

Ectoparasites of the whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835) off the Kenyan Coast: distribution within the host population and site selection on the gills

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SUMMARY

Different populations of the whitespotted rabbitfish, *Siganus sutor*, were examined for ectoparasites: adults from the Mombasa area (sampled in December 1990) and different age classes (adult, subadult and juveniles) from Gazi Bay (sampled in December 1992 and August 1993). The most common gill parasites were: the monogeneans *Pseudohaliotrema* sp., *Tetrancistrum sigani* and *Microcotyle mouvoii*, the copepods *Hatschekia* sp., *Pseudolepeophtheirus* sp. and juvenile Caligidae, and prazina larvae of the isopod *Gnathia* sp. Adult siganids had a higher parasite load than subadults. Juvenile rabbitfish did not harbour any gill parasites. Temporal differences in the parasite load of subadult rabbitfish were observed for *M. mouvoii* (highest in the December samples) and for juvenile Caligidae (highest in August). The microhabitat of the 5 most common gill parasites was species specific. Most parasite species showed distinct site preferences with respect to both gill arches and gill sectors, within the gill arches. Niche breadth of the different gill parasite species was independent of the abundance of any of the other species present. However, niche breadths of *M. mouvoii*, *Tetrancistrum* sp. and *Hatschekia* sp. increased with their own abundance. This suggests that interspecific competition for space is low and that intraspecific factors could play an important role in the microhabitat choice of these gill parasites. The hypothesis that niche restriction leads to higher intraspecific contact and an enhancement of chances to mate was tested on 2 monogenean species, *Pseudohaliotrema* sp. and *Tetrancistrum sigani*. Their highly aggregated distribution over the gill filaments, leading to increased intraspecific contact, is consistent with the hypothesis.

Key words: gill parasites, *Siganus sutor*, Indian Ocean, microhabitat use, niche.

INTRODUCTION

The whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835), is one of the most important commercial fish species in artisanal marine fisheries along the East African coast (Ntiba & Jaccarini, 1988). Rabbitfish are herbivorous (Lam, 1974), live in schools on reef flats and seagrass beds and harbour several ecto- and endoparasite species (Diamant & Paperna, 1986; Jones & Hine, 1983; Martens & Moons, 1995; Toman, 1977, 1989). Geets & Ollevier (1996) described the distribution of the endoparasitic helminths within an adult host population of *S. sutor* off the Kenyan coast. The microhabitat preferences of the intestinal helminth communities indicated a selective site segregation of the parasite species present. For testing niche theories, inter- and intraspecific interactions, and their impact on microhabitat use, parasites on the gills of marine teleost are very useful models (Rohde, 1991). The species richness of infracommunities of parasites will be influenced by bottom up processes, i.e. interspecific

interactions and niche availability (Kennedy & Guégan, 1996). Rohde (1976, 1977, 1978, 1991), studying gill parasites of fish of the Indo-Pacific and the Australian coastal waters, suggested that most gill parasite species live in low-density populations in resource-rich habitats. Whereas resource partitioning seems common and would reduce interspecific interactions, microhabitat restriction would lead to increased intraspecific competition as well as enhance the chance to find a mate. Koskivaara, Valtonen & Vuori (1992) and Bagge & Valtonen (1996) equally found no limitations of resources and an apparent lack of interspecific competition when studying 10 dactylogyrid species inhabiting the gills of roach in Finnish lakes.

The present study focuses on the ectoparasite fauna of *S. sutor* and describes the characteristics of the component communities as well as the microhabitat choice of the infracommunities of the gill parasites. The specific aim of our study was to assess whether the microhabitat use of gill parasites of a common marine fish species of the Indian Ocean, *S. sutor*, fits the prediction of the hypotheses of Rohde (1991) on the relative importance of intra- and interspecific competition and the reinforcement of reproductive barriers.

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MATERIALS AND METHODS

Five populations of whitespotted rabbitfish *Siganus sutor* (Valenciennes, 1835) were sampled. Two groups of adult rabbitfish were caught in December 1990 and 1992: 1 sample from the seagrass beds off the Mombasa coast (MADD) and 1 from Gazi Bay (60 km south of Mombasa) (GADD) respectively. Two samples of subadults were collected in Gazi Bay: 1 in December 1992 (GSUBD) and 1 in August 1993 (GSUBA). All fish were obtained from local fishermen who used cabbage-baited dematraps (traditional bottom traps). In August 1993 we also caught small juvenile siganids from Gazi Bay by beach seining (GJUVA). Table 1 gives an overview of the samples and abbreviations used further in the text. Fish were weighed, measured and fixed in 7% formaldehyde solution immediately upon landing of the fish (which was at the most 1 h after catching the fish). The MADD sample contained 33 animals, all other samples consisted of 20 individuals. Some additional fish were examined to collect living parasites for identification purposes. The parasites were fixed using the methods described by Berland (1984). The terms prevalence, intensity, mean intensity and abundance are used according to Margolis *et al.* (1982). We used data on the infracommunity level (defined as the numbers of a certain parasite species on 1 individual fish) for the calculations. The pseudobranch and the 4 gills of both left and right side of the fish were dissected and analysed for parasites in all fish of samples MADD, GSUBD and GJUVA. The gills were screened for parasites under a stereo-microscope (magnification range $\times 6$ – $\times 50$). Since there was no significant difference in parasite numbers between left and right gills in any of these samples (Wilcoxon's matched pair test, $P > 0.05$), we screened only the left gills of the fish of GADD and GSUBA. To calculate mean intensities and abundances for these last two samples, the number of parasites found was doubled, while for the other samples, intensities on left and right gills were summed.

No parasites were found on the pseudobranch (P), except in 1 fish from GSUBA harbouring 2 specimens *Gnathia* sp. Therefore the data on the pseudobranch were not included in the statistical analyses. Gill arches were numbered I to IV in anterior–posterior succession. Gill arch references were calculated using the left gills only.

