

The microecology of dactylogyrids (Monogenea: Dactylogyridae) on the gills of wild spotted rose snapper *Lutjanus guttatus* (Lutjanidae) from Mazatlan Bay, Mexico

Lilia C. Soler-Jiménez^{1,2} and Emma J. Fajer-Ávila²

¹Posgrado en Ciencias del Mar y Limnología, Unidad Mazatlán, Universidad Nacional Autónoma de México, Avenida Joel Montes Camarena s/n, Mazatlán, Sinaloa, C.P. 82040, México;

²Laboratorio de Parasitología, Centro de Investigación en Alimentación y Desarrollo, A.C. Unidad Mazatlán en Acuicultura y Manejo Ambiental, Avenida Sábalo Cerritos s/n, Mazatlán, Sinaloa, C.P. 82010, México

Abstract: The spatial distribution and coexistence of monogenean dactylogyrids was assessed on the gills of 63 specimens of wild spotted rose snapper, *Lutjanus guttatus* (Steindachner), caught in the Mazatlan Bay, Sinaloa, Mexico. Five species are reported: *Euryhaliotrema perezponcei* García-Vargas, Fajer-Ávila et Lamothe-Argumedo, 2008, *Euryhaliotrematoides* sp., *Haliotrematoides spinatus* Kritsky et Mendoza-Franco, 2009, *H. plectridium* Kritsky et Mendoza-Franco, 2009, and *H. guttati* García-Vargas, Fajer-Ávila et Lamothe-Argumedo, 2008. All except *E. perezponcei* and *H. guttati* represent new geographical records for the Pacific coast. The most prevalent dactylogyrid species was *E. perezponcei* (100%), *H. plectridium* and *H. spinatus* had >80% prevalence, and *H. guttati* and *Euryhaliotrematoides* sp. had the lowest prevalence. The mean abundance of *H. plectridium* and *E. perezponcei* was close to 60 parasites/fish, whereas *Euryhaliotrematoides* sp. and *H. guttati* had the lowest abundance. The dactylogyrid species exhibited a tendency for attachment to gill arch 2: 25% attachment occurring on gill arch 1, 30% on 2, 27% on 3 and 18% on 4, and showed a significant preference for the central sector of the gill (42%). *Haliotrematoides plectridium* had a preference for attachment to gill arches 2 and 3 and the central sector. *Haliotrematoides spinatus* tended to settle on the gill arches 2 and 3 and had a preference for the central sector. *Euryhaliotrema perezponcei* tended to settle on the gill arches 1 and 2 and the anterior gill sector. *Euryhaliotrematoides* sp. and *H. guttati* did not show a preference for any gill arch or sector. The intraspecific aggregation was stronger than the interspecific aggregation, indicating that all the dactylogyrid species on spotted rose snapper were aggregated, and there was no evidence of competition among the species.

Keywords: microhabitat, distribution, Pacific coast, *Euryhaliotrema perezponcei*, *Euryhaliotrematoides* sp., *Haliotrematoides spinatus*, *Haliotrematoides plectridium*, *Haliotrematoides guttati*

Ectoparasitic monogeneans cause problems in aquaculture worldwide; they include the dactylogyrids that affect lutjanids and barramundi in southeast Asia (Whittington 2005). Dactylogyrid monogeneans, such as *Haliotrematoides* spp. and *Euryhaliotrema* spp., are common on the gills of the wild and cultured spotted rose snapper, *Lutjanus guttatus* (Steindachner) (see Fajer-Ávila et al. 2007), a fish that is important in aquaculture (Álvarez-Lajonchere et al. 2007). High levels of infection can cause a general stress response with potentially harmful effects on the farmed fish (Del Río-Zaragoza et al. 2010).

Most species of monogeneans are restricted not only to a particular host but also to a particular body part of the host (Turgut et al. 2006). Gill-infecting dactylogyrid monogeneans commonly exhibit a narrow site-specificity (Dzika 1999, Lo and Morand 2000, Šimková et al. 2000, Turgut et al. 2006). The effect of these gill preferences is

not clear, and many host and environmental factors could be involved (Pie et al. 2006). The variation in parasite distribution on the gills could be due to a response to water currents (Llewellyn 1956, Paling 1969), differences in the area between the gill arches (Buchmann 1989), aggregation of parasites for mating (Rohde et al. 1995), avoidance of interspecific competition (Šimková et al. 2000), reinforcement of reproductive barriers to prevent hybridisation (Šimková and Morand 2008) or migration driven by host immunity (Buchmann and Bresciani 1998). Microhabitat distribution and niche restriction also seem to be affected by seasonal variation (Rohde 1991), the size and development of the host and ecological and morphological differences between monogenean species (Dzika 1999, Chapman et al. 2000, Šimková et al. 2002). Other authors suggest that several of these factors may act synergistically (Gutiérrez and Martorelli 1999, Rubio-Godoy 2008).

