

Spatial distribution and coexistence of monogenean gill parasites inhabiting two damselfishes from Moorea island in French Polynesia

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Abstract

The ectoparasite fauna of two damselfishes, *Stegastes nigricans* and *Dascyllus aruanus*, from Moorea Island in French Polynesia was investigated. Gills of these damselfishes were infected with congeneric Monopisthocotylea Monogenea belonging to the genus *Haliotrema*. *Stegastes nigricans* were found to harbour a guild of three *Haliotrema* species whereas only one species inhabited *D. aruanus*. Microhabitat distribution, inter- and intraspecific competition and interspecific associations on the gill were studied. Observations on site preference revealed no spatial segregation between the three congeneric species inhabiting the gills of *S. nigricans*. Juvenile and adult monogeneans of that guild occurred on the same microhabitat. The dominant species *Haliotrema* sp. 1 did not expand on the microhabitat when the intensity of infection increased. Interspecific association tests revealed positive and negative associations. *Haliotrema* sp. 4 expanded its distribution on the gills of *Dascyllus aruanus* when the intensity of infection increased suggesting the likelihood of intraspecific competition. Juvenile and adult monogeneans of *Haliotrema* sp. 4 appeared to segregate as a result of intraspecific competition. This competition may exist to enhance resource availability when the gill habitat is limited. Overlaps between niche breadth and species microhabitat were revealed for monogenean species inhabiting *S. nigricans*. Interspecific competition did not appear to play an important role in the distribution of *S. nigricans* congeneric ectoparasites. Reinforcement of reproductive barriers may have led to the avoidance of hybridization.

Introduction

Surveys on parasites of coral reef fishes remain scarce, although it has been emphasized that parasite species richness increases from temperate to tropical waters (Rohde, 1978a,b, 1992), but decreases from water around

mainland to remote oceanic islands (Rigby *et al.*, 1997; Lo *et al.*, 1998; but see Koskivaara *et al.*, 1992).

Marine fishes are useful models to investigate questions dealing with the ecology of parasite communities (Holmes, 1990; Rohde, 1989, 1993). Gill ectoparasites are increasingly used to estimate the evolutionary significance of intra- or interspecific interactions, reinforcement of reproductive barriers, and enhancement of mating success on niche restriction (Rohde, 1977, 1979, 1980, 1989, 1994; Ramasamy *et al.*, 1985; Adams, 1986; Koskivaara *et al.*, 1992; Rohde *et al.*, 1994; Sharples & Evans, 1995; Morand *et al.*, 1999). Recently, Geets *et al.* (1997), following

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Rohde's hypothesis (Rohde, 1991), have suggested that interspecific competition is of secondary importance for microhabitat choice. They argued that intraspecific factors such as the mating process and reinforcement of reproductive barriers affect gill-space exploitation by parasites. In order to improve the analysis of the parasite position on the habitat, each gill arch was arbitrarily divided into several regions (Lambert & Maillard, 1974; Rohde, 1976, 1977; Hanek & Fernando, 1978; Ramasamy *et al.*, 1985).

Our aim was to describe the spatial distribution of monogenean parasites on the gill arches of two species of damselfish. We tried to determine what factors (intrinsic or extrinsic) were involved in the spatial distribution of each monogenean community studied. We also tried to take into account the heterogeneity of gill habitat to allow for this effect on the distribution of parasites on the gill.

Materials and methods

Host species of the pomacentrid family (*Stegastes nigricans* and *Dascyllus aruanus*) were collected monthly between November 1994 and October 1995 at Moorea Island, French Polynesia (17°30'S, 149°50'W). A total of 341 *S. nigricans* and 337 *D. aruanus* were sampled on the fringing reef of Tiahura on the northwest coast of the island. Approximately 30 fishes of each host species were sampled each month. *Stegastes nigricans* were captured alive using rotenone powder–sand–sea water suspension which was dissipated around coral colonies. Individuals of *D. aruanus* were anaesthetized with Quinaldine (2-methoxy quinoline (Sigma Chemical, St. Louis, Missouri) mixed with 100% ethanol at a ratio of 1:1), applied from a 300 ml plastic squeeze-bottle, and captured with hand-held nets. Each damselfish was kept alive in an aquarium until rapid dissection.

