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Water temperature influencing dactylogyrid species communities in roach, *Rutilus rutilus*, in the Czech Republic

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Abstract

Dactylogyrid species (Monogenea) communities were studied in roach, *Rutilus rutilus*, collected from two localities in the basin of Morava river, Czech Republic, during the period from April to November 1997 and March to September 1998 to determine the effect of water temperature on parasite abundance, species richness and diversity. Dactylogyrid species were found to co-occur on the gills of roach with up to six species found on the same host individual. Nine dactylogyrid species were identified with the abundance of each reaching a very low level. Niche size was considered to increase with species abundance even when water temperature was high. There was a strong effect of water temperature on abundance of the common dactylogyrid species (*D. crucifer*, *D. nanus*, *D. rutili* and *D. suecicus*) as well as of the rare species *D. rarissimus*. The temporary occurrence of the rare species was found without any temperature effect. Water temperature did not affect the relationship between abundance and niche size. Niche size increased with abundance, even when the water temperature was high, which suggests that negative interspecific interactions are not important within dactylogyrid communities.

Introduction

Factors influencing the occurrence of monogenean species parasitizing the gills of fish have been considered in many studies (Rohde, 1977, 1979, 1984, 1991; Hanek & Fernando, 1978a,b; Izjumova *et al.*, 1982; Žarikova, 1986; Buchmann, 1989a; Izjumova, 1990; Koskivaara *et al.*, 1991a,b; Koskivaara & Valtonen, 1992; Bagge & Valtonen, 1996; Poulin & Rohde, 1997). Parasite abundance patterns may be influenced by both host and environmental factors (Rohde, 1984; Esch *et al.*, 1990; Rohde *et al.*, 1995), some of which are known to lead to seasonal occurrence of monogeneans by influencing the duration of their life cycle (Chubb, 1977; Hanek & Fernando, 1978a,b; Koskivaara *et al.*, 1991a,b).

Abiotic factors can significantly influence the abundance of gill monogeneans on fish. Water flow (Izjumova *et al.*, 1982; Žarikova, 1986; Ramasamy & Ramalingam, 1989; Izjumova, 1990), aquatic pollution (Koskivaara *et al.*, 1991b; Koskivaara & Valtonen, 1992; Bagge & Valtonen, 1996; Gelnar *et al.*, 1997; Valtonen *et al.*, 1997), oxygen concentration (Dorovskikh & Matrokhina, 1987) and water temperature (Hanzelová & Žitňan, 1983;

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Buchmann, 1990; Gelnar *et al.*, 1990; Izjumova, 1990; Koskivaara, 1992) have all been found to significantly affect the occurrence of monogeneans on fish.

With reference to the host factors, size (Buchmann, 1989a; Guégan *et al.*, 1992; Grutter, 1994; Guégan & Hugueny, 1994; Poulin & Rohde, 1997; Hayward *et al.*, 1998; Lo *et al.*, 1998; Sasal & Morand, 1998), age and/or sex (Hanek & Fernando, 1978a; Rohde, 1984; Žarikova, 1984; Dorovskikh & Matrokhina, 1987; Izjumova, 1990), shoaling (Gonzalez-Lanza & Alvarez-Pellitero, 1982), physiological status (Bovet, 1967; Izjumova *et al.*, 1982; Kearn, 1986), and branchial irrigation (Llewellyn, 1956; Suydam, 1971) have all been shown to exert a strong influence on infection levels of monogeneans on their fish hosts.

Among these factors, water temperature has been shown to be the most important factor influencing dactylogyrid abundance, either directly by stimulating parasite reproduction and development, or indirectly by affecting host immunity (Chubb, 1977; Kuperman & Shulman, 1978; Hanzelová & Žitňan, 1983, Koskivaara, 1992). However, these studies were undertaken in continental and septentrional conditions where distinct differences occur between summer and winter temperatures. Variation in the occurrence and abundance of monogeneans from the tropical areas may therefore be different because of little seasonal variation in water temperatures (Hafidi *et al.*, 1998).

Consequences of temperature effects on monogeneans include seasonal variation in the presence/absence of species and changes in the abundance or parasite species richness (Bychowsky, 1957; Hanek & Fernando, 1978a,b,c; Izjumova *et al.*, 1982, 1985; Dzika & Szymanski, 1989; Koskivaara *et al.*, 1991a; Koskivaara & Valtonen, 1992; Bagge & Valtonen, 1996). Generally, any increase in temperature will lead to a rise in the population density and diversity of dactylogyrids (Chubb, 1977; Koskivaara *et al.*, 1992). However, as the presence or abundance of dactylogyrids is influenced by water temperature, some dactylogyrid species are found on the gills of fish throughout the year (Chubb, 1977; Žitňan & Hanzelová, 1981). On the other hand, unfavourable environmental conditions will lead to a temporary absence of some parasite species and this in turn may facilitate colonization of empty niches by less competitive or less abundant dactylogyrid species (Paperna, 1964).

