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The microhabitat distribution of two *Dactylogyrus* species parasitizing the gills of the barbel, *Barbus barbus*

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Abstract

The microhabitat distribution of two congeneric species *Dactylogyrus carpathicus* and *D. malleus* (Monogenea) parasitizing the gills of the barbel (*Barbus barbus* L.) was investigated. We tested whether congeneric species exhibited microhabitat preference and whether interspecific interactions could be attributed to the microhabitat segregation of congeners. The outlying mean index method was used to evaluate species microhabitats. Gill variables (different microhabitats within gills) were used as environmental factors characterizing the gills. When abundances of both species were highest, and no significant difference was found between the abundance of the two species, the gill segments and gill areas were the most important factors segregating the *Dactylogyrus* species on the gills. Niche overlap was low within each of the four gill arches, and parasites were segregated in the same microhabitats within each gill arch. When abundances of both species were low, each monogenean species was segregated at the level of the gill arches. When abundances of both species increased, the niche and overlap between species increased. The distribution of both congeneric species confirmed microhabitat preference within the gills. The results suggest that microhabitat preference is dependent on species abundances, species being segregated in the case of low abundance, possibly to increasing mating opportunities. Both niche and overlap between species increased with species abundance. In the case of the high abundance of both species, microhabitat preference seems to be related to interspecific interactions between monogenean species, as previously found for endoparasitic species.

Introduction

Parasite habitat restriction and niche segregation have been studied for the past 30 years and several hypotheses have been applied to explain why parasite habitats are restricted (Paperna, 1964; Holmes, 1973; Rohde, 1979, 1991; Bush & Holmes, 1986; Stock & Holmes, 1988; Buchmann, 1989; Koskivaara *et al.*, 1992). Microhabitat specificity, a preference for certain habitats within the host (i.e. on fish gills), was observed for monogenean parasites (Rohde, 1979, 1991; Ramasamy & Ramalingam, 1989; Koskivaara *et al.*, 1992; Geets *et al.*, 1997; El Hafidi *et al.*, 1998; Gutiérrez & Martorelli, 1999).

Microhabitat distribution may be a result of intraspecific parasite interactions. Monogeneans establishing small populations on the host generally choose the same

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microhabitat, even if there is much vacant space on the fish gills. Rohde (1977) proposed that active site selection by parasites leads to increased intraspecific contacts for mating. However, it is questionable if monogeneans really choose specific gill sites for reproduction, or if the first parasite colonizing a host selects a microhabitat at random and other parasites aggregate to increase the chance of mating.

Parasite adaptations to their hosts, and especially the attachment organs of the parasite, should play an important role in explaining microhabitat specificity (Rohde, 1991; Šimková *et al.*, 2000). Microhabitat preferences of monogeneans could be the result of adaptations to the structure of host gills or to different conditions within the gills of one host due to different water currents or oxygen concentrations.

Another alternative explanation presents microhabitat specificity as a result of interspecific interactions. However, in the recent literature on ecological parasitology, there is no strict rule for estimating the intensity and consequences of interspecific competitions (Poulin, 2001). Generally, interspecific interactions in helminth communities are related to a high population density of potentially competiting species, where competition effect may be detected through numerical or functional responses in parasite communities (Poulin, 1998).

Communities of congeneric species, which present a special type of multispecies assemblages, could present a slightly different situation. Generally, congeners are complementary in their habitat utilization. Stock & Holmes (1988) suggested that one of the characteristics of interactive communities is that the presence of one species excludes the presence of other congeneric species. On the contrary, monogenean communities are formed by many congeneric species, their microhabitats can be widely overlapped, and in this case, species coexistence within hosts is reinforced by reproductive isolation (Rohde & Hobbs, 1986; Šimková *et al.*, 2002). Following Rohde (1991), when congeners possess similar features of the morphology of their attachment organs, then they should exhibit overlapping or similar microhabitats, but because of low abundance there are no important interspecific interactions restricting their niches. Šimková *et al.* (2000) mapped microhabitat distribution into the phylogeny of nine congeneric monogenean species parasitizing one host species and showed that preferred microhabitats could either be selected during evolution in order to prevent interspecific competition or may be the result of past competition.

Although many studies on monogeneans conclude that interspecific interactions do not influence microhabitat distribution, others suggest an indirect effect of interspecific interactions, mainly due to increasing parasite abundance (Paperna, 1964; Koskivaara *et al.*, 1992). Moreover, Ramasamy *et al.* (1985) showed that microhabitat preference varied with parasite abundance on the host, including the gills. They suggested that both intra- and interspecific competition may occur among gill parasites.