Each fish host was measured (total length (TL) in centimetres) and weighed before dissection. Each fish was decerebrated without bloodshed and gill arches were excised, separated, and all placed in a Petri dish containing sea-water and then examined using a dissecting microscope. Left and right arches were numbered 1 to 4 anteriorly (transverse partitioning); each gill arch was divided into four approximately equal regions dorsoventrally (sectors I, II, III, IV: longitudinal partitioning); the gill filaments were divided equally into three zones: proximal, middle and distal (vertical partitioning) (Fig. 1). Thus, 12 subequal sections were defined. The four gills of one body side represented 96 sections, with 24 sections per gill arch. Gill filaments of the four arches were counted on six fish of both host species to estimate the habitat availability of each arch. Parasites were counted and localized on each section of each arch. Special care was taken to separate adults from juveniles. Parasite identification of congeneric species was based on total body length and morphology of the haptor. Postlarvae were differentiated from adults by their small size and their translucent aspect due to the lack of vitelline follicles. For identification purposes, some monogeneans were examined, alive on a slide with a compound microscope or fixed with a drop of ammonium picrate–glycerine mixture on a slide, following the method of Malmberg (1957). Prevalence, intensity and

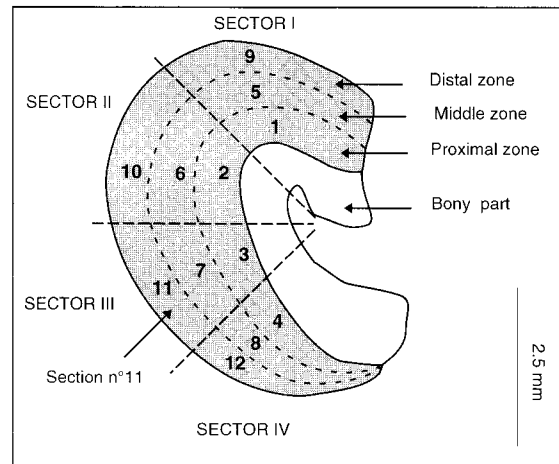


Fig. 1. Delimitation of the sectors (I, II, III, IV), zones (proximal, middle, distal) and sections (1–12) in a *Dascyllus aruanus* hemibranch.

mean intensity were used as defined by Bush *et al.* (1997). At the end of the gill observations, the sex of each fish was determined and all otoliths removed for age determination.

Data were normalized by $\log(x + 1)$ transformation to satisfy the assumption of homoscedasticity and linearity of the parametric tests. Differences in intensity between left and right gill arches for each infracommunity were tested using the Student-t test. Data on intensity of infection of four arches were pooled for each monthly host sample. An ANOVA with multiple comparisons was used to compare infection levels between gill arches. Simple linear correlations were used to reveal spatial intra and interspecific segregations of monogenean communities on the gills. To perform this test, the intensity of all parasite individuals of one species or stage (adult or juvenile) found on each section of all samples of hosts were transposed in column (section 1 to 96) for comparison with another species or stage distribution. Parasite spatial distributions among species or stages were considered as similar when linear correlations obtained were significant ($P < 0.05$).

In order to understand how the parasite microhabitat varies with an increasing intensity of infection, fish with low and high infection levels were selected and the distribution of monogeneans over their gill arches examined. To reduce any size effect, we compared the distribution of monogeneans on gills with similar surfaces. Thus, *S. nigricans* with a total length between 13.5 cm and 14 cm were selected and *D. aruanus* were grouped in two size classes (small habitat with TL < 4 cm and large habitat with TL > 4 cm). An ANOVA with multiple comparisons was used to reveal differences between the gill infections of arches, zones and a simple linear correlation was applied to reveal niche segregation.

The influence of interspecific interaction on microhabitat dispersion was studied on the *S. nigricans* guild of monogeneans. Fishes showing monospecific and pluri-specific infracommunities were selected. Individuals of similar length were chosen to reduce any habitat size

effect. The number of monogeneans on each section of each gill arch was determined. Simple linear correlations were applied to these data to examine niche segregation resulting from interspecific interactions.