The lack of information on the basic ecological features of the dactylogyrids that infect wild spotted rose snapper has hindered comparisons with cultured fish. The aim of this study was to determine which dactylogyrid species infect adult wild spotted rose snapper from Mazatlan Bay, Sinaloa, and their abundance and spatial distribution on the gills. We also attempted to analyse which factors are involved in site selection based on the relative importance of intra- and interspecific interactions.

MATERIALS AND METHODS

Host collection. A total of 63 adult spotted rose snapper, *L. guttatus*, were sampled and examined from October to December 2006 and from February to April 2007 at Mazatlan Bay, Sinaloa, Mexico (23°14'29"N, 106°24'35"W). All fish were caught by hook and line by local fishermen and were immediately transported to the laboratory for examination within 12 hours of capture. The total length (TL) from the mouth to the end of the caudal fin of each fish was measured with a conventional ichthyometer (precision ± 0.1 cm), and the wet weight was determined on a digital balance (LS 5000) (precision ± 0.1 g).

Parasite data. Monogeneans found on fresh gills were isolated, counted and observed alive with an OLYMPUS BX51 light microscope (Center Valley, PA, USA) using the 100 \times objective. All dactylogyrid species were identified using sclerotized parts of the parasite haptor (anchors, connective bars and marginal hooks) and reproductive organs (male copulatory organs and vaginal armaments) according to Plaisance and Kritsky (2004), García-Vargas et al. (2008) and Kritsky et al. (2009). Some helminth specimens were mounted unstained in Grey and Wess medium (Humason 1979) for the study of sclerotized structures, and others were stained with Gomori's trichrome (Humason 1979) and mounted in Canada balsam for the observation of internal structures. Voucher specimens from lutjanid hosts from the U.S. National Parasite Collection (USNPC; Beltsville, USA) were obtained for direct comparison and measurement. Voucher specimens of helminths were deposited in the National Collection of Helminths, Institute of Biology, National Autonomous University of Mexico (UNAM) as *Euryhaliotrematoides* sp. (CNHE 7290), *Haliotrematoides spinatus* (CNHE 7291), *Haliotrematoides plectridium* (CNHE 7292) and *Haliotrematoides guttati* (CNHE 7293).

Spatial distribution on fish gills. Only gills from the left side of the fish were dissected. The gill arches were numbered 1 to 4 from external to internal and divided into three sectors: anterior, central and posterior (Fig. 1). Each gill sector was individually placed in a separate Petri dish with several drops of filtered marine water and was monitored using a dissecting microscope (Leica Microsystems, Wetzlar, Germany) using the 2 \times objective (total magnification 20 \times). Monogeneans found on fresh gills were isolated, identified and counted from each of the twelve sectors separately. The position of each individual of the dactylogyrid species was recorded.

The association among dactylogyrid species was measured by the "aggregation model of coexistence" for parasites (modified by Morand et al. 1999), which analyses intra- and interspecific aggregation and their relative strengths in a pair of species.

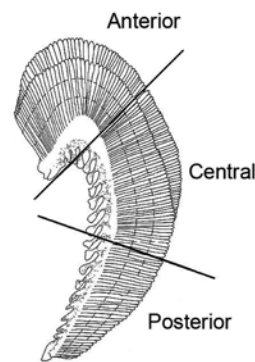


Fig. 1. Schematic drawing of gill arch showing division into three arbitrary areas.

Intraspecific aggregation (J): the proportionate increase in the number of the same dactylogyrid species on a random host relative to a random distribution;

$$J_1 = \frac{\sum_{i=1}^n \frac{n_{1i}(n_{1i}-1)}{m_1} - m_1}{m_1} = \frac{V_1}{m_1} - 1$$

where n_{1i} is the number of specimens of species 1 in patch i ; m_1 is the mean number and V_1 is the variance in the number of species 1. A value of $J = 0$ indicates that individuals are randomly distributed, whereas a value of $J = 0.5$ indicates there are 50% more conspecifics in a patch than with a random distribution.

Interspecific aggregation C: the proportionate increase in the number of heterospecific competitors relative to a random association;

$$C_{12} = \frac{\sum_{i=1}^n \frac{n_{1i}n_{2i}}{m_1} - m_2}{m_2} = \frac{Cov_{12}}{m_1m_2}$$

where Cov_{12} is the covariance between a pair of species. When $C > 0$ the two species are positively associated; when $C < 0$, the species are negatively associated. The interspecific association test was chosen to examine if the occurrence of one parasite was influenced by the existence of the other parasite species on the same host.

The relative strength of intraspecific aggregation vs. interspecific aggregation in a pair of species can be assessed using the equation,

$$A_{12} = \frac{(J_1 + 1)(J_2 + 1)}{(C_{12} + 1)^2}$$

If $A > 1$, the intraspecific aggregation is stronger than interspecific aggregation.

