

Spatial Distribution of *Dactylogyrus* (Monogenean) on the Gills of the Host Fish

Emine Turgut^{1,*}, Andrew Shinn², Rodney Wootten²

¹ Aquaculture Department, Faculty of Agriculture, Gaziosmanpaşa University, 60240, Tokat, Turkey.

² Institute of Aquaculture, Stirling University, Stirling, Scotland.

* Corresponding Author: Tel.: +90. 356 252 16 16; Fax: +90. 356 252 18 18;
E-mail: emineturgut5@yahoo.com

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Abstract

The spatial distribution of six Monogenean species, *Dactylogyrus extensus*, *Dactylogyrus auriculatus*, *Dactylogyrus difformis*, *Dactylogyrus difformoides*, *Dactylogyrus amphibothrium* and *Dactylogyrus hemiamphibothrium* on the host fish gill was investigated. There were no preference found in the distribution of *Dactylogyrus* species over the gill arches between left and right sides of the hosts. There were, however, preferences for the specific gill arches or for particular faces of the hemibranches. The first gill arch (I) was preferred by *D. amphibothrium*, gill arch II by *D. auriculatus*, gill arch III by *D. auriculatus*, *D. difformis* and *D. difformoides*, and gill arch IV by *D. difformis* and *D. difformoides*. *D. extensus*, *D. auriculatus* exhibited a preference for the inner side of the gill. Furthermore, *D. extensus* showed preference for the distal-median and distal-ventral parts of the gill, *D. auriculatus* preferred proximal-ventral, and proximal median segments and *D. difformis* and *D. difformoides* preferred distal-dorsal segments of the host fish. These specific preferences might be effected by the interaction of several factors such as differences in the water current over different parts of the gill surface, parasite density, as well as ecological and morphological differences between monogenean species.

Key words: microhabitat, niche restriction, *Dactylogyrus*

Introduction

The spatial segregation of parasites is reported to be affected by intraspecific site segregation, where microhabitat segregation is restricted to a single species and secondly, interspecific site segregation, where microhabitat selection is influenced by the presence of co-existing parasite species (Rohde, 1979; Ramasamy *et al.*, 1985; Simkova *et al.*, 2002). Thus, parasite species coexistence has been studied in the context of site segregation and niche restriction (Rohde, 1994; Matejusova *et al.*, 2002).

Most species of monogeneans are restricted not only to a particular host but also to a particular part of the host body. The microhabitat of gill-living monogeneans has been investigated by many authors (Buchmann, 1988a, b; El-Nagar *et al.*, 1993; El Hafidi *et al.*, 1998; Dzika, 1999; Chapman *et al.*, 2000; Lo and Morand, 2000; Simkova *et al.*, 2000; Simkova *et al.*, 2002; Matejusova *et al.*, 2002; Kadlec *et al.*, 2003).

Dactylogyrus species show a preference for specific parts of the gill apparatus of their host. The effect for these preferences is not clear. This work presents a study on the spatial distribution of several species of *Dactylogyrus* so that we may have a clear understanding of their preference for specific parts of the gill apparatus.

Materials and Methods

Specimens of carp were obtained from Devon,

bream and rudd from Humberside, and ruffe from Loch Lomon, Scotland, UK. Captured fish were brought in aerated bags with local water and transported to laboratory. Fish were maintained in tanks at 15°C prior to examination. Examination of fish revealed that the carp (*Cyprinus carpio*) were infected by *D. extensus*, bream (*Abramis brama*) by *D. auriculatus*, ruffe (*Gymnocephalus cernuae*) by *D. amphibothrium*, *D. hemiamphibothrium* and rudd (*Scardinius erythrophthalmus*) by *D. difformis* and *D. difformoides*. Because of the mixed infection and the morphological similarity of *D. difformis* and *D. difformoides*, it was not possible to determine the spatial distribution for each of these species separately.