Generally, monogenean communities are known for their low abundance and diversity (Rohde, 1979; Dzika & Szymanski, 1989; Hafidi *et al.*, 1998). The absence or low level of interspecific interactions is predicted and intraspecific relationships are presumed to be important (Rohde, 1979, 1991). Monogenean species (mainly congeners) have been found to coexist on the gills of fish (Buchmann, 1989b; Koskivaara & Valtonen, 1992; Geets *et al.*, 1997; Hafidi *et al.*, 1998) without a strong restriction effect on the abundance or niche size. Niche breadth exhibited cyclic seasonal changes following the seasonal changes of parasite abundance (Janovy *et al.*, 1991). However, some interactions between monogeneans have been found in high population densities as a result of the water temperature (Ramasamy & Ramalingam, 1989; Koskivaara *et al.*, 1992). Such interspecific relationships, if they exist, may lead to changes in abundance or niche restriction (Holmes, 1973; Stock & Holmes, 1988; Kennedy & Guégan, 1996; Poulin, 1998).

The aims of the present study were to determine the factors which influence the dactylogyrid community within one host species, the roach (*Rutilus rutilus* L.), with a view to: (i) evaluate the effect of water temperature on dactylogyrid species abundance, total dactylogyrid species richness and diversity, relative to sampling sites; (ii) relate parasite abundance and niche size; and (iii) evaluate the effect of water temperature on the relationship between abundance-niche size and niche overlap.

Materials and methods

From April to November 1997 and March to September 1998, a total of 328 roach, *Rutilus rutilus*, were electrofished in two localities in the basin of the Morava River (Czech Republic). A total of 194 roach from the Moravská Nová Ves locality (MNV) (N48°46′, E17°04′) and a total of 134 roach from the Rohlik locality (N48°39′, E16°56′) were investigated. The MNV locality is an oxbow lake created from a meander of the River Morava. An artificial connection with the main river channel is open only during peak discharges and during this time, fish are able to enter the oxbow. The Rohlik locality is a gravel pit artificially created during the building of a dike for flood protection. It is irregularly flooded during the spring peak discharge of the River Dyje (a tributary of the Morava). Water levels in both localities depend on the water level in the river. Captured fish were immediately placed in a tank with original local water and transported to the laboratory. During the storage of fish in the laboratory, the original water temperature was maintained and water was filtered by a routine aquarium filter. All fish were killed in the following 24 h, and the total and standard lengths of fish (cm) and weight (g) recorded. Data on fish sampling are given in table 1. *Dactylogyrus* species were collected from the gills of fish (Ergens & Lom, 1970).

All species of *Dactylogyrus* were identified using of the hard parts of the haptor (anchors, dorsal and ventral connective bars, marginal hooks) and reproductive organs (male copulatory organ and vaginal armament) according to Gussev (1985). A light microscope with phase-contrast, differential interference contrast (DIC according to Nomarski) and digital image analysis (Pro Plus 1.3 for Windows 95) were used for *Dactylogyrus* identification. No significant differences were found between the left and right gills (Buchmann, 1989b; Geets *et al.*, 1997; Hafidi *et al.*, 1998). As dactylogyrids die quickly after the death of fish, only the left side of the gill apparatus was investigated for parasite species identification.

Levels of parasitic infections were assessed using epidemiological parameters such as prevalence, intensity of infection and abundance (Bush *et al.*, 1997). Relationships between abundances for parasite species were evaluated using a Spearman rank order correlation. Following Margolis *et al.* (1982) and Bush *et al.* (1997) we defined an infracommunity as all parasite infrapopulations in a single host, a component community as all parasite infracommunities in a given host population.

Table 1. Gravimetric data on water temperature and body length of roach sampled from Moravská Nová Ves (MNV) and Rohlik from May 1997 to September 1998.