Statistical analysis. Prevalence, abundance, mean abundance and mean intensity were used as defined by Bush et al. (1997). Data were normalised by the $\ln(x+1)$ transformation to satisfy the assumption of homoscedasticity and linearity of the parametric tests. Data on the abundance of the four arches were pooled for host samples. A two-way ANOVA with multiple comparisons (Holm-Sidak method) was used to compare the mean abundance of the total number of dactylogyrids among gill arches and sectors. The microhabitat preference for each dactylogyrid species was determined by observing their position on the gill arches and sectors. The distribution of each dactylogyrid species on particular gill arches and sectors was analysed by two-way ANOVA with multiple comparisons to assess the significance of the difference.

RESULTS

The mean total length of the 63 spotted rose snapper, *L. guttatus*, sampled was 30 ± 5.51 cm. The 9179 dactylogyrids found belonged to five species: *Euryhaliotrema perezponcei* García-Vargas, Fajer-Ávila et Lamothe-Argumedo, 2008, *Euryhaliotrematoides* sp., *Haliotrematoides plectridium* Kritsky et Mendoza-Franco, 2009, *Haliotrematoides spinatus* Kritsky et Mendoza-Franco, 2009, and *Haliotrematoides guttati* García-Vargas, Fajer-Ávila et Lamothe-Argumedo, 2008.

Composition of parasite species. *Haliotrematoides plectridium* and *E. perezponcei* represented 42% and 41%, respectively, of the total number of dactylogyrids found. *Haliotrematoides spinatus* and *H. guttati* corresponded to 14% and 2%, respectively, and *Euryhaliotrematoides* sp. corresponded to 1%. The most prevalent was *E. perezponcei* (100%), with at least one individual on each fish sampled, followed by *H. plectridium* and *H. spinatus*, each of which with >80% prevalence (Table 1). The mean abundance of *H. plectridium* and *E. perezponcei* was close to 60 parasites per fish, whereas *Euryhaliotrematoides* sp. and *H. guttati* had the lowest values. The mean intensity of *H. plectridium* and *Euryhaliotrematoides* sp. was 69 and 4 parasites per fish, respectively.

Parasite aggregation. All dactylogyrid species had a value of $J > 0$, which indicated that individuals of each species were aggregated. The highest levels of intraspecific aggregation were recorded for *H. guttati* and *H. plectridium* and the lowest for *E. perezponcei* (0.47). Of the 10 values of species pairs, 8 pairs had a positive interspecific aggregation ($C > 0$), and two, *E. perezponcei* – *H. spinatus* and *E. perezponcei* – *H. guttati*, had a negative interspecific aggregation ($C < 0$). The relative strength of intraspecific aggregation on interspecific aggregation (A) was greater than 1, which indicates that intraspecific aggregation was stronger than interspecific aggregation.

Microhabitat selection. The mean abundance of all the dactylogyrids on the different gill arches did not show any statistically significant difference among gill arches 1, 2 and 3, whereas significantly fewer dactylogyrids were found on gill arch 4 ($F = 7.9$, $p < 0.001$). The distribution of parasites revealed an overall tendency of preferential settlement on the gill arches 2 and 3: 25% of all worms were found on gill arch 1, 30% on 2, 27% on 3 and 18% on 4. The mean abundance of total dactylogyrids was significantly higher ($F = 17.9$, $p < 0.001$) in the central sector than in the anterior and posterior sectors of the gill, where 42% of the parasites were located (Fig. 2A). Because

