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Microhabitat distribution and coexistence of Microcotylidae (Monogenea) on the gills of the striped mullet *Mugil cephalus*: chance or competition?

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Abstract The two monogenean species *Metamicrocotyla cephalus* and *Microcotyle mugilis* have specific microhabitats on the gills of *Mugil cephalus* on which they may or may not coexist. *M. cephalus* is found in sector 1 of the posterior hemibranch of arch I. *M. mugilis* is found on the filaments of sector 5 of the posterior hemibranch of arch I. The coexistence of these two monogenean species on the same fish does not induce a change in their respective distribution, except for a marked preference of *M. cephalus* for the left side and of *M. mugilis* for the right. This 15-month-long study shows that when the two species of monogeneans coexist the infection prevalence and intensity are higher than in cases of monospecific infection. The specific character of the microhabitat, the apparent absence of interspecific competition, and the existence of positive species interactions are discussed.

fish ectoparasites, Rhode (1991) concluded that the microhabitat of a given species did not seem to be affected by the presence of “potential competitors.” However, except for a few isolated reports (Jenkins and Behnke 1977; Koskivaara 1992) that refer to positive interactions, most studies of interspecific interactions within parasite communities refer to negative interactions.

In the work presented herein, two species of Microcotylidae (Monogenea), *Metamicrocotyla cephalus* (Azim 1939; Hargis 1954) and *Microcotyle mugilis* (Vogt 1878), were observed on the gill of *Mugil cephalus* L. 1758 from the Atlantic coast of Morocco. The goal of this study was to define the respective microhabitats of these two monogenean species in monospecific and combined infections and to understand the nature of interactions that may occur between the two species within this parasite community as well as the consequences of their interactions on the spatial structure and density of the populations.

Introduction

The structure of parasite communities has been explained in different and, sometimes, contradictory ways. For Holmes (1973) the structure of parasite communities would be due to competitive interspecific interactions that would act on the population's spatial distribution and density (interactive communities). In contrast, for Price (1980) the structure of parasite communities may result from the random assembly of species that evolve independently (isolationist communities). After studying

Materials and methods

Metamicrocotyla cephalus were sampled from catches of professional fishermen every month in the lagoon of Moulay Bousselham, Morocco, from January 1992 until March 1993. A total of 829 *Mugil cephalus* measuring between 8.5 and 41.8 cm (midcaudal length) were studied. Gills were dissected and arches, numbered I–IV from the anterior to the posterior end, were examined. After being isolated from the gills, monogeneans were studied and their species were determined according to the number, shape, and size of the sclerified structures of the haptor and the genital atrium as described by Euzet and Combes (1969).

Each individual was precisely localized on the arch according to the pattern defined by Lambert and Maillard (1975). The anterior (external) and posterior (internal) hemibranches were divided into five areas extending from the dorsal to the ventral region. Gill filaments were divided into three regions: proximal (inferior third), median, and distal (superior third; Fig. 1). A chi-square test was used to compare the number of parasites of each monogenean species found on the different regions of the gills with the number of parasites expected to be found in a balanced distribution. The terms prevalence and mean intensity were used according to the definitions of Margolis et al. (1982).

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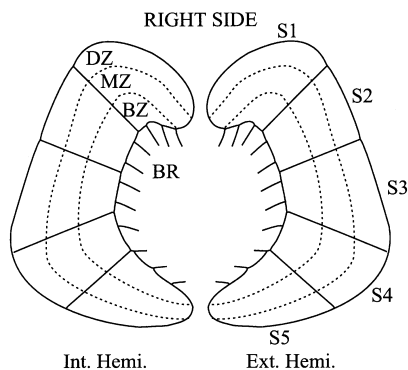


Fig. 1 Schematic diagram of a gill cutout (S Sector, BR branchiospine, Z zone, Int. Hemi. internal hemibranch, Ext. hemi. external hemibranch)

Copepods of the species *Caligus apodus* were also found on the dissected gills but were not taken into account in this study because of their small number (53) and their localization (arch II).