Several coefficients were obtained for measuring the association of parasites in the component community of *S. nigricans*, namely Dice's coefficient, to measure the degree of association and Forbes' index and phi coefficient, to measure the amount of association deviation from expectation. Chi-square tests (χ^2) with Yates correction for continuity (Yates, 1934) were used to determine the association deviation degree of significance. All *P* values less than 5% were considered to be significant.

Results

Gill habitat

The gill arches of *Stegastes nigricans* are small with a large number of filaments. Arches 1 and 2 have a similar number of gill filaments (arch 1: 70 ± 3.4 and arch 2: 70.8 ± 4.4) with a similar surface. The surface of gill arch 3 is slightly inferior with a lower number of gill filaments (64.3 ± 3.1). The 4th arch is small with differences in length between the anterior and posterior gill filaments. The mean number of posterior gill filaments is 41.6 ± 2.4 . The filaments are atrophied providing a very small surface area for parasites to settle. A mean number of 56 ± 2.9 filaments are present on the anterior side of the 4th gill arch. The number of gill filaments increases with fish length.

The gills of *Dascyllus aruanus* are similar to those of *S. nigricans* but are smaller and with a lower number of filaments. The first two arches have a similar surface with a mean number of filaments on each side of 54.7 ± 2.6 for the first arch 1 and 52 ± 1 for the 2nd arch. The surface of the 3rd arch is smaller with a mean number of 42.7 ± 0.9 gill filaments on both sides. The posterior gill filaments of the last arch are atrophied; the anterior side has 30 ± 1.2 filaments. The number of gill filaments increases with host length.

Parasite species composition

Stegastes nigricans harboured a guild of monopisthocotylean Monogenea belonging to the genus *Haliotrema* Dactylogyridae Ancyrocephalinae sensu Yamaguti 1963. In the case of *D. aruanus*, only one monogenean species also belonging to the genus

Haliotrema occurred, with a prevalence of 81.9% and was temporarily named *Haliotrema* sp.4. Three species constituted the *S. nigricans* guild of monogeneans, *Haliotrema* sp.1 being the dominant species with 94.4% prevalence, *Haliotrema* sp.2 being the least common with a prevalence of 39.0% and *Haliotrema* sp.3 with a prevalence of 47.8%. All these monogeneans are new species and the descriptions are detailed in Lo (1998). The proportional relationship of these monogeneans with host size and age in addition to other factors influencing community structure are discussed in Lo *et al.* (1998).

Microhabitat distribution

All congeneric parasite species found on *S. nigricans* showed microhabitat overlap (*H. sp.1* versus *H. sp.2*: $r=0.72$; *H. sp.1* versus *H. sp.3*: $r=0.77$; *H. sp.2* versus *H. sp.3*: $r=0.59$ with all $P < 0.0001$) which suggests a lack of interspecific segregation of habitat. None of the species studied showed a preference for the anterior or posterior side of the gill arches (t test, $P > 0.05$). Differences in the number of parasites between the left and right gill arches were found for *Haliotrema* sp.1 and *Haliotrema* sp.3 (t test, $P < 0.05$). Despite these results, only the left gill arches were evident because no differences in microhabitat preferences were revealed between the left and right gill arches ($r=0.67$; $P < 0.05$).

The majority of *Haliotrema* sp.1 (table 1) were found on the 1st and 2nd arches compared with the 3rd and 4th arches (ANOVA and multiple comparisons, $P < 0.05$). These monogenean species preferred to settle on the middle part of the gill filaments (ANOVA and multiple comparisons, $P < 0.001$) and on the 1st and 2nd sector (ANOVA and multiple comparisons, $P < 0.01$). Adults and juveniles of *H. sp.1* showed microhabitat overlap ($r=0.72$; $P < 0.0001$).

