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**ENDOPARASITIC HELMINTHS
OF THE WHITESPOTTED RABBITFISH
(*SIGANUS SUTOR* (Valenciennes, 1835))
OF THE KENYAN COAST:
DISTRIBUTION WITHIN THE HOST POPULATION
AND MICROHABITAT USE**

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Summary. The parasitic fauna of the alimentary tract of adult whitespotted rabbitfish, *Siganus sutor*, sampled in December 1990 at the Kenyan coast, was investigated. Five endoparasites were found: the digenean trematodes *Opisthogonoporoides hanumanthai*, *Gyuliauchen papillatus* and *Hexangium sigani*, the acanthocephalan *Sclerocollum rubrimaris* and the nematode *Procammalanus elatensis*. No uninfected fish, nor single species infections occurred. Parasite population data showed very high prevalences for all endoparasites, ranging from 68.18 % to 100 %. *G. papillatus* occurred with the highest mean intensity, 201.68 ± 12.54 parasites per infected fish. The parasites were overdispersed within their host's population and frequency distributions generally fitted the negative binomial function. The relationship between host size and parasite burden showed that smaller fish were more heavily infected. The infection with *O. hanumanthai* and *H. sigani* decreased significantly with total length of *S. sutor*. Study of the associations between parasites showed that the intensities of the three digenean species were significantly positively correlated. Possible transmission strategies of the digenea and impact of the feeding habits of *S. sutor* are discussed. Microhabitat preferences of the five endoparasites indicated a selective site segregation of all species.

Keywords: *Siganus sutor*, endoparasites, microhabitat, Indian Ocean.

INTRODUCTION

Siganidae or rabbitfish have a wide distribution in the Indo-Pacific, ranging from East-Africa to French Polynesia (WOODLAND, 1983). Siganids are, together with the Lethrinidae, the most important fish in the local artisanal marine fisheries along the East African coast (NTIBA & JACCARINI, 1988). Fifty percent of the total catch is made up of rabbitfish (NZIOKA, 1984). *Siganus sutor* (Valenciennes, 1835) is the dominant species at the Kenyan coast, followed by *S. luridus* (Ruppell, 1828), *S. argenteus* (Quoy and Gaimard, 1825) and *S. stellatus* Forsskål, 1775 (see NTIBA & JACCARINI, 1988). Siganids are widely recognised as potentially suitable species for mariculture (BEN-TUVIA *et al.*,

1973, LAM, 1974, HORSTMANN, 1975, LICHTOWICH & POPPER, 1975, POPPER & GUNDERMANN, 1975, VON WESTERNHAGEN & ROSENTHAL, 1976).

In view of their maricultural potential, LAM (1974) stated that "proper studies on diseases in siganids are badly needed". Most studies on parasites of marine fish in tropical regions are limited to taxonomic or zoogeographical descriptions. Ecological studies on endoparasitic helminths of fish in tropical seas and especially in the Indian Ocean are scarce. DIAMANT & PAPERNA (1986) listed the parasites of wild Red Sea rabbitfish, with special attention to the potential pathogens in mariculture. The ecology of the acanthocephalan *Sclerocollum rubrimaris* was reported in three species of rabbitfish, *Siganus rivulatus* (Forsskål, 1775), *S. argenteus* and *S. luridus* by DIAMANT (1989).

Several investigations have documented the distribution of ecto- and endoparasites of fish in the host population and their microhabitat use within their host (CROMPTON, 1973, HOLMES, 1973; 1990a, ROHDE, 1984, BATES & KENNEDY, 1991, SUKHDEO, 1990, BUCHMANN, 1991). Most of these studies present data on fish of temperate waters. The present work presents data on the distribution of five endoparasitic helminth species of *S. sutor* within the host population and on their microhabitat selection. The investigation is part of a wider research project on the parasitic fauna of *S. sutor* of the Kenyan coast. The study on ectoparasites will be presented in a separate paper (GEETS *et al.*, in prep).

MATERIAL AND METHODS

In December 1990, a sample of adult whitespotted rabbitfish *Siganus sutor* (Valenciennes, 1835) caught in the seagrass areas off the Mombasa coast, were obtained from local fishermen. Cabbage baited dematraps (traditional bottom traps) were used. They were placed in shallow water (<14 m depth) at low tide and removed at the next low tide. Upon being landed, fish were intraperitoneally injected with formaldehyde solution 7%. Total length (TL) to the nearest 0.1 cm and wet weight (WW) to the nearest 0.1 g were measured.