Since none of our parasite data were normally distributed and no satisfying transformation could be found, non-parametric tests were used. Differences in mean intensities of infection between the different host groups were tested by Kruskal–Wallis ANOVA by ranks. When an overall significant difference was found between the 4 host groups, multiple comparisons were carried out according to Siegel & Castellan (1988). P levels were

set on 0.05. The critical value for comparison of a group of 33 (MADD) and 20 (GADD, GSUBD, GSUBA) observations was 20.17 and when 2 groups of 20 fish were involved it was 22.5.

Data on infection levels of the 4 gill arches were matched (measured on the same fish) within a host group. Therefore Friedman ANOVA by ranks was used when testing the overall differences of infection of the gill arches within a host group. We followed Siegel & Castellan (1988) for *post hoc* multiple comparisons.

In order to get a better insight into the micro-habitat preferences of the gill parasites of *S. sutor*, the gills of 10 adult fish (MADD) were drawn with a drawing mirror (external and internal hemibranches drawn separately) and the exact position and number of parasites per sector was noted. Each hemibranch was divided in 8 equal sectors (Fig. 1) and the number of parasites per sector was determined. Site specificity of the parasites on these 10 fish was tested on 3 levels: between the 4 gill arches (Friedman ANOVA by ranks and multiple comparison), between external and internal hemibranches (Wilcoxon's matched pair test), and between the 8 sectors (Friedman ANOVA by ranks and multiple comparisons). When a difference of abundance on one of the first two levels (gills or hemibranches) was noticed, the Friedman ANOVA for the sectors was carried out on the numbers of parasites per separate gill arches or hemibranch, as well as on the summed data for each sector (all gills and hemibranches together).

To define spatial niche breadth, the 8 gill sectors were seen as different resources. Levins' niche breadth, $B = 1/\sum p_j^2$ where p_j is the proportion of specimens of a species found on sector j , was calculated for each infrapopulation and standardized between 0 and 1 (B_a) (Krebs, 1989). For niche overlap, Renkonen index $1 - \frac{1}{2}\sum |p_{ia} - p_{ja}|$, was used, where p_{ia} is the proportion of specimens of species i on sector a and p_{ja} the proportion of species j on sector a . Differences in both measures were tested by Wilcoxon's matched pair test. Spearman Rank correlation was used for testing correlations between niche breadth and number of parasites.

In view of the hypothesis of Rohde (1991) that niche restriction leads to higher intraspecific contact and enhancement of mating chance by the parasites, the distribution of the 2 most abundant monogenean species *Pseudohaliotrema* sp. and *Tetrancistrum sigani* on the gill filaments, was examined. An aggregated distribution of the monogeneans on certain gill filaments would result in higher opportunities for mate finding. Therefore the numbers of parasites per gill filament were counted on 5 *S. sutor* specimens. Indicators for an aggregated distribution were $s^2/m > 1$ (with s^2 the variance and m the mean) and d values > 1.96 , with $d = \sqrt{2\chi^2} - \sqrt{2\nu - 1}$ where ν is the number of degrees of freedom and $\chi^2 = s^2(n-1)/m$ (Elliott, 1977).

Table 1. Overview of samples of *Siganus sutor* taken at the Kenyan coast

Sample	Location	Maturation of fish	Date	Mean total length \pm s.d. (cm)	Mean wet weight \pm s.d. (g)	No. of fish examined
MADD	Mombasa	Adult	Dec. 1990	24.2 \pm 1.6	231.2 \pm 47.5	33
GADD	Gazi	Adult	Dec. 1992	24.6 \pm 3.7	247.6 \pm 12.0	20
GSUBD	Gazi	Subadult	Dec. 1992	13.4 \pm 1.2	37.4 \pm 8.0	20
GSUBA	Gazi	Subadult	August 1993	12.5 \pm 1.3	27.3 \pm 5.1	20
GJUVA	Gazi	Juvenile	August 1993	2.9 \pm 0.2	0.33 \pm 0.09	20

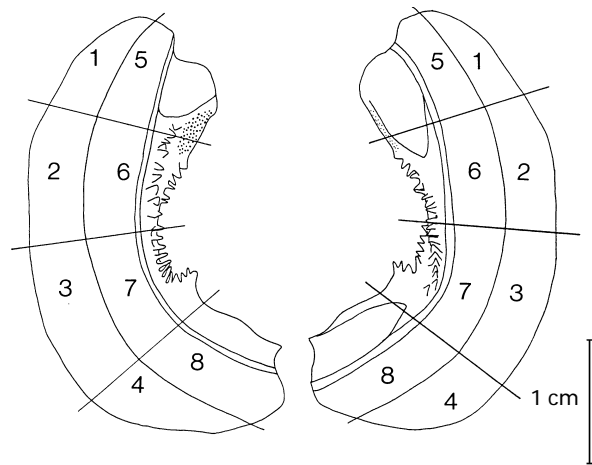


Fig. 1. Gills of *Siganus sutor* with indication of 8 gill sectors. (Left: external hemibranch, right: internal hemibranch.) 1–2–3–4: Distal sectors; 5–6–7–8: proximal sectors; 1–4–5–8: extreme sectors; 2–3–6–7: median sectors; 1–2–5–6: dorsal sectors; 3–4–7–8: ventral sectors.

Table 3. Relative proportions (%) of *Siganus sutor* infected with 0–7 ectoparasite species in 4 samples (For abbreviations of the sample code see Table 1.)

No. of parasite species	MADD	GADD	GSUBD	GSUBA
0	0	0	0	0
1	0	0	15.0	10.0
2	6.1	0	45.0	25.0
3	9.1	10.0	30.0	15.0
4	21.2	35.0	5.0	50.0
5	48.4	35.0	5.0	0
6	12.1	15.0	0	0
7	3.0	5.0	0	0

RESULTS

Species composition

Nine ectoparasite species were found on the 5 investigated populations of *S. sutor* (Valenciennes, 1835) (Table 2). Yamaguti (1953) described *Pseudohaliotrema sphincteroporos* and *P. sigani* from siganids. Our specimens were most comparable to *P.*

Table 2. Species list and abundance \pm s.d. of ectoparasites of *Siganus sutor*

(For abbreviations of the sample code see Table 1.)