Fish were killed by insertion of a pointed needle into the brain via the upper part of the eye. The total body length and weight were measured. The number of each fish species was examined and their measurements are shown in Table 1. The gills were excised and each arch placed in a separate Petri dish containing aquarium water and observed under a dissecting microscope (Olympus SZ30) at 2x-4x magnification and a binocular light microscope (Olympus CH2) at 10x-40x magnification. Gill arches from each side of the fish were numbered I-IV from the anterior gill arch below the operculum to the posterior. The surface of each hemibranch was designated as outer (i.e. that surface being the nearest to the operculum) and inner, and each hemibranch was divided into 6 sections, approximately equal in surface area. The number of worms on each gill arch

was recorded and their position plotted on a gill map as shown in Figure 1.

Statistical Analysis

Data from the distribution of *Dactylogyrus* species between the left and right sides of each gill arch, inner/ outer hemibranchs, and hemibranch segments were subjected to a four-way ANOVA. Percentages were transformed by arcsine transformation (Zar, 1984) prior to ANOVA and reversed afterwards. All statistics were executed using Minitab software

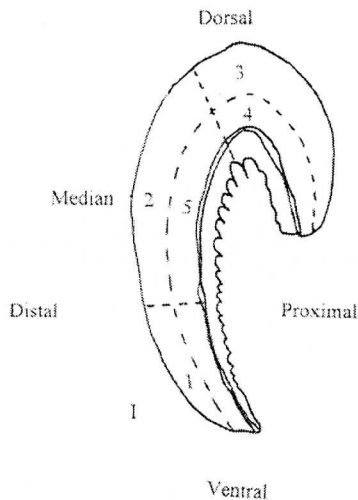


Figure 1. Illustration of gill arch showing its division into six arbitrary areas: 1. distal-ventral, 2. distal-median, 3. distal-dorsal, 4. proximal-dorsal, 5. proximal-median, 6. proximal-ventral.

Results

Spatial Distribution of *Dactylogyrus* Species

The overall number of *D. extensus* from carp, *D. auriculatus* from bream, *D. difformis* / *difformoides* from rudd, *D. amphibothrium* and *D. hemiamphibothrium* from ruffe, on the different parts of the gill apparatus is given in Table 2, 3, 4 and 7.

Dactylogyrus extensus

The number of *D. extensus* on the different parts of the gill apparatus of carp is shown in Table 2. The data analysis did not show any statistically significant difference in the number of *D. extensus* between the right and left set of gill arches of carp ($P > 0.05$). The mean number of *D. extensus* on the right and left gill arches are given in Table 8. Fewer *D. extensus* occurred on the first gill arch than on gill arches 2, 3 and 4, but these differences were not significant ($P > 0.05$). The mean number of *D. extensus* on the gill arches is given in Table 9.

There were a significantly greater number of *D. extensus* on the inner hemibranch ($P < 0.05$). The mean number of *D. extensus* on the outer and inner hemibranch is given in Table 5. There were significant differences in the number of *D. extensus* on the different gill areas ($P < 0.001$). Thus, a greater number of *D. extensus* occurred on the distal median and distal-ventral segments than on the proximal-dorsal and distal-dorsal segments of the gill. The mean number of *D. extensus* on the gill arch areas is given in Table 6.

Table 1. *Dactylogyrus* species, their hosts, mean intensity, length and weight of fish host used in spatial distribution studies

| Species | Mean intensity (range) | Host (n) | Length of fish (cm) | Weight of fish (g.) |
|-----------------------------------|------------------------|------------|---------------------|---------------------|
| <i>D. extensus</i> | 19 (5-58) | Carp (34) | 8.8 (7.2-11) | 9.6 (7-15) |
| <i>D. auriculatus</i> | 18.7 (5-44) | Bream (17) | 15.5 (13-17.6) | 31 (21-47) |
| <i>D. difformis/ difformoides</i> | 28 (11-58) | Rudd (21) | 13 (11.6-14.3) | 25 (17-34) |
| <i>D. amphibothrium</i> | 170 (42-239) | Ruffe (10) | 8.7 (7-9.5) | |
| <i>D. hemiamphibothrium</i> | 18 (3-36) | Ruffe (10) | 8.7 (7-9.5) | |