Results

Specific microhabitats

We examined the branchial distribution of *Metamicrocotyla cephalus* in monospecific infections (Table 1, Fig. 2). Of the 829 dissected fish, 143 were infected with only *M. cephalus* (prevalence 17.2%, Table 3). The distribution of the 442 parasites found in monospecific infections is reported in Table 1. The difference was not significant between the number of parasites found on the right and on the left set of the gills ($\chi^2 = 3.27, df = 1,$

$P < 0.05$). However, whatever the arch considered, the posterior hemibranchs were more likely to be colonized than were the anterior ones. Sector 1 of arch I harbored 77.8% of the parasites, whereas the other 22.2% of the infrapopulation were found on sectors 2–5 of arch I along a decreasing gradient. The median zone of the filaments harbored 67% of the parasites and, thus, constituted the preferred area of attachment for these parasites.

We also examined the branchial distribution of *Microcotyle mugilis* in monospecific infections (Table 1, Fig. 3). Of the 829 dissected fish, 84 (10.13%) were infected with *M. mugilis* only. A total of 167 parasites were found (Table 2). As in the case of *M. cephalus*, the difference was significant between the number of parasites found on the right and the left set of the gills ($P > 0.05, \chi^2 = 0.15, df = 1$), but the posterior hemibranchs were preferably infected as compared with the anterior ones. Arch I harbored 74% of these monogeneans, mostly in sector 5, whereas the other 26% were found on sector 5 of arches II–IV along a decreasing gradient before sector 4 was colonized. Parasites mostly occurred on the distal or median parts of the filaments.

Intraspecific competition and microenvironment

To test the density-dependent character of the spatial distribution we sought the saturation threshold of the preferred site for the two species. The saturation threshold is defined as the number above which additional individuals would occupy a different station.

For *M. cephalus* the way individuals filled in sector 2 of arch I during monospecific infestations indicated that when 1–4 individuals were found in sector 1, a 5th

Table 1 Monospecific infections of *Mugil cephalus* with *Microcotyle mugilis* and *Metamicrocotyla cephalus* (Ant. hemibr. Anterior hemibranch, Post. hemibr. posterior hemibranch, Prox. fil. zone proximal filament zone, Med. fil. zone median filament zone, Dist. fil. zone distal filament zone, Dif. zones different zones)

Location	Number of <i>M. cephalus</i>	% of <i>M. cephalus</i>	Number of <i>M. mugilis</i>	% of <i>M. mugilis</i>
Right side	202	45.7	86	51.5
Left side	240	54.3	81	48.5
Gill arch I	426	96.4	123	73.7
Gill arch II	15	3.4	39	23.4
Gill arch III	1	0.2	4	2.4
Gill arch IV	0	0	1	0.6
Ant. hemibr.	81	18.3	53	31.7
Post. hemibr.	359	81.2	110	65.9
Ant. & post. hemibr.	2	0.5	2	1.2
Sector 1	344	77.8	3	1.8
Sector 2	90	20.4	0	0
Sector 3	5	1.1	0	0
Sector 4	2	0.5	3	1.8
Sector 5	1	0.2	160	95.8
Branchiospine	0	0	1	0.6
Prox. fil. zone	10	2.3	2	1.2
Med. fil. zone	296	67	66	39.5
Dist. fil. zone	134	30.3	92	55.1
Dif. zones	2	0.45	6	3.59
Total numbers of parasites	442	–	167	–

Table 2 Simultaneous infections of *Mugil cephalus* with *M. mugilis* and *M. cephalus*

Location	Number of <i>M. cephalus</i>	% of <i>M. cephalus</i>	Number of <i>M. mugilis</i>	% of <i>M. mugilis</i>
Right side	547	46.8	362	54.3
Left side	621	53.2	305	45.7
Gill arch I	1116	95.5	441	66.1
Gill arch II	38	3.3	204	30.6
Gill arch III	10	0.9	22	3.3
Gill arch IV	4	0.3	0	0
Ant. hemibr.	302	25.9	238	35.7
Post. hemibr.	860	73.6	417	62.5
Ant. & post. hemibr.	5	0.4	11	1.6
Sector 1	891	76.3	0	0
Sector 2	250	21.4	1	0.1
Sector 3	17	1.5	1	0.1
Sector 4	7	0.6	4	0.6
Sector 5	2	0.2	660	99
Branchiospine	1	0.1	1	0.1
Prox. fil. zone	39	3.3	12	1.8
Med. fil. zone	697	59.7	310	46.5
Dist. fil. zone	429	36.7	314	47.1
Dif. zones	2	0.17	30	4.50
Total numbers of parasites	1168	–	667	–