Parasite species	MADD <i>n</i> = 33	GADD <i>n</i> = 20	GSUBD <i>n</i> = 20	GSUBA <i>n</i> = 20	GJUVA <i>n</i> = 20
Monogenea					
<i>Pseudohaliotrema</i> sp.	78.6 \pm 82.2	234.9 \pm 365.3	0.5 \pm 0.9	4.7 \pm 7.1	—
<i>Tetrancistrum sigani</i>	45.0 \pm 30.8	59.4 \pm 110.3	15.8 \pm 28.4	16.7 \pm 17.4	—
<i>Microcotyle mouwoi</i>	7.7 \pm 13.0	6.4 \pm 8.9	6.3 \pm 7.3	0.5 \pm 1.1	—
Copepoda					
<i>Hatschekia</i> sp.	8.5 \pm 13.1	8.0 \pm 13.5	—	—	—
<i>Caligus</i> sp.	0.03 \pm 0.2	—	—	—	0.05 \pm 0.2 ^s
<i>Pseudolepeophtheirus</i> sp.	0.5 \pm 1.1	0.1 \pm 0.4	—	—	—
<i>Bomolochus</i> sp.	—	—	0.05 \pm 0.2	—	—
Caligidae juveniles	0.8 \pm 1.1	1.5 \pm 2.4	0.5 \pm 0.9	4.6 \pm 2.8 ^G 2.6 \pm 2.9 ^s	0.7 \pm 0.9 ^s
Isopoda					
<i>Gnathia</i> sp. (larvae)	5.2 \pm 3.5	13.8 \pm 12.7	1.2 \pm 2.7	3.5 \pm 4.1	—
Mean total <i>n</i> parasites/fish	146.3 \pm 119.2	324.1 \pm 401.1	24.5 \pm 27.6	30.0 \pm 24.5	0.7 \pm 0.9 ^s

^s On the skin.^G On the gills.

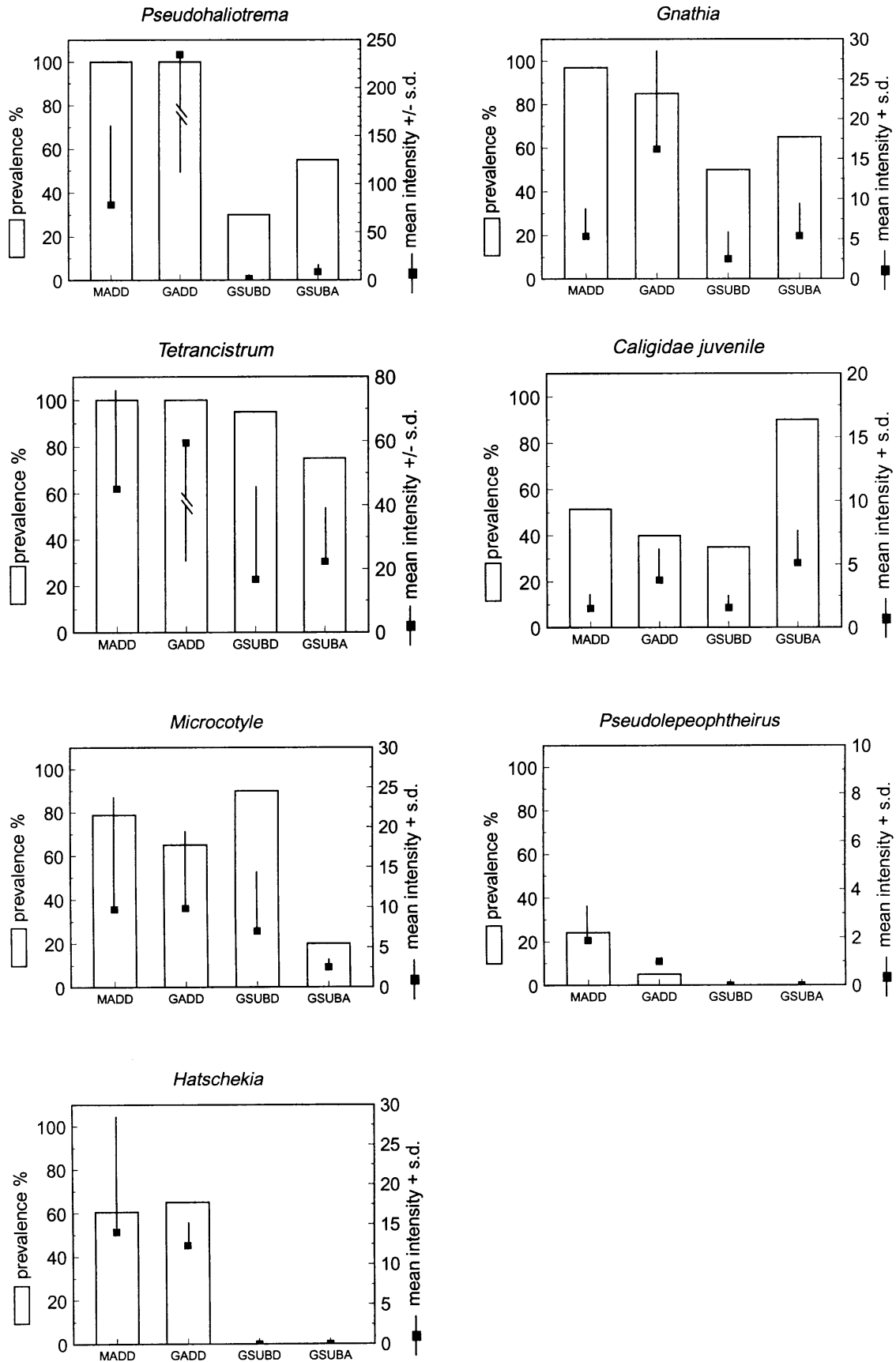


Fig. 2. Prevalence (%) and mean intensity of infection of 7 species of gill parasites in 4 populations of *Siganus sutor*.