Locality	Sampling date	Water temperature (°C)	Number of fish examined	Mean total length (in cm)±SD	Mean standard length (in cm)±SD
MNV	May/97	12	15	8.9±2.05	7.2±1.58
	Jun/97	21.5	14	10.6±0.87	8.7±0.69
	Sep/97	20.2	18	11.0±1.69	8.8±1.35
	Oct/97	13.1	20	10.6±1.12	8.5±0.89
	Nov/97	9.6	20	10.8±0.88	8.6±0.77
	Mar/98	6.9	14	11.3±1.06	9.0±0.89
	Apr/98	13	18	11.4±0.95	9.1±0.80
	May/98	19	16	11.0±1.58	8.8±1.10
	Jun/98	20	15	8.3±1.90	6.7±1.49
	Jul/98	27.7	15	10.5±2.67	8.4±2.59
	Aug/98	27.6	14	9.1±1.82	7.4±1.58
	Sep/98	14.6	15	8.1±1.55	6.5±1.22
Rohlik	May/97	17.2	12	12.1±2.82	9.9±2.34
	Jun/97	23.6	10	10.2±1.14	8.5±1.08
	Sep/97	20.7	10	8.7±2.58	7.2±2.19
	Oct/97	15.5	17	7.8±1.68	6.3±1.34
	Nov/97	10.1	4	8.7±2.79	7.2±2.31
	Apr/98	12.0	11	9.8±2.12	7.8±1.63
	May/98	18.0	15	8.5±1.74	7.0±1.60
	Jun/98	20.3	12	10.7±2.21	8.6±1.75
	Jul/98	27.6	16	9.0±1.20	7.2±0.90
	Aug/98	24.4	12	9.8±1.02	7.9±1.17
	Sep/98	15.0	15	10.2±1.76	8.3±1.41

Total dactylogyrid individuals and species richness were calculated for each individual infracommunity. The Brillouin's index was used for parasite diversity evaluation and calculated also for each infracommunity as $H = 1/N \log_e(N/N1\ N2\ N3\ \ldots NS)$ where N is total number of parasite species, N1, N2, N3…NS is the number of parasites of each species 1, 2, 3, …S.

Dactylogyrus species were classified as common (more abundant) and rare species (less abundant) species as used in Rohde *et al.* (1995). The niche size of *Dactylogyrus* species was studied and the gill apparatus was divided into four gill arches for this purpose. Each arch was divided into three gill segments (D, dorsal; M, medial; V, ventral), three gill areas (p, proximal; c, central; d, distal), two gill surfaces (in, inner; out, outer) and two gill hemibranchs (A, anterior; P, posterior) as described by Fernando & Hanek (1976) and Gelnar *et al.* (1990). A total of 144 sites were differentiated and the position of each individual parasite was recorded.

The Levin's niche size and niche overlap (Renkonen's index) were calculated for each dactylogyrid species at the infracommunity level after Geets *et al.* (1997).

Fish samples were divided into four groups by discriminant analyses depending on water temperature. The two localities were separated into four groups, fish characters (total length and weight) and abundance of all *Dactylogyrus* species were compared between the two localities. The effect of temperature on fish length and weight, the total number of dactylogyrid individuals, species richness and diversity (Brillouin's index), abundance of all *Dactylogyrus* species and niche size were tested among the four groups using the one-way Kruskal-Wallis ANOVA and cross-tested between each pair of groups using the Mann-Whitney non-parametric test (Zar, 1996).

The effect of water temperature on the relationship between abundance and niche size was computed by ANCOVA using temperature groups as cofactors (Zar, 1996).

The relationship between the abundance of dactylogyrid pairs (assessed by Spearman's correlation rank coefficient) and niche overlap (Renkonen's index) was calculated using a permutation test on distance matrices proposed by Legendre *et al.* (1994).

Results

Dactylogyrid component communities

Nine *Dactylogyrus* species were found on one host population (table 2). Four *Dactylogyrus* species (*D. crucifer*, *D. nanus*, *D. rutili* and *D. suecicus*) were considered as the common species for the two localities studied because of relatively high prevalences of 37%, 29%, 31% and 21% respectively in MNV and 37%, 24%, 22% and 16% in Rohlik. *Dactylogyrus caballeroi*, *D. fallax*, *D. rarissimus*, *D. similis* and *D. sphyrna* were considered as rare species because of their low prevalences (≤10% for all species in both localities). The highest abundance values were also found for the four common species. *Dactylogyrus fallax* was found to be more abundant at Rohlik than at MNV.

The prevalence, abundance and intensity of total dactylogyrid infections and the maximum species richness in the component community are given in table 3.

Table 2. The prevalence, mean abundance, range of intensity of infection and mean intensity of infection for nine *Dactylogyrus* species in roach examined from Moravská Nová Ves (MNV) and Rohlik.