Several studies indicated that the microhabitat selection of monogenean species could be partially related to the host immune response (Buchmann & Bresciani, 1998). Buchmann & Lindenstrom (2002) proposed that competitive exclusion between congeneric gill monogeneans could be associated with non-specific antiparasitic responses in the hosts and the different tolerance of species to the host response.

The outlying mean index method presents a multivariate technique to investigate multidimensional species niches (Thioulouse *et al.*, 1997). This method was developed to minimize the effect of abundant species and provide an evaluation of the niche specialization of the species (a species close to the origin of the axes may be considered as a more ubiquitous species, i.e. niche generalists). This method was applied for the evaluation of niche preferences for fish species (Dolédec *et al.*, 2000; Reichard *et al.*, 2002).

The aim of the present study was to apply the outlying mean index method to investigate the microhabitat distribution of two congeneric monogenean species *Dactylogyrus carpathicus* and *D. malleus*, both specific to the European common barbel, *Barbus barbus*. The effects of different abundances on microhabitat distribution of both species on the fish gills were tested:

1. In the case of relatively low parasite abundance, a narrow microhabitat restriction to facilitate mating was expected.
2. In the case of moderate parasite abundance, a random selection of microhabitats, widely overlapping between species, was expected.
3. In the case of relatively high parasite abundance, microhabitats were expected to be selected due to interspecific interactions.

Moreover, the length of the fish could contribute to the microhabitat distribution of parasite species.

Materials and methods

A total of 64 European common barbels, *Barbus barbus* L., were collected from the Danube river area, situated between the Austrian villages of Klosterneuburg and Mitterhaufen. Fish were examined during five months, the mean ± S.D. for total fish lengths in cm are given in parentheses: 11 fish in August 1993 (38.5 ± 6.39), 13 fish in April 1994 (49.69 ± 7.85), 11 fish in June 1994 (39.95 ± 7.63), 16 fish in August 1994 (29.38 ± 10.20), and 13 fish in November 1994 (54.54 ± 1.68).

Two dactylogyrid species *D. carpathicus* and *D. malleus* were identified on the fish gills using sclerotized parts of the parasite haptor (anchors, dorsal and ventral connective bars, marginal hooks) and reproductive organs (male copulatory organs and vaginal armaments) according to Gussev (1985). A light microscope equipped with phase-contrast, Nomarski differential interference contrast (DIC) and Digital Image Analysis (Micro Image for Windows, Olympus) was used for *Dactylogyrus* measurements and identification.

The left side of the gill apparatus was investigated for parasite distribution. In previous studies, no significant differences were found between the left and right sides (Buchmann, 1989; Geets *et al.*, 1997; El Hafidi *et al.*, 1998). Dactylogyrids die quickly after the death of fish, therefore only one side, i.e. the left side, of the gill apparatus was examined for parasite species. This provided the most accurate counts of parasites as the right side would have

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lost too many dactylogyrids during the time necessary for collecting parasites on the gills.

The gill apparatus was divided into four gill arches. Each arch was divided into three gill segments (D-dorsal, M-medial and V-ventral), three gill areas (p-proximal, c-central and d-distal), and two gill surfaces (in-inner and out-outer) according to Gelnar *et al.* (1990). Thus, 72 different gill sites were identified as theoretical niches for parasites within one fish. The position of each parasite (949 individuals of *D. carpathicus* and 507 individuals of *D. malleus*) was then recorded.

Parasite prevalence, abundance and intensity of infection were calculated following Bush *et al.* (1997). The abundance of both *D. carpathicus* and *D. malleus* was compared among seasons using the Kruskal-Wallis test, and cross-tested between seasons using the Mann-Whitney non-parametric test. The abundance of *D. carpathicus* and *D. malleus* was compared within each season using the Mann–Whitney test (Zar, 1999).