sphincteroporos when total body size of the monogenean was taken into account, but the form of the copulatory organs fitted more the description of *P.*

sigani. Therefore, we decided not to confine our specimens to any of the two species yet. *Pseudohaliotrematoides polymorphus indicus* sp. n., described

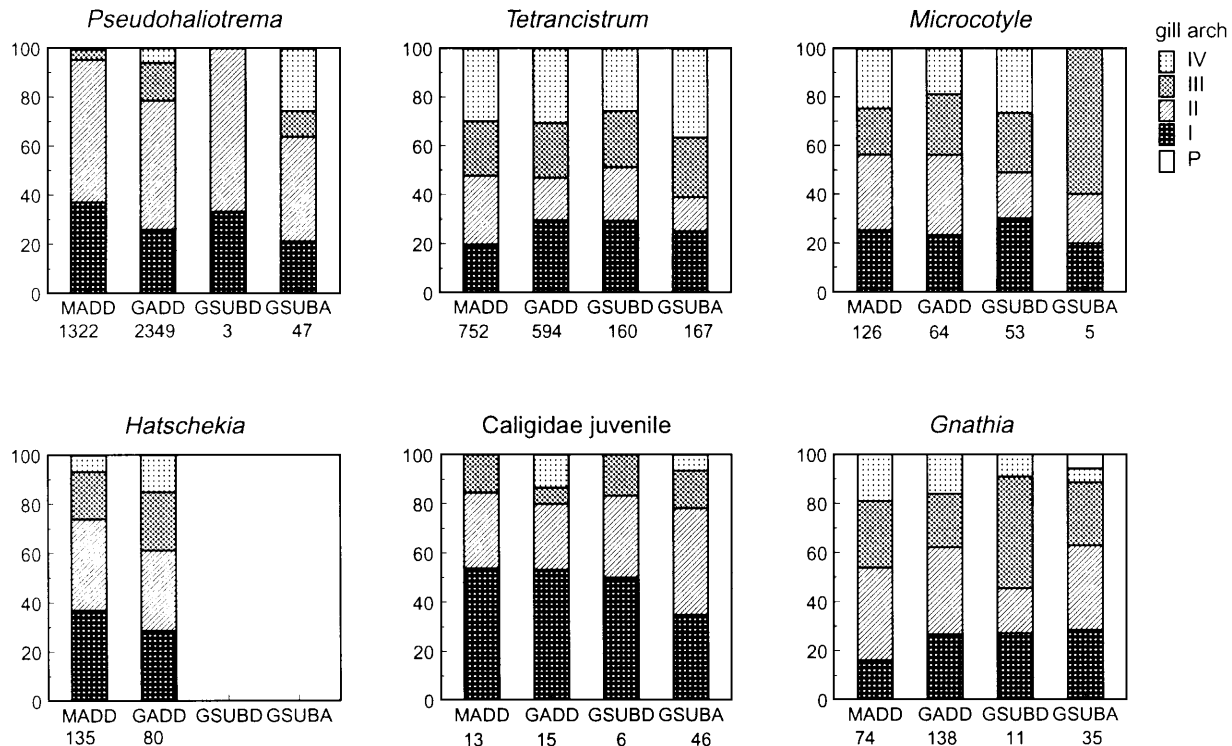


Fig. 3. Relative distribution (%) of 7 ectoparasite species over 4 gill arches (I–IV) and a pseudobranch (P) in 4 populations of *Siganus sutor*. Total number of parasites per host group is indicated below each bar.

by Paperna (1972) from a *Siganus* sp. off the Mombasa Coast, is larger and the form of the copulatory organs differs from our specimens.

The systematic place of the copepods was not always clear either. It was noted that the juvenile Caligidae found on the skin of the subadult and juvenile rabbitfish caught in August (GSUBA and GJUVA) had lunules while they were not noticed on the juvenile Caligidae found on the gills. This is an indication that the juvenile skin copepods most probably belong to the genus *Caligus*, while those of the gills would belong to the genus (*Pseudo-*) *Lepeophtheirus*. Rather than assigning these juveniles tentatively to one or another group we preferred to group the juvenile gill copepods as 'Caligidae juveniles'. One adult *Caligus* (male) was found on the skin of a juvenile siganid and 1 (male) on the gills of an adult rabbitfish (MADD). Adult *Pseudolepeophtheirus* sp. were more regularly found on the gills of the rabbitfish. One female *Bomolochus* with egg strings was noticed on the gills of a subadult fish (GSUBD).

Infection levels

Total mean number of parasites was highest for the adult siganids (mean \pm s.d.: MADD: 146.3 ± 119.2 , GADD: 324.5 ± 401.1). Subadult fishes harboured on average 24.5 ± 27.6 (GSUBD) and 30.0 ± 24.5 (GSUBA) parasites per fish. The juvenile siganids (GJUVA) did not harbour any gill parasites, only copepod skin parasites were found. Most adult

siganids harboured 4–5 species of gill parasites, while the subadults mostly had 2 or 3 parasite species in the December sample and 4 in August (Table 3).

Fig. 2 gives an overview of the prevalences and mean intensities of infection of the 7 most abundant species of gill parasites for the 4 populations of siganids. When considering the mean numbers of each parasite species in each component community, the dominant parasite species was *Pseudohaliootrema* sp. for the adult siganids (MADD and GADD) and *Tetrancistrum sigani* for the subadults (GSUBD and GSUBA).

An overall significant difference in parasite abundance between the 4 host groups was found for all parasite species (Kruskal–Wallis ANOVA, $N = 93$, D.F. = 3, $P < 0.01$ for all parasite species). In this analysis we excluded *Pseudolepeophtheirus* sp. which was only present in very low numbers. Multiple comparisons revealed that the abundances of *Pseudohaliootrema* sp., *Tetrancistrum sigani* and *Hatschekia* sp. were significantly higher in the adult host groups compared to the subadult siganids (regardless of time of sampling). For these 3 parasite species, a significant positive correlation between total length and number of parasites was found in the adult siganids of Mombasa (MADD) (Spearman Rank correlation, r_s 0.44, 0.68 and 0.42 respectively, all $P < 0.05$). The August sample of subadult rabbitfish (GSUBA) had significantly less *Microcotyle mouvoii* and significantly more Caligidae juveniles than on any of the December samples (MADD, GADD and GSUBD).