Table 2. The spatial distribution of *D. extensus* over the gill apparatus of *Cyprinus carpio*

| Gill set | Right | | | | Left | | | |
|---------------------------|----------|--------|--------|----|----------|--------|--------|----|
| No of <i>D. extensus</i> | 294 | | | | 280 | | | |
| Inner/outer hemibranch | Inner | | Outer | | Inner | | Outer | |
| No of <i>D. extensus</i> | 166 | | 128 | | 148 | | 132 | |
| Gill arches | I | II | III | V | I | II | III | V |
| No of <i>D. extensus</i> | 45 | 85 | 71 | 93 | 65 | 78 | 71 | 66 |
| Halves of primary lamella | Proximal | | Distal | | Proximal | | Distal | |
| No of <i>D. extensus</i> | 118 | | 176 | | 97 | | 183 | |
| Segments of hemibranch | Ventral | Median | Dorsal | | Ventral | Median | Dorsal | |
| No of <i>D. extensus</i> | 128 | 124 | 42 | | 108 | 125 | 47 | |

Table 3. The spatial distribution of *D. auriculatus* over the gill apparatus of *Abramis brama*

| Gill set | Right | | | | Left | | | |
|-----------------------------|----------|--------|--------|--------|----------|--------|--------|--------|
| No of <i>D. auriculatus</i> | 138 | | | | 142 | | | |
| Inner/outer hemibranch | Inner | | Outer | | Inner | | Outer | |
| No of <i>D. auriculatus</i> | 75 | | 63 | | 81 | | 61 | |
| Gill arches | I | II | III | V | I | II | III | V |
| No of <i>D. auriculatus</i> | 30 | 49 | 43 | 16 | 33 | 50 | 33 | 24 |
| Halves of primary lamella | Proximal | | Distal | | Proximal | | Distal | |
| No of <i>D. auriculatus</i> | 90 | | 48 | | 76 | | 66 | |
| Segments of hemibranch | Ventral | Median | | Dorsal | Ventral | Median | | Dorsal |
| No of <i>D. auriculatus</i> | 61 | 54 | | 23 | 51 | 55 | | 36 |

Table 4. The spatial distribution of *D. difformis* / *difformoides* over the gill apparatus of *Scardinius erythrophthalmus*

| Gill set | Right | | | | Left | | | |
|--|----------|--------|--------|--------|----------|--------|--------|--------|
| No of <i>D. difformis/difformoides</i> | 285 | | | | 317 | | | |
| Inner/outer hemibranch | Inner | | Outer | | Inner | | Outer | |
| No of <i>D. difformis/difformoides</i> | 159 | | 126 | | 166 | | 151 | |
| Gill arches | I | II | III | V | I | II | III | V |
| No of <i>D. difformis/difformoides</i> | 44 | 67 | 82 | 92 | 51 | 67 | 96 | 103 |
| Halves of primary lamella | Proximal | | Distal | | Proximal | | Distal | |
| No of <i>D. difformis/difformoides</i> | 138 | | 147 | | 138 | | 179 | |
| Segments of hemibranch | Ventral | Median | | Dorsal | Ventral | Median | | Dorsal |
| No of <i>D. difformis/difformoides</i> | 63 | 100 | | 122 | 91 | 104 | | 122 |

Table 5. Comparison of the mean number of *Dactylogyrus* species distributed on the inner and outer hemibranchs of the gills of the host fish

| Species | <i>D. extensus</i> | <i>D. auriculatus</i> | <i>D. difformis / difformoides</i> |
|------------|--------------------|-----------------------|------------------------------------|
| Hemibranch | Mean \pm SD | Mean \pm SD | Mean \pm SD |
| Inner | 4.0 \pm 1.9 a | 3.7 \pm 2.6a | 3.8 \pm 1.9a |
| Outer | 3.3 \pm 2.2b | 2.9 \pm 2.6b | 3.5 \pm 1.8 a |

*Values with the same superscript letter are not significantly different (P<0.05)