Twenty two specimens of *S. sutor* (24.9 ± 1.9 cm mean TL, 249.2 ± 62.1 g mean WW) were examined for endoparasites. The alimentary tract was divided into stomach and intestine. From the pyloric sphincter up to the anus, the intestine was cut into four equal parts and parasite load was counted for each section. For identification purposes, additional live parasite specimens were obtained from *S. sutor* from the same area and immediately fixed using the methods described by BERLAND (1984) and PRITCHARD & KRUSE (1982). The acanthocephalan was identified using the the description of SCHMIDT & PAPERNA (1978).

The terms prevalence, intensity, mean intensity and abundance were used as indicated by MARGOLIS *et al.* (1982).

The frequency distributions of the parasites were compared with the theoretical Poisson and negative binomial functions. The number of frequency classes was determined using the following equation $Q = 1 + 3.3 \log N$, with Q the number of classes and N the maximal number of a particular parasite recorded (ROBERT *et al.*, 1990). The expected values for the Poisson series were calculated in Lotus 123R4 for Windows with the @POISSON function, those for the negative binomial function were calculated using

PROBNEGB in SAS version 6.08. The k values were calculated with the maximum likelihood equation (ELLIOTT, 1977). Goodness of fit was tested using the chi square test. Variance to mean ratio as well as k values were used as indices of dispersion. Variance to mean ratio will approximate unity if there is an agreement with a Poisson series. If variance to mean ratio is greater than 1, a contagious or aggregated distribution is suspected. The H_0 hypothesis that parasite species (total number) were equally distributed over the four different areas of the intestine was tested using G and chi square tests (SOKAL & ROHLF, 1987; 1995). Analysis of correlations of occurrence of two parasite species was done using Spearman's rank correlation coefficient r_s , since data on intensities of infection were not normally distributed. Statistica software (release 4.1) was used for most statistical analysis.

RESULTS

Five endoparasite species were found in the alimentary tract of *Siganus sutor*: the digenean trematodes *Opisthagonoporoides hanumanthai* Madhavi, 1971, *Gyliachuca papillatus* (Goto & Matsudaira, 1918), *Hexangium sigani* Goto & Okazi, 1929, the acanthocephalan *Sclerocollum rubrimaris* Schmidt & Paperna, 1978 and the nematode *Procammalanus elatensis* Fusco & Overstreet, 1979.

In Table 1 the quantitative data on the five endoparasites are given. Prevalence was very high for all species, ranging between 68.2 % for *H. sigani* up to 100 % for *G. papillatus*. The digenean *G. papillatus* reached the highest mean intensity, 201.68 ± 12.54 parasites per infected fish, the acanthocephalan *S. rubrimaris* was the least common with a mean intensity of 2.72 ± 0.12 . *G. papillatus* accounted for 52.2 % of the total of 8496 parasites recovered from the 22 rabbitfish. Of all fish examined, 54.5 % were infected with all five endoparasites. Neither uninfected fish, nor single-species infections were recorded (Table 2).

TABLE 1

Quantitative data on the endoparasites of Siganus sutor

Parasite species	Total number of parasites (%)	Maximum intensity	Prevalence (%)	Mean intensity \pm s.d.	Abundance \pm s.d.
<i>O. hanumanthai</i>	3254 (38.3)	691	81.8	180.77 ± 11.01	147.91 ± 8.73
<i>G. papillatus</i>	4437 (52.2)	1317	100.0	201.68 ± 12.54	201.68 ± 2.54
<i>H. sigani</i>	317 (3.7)	125	68.2	21.13 ± 2.27	14.41 ± 1.35
<i>S. rubrimaris</i>	49 (0.01)	9	81.8	2.72 ± 0.12	2.22 ± 0.10
<i>P. elatensis</i>	439 (5.2)	53	90.9	21.95 ± 0.64	19.95 ± 0.63

TABLE 2

Relative proportion (%) of *Siganus sutor* infected with 0 to 5 endoparasite species.
(Total number of fish examined = 22)

Number of parasite species	Percentage <i>S. sutor</i> infected
0	0
1	0
2	9.1
3	13.6
4	22.7
5	54.5