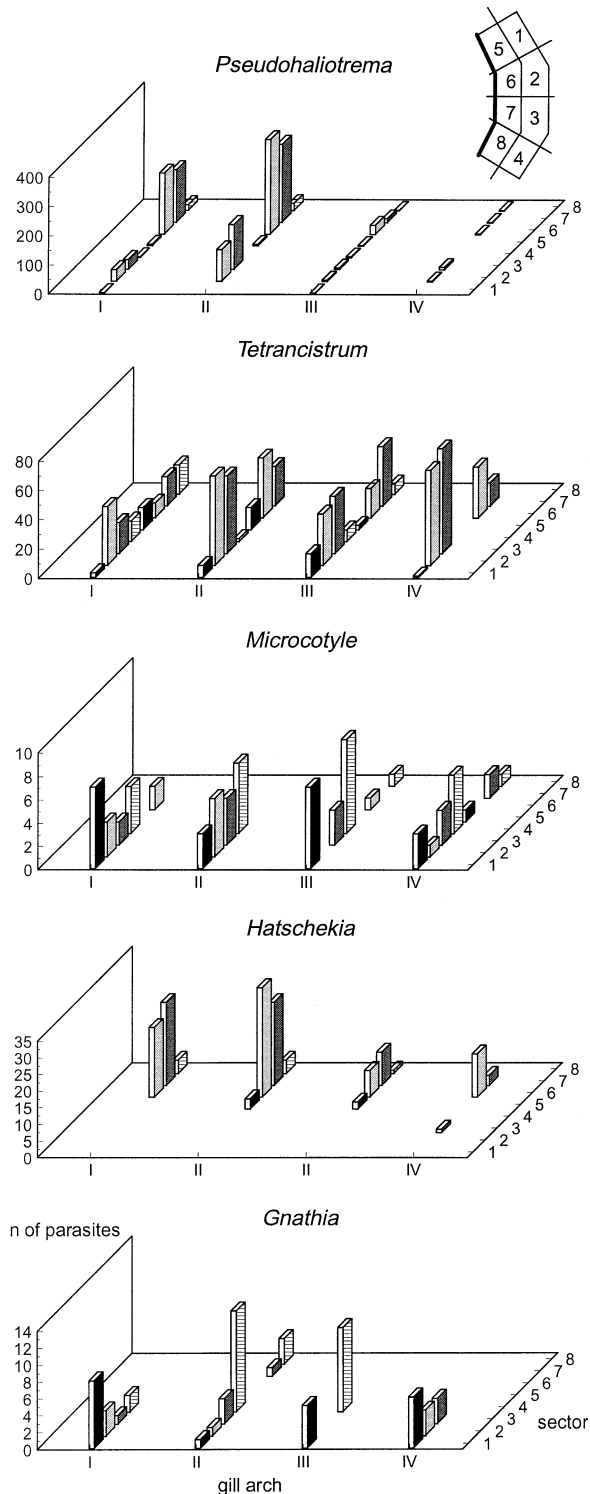


Fig. 4. Distribution of ectoparasite species of *Siganus sutor* over 8 gill sectors. A schematic drawing of a gill with indication of the sectors is given on top. (Numbers of parasites per sector were summed for all 10 investigated fish.)

Microhabitat preference

None of the parasite species showed a preference for the left or right gill arches (Wilcoxon's matched pair test, $P > 0.05$). Therefore only parasite numbers of the left gill arches were used in the study of site preference between the gill arches (Fig. 3). Most

parasite species showed a consistent habitat choice, independent of the sampling place, sampling time or maturation of their siganid hosts. When a correction was made for the relative size of the gills, no changes in patterns of distribution occurred (Geets, unpublished data). Thus, differences in size of the gills did not explain the gill arch preference.

Pseudohaliotrema sp. was more abundant on the first 2 gill arches in all 4 siganid populations (Friedman ANOVA and multiple comparisons, $P < 0.001$). *Tetrancistrum sigani* was observed more on the 1st and the 4th gill arch, but the difference was only significant for the adult siganids of Gazi (GADD), where the mean intensity was highest.

Microcotyle mouwoi and *Gnathia* sp. did not show a clear preference for a certain gill arch. *Hatschekia* sp. and Caligidae juveniles were more abundant on the first 2 gill arches, but this difference was not significant for *Hatschekia* sp. in the GADD group and for the juvenile Caligidae in the GSUBD group.

The distribution of the parasites over the 8 gill sectors is shown in Fig. 4. Numbers of Caligidae were too low and therefore not included in the analysis. A Friedman ANOVA on the summed data of all 4 gill arches for each sector, indicates that *Pseudohaliotrema* sp. was not equally distributed over the gill sectors ($P < 0.01$). The median sectors (2, 3, 6, 7) carried the highest parasite load. The median proximal sectors (6, 7) had the highest number of *Pseudohaliotrema* sp. and their number differed significantly from all extreme sectors (1, 4, 5, 8) but not from the median distal sectors (2, 3). Because *Pseudohaliotrema* sp. was more abundant on the first 2 gill arches than on the 3rd and 4th, the distribution of the parasite over the gill sectors was also tested separately for each gill arch. The same patterns of distribution over the 8 gill sectors were found when gill arch I and II were analysed separately. On gill III and IV, the parasites were also aggregated in the median proximal sectors but the differences were not significant because of low numbers of parasites (Fig. 4). No significant difference between numbers of *Pseudohaliotrema* sp. on the external and internal hemibranch was found.