Table 6. Distribution of *Dactylogyrus* species on the segments of the gill arch areas of the host fish

| Species | <i>D. extensus</i> | <i>D. auriculatus</i> | <i>D. difformis/difformoides</i> |
|---------------------|-----------------------------|-----------------------------|----------------------------------|
| Hemibranch | Mean \pm SD | Mean \pm SD | Mean \pm SD |
| 1. distal-ventral | 4.6 \pm 2.0 ^c | 2.9 \pm 2.3 ^{ab} | 2.7 \pm 1.8 ^a |
| 2. distal-median | 5.3 \pm 1.7 ^c | 3.4 \pm 2.7 ^{ab} | 3.8 \pm 1.8 ^{ab} |
| 3. distal-dorsal | 2.8 \pm 1.5 ^{ab} | 2.4 \pm 2.2 ^a | 4.9 \pm 1.8 ^b |
| 4. proximal-dorsal | 1.8 \pm 1.7 ^a | 2.7 \pm 2.5 ^{ab} | 3.3 \pm 1.8 ^{ab} |
| 5. proximal-dorsal | 3.5 \pm 1.8 ^b | 3.9 \pm 2.7 ^{ab} | 3.7 \pm 1.8 ^{ab} |
| 6. proximal-ventral | 3.8 \pm 1.6 ^{bc} | 4.4 \pm 2.8 ^b | 3.6 \pm 1.6 ^{ab} |

*Values with the same superscript letter are not significantly different (P<0.05)

Table 7. The spatial distribution of *D. amphibothrium* and *D. hemiamphibothrium* over the gill apparatus of *Gymnocephalus cernuae*

| Gill set | Right | | | | Left | | | |
|-----------------------------------|-------|-----|-----|-----|------|-----|-----|-----|
| No of <i>D. amphibothrium</i> | 818 | | | | 887 | | | |
| No of <i>D. hemiamphibothrium</i> | 86 | | | | 93 | | | |
| Gill arches | I | II | III | IV | I | II | III | IV |
| No of <i>D. amphibothrium</i> | 144 | 221 | 234 | 219 | 197 | 229 | 250 | 211 |
| No of <i>D. hemiamphibothrium</i> | 37 | 22 | 18 | 9 | 48 | 27 | 18 | 0 |

Table 8. Comparison of the mean number of *Dactylogyrus* species distributed on the right and left sets of the gills of the host fish

| Species | <i>D. extensus</i> | <i>D. auriculatus</i> | <i>D. difformis/ difformoides</i> | <i>D. amphibothrium</i> | <i>D. hemiamphibothrium</i> |
|---------|----------------------------|----------------------------|-----------------------------------|-----------------------------|-----------------------------|
| Side | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD |
| Right | 3.6 \pm 2.3 ^a | 3.1 \pm 2.6 ^a | 3.6 \pm 1.8 ^a | 14.4 \pm 1.4 ^a | 13.8 \pm 3.7 ^a |
| Left | 3.7 \pm 1.8 ^a | 3.4 \pm 2.6 ^a | 3.8 \pm 1.9 ^a | 15.2 \pm 1.7 ^a | 12.5 \pm 8.7 ^a |

*Values with the same superscript letter are not significantly different (P<0.05)

Table 9. Comparison of the mean number of *Dactylogyrus* species on the gill arches I, II, III, IV of the host fish

| Species | <i>D. extensus</i> | <i>D. auriculatus</i> | <i>D. difformis/ difformoides</i> | <i>D. amphibothrium</i> | <i>D. hemiamphibothrium</i> |
|-------------|----------------------------|-----------------------------|-----------------------------------|-----------------------------|------------------------------|
| Gill arches | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD |
| I | 3.0 \pm 2.0 ^a | 3.2 \pm 2.4 ^a | 2.8 \pm 1.7 ^a | 13.2 \pm 2.4 ^a | 19.9 \pm 3.8 ^a |
| II | 4.0 \pm 1.9 ^a | 4.2 \pm 2.9 ^b | 3.5 \pm 1.7 ^{ab} | 15.4 \pm 0.4 ^a | 15.1 \pm 1.3 ^{ab} |
| III | 3.7 \pm 2.1 ^a | 3.5 \pm 2.6 ^{ab} | 4.1 \pm 1.9 ^b | 15.6 \pm 0.9 ^a | 12.9 \pm 1.3 ^b |
| IV | 3.8 \pm 2.1 ^a | 2.3 \pm 2.1 ^a | 4.3 \pm 1.8 ^b | 15.0 \pm 0.3 ^a | 4.5 \pm 5.3 ^c |

*Values with the same superscript letter are not significantly different (P<0.05).