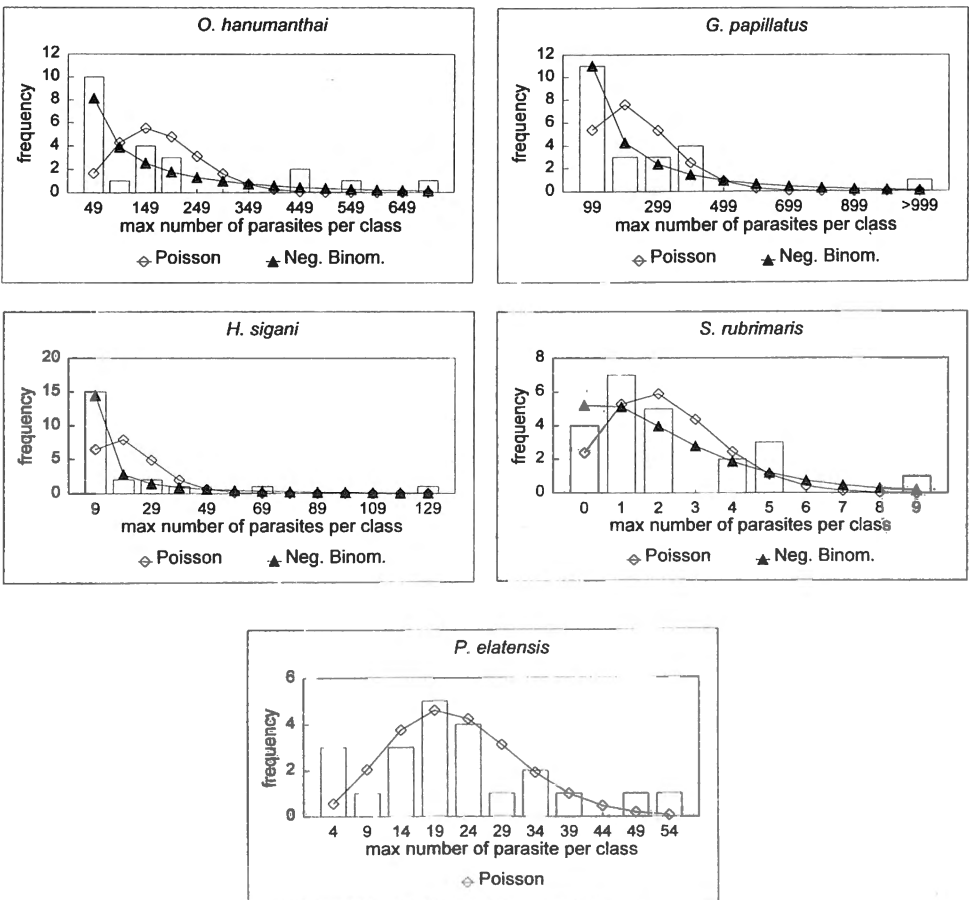


Fig. 1. – Frequency distribution of five endoparasite species of *Siganus sutor* with fitting of Poisson and negative binomial distribution.

The distribution of the endoparasites in the host population is shown in Fig. 1. Variance (s^2) to mean (m) ratio and k -values (Table 3) are both used as indices of dispersion: $s^2/m > 1$ and $1/k$ are both measures for clumping of the individuals in the host population. All five endoparasite species were overdispersed (aggregated) throughout the rabbitfish population. *O. hanumanthai* and *G. papillatus* showed a very high aggregation in the host's population. A few hosts carried an enormous amount of parasites, eg. the maximum intensity of infection in one host was 1317 for *G. papillatus* and 691 for *O. hanumanthai*.

TABLE 3

*Indices of dispersion, s^2/m and k -value, for the five endoparasite species of *Siganus sutor**

<i>Parasite species</i>	s^2/m	k -value
<i>O. hanumanthai</i>	249.58	0.59
<i>G. papillatus</i>	377.64	0.53
<i>H. sigani</i>	52.31	0.28
<i>S. rubrimaris</i>	2.26	0.74
<i>P. elatensis</i>	9.40	2.36