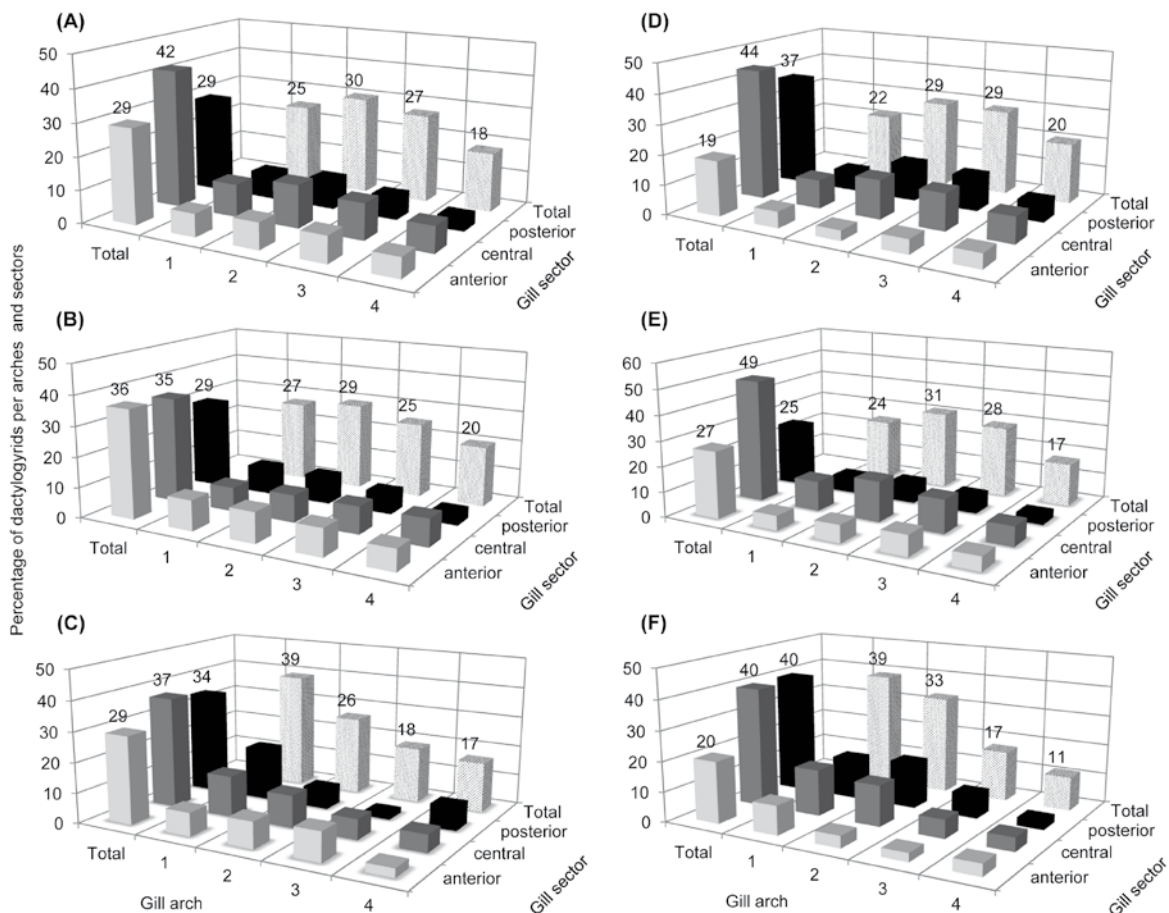


Fig. 2. Percentage of dactylogyrids on the gill arches and sectors of *Lutjanus guttatus*. Total dactylogyrids (A), *Euryhaliotrema perezponcei* (B), *Euryhaliotrematoides* sp. (C), *Haliotrematoides spinatus* (D), *H. plectridium* (E), *H. guttati* (F).

Table 1. The prevalence, mean abundance (\pm Standard Deviation, SD) and mean intensity (\pm SD) of dactylogyrid species collected from the gills of the spotted rose snapper, *Lutjanus guttatus*, from Mazatlan Bay (n = 63).

	<i>Euryhaliotrema perezponcei</i>	<i>Euryhaliotrematoides</i> sp.	<i>Haliotrematoides spinatus</i>	<i>Haliotrematoides plectridium</i>	<i>Haliotrematoides guttati</i>
Prevalence (%)	100	39.7	81.0	88.9	50.8
Mean abundance	59.8 \pm 52.9	1.6 \pm 2.7	20.1 \pm 24.5	61.3 \pm 68.7	2.8 \pm 4.1
Mean intensity	59.8 \pm 52.9	4.1 \pm 2.7	24.9 \pm 25.0	69.0 \pm 69.2	5.5 \pm 4.7
Range of intensity	1–218	0–12	0–99	0–317	0–24

of their rare occurrence, *Euryhaliotrematoides* sp. and *H. guttati* were not included in the general analysis.

The distribution of some dactylogyrid species across microhabitats was not random. The analysis for *E. perezponcei* showed significant differences in the number of parasites in arches 1 and 2 relative to arch 4 ($F = 4.34$, $p < 0.05$), which had the lowest number of parasites. However, this species had a tendency of preference to be found on gill arches 1 and 2, with 27% on gill arch 1, 29% on 2, 25% on 3 and 20% on 4. On the anterior gill sector, a significantly higher abundance of *E. perezponcei* (36%) compared with the posterior sector (29%) was found ($F = 3.37$, $p < 0.05$), whereas the central sector (35%) did not show a difference between the anterior and posterior arches (Fig. 2B). *Euryhaliotrematoides* sp. apparently did not have a preference for a gill arch or sector but had a tendency to be located on gill arch 1 (39% on gill arch 1, 26% on 2, 18% on 3 and 17% on 4) and the central sector (37%) (Fig. 2C). *Haliotrematoides spinatus* did not show a preference for any gill arch but tended to be located on arches 2 and 3 (22% on gill arch 1, 29% on 2, 29% on 3 and 20% on 4%); however, a significant increase of individuals was found on the central (44%) and posterior (37%) sectors ($F = 18.1$, $p < 0.001$) (Fig. 2D). *Haliotrematoides plectridium* preferred gill arches 2 and 3 (24% on gill arch 1, 31% on 2, 28% on 3 and 17% on 4) compared with 4 ($F = 4.68$, $p < 0.001$) and the central sector (49%) ($F = 16.31$, $p < 0.001$) (Fig. 2E). *Haliotrematoides guttati* showed a significant preference for gill arches 1 (39%) and 2 (33%) compared with 3 (17%) and 4 (11%) ($F = 7.35$, $p < 0.001$) as well as for the central (40%) and posterior (40%) sectors ($F = 4.12$, $p < 0.005$) (Fig. 2F).