Tetrancistrum sigani showed no preference for the external or internal hemibranchs, nor for any of the 4 gill arches. Regarding the distribution over the gill sectors, the median distal sectors (2, 3) had significantly ($P < 0.01$) more *T. sigani* than any of the extreme sectors (1, 4, 5, 8), but they did not differ significantly from the median proximal sectors (6, 7).

Microcotyle mouwoi infected the external hemibranchs more than the internal (Wilcoxon's matched pair test, $P < 0.05$). Total counts on the distal areas (1+2+3+4) outnumbered those of the proximal areas (5+6+7+8), Wilcoxon's matched pair test, $P < 0.01$. Parasite loads on the external and internal hemibranchs tested separately gave concordant results.

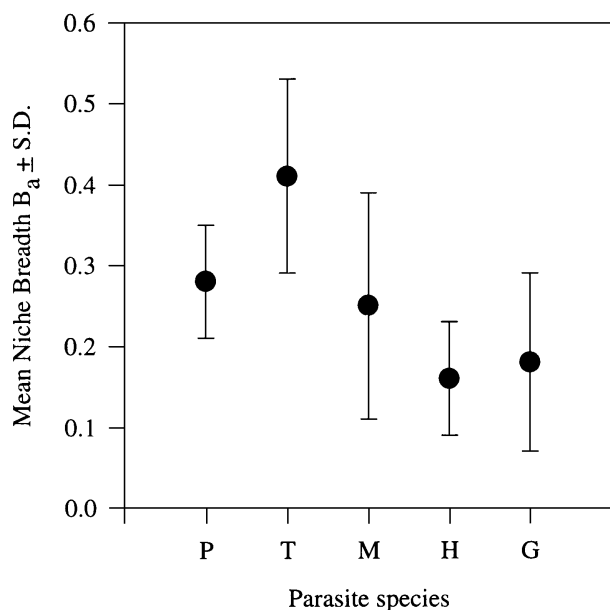


Fig. 5. Levins' mean niche breadth $B_a \pm S.D.$ for 5 ectoparasite species of *Siganus sutor*. (P, *Pseudohaliootrema* sp.; T, *Tetrancistrum sigani*; M, *Microcotyle mouzoi*; H, *Hatschekia* sp., G, *Gnathia* sp.).

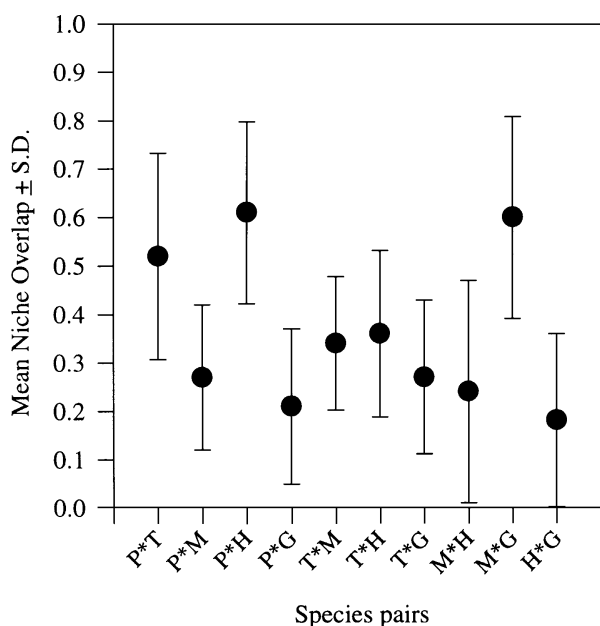


Fig. 6. Renkonen mean niche overlap $\pm S.D.$ between pairs of gill parasites of *Siganus sutor*. (P, *Pseudohaliootrema* sp.; T, *Tetrancistrum sigani*; M, *Microcotyle mouzoi*; H, *Hatschekia* sp.; G, *Gnathia* sp.).

Hatschekia sp. was found more on the first 2 gills ($P < 0.05$), but no preference on the level of the hemibranchs was seen. *Hatschekia* sp. was observed almost exclusively in the proximal areas (5+6+7+8) near the filament base ($P < 0.01$) and most often on the median proximal sectors (6, 7) ($P < 0.05$).

Gnathia sp., which showed no preference for any of the gills or hemibranchs, was found mostly on the distal sectors (1+2+3+4), towards the tip of the gill

filaments ($P < 0.01$). Within this distal region, the extreme sectors (1+4) were more likely to be parasitized than the median part (2+3) ($P < 0.01$).

The highest mean niche breadth was noted for *T. sigani* and the lowest for *Hatschekia* sp. and *Gnathia* sp. (Fig. 5). Friedman ANOVA and multiple comparisons showed a significant difference ($P < 0.05$) between the highest and the lowest values. Niche breadths of *T. sigani*, *M. mouzoi* and *Gnathia* sp. increased with increasing abundance of these species (Spearman Rank correlation $r_s = 0.72$, 0.83 and 0.79 respectively, $P < 0.05$). This was not the case for *Pseudohaliootrema* sp. and *Hatschekia* sp. For all 5 species, the niche breadth of one species was independent of changes in abundance of any of the other species present.

Hatschekia sp. and *Gnathia* sp. have the lowest niche overlap when compared to all other species pairs (Fig. 6). The highest overlap was found between *Pseudohaliootrema* sp. and *Hatschekia* sp. and between *M. mouzoi* and *Gnathia* sp..

The hypothesis of Rohde (1977) of reinforcement of reproductive barriers, based on non-competitive and intraspecific mechanisms which bring about aggregation of individuals of 1 species, even in the absence of the other species, was tested for the 2 most abundant monogeneans *Pseudohaliootrema* sp. and *T. sigani*. Individuals of both monogenean species were found more often on the same filaments than expected from chance events alone (Fig. 7). High s^2/m values (> 1) and d values significantly higher than 1.96 confirmed their clumped distribution. The pattern was similar for all fish in the sample, independent of the degree of infection. In Fig. 7, only the data for the most infected fish as well as for the least infected fish are represented.