Dactylogyrus auriculatus

The number of *D. auriculatus* on the different parts of gill apparatus of bream is shown in Table 3. The data analysis did not show any statistically significant differences in the number of *D. auriculatus* between the right and left set of gill arches of bream (P> 0.05). The mean number of *D. auriculatus* on the right and gill arches is given in Table 8. The data analysis showed statistically significant differences in the number of *D. auriculatus* between the gill arches. A significantly greater number of *D. auriculatus* occurred on the second and third gill arches. The mean number of *D. auriculatus* on the gill arches is given in Table 9. There were a significantly greater number of *D. auriculatus* on the inner hemibranch (P<0.05). The mean number of *D. auriculatus* on the outer and inner hemibranch is given in Table 5. There were significant differences in the number of *D. auriculatus* on the different gill arch areas (P<0.01). A greater number of *D. auriculatus* occurred on the proximal-ventral and proximal-median segments than on the proximal-dorsal, distal dorsal segments of the gill. The mean number of *D. auriculatus* on the gill arch areas is given in Table 6.

Dactylogyrus difformis/ difformoides

There was a mixed infection of *D. difformis* and *D. difformoides* on rudd. Due to these mixed infections and difficulty on identification of these two species, spatial distribution for these two species could not be done individually. The spatial distribution of these species was mentioned in this work together as *D. difformis/ difformoides*. The number of *D. difformis/ difformoides* on the different parts of the gill apparatus of rudd is shown in Table 4. The data analysis did not show any statistically significant difference in the number of *D. difformis/*

difformoides on the right and left gill arches are given in Table 8. A significantly greater number of *D. difformis/ difformoides* occurred on the third and fourth gill arches than on the first and second gill arches (P<0.001). The mean number of *D. difformis/ difformoides* on the gill arches is given in Table 9. The data analysis did not show statistically significant differences in the number of *D. difformis/ difformoides* between the inner and outer hemibranch (P>0.05). The mean number of *D. difformis/ difformoides* on the outer and inner hemibranch is given in Table 5. There were significant differences in the number of *D. difformis/ difformoides* on the different gill areas (P<0.001). A greater number of *D. difformis/ difformoides* occurred on the distal-dorsal than on the proximal ventral, proximal dorsal and distal ventral segments of the gill. The mean number of *D. difformis/ difformoides* on the gill arch areas is given in Table 6.

Dactylogyrus amphibothrium

The number of *D. amphibothrium* on the different parts of the gill apparatus of ruffe is shown in Table 7. The data analysis did not shown any statistically significant differences in the number of *D. amphibothrium* between the right and left set of gill arches of ruffe (P>0.05). The mean number of *D. amphibothrium* on the right and left gill arches is given in Table 8. The data analysis did not show any statistically significant differences in the number of *D. amphibothrium* between the gill arches of ruffe (P>0.05). The mean number of *D. amphibothrium* on the gill arches is given in Table 9.

Dactylogyrus hemiamphibothrium

The number of *D. hemiamphibothrium* on the different parts of gill apparatus of ruffe is shown in Table 7. The data analysis did not show any

statistically significant difference in the number of *D. hemiamphibothrium* between the right and left set of gill arches of ruffe ($P > 0.05$). The mean number of *D. hemiamphibothrium* on the right and left gill arches is given in Table 8. There were a significantly greater number of *D. hemiamphibothrium* on the first gill arches than on the gill arch 2, 3 and 4 ($P < 0.001$). The mean number of *D. hemiamphibothrium* on the gill arches is given in Table 9.

Discussion

There are many studies on the microhabitat distribution of monogeneans on the gills of their host (Dzika and Szymanski, 1989; El Hafidi et al., 1998; Simkova et al., 2000; Chapman et al., 2000; Lo and Morand, 2000; Simkova et al., 2000, 2002; Matejusova et al., 2002; Kadlec et al., 2003). In the present study, the *Dactylogyrus* species examined showed preferences for particular branchial arches or certain parts of the gill arches. None of the species studied showed any significant differences in distribution between the right and left sets of gills. However, preference for the right side was recorded by *D. amphibothrium* (Wootten, 1974) and *Microcotyle mugilis* and also preference for the left side was reported by *Metamicrocotyle cephalus* (El Hafidi et al., 1998).