Locality	*Dactylogyrus* species	Prevalence of infection %	Mean abundance ±SD	Intensity of infection (min–max)	Mean intensity of infection±SD
MNV	*D. caballeroi*	2	0.03±0.19	0–2	1.25±0.43
	D. crucifer	37	0.85±1.48	0–7	2.29±1.60
	D. fallax	1	0.01±0.07	0–1	1.00±0.00
	D. nanus	29	0.44±0.81	0–4	1.54±0.76
	D. rarissimus	10	0.18±0.65	0–6	1.79±1.20
	D. rutili	31	0.66±1.28	0–8	2.15±1.45
	D. similis	1	0.02±0.23	0–3	2.00±1.00
	D. sphyrna	7	0.08±0.31	0–2	1.14±0.35
	D. suecicus	21	0.37±0.87	0–5	1.76±1.05
Rohlik	*D. caballeroi*	8	0.11±0.40	0–2	1.36±0.48
	D. crucifer	37	1.39±2.89	0–19	3.72±3.68
	D. fallax	10	0.34±1.76	0–18	3.29±4.45
	D. nanus	24	0.61±1.48	0–9	2.56±2.03
	D. rarissimus	7	0.12±0.44	0–2	1.60±0.49
	D. rutili	22	0.40±0.90	0–4	1.80±1.05
	D. similis	2	0.04±0.44	0–6	3.00±2.00
	D. sphyrna	4	0.06±0.32	0–3	1.33±0.75
	D. suecicus	16	0.26±0.74	0–5	1.67±1.04

Dactylogyrid infracommunities

Data were used for 199 dactylogyrid communities of roach (960 dactylogyrid individuals) from the two study sites and the mean and maximum species richness at the infracommunity level are given in table 3.

At Rohlik the maximum number of parasites of one species per fish was 19 individuals of *D. crucifer*, and a high intensity of 18 individuals per fish was also found for *D. fallax*. At MNV a lower intensity of infection per fish was found. The maximum at this locality was seven individuals of *D. crucifer* but only one specimen of *D. fallax*. *Dactylogyrus caballeroi*, *D. rarissimus* and *D. sphyrna* in Rohlik and *D. caballeroi*, *D. fallax* and *D. sphyrna* in MNV had the lowest intensity of infection per fish.

Positive associations between dactylogyrid species are given in table 4. A significant positive relationship was found between pairs of the common dactylogyrid species in both localities. These pairs were *D. crucifer–D. nanus*, *D. crucifer–D. rutili*, *D. rutili–D. nanus*, *D. rutili–D. suecicus*, *D. nanus–D. suecicus* in both localities and *D. crucifer–D. suecicus* in Rohlik only. A positive correlation was also found between *D. rarissimus* and the three common species *D. crucifer*, *D. nanus* and *D. rutili*, but no relationship was found between the abundance of *D. rarissimus* and *D. suecicus*. The abundance of *D. crucifer* was correlated with abundance of *D. sphyrna* in both localities. In Rohlik a significant positive correlation was found when *D. caballeroi* and *D. fallax* were more abundant. The abundance of *D. caballeroi* was positively correlated with abundance of *D. crucifer*, *D. rarissimus*, *D. rutili* and *D. sphyrna*. The abundance of *D. fallax* was positively correlated with abundance of *D. crucifer*, *D. similis* and *D. sphyrna*. A positive correlation between other dactylogyrid pairs (table 4) was found, but at least one has a low abundance.

Influence of water temperature on dactylogyrid abundance, species richness and diversity

As there was a temperature effect on the dactylogyrid abundances, fish samples were divided into four groups of increasing water temperature from group 1 to 4 by

Table 3. Characters of total dactylogyrid infections in the component community, species richness at the intra- and component community in roach from Moravská Nová Ves (MNV) and Rohlik.

Sampling locality	MNV	Rohlik
Total prevalence of dactylogyrid infection	65%	60%
Mean abundance of dactylogyrid infection	2.90 ± 3.36	3.83 ± 6.15
Mean intensity of dactylogyrid infection	4.47 ± 3.23	6.33 ± 6.83
Intensity of infection (min-max)	0–19	0–41
Maximum species richness in the infracommunity	5	6
Mean species richness in the infracommunity	1.39 ± 1.35	1.31 ± 1.49
Species richness in the component community (maximum during one sampling season)	7	7

Table 4. Positive associations between pairs of *Dactylogyrus* species (Spearman correlation rank coefficient).

	D. crucifer	*D. fallax*	*D. nanus*	*D. rarissimus*	*D. rutili*	*D. similis*	*D. sphyrna*	*D. suecicus*
MNV								
D. caballeroi	**0.036*** R = 0.151	0.885	0.998	0.509	0.187	0.838	0.576	0.302
D. crucifer		0.386	**0.032** R = 0.154	**0.011** R = 0.183	**0.016** R = 0.173	0.926	**0.017** R = 0.172	0.067
D. fallax			0.532	**0.004*** R = 0.207	0.513	0.919	0.781	0.609
D. nanus				**0.017** R = 0.171	**0.000** R = 0.307	0.640	0.866	**0.002** R = 0.227
D. rarissimus					**0.000** R = 0.355	0.642	0.203	0.196
D. rutili						0.762	0.675	**0.000** R = 0.402
D. similis							**0.020*** R = 0.168	0.401
D. sphyrna								0.081
Rohlik								
D. caballeroi	**0.007** R = 0.234	0.350	0.843	**0.009** R = 0.226	**0.036** R = 0.181	0.673	**0.025*** R = 0.194	0.163
D. crucifer		**0.004** R = 0.247	**0.000** R = 0.326	**0.003** R = 0.253	**0.000** R = 0.369	0.998	**0.024** R = 0.195	**0.006** R = 0.237
D. fallax			0.100	0.266	0.911	**0.000*** R = 0.351	**0.000** R = 0.396	0.890
D. nanus				**0.000** R = 0.433	**0.000** R = 0.394	0.434	0.626	**0.003** R = 0.256
D. rarissimus					**0.000** R = 0.381	0.689	0.481	0.651
D. rutili						0.452	0.308	**0.001** R = 0.292
D. similis							0.760	0.544
D. sphyrna								**0.017*** R = 0.207