Calculations and figures were made with ADE-4 software http://pbil.univ-lyon1.fr/ADE-4/ (Thioulouse *et al.*, 1997) using the outlying mean index (OMI) method of multivariate statistical analysis to investigate multidimensional niches. The first step consisted of running a normalized principal component analysis (PCA) on the environmental table, i.e. the table characterizing different gill sites by defined microhabitats. Each of the potential sites was considered as a different habitat for the *Dactylogyrus* species. The principal component analysis was performed on a covariance matrix. Relative inertia for each axis was computed and the seven first axes representing at least 95% of the total inertia were kept for the remaining analysis. Then, in a second step, the faunistic table (presenting species abundances in each microhabitat) was associated with the centered table of the row profiles resulting from the PCA analysis. This associated table contains the average position of each species on each gill variable. In the third step, the OMI analysis was performed on the associated table. Niche parameters to describe the marginality (expressed as the OMI) and the tolerance (expressed as tolerance index) of species were computed and tested. Both indexes present the variability of responses of the species to niche variables. A permutation test (10000 permutations) was performed as a global test on the average marginality of both species. The statistical significance justified a plot of the species positions on an ordination diagram. The OMI (or species marginality) measures the distances between the mean habitat conditions used by the species and represents a deviation of the average position of species from the origin G (which corresponds to the overall mean habitat). The tolerance index (or index of niche breadth) represents a measurement of the niche breadth of species on the gills. The total inertia represents a quantification of the influence of the environment variables on the niche separation of species and contributes to the characterization of the global niche overlap of species.

The OMI analysis was undertaken for each season separately because of differences in species abundances between seasons. Gill arches, segments, areas and surfaces were considered as environmental variables. When the permutation test revealed a significant influence of environmental variables on species distribution in host samples within one season, the OMI analysis was carried out for each gill arch separately to test the microhabitat preference within gill arches.

The graphic representation of the two first OMI axes for the environmental table (the potential niches for the parasite species) is given on top of the representation of microhabitat distribution for each parasite species in the multidimensional niche space (in this case, the gills or gill arch). For each parasite species, frequencies of the average position on the gills or gill arch and ellipses, including an equal percentage of values for each species were plotted.

Results

Species occurrence on fish between and within seasons

The values of parasite prevalence, mean abundance, mean intensity of infection and range of intensity are given in table 1. In four of the five seasons investigated, *D. carpathicus* reached a higher mean abundance and mean intensity of infection than *D. malleus*. In April 1994, *D. malleus* reached higher values of mean abundance and intensity of infection than *D. carpathicus*. The maximum prevalence of *D. carpathicus* was reached in August 1993 and April 1994 whilst the highest value of prevalence of *D. malleus* was reached in April 1994. The highest number of parasites on one fish (one side only) was 92 for *D. carpathicus* and 102 for *D. malleus*, both recorded in April 1994.

The abundances of both species were compared among seasons and cross-compared between seasons.

Table 1. The prevalence, intensity of parasite infection (range and mean ± standard deviation) and abundance of infection (mean ± standard deviation) of barbel with *Dactylogyrus carpathicus* and *D. malleus*.

	D. carpathicus				*D. malleus*			
	Prevalence (%)	Intensity		Abundance Mean ± SD	Prevalence (%)	Intensity		Abundance Mean ± SD
		Range	Mean ± SD			Range	Mean ± SD	
August 1993	100	4–34	17.18 ± 9.50	17.18 ± 9.50	64	1–48	10.71 ± 15.87	6.82 ± 17.93
April 1994	100	2–92	23.85 ± 22.79	23.85 ± 22.79	92	2–102	30.42 ± 29.14	28.08 ± 29.15
June 1994	73	2–24	13.00 ± 7.58	9.45 ± 8.68	45	1–3	1.80 ± 0.75	0.82 ± 1.03
August 1994	75	3–74	19.83 ± 18.24	14.88 ± 17.98	69	1–14	4.55 ± 3.60	3.13 ± 3.66
November 1994	77	3–26	10.80 ± 7.93	8.31 ± 8.31	38	1–3	1.60 ± 0.80	0.62 ± 0.92

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Although the Kruskal-Wallis test revealed no significant difference among seasons for *D. carpathicus*, when comparing its abundance between seasons using the Mann-Whitney test, *D. carpathicus* was more abundant in April 1994 than in June 1994 ($U = 33.500$, $P = 0.028$) and November 1994 ($U = 36.500$, $P = 0.043$). No difference was found between the abundance of *D. carpathicus* when comparing April 1994 to August 1993 and August 1994 ($P > 0.05$). Moreover, the abundance of *D. carpathicus* was significantly higher in August 1993 ($U = 36.500$, $P = 0.043$) and in August 1994 ($U = 56.000$, $P = 0.034$) than in November 1994.

When comparing the abundance of *D. malleus* among seasons, the Kruskal-Wallis test revealed significant difference ($H = 22.757$, $P = 0.0001$). The highest abundance was reached in April 1994 (Mann-Whitney test, $P < 0.01$ between April 1994 and each other season). No other differences were found between seasons.