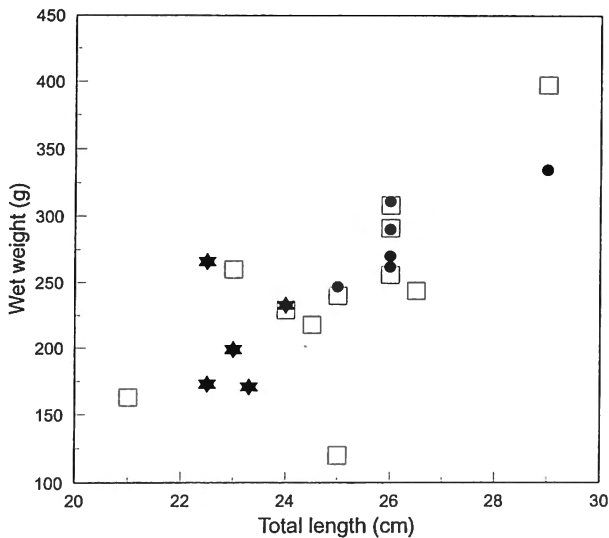
Poisson series and negative binomial distribution were fitted to the frequency distributions. A goodness of fit chi square test showed that none of the parasites were randomly distributed in the host population ($P < 0.001$ for the Poisson series). Almost all endoparasite distributions could be described by the negative binomial distribution ($P > 0.05$), except for the distribution of the nematode *P. elatensis*. Although an aggregated distribution was expected from the high variance to mean ratio for *P. elatensis*, the negative binomial distribution was not a good theoretical function to describe this frequency distribution.

A Spearman 's rank correlation (Table 4) between total length and number of parasites of each species showed significant negative correlations for *O. hanumanthai* and *H. sigani*. The total parasite load was also significantly negatively correlated with the size of the host. Of the total number of parasites found, *O. hanumanthai* accounted for 38.3 % and *H. sigani* for 3.7 %, so this could partly explain the negative correlation of the total number of parasites with the total length. But, on the other hand, *G. papillatus*, which accounts for 52.2 % of all the parasites, did not show a significant negative correlation between intensity of infection and host size. The relation between total length and wet weight of the fish with an indication of the six least parasitized specimens (total number of parasites < 100) and of the five most heavily parasitized hosts (total number of parasites > 600) is shown in Fig. 2. Mean weight and mean total length were considerably lower for the heavily parasitized siganids.

TABLE 4

Spearman's Rank Correlation (r_s) between total length (TL) of *Siganus sutor* and intensities of infection. Significant correlations are indicated in bold

Pair of variables	r_s	p-level
TL- <i>O. hanumanthai</i>	-0.74	<0.001
TL- <i>G. papillatus</i>	-0.12	>0.05
TL- <i>H. sigani</i>	-0.69	<0.001
TL- <i>S. rubrimaris</i>	-0.27	>0.05
TL- <i>P. elatensis</i>	-0.37	>0.05
TL-total n of parasites	-0.53	<0.05



	< 100 parasites ●	> 600 parasites ★
Mean total length ±SD (cm)	26.3 ±1.4	23.1 ±0.6
Mean wet weight ±SD (g)	285.7 ±32.5	208.4 ±40.8

Fig.2.—Relation between total length and wet weight of *Siganus sutor* with indication of the least parasitized individuals (solid circle) (< 100 parasites / fish) and the heaviest parasitized fish (star) (>600 parasites / fish). Mean total length and mean wet weight and their standard deviations are indicated in the accompanying table and are significantly different for both groups (T-test, $P < 0.001$).

The interrelationship between parasites is demonstrated in Table 5 by the Spearman 's rank correlation coefficients (r_s). For this comparison, only rabbitfish containing at least one of the two parasite species involved, were included. All three digenean parasites showed significant positive correlations with each other. Thus, there seems to be an asso-

ciation between the numbers of digenean parasites found in *S. sutor*. No correlation between the numbers of the acanthocephalan *S. rubrimaris* or the nematode *P. elatensis* and the other parasite species could be found.

TABLE 5

Correlation between intensities of infection of five endoparasites of *Siganus sutor* (r_s = Spearman's rank correlation coefficient). Significant correlations are indicated in bold.