Bold, $P < 0.05$; *low abundance at least of one species; MNV, Moravská Nová Ves.

carrying out a discriminant analysis (table 5). The prevalence, mean abundance, range of intensity of infection and mean intensity of infection in the four groups are given in table 6. Fish length and weight were compared in each group separately between the two localities. Total dactylogyrid abundance and the abundance of each species were tested between the two localities (table 7). A weak but significant difference was found for fish length between localities in group 2 ($P = 0.045$). A significant difference was found between the two localities in the abundance of *D. fallax* (in groups 2 and 3), *D. rarissimus* (in group 3) and *D. caballeroi* (in group 4). These differences were mainly due to the absence of the species in one of the localities. Differences were also found for the three common species: *D. rutili* (in groups 3 and 4) and *D. suecicus* (in groups 2 and 4) when those species were more abundant at MNV whereas *D. nanus* (differences in group 3) was more abundant at Rohlik.

Host characters (total length, standard length and weight) were compared among the four groups (table 8). The effect of water temperature was tested on the

Table 5. Roach samples divided by discriminant analysis into four seasonal groups depending on water temperature in Moravská Nová Ves (MNV) and Rohlik.

Fish group	Sampling date	Total number of fish	Number of fish at MNV	Number of fish at Rohlik	Mean temperature ±SD (in °C)
1	Nov 97, Mar 98	38	34	4	8.66±1.35
2	Apr 97, Oct 97 Apr 98, Sep 98	111	68	43	13.65±1.29
3	May 97, Jun 97, Sep 97 May 98, Jun 98	112	63	49	19.60±1.30
4	Jun 97, Jul 98 Aug 98, Sep 98	67	29	38	26.45±1.70

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Table 6. The prevalence, mean abundance, range of intensity of infection and mean intensity of infection of nine *Dactylogyrus* species in four fish groups divided by temperature differences.

	Group 1			Group 2			Group 3			Group 4		
Parasite species/locality	Prevalence %	Abundance ±SD	Intensity ±SD	Prevalence %	Abundance ±SD	Intensity ±SD	Prevalence %	Abundance ±SD	Intensity ±SD	Prevalence %	Abundance ±SD	Intensity ±SD
MNV												
D. caballeroi	3	0.03 ± 0.17	1.00	3	0.04±0.27	1.50±0.50	2	0.02±0.12	1.00	–	–	–
D. crucifer	29	0.53 ± 1.12	1.80 ± 1.40	25	0.46±0.99	1.82±1.20	51	1.37±1.90	2.69±1.88	45	1.03±1.38	2.31±1.14
D. fallax	3	0.03 ± 0.17	1.00	–	–	–	–	–	–	–	–	–
D. nanus	24	0.26 ± 0.50	1.13 ± 0.33	24	0.40±0.82	1.69±0.85	30	0.44±0.75	1.47±0.60	45	0.76±1.04	1.69±0.91
D. rarissimus	3	0.03 ± 0.17	1.00	4	0.09±0.45	2.00±0.82	8	0.14±0.53	1.80±0.75	34	0.62±1.22	1.80±1.47
D. rutili	9	0.15 ± 0.55	1.67 ± 0.94	22	0.50±1.29	2.27±1.88	33	0.63±1.06	1.90±0.97	72	1.72±1.66	2.38±1.50
D. similis	–	–	–	3	0.06±0.38	2.00±1.00	–	–	–	–	–	–
D. sphyrna	6	0.09 ± 0.37	1.50 ± 0.50	3	0.04±0.27	1.50±0.5	11	0.11±0.31	1.00	10	0.10±0.30	1.00
D. suecicus	12	0.21 ± 0.72	1.75 ± 1.30	15	0.28±0.85	1.90±1.37	16	0.22±0.55	1.40±0.49	59	1.10±1.18	1.88±0.96
Rohlik												
D. caballeroi	–	–	–	5	0.07±0.33	1.50±0.50	8	0.12±0.43	1.50±0.50	28	0.16±0.43	1.20±0.40
D. crucifer	–	–	–	16	0.30±1.09	1.86±2.10	39	1.67±3.17	4.32±3.81	63	2.39±3.51	3.79±3.76
D. fallax	–	–	–	12	0.21±0.63	1.80±0.75	18	0.76±2.79	4.11±5.34	–	–	–
D. nanus	25	0.25 ± 0.43	1.00	12	0.30±0.95	2.60±1.36	12	0.16±0.51	1.33±0.75	74	1.58±2.23	3.00±2.28
D. rarissimus	–	–	–	5	0.07±0.33	1.50±0.50	–	–	–	42	0.34±0.70	1.63±0.48
D. rutili	–	–	–	9	0.09±0.29	1.00	14	0.29±0.81	2.00±1.07	51	0.95±1.21	1.89±1.07
D. similis	–	–	–	5	0.14±0.76	3.00±2.00	–	–	–	–	–	–
D. sphyrna	–	–	–	–	–	–	10	0.14±0.49	1.40±0.80	3	0.03±0.16	1.00
D. suecicus	–	–	–	2	0.05±0.30	2.00	18	0.31±0.76	1.66±0.94	37	0.47±0.97	1.64±1.15