Haliotrema sp.2 (table 1) showed no particular preference between the first three arches (ANOVA and multiple comparisons, $P > 0.05$) but was significantly less abundant on the 4th arches. (ANOVA and multiple comparisons, $P < 0.05$). Individuals of this monogenean species preferred to inhabit the middle and the proximal zones of the gill filaments (ANOVA and multiple comparisons, $P < 0.05$) and no significant differences between sectors I, II and III were found. Sector IV was the least infected and differed significantly from the first and second sector (ANOVA and multiple comparisons, $P < 0.05$). Although the abundance of juveniles of *H. sp.2* was low, the juveniles showed microhabitat overlap with the adults ($r=0.28$; $P < 0.0001$).

Table 1. The number of monogeneans of the genus *Haliotrema* inhabiting the left gills of *Stegastes nigricans* and *Dascyllus aruanus*.

Species	Gill-arch number				Sectors				Zones		
	1	2	3	4	I	II	III	IV	Distal	Middle	Proximal
<i>Haliotrema</i> sp.1	3028	2859	1678	351	2026	4321	1300	269	1406	4905	1605
<i>Haliotrema</i> sp.2	75	59	45	13	40	111	36	5	19	103	70
<i>Haliotrema</i> sp.3	141	304	112	19	116	323	116	21	152	390	34
<i>Haliotrema</i> sp.4	323	390	192	13	303	363	193	59	355	501	62

Table 2. The frequency (%) of gill sections inhabited by *Haliotrema* sp.1 on the left gill arches of *Stegastes nigricans* in low (7–47 monogeneans per fish) and high (90–262 monogeneans per fish) infection intensities.

Gill arch number	Frequency of inhabited gill sections (left arches)	
	Low infection (N = 30 fishes)	High infection (N = 20 fishes)
1	83.3	100
2	79.2	100
3	70.8	87.5
4	54.2	45.8

The distribution of *Haliotrema* sp.3 on the gills of *S. nigricans* is given in table 1. This species was the most abundant on the 2nd gill arch compared with the 1st arch and the 3rd arch but less abundant on the 4th arch (ANOVA and multiple comparisons, $P < 0.05$). Along the gill filaments, individuals of *H. sp.3* preferred the middle zone compared with the distal one and avoided the proximal zone (ANOVA and multiple comparisons, $P < 0.05$). With reference to the distribution over the gill sectors, the median-dorsal sector II carried significantly more *Haliotrema* sp.3 than any of the other sectors (ANOVA and multiple comparisons, $P < 0.05$). No significant difference was found between sectors I and III and the ventral sector IV had the lowest parasite load (ANOVA and multiple comparisons, $P < 0.0001$). Very few juveniles of *H. sp.3* were found, but their distribution did not differ significantly from that of adults ($r = 0.16$; $P < 0.05$).

Haliotrema sp.4 from *D. aruanus* (table 1), showed some preferences for specific gill arches (ANOVA, $P < 0.0001$). This monogenean was more abundant on the two first gill arches than on the 3rd and less abundant on the 4th arch (ANOVA and multiple comparisons, $P < 0.01$). Along the gill filaments, the highest parasite load was found on the middle and distal zones, whereas the proximal part of the filaments was avoided (ANOVA and multiple comparisons, $P < 0.0001$). For the longitudinal partitioning, dorsal sectors 1 and 2 were preferred to the others (ANOVA and multiple comparisons, $P < 0.005$) while sector 4 was avoided. The microhabitat distributions of juveniles and adults of *H. sp.4* were not correlated ($r = 0.008$; $P > 0.05$).

Table 3. The distribution of *Haliotrema* sp.4 inhabiting the left gills of *Dascyllus aruanus* in small (TL < 4 cm) and large (TL > 4 cm) gill habitats and in low (1–4 monogeneans per fish) and high (11–55 monogeneans per fish) infection intensities.