DISCUSSION

The largest genus in the family Lutjanidae is *Lutjanus*, with 68 valid species (Froese and Pauly 2010), 20 of which have been found infected by dactylogyrids. Three dactylogyrid genera, *Euryhaliotrema* Kritsky et Boeger, 2002, *Haliotrematoides* Kritsky, Tingbao et Yuan, 2009 and *Tetrancistrum* Goto et Kikuchi, 1917, include species that have been found on the gills of snappers (Kritsky et al. 2009). Fifteen species of *Euryhaliotrema* are currently known from snappers worldwide (Kritsky and Boeger 2002, Li 2005, 2006, Li et al. 2005, Pan and Zhang 2006, Fuentes Zambrano and Silva Rojas 2006, García-Vargas et al. 2008) and 22 of *Haliotrematoides* (Kritsky et al. 2009). In Mexico, four species of *Haliotrematoides*

have been found on lutjanids from the Atlantic (Zhukov 1976). *Euryhaliotrema perezponcei* and *H. guttati* were described from the spotted rose snapper, *L. guttatus*, on the north-western coast of Mexico (García-Vargas et al. 2008). The morphological characteristics of the dactylogyrid species found in this study matched the descriptions of *E. perezponcei* and *H. guttati* by García-Vargas et al. (2008) and of *H. plectridium* and *H. spinatus* by Kritsky et al. (2009). The description of a new *Euryhaliotrematoides* species is underway.

Most populations of fish parasites in natural waters are limited by transmission events (Kennedy 1997). Ectoparasitic metazoans on fish in natural waters often occur in low numbers; for these parasites, site specificity can facilitate mating in these low-density populations (Rohde 1994). The intensity of infection by dactylogyrids on the gills of spotted rose snapper varied according to the dactylogyrid species. In this study, *H. spinatus* had an intensity of infection (25 parasites per fish infected) similar to that found for *H. johnei* (Tripathi, 1959) (= *Euryhaliotrema johnei* (Tripathi, 1959) (Kritsky et Boeger, 2002)) (29 parasites per fish infected) in the wild golden snapper *Lutjanus johnii* (Bloch) (see Leong and Wong 1987). However, *H. plectridium* and *E. perezponcei* had the highest intensity of infection (59 and 69 parasites per fish, respectively), which is in contrast with the value (10.6; $n = 17$) previously reported by Bosques Rodríguez (2004) for *H. heteracantha* (Zhukov, 1976) on *Lutjanus synagris* (Linnaeus). The prevalence of *Haliotrematoides* spp. in the present study was high, but the prevalence of *H. plectridium* (89%) and *H. spinatus* (81%) was similar to that reported for *Haliotrema abaddon* Kritsky et Stephens, 2001 from *Glaucosoma hebraicum* Richardson (see Kritsky and Stephens 2001) and for *Pseudohaliotrema* sp. on *Siganus sutor* (Valenciennes) (Geets et al. 1997). The prevalence of *E. perezponcei* (100%) was similar to the value previously reported (94.73%) on this host species (García-Vargas et al. 2008). These results are consistent with other data on the frequency of the occurrence of dactylogyrid species on the gills of snappers (Kritsky et al. 2009).

The microhabitat of gill-living monogeneans has been investigated by many authors (Dzika 1999, Lo and Morand 2000, Simková et al. 2000, Šimková et al. 2002, Matejusová et al. 2002), and it has been shown that many species have clearly defined microhabitats (Wootton 1974, El Hafidi et al. 1998, Dzika 1999, Lo and Morand

2000, 2001, Turgut et al. 2006, Rubio-Godoy 2008). In the present study, the most abundant dactylogyrid species, *H. plectridium*, preferred the gill arches 2 and 3, whereas the second-most abundant species, *E. perezponcei*, tended to settle on the gill arches 1 and 2, indicating that these two dactylogyrid species were the main contributors to the microhabitat distribution. The least-abundant species, *Euryhaliotrematoides* sp. and *H. guttati*, did not show a preference for a gill arch but had the tendency to settle on the gill arches 1 and 2, whereas a higher percentage of *H. spinatus* was found on the gill arches 2 and 3. Thus, the results indicated that the second gill arch of the spotted rose snapper harboured the five dactylogyrids species found in this study, which had a tendency to be attached on the most exterior gill arches. This preference is similar to that for the first two gill arches reported by Geets et al. (1997) for *Pseudohaliotrema* sp. on *Siganus sutor* and consistent with the microhabitat distribution found by Rubio-Godoy (2008) for *Discocotyle sagittata* on cultured rainbow trout.