DISCUSSION

Species composition

Studies on the parasite fauna of different species of siganid fish have been conducted in the Red Sea (Diamant & Paperna, 1986), on the Philippine siganids (Jones & Hine, 1983) and in the Seychelles (Toman, 1977, 1989). In a paper on the metazoan parasites of *S. sutor* from Nyali Beach (Kenya), Martens & Moons (1995) reported 8 gill parasites. Although the reported species richness is mainly in accordance with our findings, some differences were noticed. Martens & Moons (1995) mentioned 2 species of *Pseudohaliootrema* (sp. 1 and sp. 2). In our study, the examined *Pseudohaliootrema* specimens found on the gills of *S. sutor* did not show clear morphological differences which would indicate the presence of more than 1 species. Since no description of the 2 species was included in the study of Martens & Moons (1995), assigning our specimens to one or other was not possible.

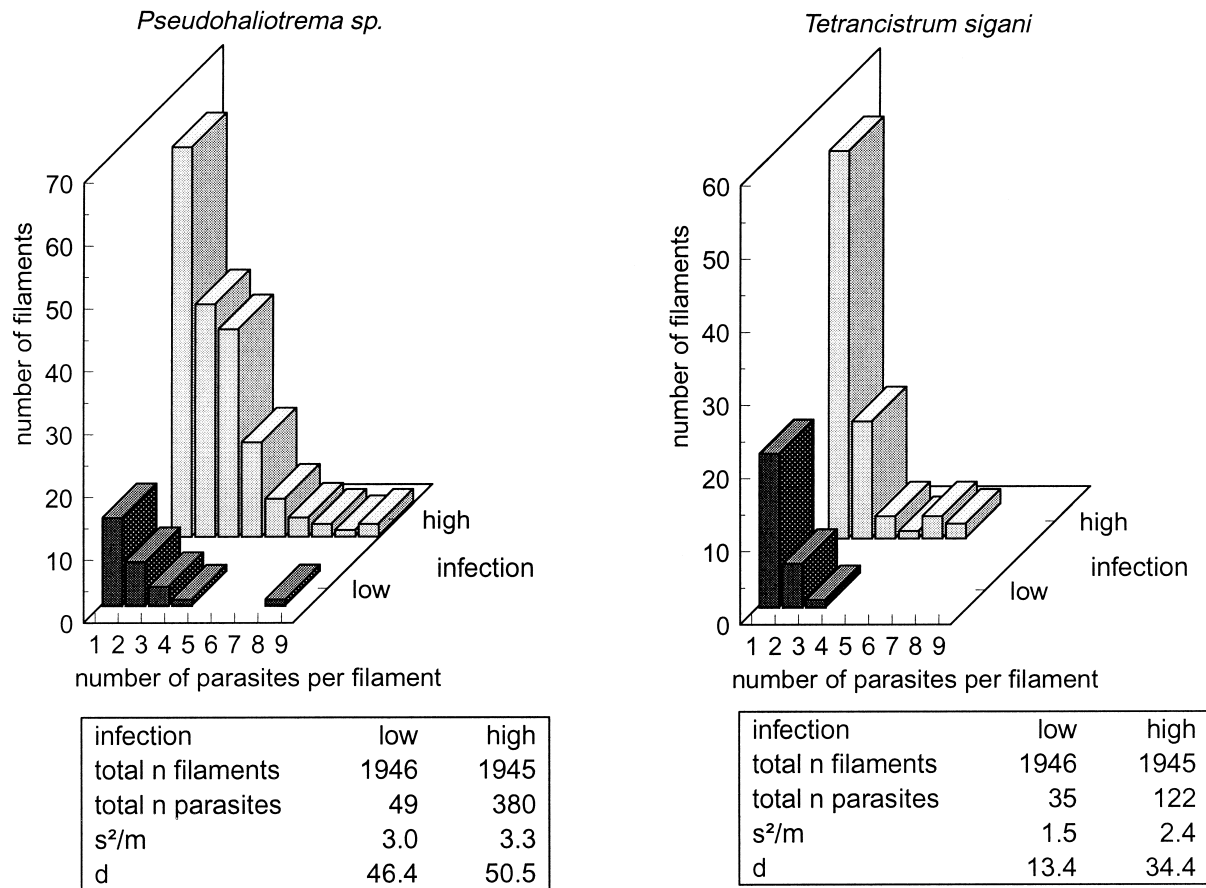


Fig. 7. Frequency distribution of *Pseudohaliotrema* sp. and *Tetrancistrum sigani* on gill filaments of *Siganus sutor*, at low and high intensities of infection.

Apart from *M. mouzvoi*, found in our study, Martens & Moons (1995) reported a second larger Microcotylidae species. Thoney & Munroe (1987) noted a considerable intraspecific variation in *M. sebastis*, *M. pomatomi* and *M. hiatulae*. For the latter species they demonstrated a strong correlation between clamp number and length of the monogenean, and clamp number could therefore be used as a growth indicator. The *M. mouzvoi* specimens in our study also varied considerably in size and clamp number, but no other morphological differences were noticed (Geets, personal observation). Therefore we considered the specimens to belong to 1 species.

Infection levels

The fact that only copepod skin parasites and not one gill parasite was found on the small juvenile siganids (GJUVA) was quite remarkable, considering the high prevalence and mean intensity of gill parasites on the subadult and adult rabbitfish. Loss of gill parasites because of the difference in sampling technique (beach seining against bottom traps) can be ruled out since the juvenile fish were caught alive and immediately fixed upon capture. Possibly these small juveniles acquire the gill parasites mainly when

schooling together with larger, already parasitized rabbitfish. During sampling not one larger specimen was caught together with the juveniles, leading to the assumption that contact and subsequent transfer of parasites might not have taken place yet.

When comparing the infection levels of the subadult siganids of December (GSUBD) and those of August (GSUBA), temporal differences in parasite load were observed from *M. mouzvoi* (highest in December) and Caligidae infections (highest in August). Seasonal changes in infection patterns of fish parasites are well known in temporal regions, but studies in tropical areas are more scarce. Grutter (1994) reported a 7-fold increase in number of dactylogyridean monogeneans on *Siganus doliatus* from the Australian Great Barrier Reef from May 1992 to January 1993.