Although slightly more *D. extensus* occurred on the second gill arch in carp, this was not found to be statistically significant. However, significantly, more *D. auriculatus* located on the second and third gill arches of bream and *D. difformis/ difformoides* was located on the third and fourth gill arches. The results coincide with the findings of some workers who found the highest number of *Dactylogyrus* occurred on the third gill arch and the lowest number of worms attached to the first gill arch (Wootten, 1974; Koskivaara et al., 1992) and the highest number of *Neodiplozoon polycotyleus* was located on the second gill arch (Chapman et al., 2000). However, Dzika & Szymanski (1989) reported that *D. auriculatus* mostly preferred the first gill arch with the lowest number of worms on the third gill arch; this coincides with our results as significantly more *D. hemiamphibothrium* was located on the first gill arches.

Monogenans also showed a preference for the different part of the gill (El Hafidi et al., 1998; Chapman et al., 2000; Kadlec et al., 2003). Greater number of *D. extensus* attached to the distal-median and distal-ventral halves of the gill filament, with fewer worms attached to the dorsal segment of the hemibranch and a greater number of *D. difformis/ difformoides* occurred on the distal dorsal part of the gill. Schaperclaus (1991) also found that *D. extensus* was mostly located on the distal part of the gill filaments. *D. vastator* prefers to attach to the terminal edge of the gill filaments. Similarly, *D. hemiamphibothrium* was found to prefer to the terminal edge of the filament. *D. auriculatus* occurred

in the proximal-ventral and proximal-median halves of the hemibranch. This finding was not consistent with the results of Dzika & Szymanski (1989), who recorded that *D. auriculatus* seemed to prefer to locate on the distal and median segment of the gill. *D. zandti*, *D. falcatus*, *D. wunderi* prefer to attach to the proximal section of the hemibranch (Dzika & Szymanski, 1989). Furthermore, some monogenean species tend to attach to the inner hemibranch of the gill (El Hafidi et al., 1998). In the present study, a greater number of *D. extensus* and *D. auriculatus* were found on the inner rather than the outer face of the hemibranch.

Differences in the water current over the different parts of gill surface have been considered important in determining the distribution of parasites on the gills (Wootten, 1974; Kadlec et al., 2003). The strongest water current passes through the middle part of the gill arches, thus creating convenient conditions for parasite settlements. The volume of the passing water may influence the aerobic conditions in certain gill parts, thus facilitating parasite settlement but also reflected the greater surface area available for parasite attachment on these gills (Wootten, 1974). This result might explain the present findings that the greatest number of *D. extensus*, *D. auriculatus* and *D. amphibothrium* occurred on the second and third gill arches.

Many monogenean species show a preference for specific parts of the gill apparatus of their host. In this study, no significant preferences were found in the distribution of *Dactylogyrus* species on the gill arches between the left and right sides of its host. There was however, a significant preference for specific gill arches or for particular faces of the hemibranchs. A preference for specific regions of the gill arches was also found in this work. These specific preferences might be effected by the interaction of several factors such as differences in the hydrostatic pressure of the branchial pump (Hughes & Shelton, 1958), coughing action (Bijtel, 1949), water current over the gill surface (Paling, 1968; Wootten, 1974) during the respiratory cycle (Hanek and Fernando, 1978; Ramasamy et al., 1985). Furthermore, microhabitat distribution and niche restriction in some species seem to be affected by seasonal variation, probably reflecting changes in parasite population (Rohde, 1991), the size and development of the host and ecological and morphological differences between monogenean species (Dzika, 1999; Chapman et al., 2000; Simkova et al., 2002). Some authors have also suggested that parasite mating has strong influence on the restriction of microhabitat. Crowding effects and narrow microhabitats increase the chance of mating opportunities. On the other hand, microhabitat segregation among closely related species causes reproductive barriers against hybridization (Holmes, 1990; Rohde, 1994; Simkova et al., 2002).

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