The variation in the force and direction of the flow of water across the four gill arches may influence the settlement of parasites (Llewellyn 1966). Rubio-Godoy and Tinsley (2002) reported a correlation between the proportion of the number of *D. sagittata* and the current flowing over each gill arch of *Oncorhynchus mykiss*. In the present study, the highest volume of water passing over the most exterior gill arches of spotted rose snapper may improve the aerobic conditions to favour the greatest number of dactylogyrids, in proportion to the respiratory current flowing over each arch. The high abundance of *H. plectridium* (49%), *E. perezponcei* (35%), *H. spinatus* (44%), *H. guttati* (40%) and *Euryhaliotrematoides* sp.

(37%) found on the central gill sector, in contrast with anterior and posterior sectors, matches the greater surface area available for the settlement of parasites on the gill arches and corresponds with the locations on those gill arches that receive the strongest water flow (Paling 1968, Lo and Morand 2000).

In terms of inter- or intraspecific interaction, the 'aggregation model of coexistence' postulates that if species using the same type of resource are distributed in such a way that interspecific aggregation is reduced relative to intraspecific aggregation, species coexistence is facilitated. In the present study, there was no observed overlap in the use of the microhabitats. Moreover, the species of monogeneans studied here exhibited a weak positive interspecific association, and the value of intraspecific aggregation ($J > 0$) of dactylogyrid species indicated an aggregated distribution. The restriction in the selection of monogenean microhabitats to specific gill arches and sectors could facilitate species coexistence and opportunities to mate (Rohde 1991, Lo and Morand 2001), avoid competition (Šimková et al. 2000) and reinforce the reproductive barriers to prevent hybridisation (Šimková and Morand 2008). The reduction in competition is also reflected by the relative strength of intraspecific aggregation versus interspecific aggregation ($A > 1$), facilitating the coexistence of species.

The increase of parasite load favours the aggregation of congeners within the hosts, which could be pathogenic in farmed fish. However, the main factor that contributes to settlement in a specific microhabitat has not been defined, and the spatial preference might be correlated with physiological, environmental, ecological and physical factors (Rohde 1994). More studies are required to clarify this.

REFERENCES

- ÁLVAREZ-LAJONCHERE L., REINA-CAÑEZ M., CAMACHO-HERNÁNDEZ M., KRAUL S. 2007: Design of a pilot-scale tropical marine fin fish hatchery for a research center at Mazatlan, Mexico. *Aquac. Eng.* 36: 81–96.
- BOSQUES RODRÍGUEZ L. 2004: Metazoan parasites of snappers, Lutjanidae (Pisces) from Puerto Rico. MSc Thesis, University of Puerto Rico, Mayagüez, Puerto Rico, 178 pp.
- BUCHMANN K. 1989: Microhabitats of monogenean gill parasites of European eel (*Anguilla anguilla*). *Folia Parasitol.* 36: 321–329.
- BUCHMANN K., BRESCIANI J. 1998: Microenvironment of *Gyrodactylus derjavini* on rainbow trout *Oncorhynchus mykiss*: association between mucous cell density in skin and site selection. *Parasitol. Res.* 84: 17–24.
- BUSH A., LAFFERTY K., LOTZ J., SHOSTAK A. 1997: Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83: 575–583.
- CHAPMAN L.J., LANCIANI C.A., CHAPMAN C.A. 2000: Ecology of a diplozoan parasite on the gills of the African cyprinid *Barbus neumayeri*. *Afr. J. Ecol.* 38: 312–320.
- DEL RÍO-ZARAGOZA O., FAJER-ÁVILA E., ALMAZAN-RUEDA P. 2010: Haematological and gill responses to an experimental infection of dactylogyrid monogeneans on the spotted rose snapper *Lutjanus guttatus* (Steindachner, 1869). *Aquacult. Res.* 41: 1592–1601.
- DZIKA E. 1999: Microhabitats of *Pseudodactylogyrus anguillae* and *P. bini* (Monogenea: Dactylogyridae) on the gills of large-size European eel *Anguilla anguilla* from Lake Gaj, Poland. *Folia Parasitol.* 46: 33–36.
- EL HAFIDI F., BERRADA-RKHAM O., BEMAZZOU T., GABRION C. 1998: Microhabitat distribution and coexistence of Microcotylidae (Monogenea) on the gills of the striped mullet *Mugil cephalus*: chance or competition? *Parasitol. Res.* 84: 315–320.
- FAJER-ÁVILA E., VELÁSQUEZ-MEDINA S., BETANCOURT-LOZANO M. 2007: Effectiveness of treatments against eggs, and adults of *Haliotrema* sp. and *Euryhaliotrema* sp. (Monogenea: Ancyrocephalinae) infecting red snapper, *Lutjanus guttatus*. *Aquaculture* 264: 66–72.
- FROESE R., PAULY D. (Eds.) 2010: FishBase. World Wide Web electronic publication, www.fishbase.org, version 06/2010.
- FUENTES ZAMBRANO J.L., SILVA ROJAS C.L. 2006: Una nueva especie de *Euryhaliotrema* Kritsky y Boeger, 2002 (Monogenea) encontrada en branquias de *Lutjanus griseus* (Perciformes: Lutjanidae) de la Isla de Margarita, Venezuela. *Bol. Inst. Oceanogr. Venez.*, Univ. Oriente 45: 3–7.
- GARCÍA-VARGAS F., FAJER-ÁVILA E., LAMOTHE-ARGUMEDO R. 2008: Two new species of Dactylogyridae (Monogeneoidea) on spotted rose snapper, *Lutjanus guttatus* (Osteichthyes: Lutjani-