When comparing the abundances of *D. carpathicus* and *D. malleus* within each season, in four of the five seasons investigated, *D. carpathicus* was more abundant than *D. malleus* (Mann–Whitney test, $P = 0.005$ for August 1993, $P = 0.026$ for June 1994, $P = 0.039$ for August 1994, $P = 0.010$ for November). Only in April 1994, was no difference ($P = 0.463$) found between abundance of *D. carpathicus* and *D. malleus*.

Effect of host size on parasite abundance

The total and standard lengths of fish were tested among seasons and significant differences in fish size were found among different seasons (Kruskal-Wallis test, for total length, $H = 38.250$, $P < 0.0001$). The Mann-Whitney tests between seasons revealed that the highest fish size was reached in April 1994 samples and November 1994 samples ($P < 0.01$). No difference was found between fish size in August 1993 and June 1994. The lowest fish size was reached in the sample of August 1994. When testing for parasite abundance increasing with host size, no effect of host size (total fish length) on parasite abundance of *D. carpathicus* and *D. malleus* was found in any season (linear regression, $P > 0.05$).

OMI analysis on microhabitat distribution of parasites

The results of the OMI analysis are given in tables 3–5 and figs 1–3. Gill variables were important for the parasite distribution on fish gills in three seasons (April 1994, June 1994, August 1994) when the permutation test on the average marginality of parasite species was significant ($P < 0.001$ in April 1994 and $P < 0.05$ in June and August 1994). Considering the marginality of separated species in each of the three seasons, in April 1994 both parasite species ($P < 0.0001$), in June 1994 only *D. malleus* ($P = 0.013$) and in August 1994 only *D. carpathicus* ($P = 0.008$) showed a significant deviation of their niche from the origin. In two seasons (August 1993, November 1994) the permutation test did not reveal significant results which would suggest that species are indifferent to their microhabitats as predicted by the null hypothesis. For each of three seasons (April 1994, June 1994 and August 1994) the analysis was repeated considering each arch separately, and the results of the permutation test showed that gill variables were only important for parasite separation within gill arches

Table 2. The abundance of infection (mean ± standard deviation and maximum abundance for one fish individual) for *Dactylogyrus carpathicus* and *D. malleus* on different gill arches.

		D. carpathicus		*D. malleus*	
		Abundance		Abundance	
	Gill arch	Mean ± SD	Maximum	Mean ± SD	Maximum
August 1993	First	3.27 ± 4.38	15	1.64 ± 3.17	8
	Second	4.91 ± 2.02	9	1.09 ± 2.17	7
	Third	6.00 ± 5.29	16	2.64 ± 6.87	23
	Fourth	3.00 ± 3.00	10	1.45 ± 3.08	10
April 1994	First	3.54 ± 4.37	16	2.69 ± 2.63	9
	Second	5.31 ± 4.94	18	7.46 ± 11.12	34
	Third	7.08 ± 7.43	27	13.69 ± 15.74	51
	Fourth	7.92 ± 8.62	31	4.23 ± 3.68	12
June 1994	First	0.75 ± 0.89	2	0	0
	Second	3.63 ± 3.02	7	0.13 ± 0.35	1
	Third	5.5 ± 4.60	10	0.13 ± 0.35	1
	Fourth	3.13 ± 2.53	7	0.88 ± 1.13	3
August 1994	First	3.46 ± 3.84	15	0.85 ± 1.14	3
	Second	5.62 ± 6.50	24	1.08 ± 1.44	5
	Third	5.08 ± 4.62	15	0.77 ± 1.54	4
	Fourth	4.15 ± 5.41	20	1.15 ± 1.63	5
November 1994	First	2.40 ± 2.67	7	0.10 ± 0.32	1
	Second	3.40 ± 2.63	9	0.10 ± 0.32	1
	Third	2.90 ± 2.42	7	0.30 ± 0.67	2
	Fourth	2.10 ± 2.42	6	0.30 ± 0.48	1

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Table 3. Niche parameters for *Dactylogyrus carpathicus* and *D. malleus* (by the season or gill arches).