See table 5 for details of the four fish groups.

Table 7. Comparison of the abundance of nine *Dactylogyrus* species in four fish groups in Moravská Nová Ves and Rohlik.

	Group 1	Group 2	Group 3	Group 4
Fish total length	0.105	**0.045**	0.241	0.894
Fish weight	0.118	0.307	0.277	0.506
Abundance total dactylogyrids	0.352	0.218	0.307	0.824
D. caballeroi	0.732	0.639	0.093	**0.044**
D. crucifer	0.217	0.248	0.476	0.074
D. fallax	0.732	**0.004**	**<0.001**	–
D. nanus	0.974	0.163	**0.020**	0.226
D. rarissimus	0.732	0.966	**0.045**	0.272
D. rutili	0.542	0.060	**0.024**	**0.036**
D. similis	–	0.633	–	–
D. sphyrna	0.623	0.259	0.909	0.190
D. suecicus	0.475	**0.037**	0.703	**0.010**

Bold, $P < 0.05$; see table 5 for details of the four fish groups.

Table 8. Host characters compared among four groups (Kruskal-Wallis test, bold, $P < 0.05$) and between two fish groups in Moravská Nová Ves (MNV) and Rohlik (Mann-Whitney test, groups are given in decreasing order, $P < 0.05$).

	Total (MNV and Rohlik)	Fish group number	MNV	Fish group number	Rohlik	Fish group number
Fish total length	**0.003**	$1 > 3 > 2 = 4$	0.016	$1 > 2 = 3 = 4$	0.209	
Fish standard length	**0.004**	$1 > 3 > 2 = 4$	**0.013**	$1 > 2 = 3 = 4$	0.169	
Fish weight	**0.017**	$1 = 3 > 2 = 4$	0.066		**0.008**	$3 > 1 = 2 = 4$

See table 5 for details of the four fish groups.

Table 9. Influence of water temperature on the abundance of each dactylogyrid species, total dactylogyrid abundance, species richness and diversity (Brillouin's index), all variables compared amongst four fish groups by the Kruskal-Wallis test (bold, $P < 0.05$) and cross–tested between groups by the Mann-Whitney test; fish groups are given in decreasing order ($P < 0.05$).

Dactylogyrus species	Total (MNV and Rohlík)	Fish group number	MNV	Fish group number	Rohlik	Fish group number
D. caballeroi	0.314		0.784		0.534	
D. crucifer	**<0.001**	$4 = 3 > 2 = 1$	**0.003**	$4 = 3 > 2 = 1$	**<0.001**	$4 = 3 > 2 = 1$
D. fallax	0.084		0.195		**0.042**	$3 > 2 > 1 = 4 = 0^*$
D. nanus	**<0.001**	$4 > 3 = 2 = 1$	0.145		**<0.001**	$4 > 3 = 2 = 1$
D. rarissimus	**<0.001**	$4 > 3 = 2 = 1$	**<0.001**	$4 > 3 > 2 > 1$	**<0.001**	$4 > 2 > 1 = 3 = 0^*$
D. rutili	**<0.001**	$4 > 3 > 2 > 1$	**<0.001**	$4 > 3 > 2 > 1$	**<0.001**	$4 > 3 > 2 > 1 = 0^*$
D. similis	**0.048**	$2 > 1 = 3 = 4 = 0^*$	0.293		0.234	
D. sphyrna	0.054		0.310		0.100	
D. suecicus	**<0.001**	$4 > 3 = 2 = 1$	**<0.001**	$4 > 3 = 2 = 1$	**0.010**	$4 = 3 > 2 = 1$
Total dactylogyrids	**<0.001**	$4 > 3 > 2 = 1$	**<0.001**	$4 > 3 > 2 = 1$	**<0.001**	$4 > 3 > 2$
Species richness	**<0.001**	$4 > 3 > 2 = 1$	**<0.001**	$4 > 3 > 2 = 1$	**<0.001**	$4 > 3 = 2$
Brillouin's index	**<0.001**	$4 > 3 > 2 = 1$	**<0.001**	$4 > 3, 3 = 2, 3 > 1, 1 = 2$	**<0.001**	$4 > 3 = 2$