Table 3 Distribution of *M. mugilis* and *M. cephalus* in the *Mugil cephalus* population of Moulay Bouselham, Morocco

Type of infection	Monospecific	Monospecific	Bispecific	Bispecific
Parasite species	<i>M. cephalus</i>	<i>M. mugilis</i>	<i>M. cephalus</i>	<i>M. mugilis</i>
Number of fish	829	829	829	829
Number of infected fish	143	84	195	195
Number of parasites	442	167	1168	667
Prevalence (%)	17.2	10.13	23.5	23.5
Abundance	0.53	0.20	1.40	0.80
Mean intensity	3.09	2.06	6.1	3.05
SD	3.69	1.63	7.60	3.69

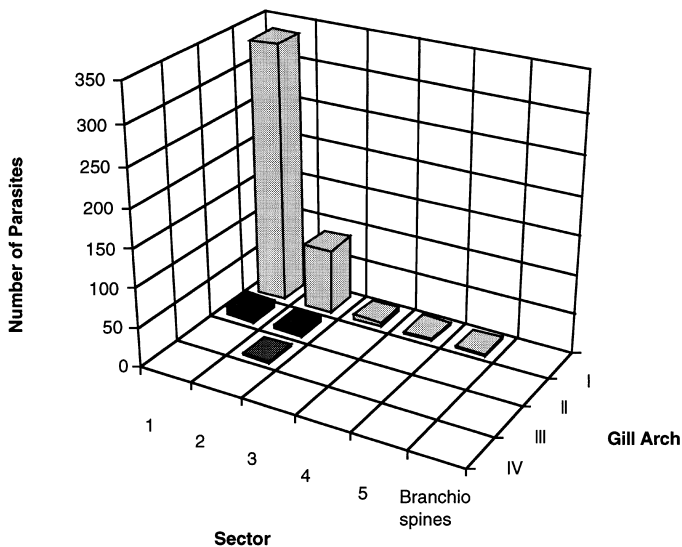


Fig. 2 Branchial distribution of *Metamicrocotyla cephalus* in monospecific infection of *Mugil cephalus*

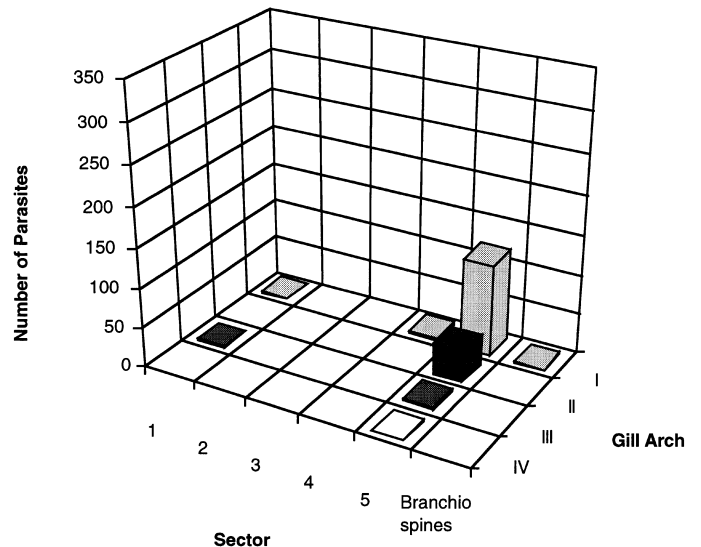


Fig. 3 Branchial distribution of *Microcotyle mugilis* in monospecific infection of *Mugil cephalus*

individual would be found in the next sector in 25% of cases. However, when there were 5 or more individuals in the infrapopulation, additional parasites would be found in sector 2 in 70% of cases. Therefore, the distribution of *M. cephalus* in the different sectors of arch I followed a gradient and appeared to be a function of the size of the infrapopulation; colonization of the adjacent sector seemed to occur after a threshold of four parasites had been reached in the preferred sector. However, there were exceptions: on one fish, ten *M. cephalus* were found in sector 1, whereas no colonization of sector 2 had occurred, and on another, seven *M. cephalus* were found in sector 2, whereas sector 1 was vacant.