	Season	Gill arches	Species inertia	OMI	Tolerance index
D. carpathicus	April 1994	All	1.862	0.178	1.425
D. malleus			2.049	0.345	1.343
D. carpathicus	April 1994	First	1.206	0.162	0.876
D. malleus			1.394	0.222	0.826
D. carpathicus	April 1994	Second	0.951	0.147	0.470
D. malleus			1.313	0.417	0.511
D. carpathicus	April 1994	Third	1.057	0.293	0.555
D. malleus			1.217	0.234	0.643
D. carpathicus	April 1994	Fourth	1.194	0.098	0.901
D. malleus			1.321	0.278	0.789
D. carpathicus	June 1994	All	1.94	0.015	1.573
D. malleus			1.768	0.632	0.979
D. carpathicus	August 1994	All	1.981	0.037	1.714
D. malleus			2.110	0.072	1.813

Table 4. Relative contribution of each microhabitat to the two factorial axes (FA) in outlying mean index analyses for seasonal samples of gills of barbel infected with *Dactylogyrus carpathicus* and *D. malleus*.

	April 1994		June 1994		August 1994	
Gill variables	FA1	FA2	FA1	FA2	FA1	FA2
First arch	35.13	64.86	35.66	64.33	75.9	24.09
Second arch	50.71	49.28	96.23	3.76	76.24	23.75
Third arch	71.21	28.78	73.65	26.34	90.06	9.93
Fourth arch	89.94	10.05	99.15	0.84	76.22	23.77
Dorsal segment	28.06	71.93	60.93	39.06	61.36	38.63
Medial segment	99.97	0.02	61.09	38.9	24.5	75.49
Ventral segment	9.40	90.59	59.06	40.93	89.24	10.75
Distal area	64.02	35.97	85.53	14.46	83.15	16.84
Central area	85.77	14.22	57.18	42.81	92.45	7.54
Proximal area	99.66	0.33	33.92	66.07	99.99	0
Inner surface	45.61	54.38	99.95	0.04	19.48	80.51
Outer surface	45.61	54.38	99.95	0.04	19.48	80.51

Table 5. Relative contribution of each microhabitat to the two factorial axes (FA) in outlying mean index analyses for gill arches in barbel infected with *Dactylogyrus carpathicus* and *D. malleus*, April 1994.

	First		Second		Third		Fourth	
Gill arches	FA1	FA2	FA1	FA2	FA1	FA2	FA1	FA2
Dorsal segment	14.36	85.63	90.64	9.35	28.37	71.62	13.38	86.61
Medial segment	79.24	20.75	94.25	5.74	98.06	1.93	22.74	77.25
Ventral segment	83.67	16.32	5.56	94.43	4.21	95.78	8.35	91.64
Distal area	41.99	58	49.47	50.52	26.54	73.45	65.98	34.01
Central area	96.77	3.22	99.00	0.99	94.68	5.31	87.63	12.36
Proximal area	99.56	0.43	99.81	0.18	98.62	1.37	99.56	0.43
Inner surface	70.33	29.66	–	–	–	–	47.84	52.15
Outer surface	70.33	29.66	–	–	–	–	47.84	52.15

in April 1994 ($P < 0.001$). When analysing gill arches separately for the two remaining seasons (June 1994 and August 1994), species were distributed independently of gill variables ($P > 0.05$).

The total inertia of the OMI analysis was lowest in August 1994 (0.044), indicating a high niche overlap of species (fig. 3). The highest value of total inertia was found in April 1994 (0.290), indicating species separation

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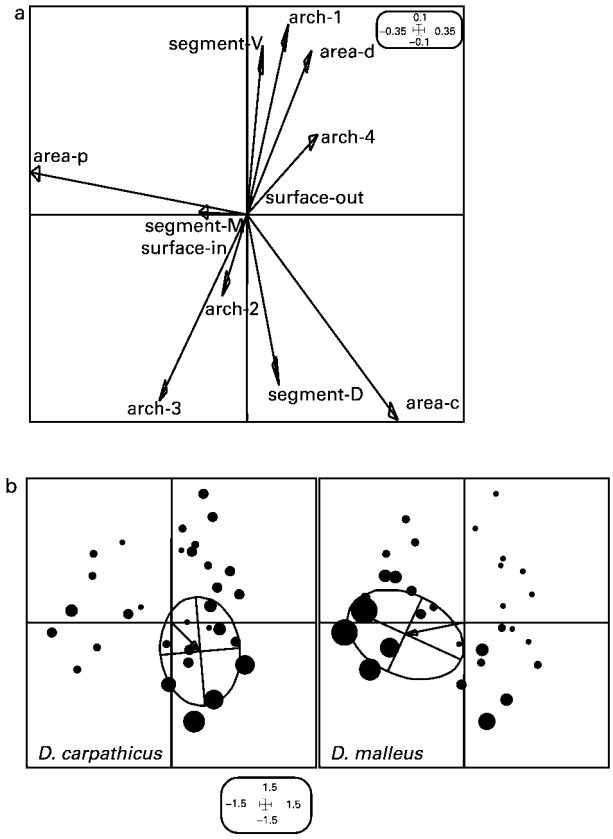

Fig. 1. Graphic representation using the first and the second OMI axes in April 1994 to describe (a) canonical representation of gill variables of the barbel, and (b) microhabitat distribution of *Dactylogyrus carpathicus* and *D. malleus* using mapping of parasite frequencies. The ellipses represent the average niche size for each mongenean species.