*0 indicates no parasites in the group; MNV, Moravská Nová Ves; see table 5 for details of the four fish groups.

abundance of each dactylogyrid species, species richness and diversity (table 9) and a relationship between water temperature and total dactylogyrids was found in both localities. When each species was compared separately, the Kruskal-Wallis non-parametric test revealed a significant difference in the abundance of five species (*D. crucifer*, *D. rarissimus*, *D. rutili*, *D. suecicus* in both localities, *D. nanus* in Rohlik only) among groups. Each pair of groups was cross-tested with a Mann-Whitney non-parametric test, and this demonstrated an increase in abundance with group number, i.e. water temperature. The most abundant species, *D. crucifer*, had the highest abundance in groups 3 and 4. The other four species were more abundant in group 4, when temperature was at its highest. No relationship between temperature and abundance was found for *D. caballeroi*, *D. similis* and *D. sphyrna*. There was a significant difference between groups for *Dactylogyrus fallax* in Rohlik. The highest abundance was found in group 3 and the lowest in group 4 (when the temperature was at its highest) for this species.

Parasite species richness and diversity (Brillouin's

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Table 10. Linear regression (R) between abundance (A) and niche breadth (B) for each of the nine *Dactylogyrus* species studied.

Dactylogyrus species	MNV	R	Rohlik	R
D. caballeroi	–	–	B=0.910*A+0.005	0.976
D. crucifer	B = 0.674*A + 0.176	0.905	B=0.778*A+0.080	0.976
D. fallax	–	–	B=0.484*A+0.124	0.943
D. nanus	B = 0.911*A + 0.011	0.971	B=0.914*A+0.023	0.984
D. rarissimus	B = 0.780*A + 0.023	0.963	B=0.927*A+0.002	0.980
D. rutili	B = 0.766*A + 0.105	0.954	B=0.898*A+0.021	0.977
D. similis	–	–	B=0.725*A+0.003	0.997
D. sphyrna	–	–	B=0.536*A+0.012	0.855
D. suecicus	B = 0.823*A + 0.032	0.960	B=0.886*A+0.024	0.969

$P < 0.05$; MNV, Moravská Nová Ves. A linear regression model was not obtained for four of *Dactylogyrus* species because of low abundance.

index) were tested among the four groups (table 9). Significant differences in parasite species richness and parasite diversity between the groups were found. Highest values were recorded in group 4 in both localities. No significant differences were found between groups 1 and 2, when the temperature was at its lowest.

Abundance, niche size and overlap

Relationships between abundance and niche breadth are given in table 10. *Dactylogyrus caballeroi*, *D. fallax*, *D. similis* and *D. sphyrna* were not evaluated at MNV because of low abundance on the gills of roach. Niche size was found to increase with abundance for each of the other dactylogyrid species.

No water temperature effect on relationship between abundance and niche size was found in either locality (ANCOVA, for all dactylogyrid species $P > 0.05$). Niche overlap between dactylogyrid pairs also increased with dactylogyrid abundance, i.e. a positive relationship between the abundance of dactylogyrid pairs (assessed by Spearman's correlation rank coefficient) and niche overlap was found in both localities ($b = 0.449$, $R^2 = 0.202$, $P = 0.018$ in MNV and $b = 0.480$, $R^2 = 0.231$, $P = 0.002$ in Rohlik).

Because of the low abundance of dactylogyrid species in the present study, niche overlap was only found between common species and was low. Niche overlap was not influenced by temperature (Mann-Whitney test, $P > 0.05$).

Discussion

Monogenean communities are known for their low parasite diversity and abundance (Rohde, 1977, 1979; Dzika & Szymanski, 1989; Hayward *et al.*, 1998) and an absence of niche saturation is usually considered to be due to their aggregated distribution. However, high numbers of congeneric species belonging to the genus *Dactylogyrus* may be found in the same fish species (Kennedy & Bush, 1992; Koskivaara & Valtonen, 1992). In the present study, nine dactylogyrid species were identified on the gills of roach and the maximum number of dactylogyrid species parasiting the gills of one host was six. The abundance of all species was low. Four species, *D. crucifer*, *D. nanus*, *D. rutili* and *D. suecicus*, were considered as common species. The other five species were considered rare with a temporary occurrence. The presence of these species was concentrated in a short period of time, i.e. spring or autumn.