To determine if the presence of *M. mugilis* in sector 5 of arch II was a function of the number of individuals attached on arch I, we considered all fish that were parasitized with only this monogenean species and had parasites on sector 5 of arch II. In 21% of the fish, parasites were attached in sector 5 of arch II, whereas only one parasite was found on preferred arch I. In 49% of the fish, parasites were found in sector 5 of arch II, whereas sector 5 of arch I was vacant. Therefore, the distribution of *M. mugilis* on sector 5 of the different arches followed a pattern that did not depend on intraspecific competition. As a result, it may be concluded that there was no saturation threshold for the preferred site of this parasite.

Coexistence and spatial distribution

Of the 829 dissected fish, 195 fish were simultaneously infected with both species of Microcotylidae. There was no difference in the spatial distribution of the two species in the branchial cavity when they coexisted as compared with the respective monospecific infections (see Table 2). However, there was an increase in the microhabitat size for both species; more *M. cephalus* were found on the median part of the filaments. Finally, there was a significant difference between the distribution of the two monogenean species relative to the side of the fish in combined infections. In this case, *M. cephalus* preferred the left side and *M. mugilis* preferred the right side ($\chi^2 = 9.11$, $df = 3$, $P > 0.05$).

Coexistence and aggregation processes

Overall, *Mugil cephalus* was parasitized less heavily (in terms of mean intensity) by *M. mugilis* than by *M. cephalus*: however, whatever the parasite species observed, the prevalence and mean intensity were higher when the two species coexisted (Table 3). This increase in the infrapopulation densities may explain the increased size of the respective microhabitats. Co-existence of both monogenean species was observed in fish measuring 15 cm or more, and the prevalence increased progressively with the size of the fish. All fish measuring 40 cm or more were simultaneously parasitized with both monogenean species.

Simultaneous infections with both monogenean species occurred throughout the 15-month-long sampling period, with peaks being noted in February and August (Figs. 4, 5). Monospecific infection with *M. mugilis* varied greatly, although such infections occurred continuously.

Discussion

Spatial segregation and interspecific competition

The study of the spatial distribution of the infrapopulations of both microcotylid species indicates the preferred microhabitat of each species. The microhabitat of *Metamicrocotyla cephalus* is sector 1 on the posterior hemibranch of arch I, with individuals being attached in the median region of the filaments. The microhabitat of *Microcotyle mugilis* is sector 5 of the posterior hemibranch of arch I, with individuals being attached in the distal and median regions of the filaments. The spatial distribution of either parasite species did not change when they coexisted on the host. The presence of both monogenean species did not induce any decrease in or shifting of their respective microhabitats. Furthermore, whatever the size of both species infrapopulations, av-