Gill habitat	Gill-arch number				Sectors				Zones		
	1	2	3	4	I	II	III	IV	Distal	Middle	Proximal
Small habitat											
Low intensity	17	14	13	2	17	19	5	5	16	20	10
High intensity	11	23	9	1	13	18	10	3	19	22	3
Large habitat											
Low intensity	22	19	13	20	20	25	5	4	21	26	7
High intensity	86	85	33	5	62	65	62	20	84	117	8

Effect of the increase in infection intensities of parasites on habitat use

The effect of an increase in the intensity of infection on *S. nigricans* gills was tested only for *Haliotrema* sp.1, which is the dominant species of the guild. A total of 30 hosts with low infection intensities (i.e. with 7 to 47 monogeneans per fish) and 20 hosts with high infection intensities (i.e. with 90 to 262 monogeneans per fish) of similar size were examined. Gill distributions of *Haliotrema* sp.1 with low and high intensity of infections were significantly correlated ($r = 0.84$; $P < 0.0001$). The percentage of sections inhabited by at least one parasite increased with the intensity of infection but the distribution of parasites between gill arches remained unchanged (table 2).

For *D. aruanus* hosts, the effect of the increase in the number of *Haliotrema* sp.4 was studied on small (TL < 4 cm) and large (TL > 4 cm) gill habitats (table 3). In the case of small habitats, an increase in parasite intensity did not induce habitat expansion as the microhabitat distributions were similar ($r = 0.3$; $P < 0.01$). No preferences were noted between the first three arches; only arch 4 was avoided (ANOVA and multiple comparisons, $P < 0.001$). For large gill habitats, the distribution of *H. sp.4* in low and high intensities of infection were not different ($r = 0.5$; $P < 0.0001$). Arches 1 and 2 were preferred to 3 and 4 in fish with heavy parasite loads (ANOVA and multiple comparisons, $P < 0.001$). Similarly, middle and distal zones of the gill filaments were preferred to the proximal ones (ANOVA and multiple comparisons, $P < 0.0001$). No significant differences were revealed between sectors I, II and III. The number of occupied sections for each gill arch increased, with a colonization of the microhabitats left empty in low infection intensity of parasites (table 4).

Microhabitat distribution in mono- and plurispecific infections

A sample of 42 *S. nigricans* (mean TL = 10.5 ± 2.2 cm) infected by the dominant species *Haliotrema* sp.1 in monospecific infections was used for this survey. For the plurispecific infection, the microhabitat distribution of monogeneans species was studied on 42 *S. nigricans* (mean TL = 13.7 ± 1.4 cm). Three kinds of associations were found on *S. nigricans* gills with the constant presence of the dominant species *H. sp.1*. These guilds were formed at 29.3% of *H. sp.1*–*H. sp.3* species pairs, at 20.8%

Table 4. The frequency (%) of gill sections inhabited by *Haliotrema* sp.4 on the left gill arches of large *Dascyllus aruanus* (TL > 4 cm) in low (1–4 monogeneans per fish) and high (11–55 monogeneans per fish) infection intensity.

Gill arch number	Low infection (N = 30 fish)	High infection (N = 30 fish)
1	50	70.8
2	37.5	75
3	33.3	50
4	0	16.7

of *H. sp.1*–*H. sp.2* and finally 18.2% comprise the three *Haliotrema* species. Only fish with a guild composed of *H. sp.1* and *H. sp.3* were selected to study the microhabitat distribution because of the low numbers of *H. sp.2* recorded on hosts infected by this species. The distribution of *Haliotrema* sp.1 in single infections was significantly correlated with the distribution found when *H. sp.3* were present ($r=0.86$; $P < 0.0001$).

Interspecific associations

Differing association coefficients obtained between pairs of monogenean species infecting *S. nigricans* are given in fig. 2. The values of Dice’s coefficient were important for some parasite associations. The highest

value was found for the *H. sp.1*–*H. sp.3* species pair followed by *H. sp.1*–*H. sp.2* and finally the *H. sp.2*–*H. sp.3* species pair. Phi coefficients revealed positive associations for *H. sp.1*–*H. sp.2* and *H. sp.1*–*H. sp.3* species pairs and a negative one for the *H. sp.2*–*H. sp.3* species pair, although this last value was close to zero. However, Forbes’ index of each pair was close to the calculated value, suggesting that these observed associations were a stochastic assemblage. Chi-square tests (χ^2) showed that only guilds formed of *H. sp.1*–*H. sp.2* and *H. sp.1*–*H. sp.3* species pairs had a significant association deviation degree ($P < 0.001$).