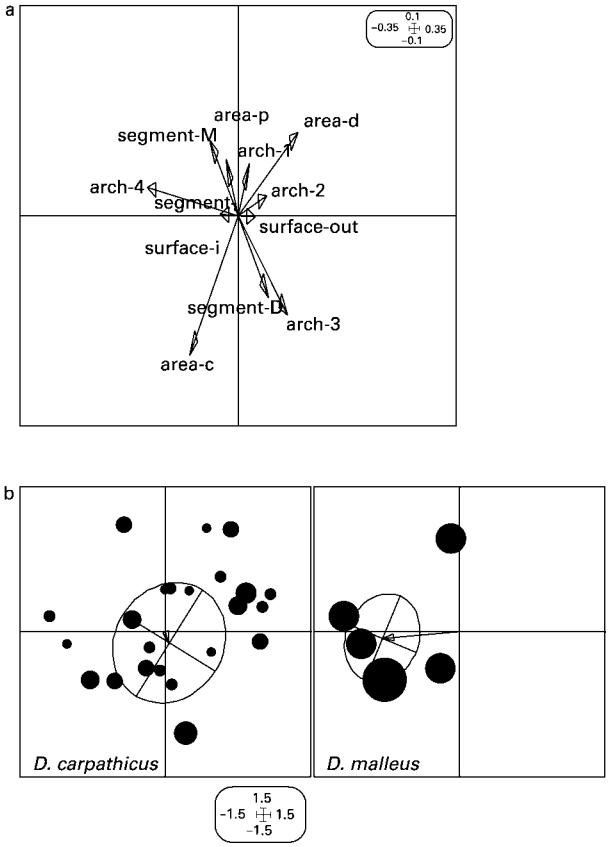

Fig. 2. Graphic representation using the first and the second OMI axes in June 1994 to describe (a) canonical representation of gill variables of the barbel, and (b) microhabitat distribution of *Dactylogyrus carpathicus* and *D. malleus* using mapping of parasite frequencies. The ellipses represent the average niche size for each mongenean species.

on the gills (fig. 1). In April 1994, when considering gill arches separately, the best separation of species was reached within the second and third gill arches (total inertia 0.305 and 0.254 respectively) when the values of mean abundance for *D. malleus* were higher than within the first and fourth gill arches (table 2).

The values of species inertia (presenting the quantification of microhabitat position on species separation), the OMI and tolerance index are shown in table 3. Species inertia was generally higher for *D. malleus*. A small deviation of the average position of species from the origin (expressed as OMI) was recorded for both *Dactylogyrus* species in August 1994. In June 1994, the value of OMI was low for *D. carpathicus*, indicating its position close to the origin whilst the OMI of *D. malleus* showed its mean microhabitat position well separated from *D. carpathicus*. In April 1994, both species were distant from the origin in the total analysis as well as in the analyses of the separated arches. In the first, second and fourth gill arches, OMI values for *D. carpathicus* were lower than for *D. malleus*. In the third gill arch when mean abundance of *D. malleus* was the highest (table 2), the OMI of both species were approximately similar.

The tolerance index presents measurements of the niche breadth (table 3). In April 1994 when *D. carpathicus* reached the highest abundance, it had a lower tolerance index than in June 1994 and August 1994 when its abundance reached lower values (tables 1 and 3). The tolerance index of *D. malleus* followed a similar trend. However, in June 1994, when the abundance of *D. malleus* reached the lowest values when comparing three seasons investigated, the tolerance index indicated a relatively high niche breadth. When comparing the tolerance index of *D. carpathicus* and *D. malleus* within gill arches for April 1994, tolerance index values were similar for both species within each of the gill arches, but were different in different gill arches, i.e. higher values in the first and fourth gill arches indicating broader niches and lower values in the second and third arches indicating narrow niches (see table 2 for comparison of mean abundances in gill arches).