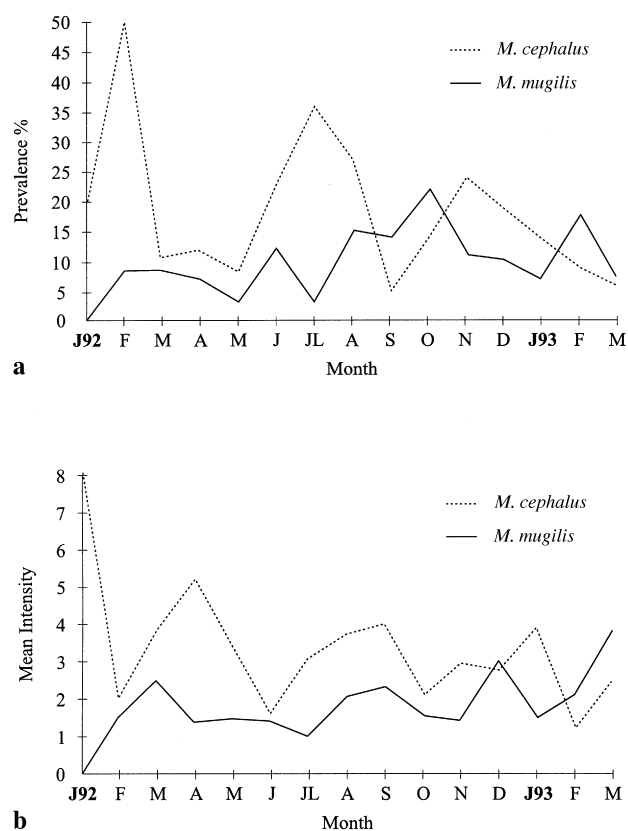


Fig. 4a, b Monospecific infections of *Mugil cephalus* with *M. cephalus* and *M. mugilis*. a Monthly evaluation of prevalence. b Monthly evaluation of mean intensity

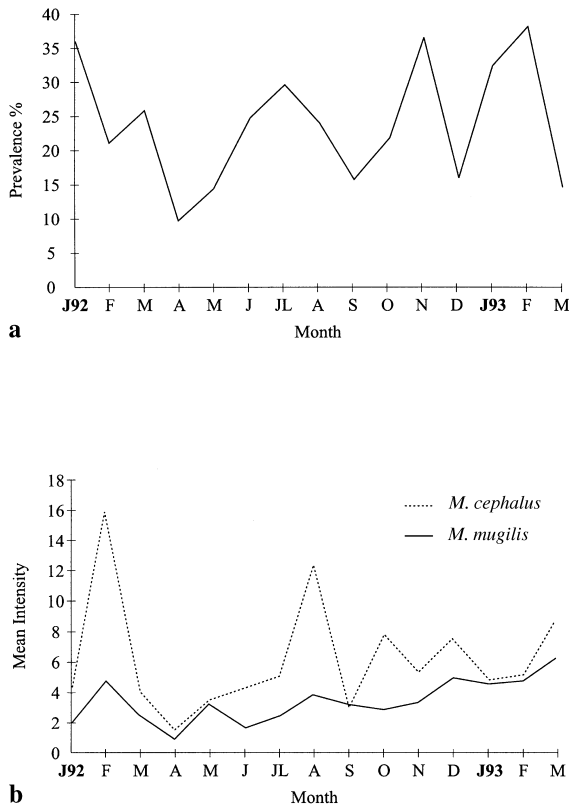


Fig. 5a, b Simultaneous infections of *Mugil cephalus* with *M. mugilis* and *M. cephalus*. **a** Monthly variations in prevalence. **b** Monthly variations in mean intensity

erage intensities remained low (Table 4) and numerous potential niches remained vacant. Thus, as Combes (1995) suggested, the absence of competition or the presence of low-level of interspecific competition does not make each species extend its niche over the entire available space. These results raise the following question: what could be the constraints that may explain this niche restriction in the absence of apparent interspecific competition?

Works by numerous authors have established a marked preference of monogeneans for particular sites on the gills (see Wooten 1974; Rhode 1982). In the Microcotylidae this is the case for *M. salpae* Parona and Perugia 1980 on *Box salpa* (Ktari 1969), for *Polylabris*

tubicirrus (Paperna and Kohn 1964) and *Atriatster heterodus* (Lebedev and Paruchin 1969) on *Diplodus sargus* (Noisy and Euzet 1979), and for *M. chrysoiphrii* (van Beneden and Hesse 1863) on *Spratus aurata* (Noisy and Maillard 1980; Oliver 1984). Is the distribution of these parasites linked to the structure of the gills and the respiratory current as suggested by Davey (1980) and Llewellyn (1956)? The variation in the flow of water from one gill arch to another (Paling 1967; Wooten 1974) and even, sometimes, from one part of the hemibranch to another (Wooten 1974) may explain the localization of these monogeneans on the first arch. In effect, these parasites may have a reduced ability to maintain themselves against the respiratory current. The localization of *M. cephalus* in the median zone of the first sector may reflect a preference of this parasite for a site that is less oxygenated but in which the water flow is maximal. *M. mugilis* is found in the distal zone of the 5th sector, where greater water flow occurs as compared with the other sites, and may be attached there because of its large number of clamps.