Discussion

Microhabitat organization of gill monogeneans

Species of *Haliotrema* spp. found on *S. nigricans* and the species *Haliotrema* sp.4 infecting *D. aruanus* showed a similar distribution. In plurispecific infections, the ectoparasites of *S. nigricans* overlapped, although some preferences were noted according to the position on gills. All monogeneans showed a high preference for the 1st and 2nd arch with a constant low level of infection for the 4th arch. However, few differences were revealed between species. Most individuals of *Haliotrema* sp.1 were found on arch 1. Individuals of *H. sp.3* were found on the 2nd arch, whereas individuals of *H. sp.2* and *H. sp. 4* colonized equally the first three arches (respectively on *S. nigricans* and *D. aruanus*).

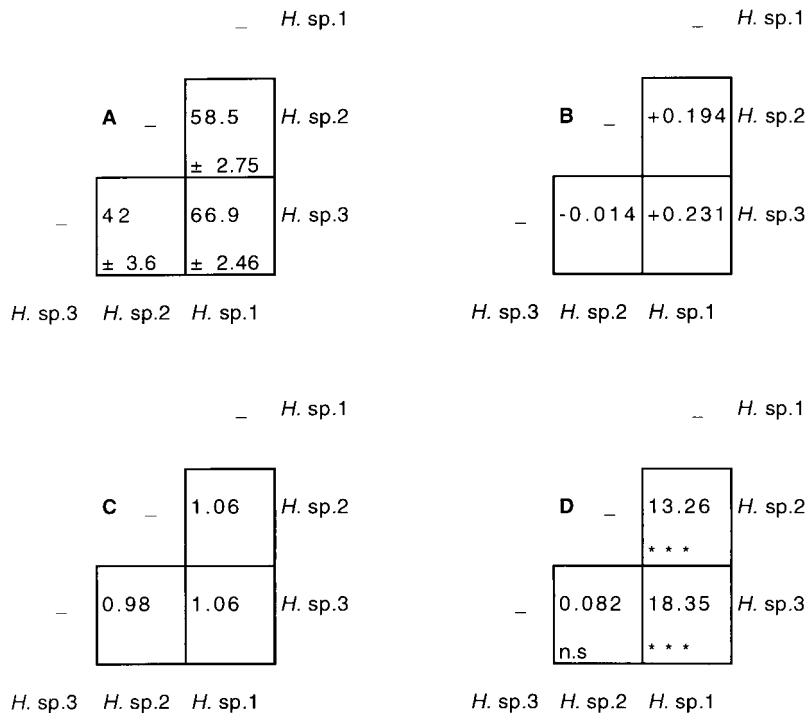


Fig. 2. Different association coefficients performed between pairs of monogenean species infecting *Stegastes nigricans* gills. A, Dice’s coefficient (\pm S.E. at 5% error); B, phi coefficient; C, Forbes’ index; D, Chi-square tests and association deviation degrees of significance (***, $P < 0.001$; n.s., $P > 0.05$).

Several explanations have been proposed to explain the transverse partitioning distribution of gill ectoparasites. Suydam (1971) suggested that the distribution of one of the monogenean species he studied was the result of the force and the direction of water currents over the gill arches. Later, Wootton (1974) showed, using the glochidia of *Anodonta cygnea* as passive 'marker parasites', that the larger gill arches receiving most of the water flow were the most infected. For *S. nigricans*, the largest arches, both in surface area and number of gill filaments, are the 1st and the 2nd, followed by the 3rd and the 4th arches. Thus, the distribution of the monogeneans seems to be influenced mainly by extrinsic factors such as surface area of the gill arch and the number of filaments. However, the distribution of *H. sp.3* does not reflect a purely passive invasive process distribution as in the case of other monogeneans. Indeed, arch 1 appeared to be avoided but not arch 2; this may be due to post-settlement migrations as suggested by Paling (1969). *Haliotrema sp.3* is the largest of the guild ($462 \pm 94 \mu\text{m}$) and is able to elongate its body to twice its body length when crossing gill filaments (personal observation). As distal parts of filaments of neighbouring arches are in regular contact (Bitjel, 1949), these parasites may migrate from one arch to the next without major problems. Other monogenean species of the guild are very small (less than $300 \mu\text{m}$), hence their movements are reduced to a small area of the gill filaments and migration between arches is unlikely. Thus, the distribution pattern of these small monogeneans may be influenced more by extrinsic factors such as surface area of the arch or the number of gill filaments. This hypothesis agrees with the results of Rohde (1980) on the distribution of a small prolific Ancyrocephalinae which was correlated with the number of gill filaments and the surface of arches of *Gadus morhua*.