The significantly higher number of *Pseudohaliotrema* sp., *T. sigani* and *Hatschekia* sp. on adult rabbitfish in comparison with subadult, regardless of time of sampling and the significant positive correlation of abundance with fish length, suggests that these gill parasites accumulate during the life-time of the fish. Martens & Moons (1995), who investigated rabbitfish from 7 to 21 cm, also indicate a positive correlation between total gill parasite numbers and fish length. Grutter (1994) did not find a correlation

between total number of gill parasites per fish and length of *S. doliatus*, but a limited number of fish of a relatively small size range (14–18 cm) was investigated. Variation in parasite communities between adult siganids of Mombasa and Gazi was minor and more due to parasite numbers than to species composition.

Microhabitat preference

Each parasite species showed a specific distribution over 4 gill arches as well as over the 8 gill sectors within each arch. Site specificity at the level of the arches did not vary between the different host populations. Koskivaara *et al.* (1992) showed that the gill arch preference could differ seasonally in *Dactylogyrus* sp. on roach (*Rutilus rutilus*). Although we could only compare December (long rain season) and August samples (short rain season), no clear differences in microhabitat choice of the gill parasites was noticed. In the study of Martens & Moons (1995), samples were taken at the end of the rain season (April–May) and overall distribution of gill parasites was in accordance with our results. Therefore, seasonal variation in site selectivity of the siganid gill parasites is not expected.

Different explanations have been given for the frequently observed microhabitat selection of gill parasites of fish. Llewellyn (1956) postulated that differences in water volumes passing over the 4 gill arches might be reflected in differences in opportunities of parasites to attach. But, larvae attached to the gills with greater water current might have lower survival rates, because they have to struggle more against the greater current. Experiments by Paling (1968) on brown trout (*Salmo trutta* forma *fario* L.) showed a significant greater water volume passing over the 2nd and 3rd gill than over the 1st and the 4th. Suydam (1971), who studied the micro-ecology of 3 monogenean species on different hosts, concluded that the distribution of 1 of the species, *Declidophora maccallumi*, was a result of the force and direction of the ventilating current. If water current would have been the determining force, then a II-III-I-IV pattern of infection intensity should occur. The distribution of none of the gill parasites of *S. sutor* fitted this pattern. If a lower survival of parasites on more ventilated gills would determine the distribution of the gill parasites, a IV-I-III-II pattern would result. As *Tetrancistrum sigani* occupies predominantly the 1st and 4th gill arch, the distribution of this species would fit this explanation, if it was not that they prefer to expose themselves on the median distal sectors, where water current is high, instead of hiding in the calmer proximal gill areas.

Ramasamy *et al.* (1985) observed that parasites living on the exposed distal half of the gills often have additional clamps or suckers to attach. They

used this to explain the site selectivity of 4 monogenean and a copepod species on the gills of *Scomberoides* spp. The distribution of the gill parasites of *S. sutor* observed by us fits the expected pattern. *Pseudohaliotrema* sp., the smallest of the gill parasites, was found mostly near the gill basis on the median proximal site, while *T. sigani*, which is about twice as big and has larger clamps, used the more exposed median distal sites. *Microcotyle mouwoi* and *Gnathia* sp. both had strong developed attachment organs and were found on the distal region, while the smaller *Hatschekia* sp., using its second antennae to attach to the gills (Kinne, 1984), inhabited the more sheltered proximal sectors.

Besides the different ability to attach to the gills, the gill parasites also have different feedings habits and the site preference might be related to access to food. Generally, polyopisthocotylean monogenea (e.g. *M. mouwoi*) feed on blood and Monopisthocotylea (e.g. *Pseudohaliotrema* sp. and *T. sigani*) on mucus. Gnathiid prazinae are sucking blood. *Microcotyle mouwoi* and *Gnathia* sp. were mostly firmly attached on the distal half of the gill filaments, where the gill filaments are thinner, and possibly more easily perforated to reach the blood vessels.

Holmes (1973) suggested that the continued interspecific interaction between parasite species leads to niche diversification and that site segregation is an important part of niche specialization. It was also noted, however, that selective site segregation, in which the parasite species occupies a restricted microhabitat, independent of the presence or absence of other parasite species, is far more common than interactive site segregation. Thus interspecific competition would then not be the direct driving force of habitat restriction. Rohde (1978, 1991) pointed out that many potential niches for ectoparasites of fish are empty and claimed that this reduces the importance of interspecific competition as a cause for niche restriction. In our study, the niche breadth of gill parasites of *S. sutor* did not change (or sometimes even increased) with increasing abundance of other species present. This indicates that interspecific competition or interactive site segregation is probably not important for the microhabitat choice of these gill parasites. *Dactylogyrus* species on the gills of roach also showed a lack of interspecific competition amongst most species, even during high population densities in summer (Koskivaara *et al.* 1992, Bagge & Valtonen, 1996).

In our study on *S. sutor*, increasing niche breadth of *M. mouwoi*, *T. sigani* and *Gnathia* sp. with higher densities suggests an effect of intraspecific competition for space in those species. However, this was not observed for *Pseudohaliotrema* sp. which is numerously the most dominant species and where, in some cases, infection levels of several hundreds of parasites per fish were observed.

Rohde (1991) assumed that intraspecific factors are largely responsible for niche restriction, and that an important function of niche restriction is to improve the chance to mate. In the case of *Pseudohaliootrema* sp. and *T. sigani*, both capable of reproducing on the gills of *S. sutor*, our results are consistent with this hypothesis as the parasites were not only restricted to certain area of the gills, but also aggregated on certain gill filaments. Lebedev (1978), however, argued that improved reproduction potential was not the cause but the result of site selection of the parasite. More detailed studies that include information on stage of maturation and/or sex of the parasites together with a very detailed study of their site selection (for gill parasites up to the level of the filaments) are required to get more insight into these phenomena.

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