- dae), from the coasts of Nayarit and Sinaloa, Mexico. *Zootaxa* 1729: 61–68.
- GEETS A., COENE H., OLLEVIER F. 1997: Ectoparasites of the whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835) off the Kenyan Coast: distribution within the host population and site selection on the gills. *Parasitology* 115: 69–79.
- GUTIÉRREZ P.A., MARTORELLI S.R. 1999: Hemibranch preference by freshwater monogeneans a function of gill area, water current, or both? *Folia Parasitol.* 46: 263–266.
- HUMASON G.L. 1979: *Animal Tissue Techniques*. 4th Ed. W.H. Freeman and Company, San Francisco, 661 pp.
- KENNEDY C.R. 1997: Long-term and seasonal changes in composition and richness of intestinal helminth communities in eels *Anguilla anguilla* of an isolated English river. *Folia Parasitol.* 44: 267–273.
- KRITSKY D.C., BOEGER W.A. 2002: Neotropical Monogenoidea 41: New and previously described species of Dactylogyridae (Platyhelminthes) from the gill of marine and freshwater perciform fishes (Teleostei) with proposal of new genus and a hypothesis on phylogeny. *Zoosystema* 24: 7–40.
- KRITSKY D.C., STEPHENS F. 2001: *Haliotrema abaddon* n. sp. (Monogenoidea: Dactylogyridae) from the gills of wild and maricultured West Australian dhufish, *Glaucosoma hebraicum* (Teleostei: Glaucosomatidae), in Australia. *J. Parasitol.* 87: 749–754.
- KRITSKY D.C., TINGBAO Y., YUAN S. 2009: Dactylogyrids (Monogenoidea, Polyonchoinea) parasitizing the gills of snappers (Perciformes, Lutjanidae): Proposal of *Haliotrematoides* n. gen. and descriptions of new and previously described species from marine fishes of the Red Sea, the eastern and Indo-west Pacific Ocean, Gulf of Mexico and Caribbean Sea. *Zootaxa* 170: 1–51.
- LEONG T., WONG S. 1987: Parasites of wild and diseased juvenile golden snapper, *Lutjanus johni* (Bloch), in floating cages in Penang, Malaysia. *Asian Fish. Sci.* 1: 83–90.
- LI H.Y. 2005: Description of two species (including a new one) in *Euryhaliotrema* Kritsky & Boeger, 2002. *J. Dalian Fish. Univ.* 20: 186–191. (In Chinese.)
- LI H.Y. 2006: One new species of the genus *Euryhaliotrema* (Monogenea, Ancyrocephalidae). *Acta Zootaxon. Sin.* 31: 317–320. (In Chinese.)
- LI H.Y., YAN X., YU L., LAN Q., HUANG X. 2005: Description of two new species of Ancyrocephalidae (Monogenoidea). *J. Guangxi Norm. Univ.* 23: 86–89. (In Chinese.)
- LLEWELLYN J. 1956: The host-specificity, micro-ecology, adhesive attitudes, and comparative morphology of some trematode gill parasites. *J. Mar. Biol. Assoc.* 35: 113–127.
- LLEWELLYN J. 1966: The effect of fish host upon the body shape of their monogenean parasites. *Proc. First Int. Congress Parasitol.* 1: 543–545.
- LO C.M., MORAND S. 2000: Spatial distribution and coexistence of monogenean gill parasites inhabiting two damselfishes from Moorea Island in French Polynesia. *J. Helminthol.* 74: 329–336.
- LO C.M., MORAND S. 2001: Gill parasites of *Cephalopholis argus* (Teleostei: Serranidae) from Moorea (French Polynesia): site selection and coexistence. *Folia Parasitol.* 48: 30–36.
- MATEJUSOVÁ I., ŠIMKOVÁ A., SASAL P., GELNAR M. 2002: Microhabitat distribution of *Pseudodactylogyrus anguillae* and *P. bini* among and within gill arches of the European eel (*Anguilla anguilla* L.). *Parasitol. Res.* 89: 290–296.
- MORAND S., POULIN R., ROHDE K., HAYWARD C. 1999: Aggregation and species coexistence of ectoparasites of marine fishes. *Int. J. Parasitol.* 29: 663–672.