The two axes of OMI analyses, representing 100% of the total marginality were plotted to seasonally represent the species segregation and niche breadth of different species abundance (figs 1 to 3). The relative contributions of each microhabitat on the first and second factorial axes are

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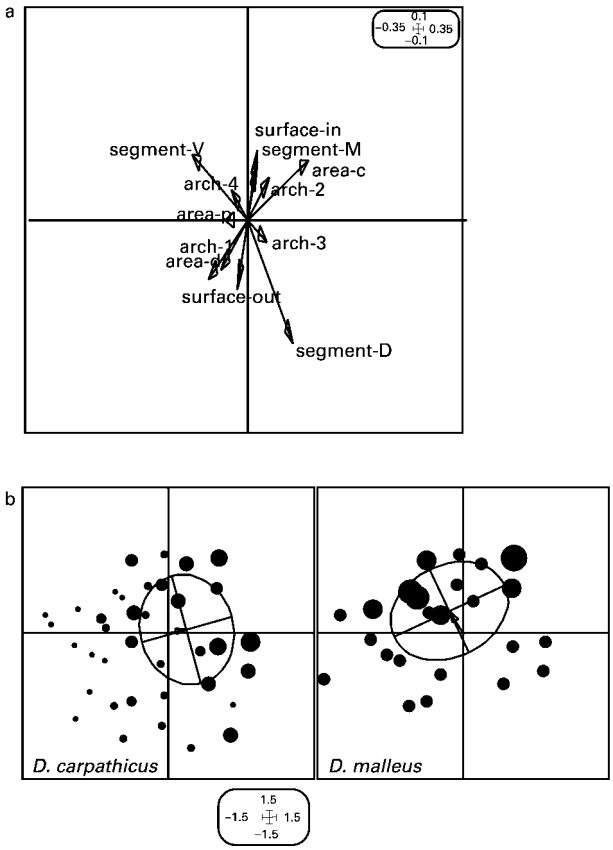

Fig. 3. Graphic representation using the first and the second OMI axes in August 1994 to describe (a) canonical representation of gill variables of the barbel, and (b) microhabitat distribution of *Dactylogyrus carpathicus* and *D. malleus* using mapping of parasite frequencies. The ellipses represent the average niche size for each monogenean species.

given in table 4 for the three different seasons and in table 5 for the separate gill arches in April 1994. The relative contributions of microhabitats were different when comparing three seasons (table 4). In April 1994, medial segment and proximal area to the first factorial axis (FA1), and the ventral segment to the second factorial axis (FA2), were the most contributing factors. In June 1994, the second and fourth gill arches as well as both surfaces presented the highest contribution to the first factorial axis. In August 1994, the third gill arch and both central and proximal areas to the first factorial axis and surface position to the second factorial axis were factors indicating the highest relative contribution.

When considering microhabitat distribution for separated gill arches in April 1994, the most contributing gill factors were the central and proximal areas (table 5). Moreover, dorsal and medial segments in the second gill arch and the medial segment in the third gill arch had a high relative contribution to the first factorial axis (more than 90%). The greatest contributing factor to the second factorial axis was the ventral segment in the second, third and fourth gill arches. The dorsal segment contributed highly to the second axis in the first and fourth gill arches. No parasites were found in the outer gill surface in the second and third gill arches, therefore this surface position was not evaluated. The microhabitat preference was recorded for both *Dactylogyrus* species. *Dactylogyrus carpathicus* preferred central gill areas whilst *D. malleus* was segregated to the proximal areas. Moreover, *D. carpathicus* was situated more in the dorsal segments and *D. malleus* in medial segments. This final segregation was more apparent in the second and third gill arches.

Discussion

Many parasites have restricted microhabitats on hosts (Holmes, 1973; Rohde, 1979, 1991; Geets *et al.*, 1997). Generally, parasite communities are divided into isolationist and interactive in relation to their niche (Stock & Holmes, 1988). In the case of isolationist communities, fundamental and realized niches should be similar, whereas niche breadths and overlap may increase with increasing population sizes. Parasites should show either a random distribution or a preferred habitat as a result of adaptation to the host. In the case of interactive communities, fundamental niches should be broad, and realized niches reduced in the presence of other species. However, the relationship between overlap and competition can be misleading because an inverse relationship between competition and niche overlap may occur (Pianka, 1976; Tokeshi, 1999). In addition, Poulin (2001) suggested that it is difficult to assess the importance of species interaction in helminth communities.