In the present investigation, all monogenean species preferred the middle zone of the gill filaments. Distal zones were colonized by the largest monogenean species (i.e. *H. sp.3* and *H. sp.4*). Distal zones of gill filaments are known to be the most exposed to respiratory currents (Hughes, 1966) but, once settled, monogeneans appear to be unaffected by hydrodynamic constraints. Other factors are likely to be involved in the microhabitat choice of these species.

Longitudinal partitioning showed that all *Haliotrema* species of both species of damselfishes preferred dorsal sectors (sector I and then II or III). In all cases, the ventral sector IV which is the most exposed to water current (Wootton, 1974) was avoided. However, if sectors I, II and III offered similar habitat surfaces, sector IV provides a smaller surface area due to the reduced length of the gill filaments towards the ventral side. The effect of gill surface size on parasite distribution is therefore likely to be the main factor here rather than hydrodynamic influences.

Differences between the left and right gill arches for *H. sp.1* and *H. sp.3* have been reported in other studies dealing with monogenean species (Wiles, 1968; Wootton, 1974), but these differences in parasite intensity remain unexplained. In the present study, differences in the number of parasites found between left and right gills can be explained by the protocol used to observe the gills

and the time spent in examining gills (about 30 min is needed per side in heavy infections of *S. nigricans*), and the consequent loss of parasites.

Intraspecific microhabitat interactions

Niche expansions induced by an increase in intensity of parasite infection have been observed in several populations of gill parasites (Anderson, 1974; Arme & Halton, 1974; Silan, 1984; Ramasamy *et al.*, 1985). For example, Anderson (1974) showed that individuals of *Diplozoon paradoxum* were evenly distributed in heavy infections but settled to specific sites in low levels of infection intensity. Moreover, Arme & Halton (1974) noted that the niche of *Declidophora merlangi* expanded gradually. In low intensities, 80% of *D. merlangi* occurred on the first arch, whereas only the second, third and fourth arches were occupied in heavy infections. Ramasamy *et al.* (1985) showed that two monogenean species (*Vallisia indica* and *Dionchus remorae*) of *Scomberoides* spp. also expanded their microhabitat in heavy infections. For *S. nigricans*, the dominant species *Haliotrema sp.1* did not show any significant expansion of microhabitat along the four gill arches when parasite intensity increased. Only a few parasites were found on sectors which were usually avoided and thus parasite expansion on gill habitat as described by Anderson (1974) or Arme & Halton (1974) was not found here. A lack of niche expansion was demonstrated by Rohde (1991) when he studied the monogenean parasite *Kuhnia scombri* of *Scomber australicus*. He found that an increase in parasite abundance was not sufficient to saturate the gill habitat. As suggested by Anderson (1974) and Rohde (1979), the maximal parasite carrying capacity is rarely reached in natural conditions.

The gill habitat of *S. nigricans* does not seem to be filled by the dominant species *H. sp.1*, as shown by the low abundance value (37.9 ± 38.1 parasite per fish) compared with the optimal infection intensity observed on one fish (262 parasites). These values reflect the low intensities of infrapopulations generally observed in the natural environment and provide an estimate of the gill carrying capacity of *S. nigricans*. The possibility for a host to support a significant number of parasite species may reduce intraspecific competition. In that case, if intraspecific competition between *H. sp.1* does exist, it may occur only after extrinsic factors determine the optimal distribution of these monogeneans. The other species of the guild *H. sp.2* and *H. sp.3* were not studied because of the low infrapopulation intensities and prevalence observed (see Lo *et al.*, 1998), as these were too small to induce competing mechanisms. Several authors have underlined the importance of intensity and prevalence of infrapopulations to induce intra- or interspecific competition (Dobson, 1985; Holmes, 1987, 1990).