- PALING J.E. 1968: A method of estimating the relative volumes of water flowing over different gills of a freshwater fish. *J. Exp. Biol.* 48: 533–544.
- PALING J.E. 1969: The manner of infection of trout gills by the monogenean parasite *Discocotyle sagittata*. *J. Zool. (Lond.)* 159: 293–309.
- PAN J., ZHANG J. 2006: Monogenea of marine fishes from Hainan Island, China. VIII. Two new species of *Euryhaliotrema* Kritsky & Boeger, 2002 (Dactylogyridae) from *Lutjanus argentimaculatus* (Teleostei: Lutjanidae). *Syst. Parasitol.* 64: 125–130.
- PIE M.R., ENGERS K.B., BOEGER W.A. 2006: Density-dependent topographical specialization in *Gyrodactylus anisopharynx* (Monogenoidea, Gyrodactylidae): boosting transmission or evading competition? *J. Parasitol.* 92: 459–463.
- PLAISANCE L., KRITSKY D.C. 2004: Dactylogyrids (Platyhelminthes: Monogenoidea) parasitizing butterfly fishes (Teleostei: Chaetodontidae) from the coral reefs of Palau, Moorea, Wallis, New Caledonia, and Australia: species of *Euryhaliotrematoides* n. gen. and *Aliatrema* n. gen. *J. Parasitol.* 90: 328–341.
- ROHDE K. 1991: Intra- and interspecific interactions in low density populations in resource-rich habitats. *Oikos* 60: 91–104.
- ROHDE K. 1994: Niche restriction in parasites: proximate and ultimate causes. *Parasitology* 109: S69–S84.
- ROHDE K., HAYWARD C., HEAP M. 1995: Aspects of the ecology of metazoan ectoparasites of marine fishes. *Int. J. Parasitol.* 25: 945–970.
- RUBIO-GODOY M. 2008: Microhabitat selection of *Discocotyle sagittata* (Monogenea: Polyopisthocotylea) in farmed rainbow trout. *Folia Parasitol.* 55: 270–276.
- RUBIO-GODOY M., TINSLEY R.C. 2002: Trickle and single infection with *Discocotyle sagittata* (Monogenea: Polyopisthocotylea): effect of exposure mode on parasite abundance and development. *Folia Parasitol.* 49: 269–278.
- ŠIMKOVÁ A., DESDEVISES Y., GELNAR M., MORAND S. 2000: Coexistence of nine gill ectoparasites (*Dactylogyrus*: Monogenea) parasitising the roach (*Rutilus rutilus* L.): history and present ecology. *Int. J. Parasitol.* 30: 1077–1088.
- ŠIMKOVÁ A., MORAND S. 2008: Co-evolutionary patterns in congeneric monogeneans: a review of *Dactylogyrus* species and their cyprinid hosts. *J. Fish Biol.* 73: 2210–2227.
- ŠIMKOVÁ A., ONDRAČKOVÁ M., GELNAR M., MORAND S. 2002: Morphology and coexistence of congeneric ectoparasite species: reinforcement of reproductive isolation? *Biol. J. Linn. Soc.* 76: 125–135.
- TURGUT E., SHINN A., WOOTTEN R. 2006: Spatial distribution of *Dactylogyrus* (Monogenan) [sic] on the gills of the host fish. *Turk. J. Fish. Aquat. Sci.* 6: 93–98.
- WHITTINGTON I. 2005: Monogenea Monopisthocotylea (ectoparasitic flukes). In: K. Rohde (Ed.), *Marine Parasitology*. CSIRO Publishing, Melbourne, Australia, pp. 63–72.
- WOOTTEN R. 1974: The spatial distribution of *Dactylogyrus amphibothrium* on the gills of ruffe *Gymnocephalus cernua* and its relation to the relative amounts of water passing over the parts of the gills. *J. Helminthol.* 48: 167–174.
- ZHUKOV E.V. 1976: [New species of the genus *Haliotrema* Johnston and Tiegs, 1922, from the Gulf of Mexico fishes of the family Lutjanidae.] In: *Fauna, Systematics and Phylogeny of Monogenoidea*. Proceedings, Institute of Biology and Pedology, Far-East Science Centre, Academy of Sciences of the U.S.S.R., New Ser. 35: 33–47. (In Russian.)