According to Llewellyn (1956), parasites with a large number of clamps would be more or less sessile and the oncomiracidium would be the one selecting the microhabitat (Ramasamy et al. 1984). The pair of clamps that appears precociously in the *M. mugilis* oncomiracidium (Euzet and Combes 1969) may reinforce the ability for this parasite to attach to the distal region of sector 5 of arch I. In *M. cephalus* a reduced number of clamps may explain why the parasite is rejected to the median region of the first sector of arch I despite the presence of a posterior peduncle that might increase adherence and the ability of the parasite to wrap around several filaments.

Thus, although the heterogeneity of the gill apparatus, the physiology of the host, and the structure of the larval and adult haptors may explain the spatial distribution of the two monogenean species, the advantage of this type of distribution remains to be determined. As suggested by Rhode (1977), the aggregation of adults in a small number of sites may favor chances of mating in cross-fertilizers.

Spatial segregation and intraspecific competition

Whatever the advantages of the type of distribution observed, the aggregation of individuals in a narrow space would be expected to increase intraspecific interactions. Although a saturation threshold for the preferred site is observed only during monospecific infestations by *M. cephalus*, the microhabitat of each species enlarges during simultaneous infestations. This observation fits Holmes' conclusions (1961, 1962, 1973) about intestinal parasites for which niche extension is a consequence of intraspecific competition. Although intraspecific competition is not obvious for the monogenean species and depends on the size of the infrapopulations, it is more likely to be at the origin of

Table 4 Preferred localization of *M. mugilis* and *M. cephalus* in *Mugil cephalus*

Species	<i>M. cephalus</i>	<i>M. mugilis</i>
Location		
Side	^a Left -right	^a Right -left
Arch	1	1
Hemibranch	Posterior	Posterior
Sector	1	5
Filament zone	Median	Distal & median

^a The site preferred by each of the two parasite species coexisting in the same fish is indicated in **bold face**

shifting to the microhabitat than is interspecific competition; that is, the effects of this type of competition appear to be opposite to those expected from interspecific competition (Pianka 1974).

Coexistence and positive interactions

That two species cohabit without shifting their niche does not imply that reciprocal pressures are not exerted. Prevalences and mean intensities are higher when *Mugil cephalus* is parasitized simultaneously with both Microcotylidae species, as also happens in *Dactylogyrus* communities parasitizing the roach *Rutilus rutilus* (Koskivaara 1992). According to Rhode (1994), these types of positive interaction between fish ectoparasites parasitizing the same host are more frequent than negative interactions (of 4000 marine fish belonging to 100 species, 35 positive interactions were recorded versus 2 negative ones).

The increase in infrapopulations during multispecific infestations may mean either that the recruitment of the two species is, in most cases, simultaneous or that the attachment of one of the species' larvae is favored by the presence of individuals of the other species. Facilitated infestations of the second species may be caused by a nonspecific immunosuppressive action of the first species, as has been shown in nematodes by Jenkins and Behnke (1977). This mechanism could be facilitated by an equivalent susceptibility of the host linked to the two closely related parasites (Dobson 1985). The strict specificity of *M. cephalus* for *Mugil cephalus* as opposed to the wide specificity of *M. mugilis* (Euzet and Combes 1969) may also explain the differences in parasitism between the two Microcotylidae species.

The preference of parasites to attach to previously parasitized fish may increase the parasitic load and favor aggregation of the infracommunities within the hosts and not of each species' infrapopulation. This implies that one could distinguish two subpopulations of *M. cephalus*, one of fish without Microcotylidae and the other of fish infected simultaneously with both monogenean species.

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