The best way for indicating competition is to compare fundamental and realized niches (Poulin, 1998). Stock & Holmes (1988) found that for intestinal endoparasites different species are positioned along the intestine. Wider overlap was found between fundamental niches than between realized niches. A different situation occurs in the case of monogeneans living on the gills. When considering communities of congeneric monogenean species, generally, a higher number of congeneric species can be recorded in one host (Kennedy & Bush, 1992; Koskivaara *et al.*, 1992; Šimková *et al.*, 2000) and their niches are widely overlapped (Rohde, 1991). Moreover, gills present unsaturated space for parasite colonization and interspecific interactions are not thought to restrict niches.

Rohde (1977, 1991) pointed out that the most important factor responsible for restricting niches is selection to increase intraspecific contacts to facilitate mating. However, there is no convincing reason to exhibit microhabitat specificity for mating as the random selection of niches could also contribute to increasing intraspecific contacts. Restricted niches of monogeneans have often been explained from the mating hypothesis point of view (Geets *et al.*, 1997; El Hafidi *et al.*, 1998).

The present study was carried out in natural conditions for the fish. We could not compare fundamental and realized niches, but we tried to show the influence of parasite abundance on microhabitat distribution of congeneric species, and to consider whether interspecific interactions could be a factor attributed to microhabitat specificity. The best way to answer this question was presented by a model of fish species parasitized only by two congeneric specific monogeneans, i.e. *D. carphathicus* and *D. malleus* in the present

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study. Previously, Ramasamy *et al.* (1985) studied the microhabitat distribution of non-congeneric monogenean species and suggested that microhabitat specificity varied with parasite density on hosts or among different gill parts of the hosts and, in addition, interspecific interactions could occur among gill parasites.

The present results showed that the character of monogenean communities departs mainly from species abundance. However, fish size seems to be a factor partially influencing monogenean distribution on the gills. Buchmann (1989) suggested that different microhabitats of congeners depend on host size. We found no relationship between parasite abundance and fish length in any of the seasons investigated. However, when comparing August 1993 and August 1994, different fish sizes between seasons could explain the differences for microhabitat distribution of parasites. In August 1994, when fish reached a lower size we expected a lower gill size and narrow microhabitats were defined on the fish gills. Thereafter, we could explain that the different microhabitats were important for species distribution in August 1994, but species were distributed indifferently on microhabitats in August 1993 when fish size reached higher values.

Nevertheless, the present study suggests that species abundance could be a factor influencing microhabitat preference in the case of congeneric species. When considering the case of low abundance of both species, i.e. the abundance of the first species was higher than that of second species, then the first species showed no statistically proven preference and tended to occupy a broad niche. The second species was more restricted at the level of the gill arches, and its restriction follows the hypothesis of increasing intraspecific contacts to facilitate mating chances (Rohde, 1977, 1991). When parasites live in moderate abundance, their niches increase as well as overlap. In these conditions, no effect of the more abundant *D. carpathicus* on microhabitat restriction of *D. malleus* was found, and interspecific competition had little influence in limiting the species overlap. The third case in the present study is when the abundance of both congeneric species increased, although niche saturation could not be assumed in this case. *Dactylogyrus malleus* reached a significantly higher abundance than in the first two cases and showed no difference in the abundance of *D. carpathicus*. The niches of both congeners were greatly segregated and a low overlap was found within all gill arches. Moreover, there was a trend for microhabitat preference for both species and similar results were obtained when analysing arch by arch separately. The microhabitats selected due to interspecific interactions could be explained by the different morphology of the attachment organs of *Dactylogyrus*. In the case of *D. carpathicus* and *D. malleus*, the form of the central hooks, i.e. the anchors and ventral connective bar differs greatly and this supports the hypothesis of morphological niche segregation of monogeneans (Rohde, 1991). Another hypothesis, by Buchmann & Lindenstrom (2002), suggests that the microhabitat selection by congeneric monogeneans in the case of increasing abundance could be explained by different tolerances to the host immune reaction, and then one congeneric species out competes the other one. Even if the microhabitats of *D. carpathicus* were restricted in the case of high abundance of *D. malleus*, such a hypothesis was not confirmed in the present case, as the host immune response was not studied.

Previous studies on gill parasite distribution have analysed the microhabitat distribution only among gill arches, i.e. one-dimensional or two-dimensional niches (Koskivaara *et al.*, 1992; Bagge & Valtonen, 1996). Several studies have compared the niche occupation following the microhabitat partitioning within gill arches but the analyses have been performed by taking all arches together and no analysis has been carried out to compare the microhabitat partitioning of species within separated arches (Wootten, 1974; Rohde *et al.*, 1994). The OMI analysis seems to be the most useful method for determining the importance of interspecific and intraspecific relationships in the case of multidimensional microhabitats for parasites.

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