Different host parameters and environmental factors have been shown to influence the abundance of monogenean species. Among these factors, water temperature and host body length have often been discussed as important in determining species richness in monogenean communities. For example, Poulin & Rohde (1997) suggested that both water temperature and host size may affect parasite abundance (including monogeneans) but only water temperature seemed to be important for ectoparasites. Our results showed that water temperature influenced dactylogyrids, although we cannot confirm the effect of host length because of the small difference between the fish investigated. However, host size has been reported to be a major determinant of monogenean species richness (Buchmann, 1989a; Guégan & Hugueny, 1994; Guégan & Morand, 1996).

Water temperature is considered as a major factor in regulating the seasonal occurrence of monogeneans even if the monogenean community structure is a result of different environmental factors (Chubb, 1977; Koskivaara, 1992). Generally, the effect of seasonality has been shown to influence monogenean community structure. The abundance of monogeneans has been shown to be influenced by seasonal changes in water temperature (Hanek & Fernando, 1978a,b; Hanzelová & Žitňan 1985, Koskivaara *et al.*, 1991a,b; Bagge & Valtonen 1996). However, the effect of temperature differed among parasite species. For instance, gyrodactylids occur generally on fish when the temperature is low (Koskivaara *et al.*, 1991b). The effect of water temperature on parasite diversity and/or abundance has been found for dactylogyrids (Hanzelová & Žitňan, 1983; Koskivaara *et al.*, 1991a, 1992) as dactylogyrid abundance and diversity increase with temperature. In the present case, total dactylogyrid abundance, species richness and diversity also increased with water temperature in both sampling sites, although there was a difference in origin. The abundance of the common species *D. crucifer*, *D. nanus*, *D. rutili* and *D. suecicus* as well as the abundance of *D. rarissimus* increased with increasing water temperature.

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These five species were typically found to co-occur on the gills of roach mainly during the summer. The rare species, *Dactylogyrus fallax* was more abundant when temperature decreased. We found no effect of temperature on the abundance of other rare species such as *D. cabelleroi*, *D. similis* and *D. sphyrna*. Their presence on the gills was typically in the period of lower water temperature when the abundance of the four common species and *D. rarissimus* was low.

The structure of dactylogyrid communities parasitizing the gills of roach has previously been studied in freshwater lakes in Finland (Koskivaara *et al.*, 1991a,b, 1992; Koskivaara, 1992; Koskivaara & Valtonen, 1992; 1992; Bagge & Valtonen, 1996; Valtonen *et al.*, 1997). In these studies, the presence of *D. micracanthus*, a rare species, and *D. vistulae*, a species with very low prevalence and abundance, showed differences compared with our dactylogyrid communities. In the present study, *D. rutili* was considered to be an abundant species and *D. rarissimus* was considered a rare species in dactylogyrid communities. Both dactylogyrid species are specialists of roach. The abundance of both dactylogyrid species was affected by water temperature, with abundance being highest when the water temperature was also at its highest. Differences in the structure of dactylogyrid communities may be the result of a range of water temperatures. The mean water temperatures under the conditions of lakes in Finland was 10°C, with the highest temperature being 18–20°C in July–August, whereas the mean water temperature in the Czech Republic during the time of investigation was 17.8°C with the maximum range of 24.4–27.7°C in July–August. Moreover, temperatures in northern latitudes change more rapidly than in southern latitudes.

For communities of congeneric species, a stable coexistence is predicted without any evidence of negative interspecific interactions (Rohde, 1979; Kennedy & Moriarty, 1987). The abundances of congeneric dactylogyrids in individual fish were significantly higher in multi-species infections, i.e. species coexistence (Koskivaara, 1992; Hafidi *et al.*, 1998). We found a positive relationship between the abundance of dactylogyrid species, mainly when species were more abundant and this suggests only positive interspecific associations.

If competition exists in parasite communities, it may be detected by changes in abundance as a numerical response of competition, or in niche size as a functional response of competition under natural environmental conditions (Poulin, 1998). Several studies on monogeneans supported such evidence for interspecific interactions at the time of highest species diversity (Ramasamy & Ramalingam, 1989; Koskivaara *et al.*, 1992) or suggested the possibility of competitive exclusion (Paperna, 1964). However, the present results cannot support this assumption because dactylogyrid communities were studied during the summer season when parasite abundance was low. Abundance as well as niche size increased with water temperature and niche overlap was very low even for pairs of common species. Negative interspecific interactions between species were not found because of the seasonality effect induced by water temperature so that the existence of positive interactions between parasite species is supported.

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