The response of *H. sp.4* to an increase in infrapopulations intensity differed depending on the size of the gill habitat size of *D. aruanus*. On a small host habitat, the microhabitat did not seem to expand significantly in high parasite loads whereas, on the larger habitat, an increase in infrapopulation intensity led to an extension of the microhabitat with colonization of empty niches along the anterior-posterior axis of the gills. These results suggest a possible effect of intraspecific competition for

space although no microhabitat expansion was observed on the small habitat. In heavy infections on small habitats, individuals of *H. sp.4* may be quickly rejected to marginal sites where conditions are inadequate for survival. On the larger host habitat, the surface area is larger and the carrying capacity of habitat is less likely to have been reached so microhabitat extension was more visible because parasites found sufficient resources even on sites usually avoided. In both cases, the distribution of *H. sp.4* did not differ significantly so parasites always occurred on the preferred sites on the gills. In fact, intraspecific competing processes aim to manage the use of space to protect limited resources of these mucus and epithelial cell eaters (Llewellyn, 1966).

Interactions between juvenile and adult monogeneans have been demonstrated by Silan (1984) studying a guild of *Diplectanum* spp. parasites of *Dicentrarchus labrax*. He revealed the existence of a centrifugal migration of these monogeneans from the proximal to the distal part of the gill filaments during their growth. Other authors such as Rohde (1980) have not shown any segregation between juvenile and adult monogeneans. Our study on the guild parasites of *S. nigricans* did not show any interaction for space between adults and juveniles for any of the three *Haliotrema* species studied. In the case of *H. sp.4* found on *D. aruanus*, the lack of a correlation between juveniles and adults suggests a possible segregation induced by intraspecific competition. However, when the distribution of juveniles was studied along the different partitions of the gill, we could not clearly reveal site segregation as shown by Silan (1984). In fact, these monogenean stages showed high overlap in their distribution and only the 1st arch was avoided by juveniles. These results suggest the maintenance of the gill distribution of these *Haliotrema* species, when settled, is likely to be induced in part by extrinsic factors.

Interspecific microhabitat interactions and associations

Ecologists have argued that when several congeneric species use the same habitat and resources, this generally leads, by competitive processes, to either the exclusion of one or several species or to niche segregation (cf. Barbault, 1981; Combes, 1995). All *Haliotrema* species occurring on the gills of *S. nigricans* showed a high overlap in their distribution, although some preferred certain gill arches, zones or sectors. Furthermore, the distribution of the dominant species *Haliotrema* sp.1 did not change either in single or in concurrent infections. Niche overlap appears to be common in monogeneans found on the gills (e.g. Rohde *et al.*, 1994). Another study on a guild of *Dactylogyryus* species inhabiting the gills of *Abramis brama* also revealed no differences between the distribution of the four congeneric monogeneans (Dzika & Szymanski, 1989). As suggested by Rohde & Hobbs (1986), congeneric species can share similar overlapping microhabitats when they are reproductively isolated. Like the congeneric *Haliotrema* species found by Rohde *et al.* (1994) on the gills of *Lethrinus miniatus*, the three *Haliotrema* species in the present study showed clear differences in the size and shape of the copulatory organs as well as body size (Lo, 1998). Thus, reinforcement of reproductive barriers, as hypothesized by Rohde (1994), may explain

the lack of niche segregation between congeneric monogenean species.

Positive associations were found between the dominant species *H. sp.1* and the other species, which supports the conclusion of Rohde (1991). In the present study, the positive associations were significant, whereas a negative one between *H. sp.2* and *H. sp.3* was not significant. Rohde *et al.* (1994) suggested that positive interactions can be the result of a positive correlation between infection intensities and host length. This may be the case here (Lo *et al.*, 1998). Alternatively, significant positive associations may also be the result of the constant occurrence of the dominant species *Haliotrema* sp.1. Finally, it appears that the present results support the conclusion of Rohde (1994) suggesting that interspecific competition does not play a major role in habitat organization of gill parasites.

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