Number of pairs r_s Probability	<i>O. hanumanthai</i>	<i>G. papillatus</i>	<i>H. sigani</i>	<i>S. rubrimaris</i>
<i>G. papillatus</i>	22 0.437 < 0.05			
<i>H. sigani</i>	18 0.691 < 0.01	22 0.633 < 0.01		
<i>S. rubrimaris</i>	22 0.147 > 0.05	22 -0.154 > 0.05	21 -0.33 > 0.05	
<i>P. elatensis</i>	21 0.328 > 0.05	22 0.313 > 0.05	20 0.382 > 0.05	22 0.011 > 0.05

Microhabitat preferences of the five parasite species in the alimentary tract of *S. sutor* are shown in the histograms in Fig. 3. The stomach of *S. sutor* harboured no parasites. The H_0 hypotheses for the chi square as well as for the G test stated that the total number of parasites of each species was equally distributed over the four (equal) parts of the intestine. Both tests rejected this hypothesis ($P < 0.001$). The distribution of each of the parasite species was not equal over the intestine but showed a distinct pattern of preference.

The three digenean species preferred the two most posterior parts, I3 and I4, but each species showed a distinct microhabitat preference within this posterior region. *O. hanumanthai* was found in the I3 region in 71.5 % of the cases, *G. papillatus* showed a preference for the I4 region (95.4 %) and *H. sigani* was distributed over both areas but with a slight preference for the I4 region (41.6 % in I3, 58.4 % in I4).

The acanthocephalan *S. rubrimaris* attached most frequently (65.3 %) to the first quarter of the intestine (I1), with decreasing numbers towards the rectum. *P. elatensis*, the nematode, seemed the least site specific of the five species. It was abundant in the first three quarters of the intestinal tract, but rarely occurred in the most posterior part (4.8 %). Each of the four intestinal sectors was characterized by the abundant presence of different parasite species: I1 by *S. rubrimaris*, I2 by *P. elatensis*, I3 by *O. hanumanthai* and I4 by *G. papillatus*, which suggests a spatial niche segregation of the species.

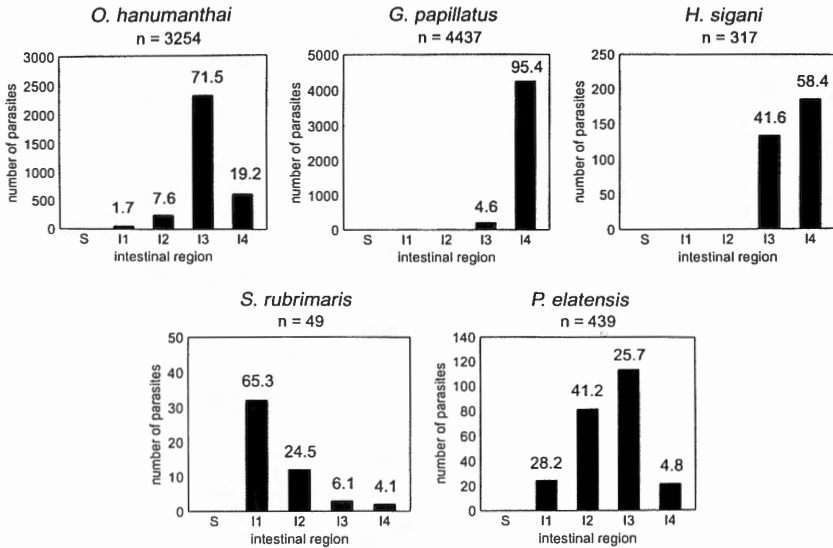


Fig. 3. – Distribution of five helminth species along the alimentary tract of *Siganus sutor*. Relative proportion (%) of the total number of parasites are given on top of each bar. (S = stomach, I1-I4 = four sections of the intestine from pyloric sphincter to anus.).

DISCUSSION

Siganids are herbivorous fish which incidentally take in invertebrate food items (LAM, 1974, SUYEHIRO, 1942). *Siganus sutor* lives in schools on reef flats and seagrass beds. Although herbivorous fish are generally considered to harbour less intestinal parasites than carnivorous or omnivorous fish, this is certainly not the case for *S. sutor*, considering the high prevalences and mean intensities of parasites found in our study.

Up to now, most parasitological studies on siganids were carried out on species of the Red Sea (DIAMANT & PAPERNA, 1986), the Philippines (JONES & HINE, 1983) and the Seychelles (TOMAN, 1977; 1989). DIAMANT & PAPERNA (1986) list thirty five parasite species (12 ecto- and 23 endoparasites) on three rabbitfish species, *Siganus argenteus*, *S. luridus* and *S. rivulatus* (Forsskål, 1775) of the Red Sea. All five endoparasites considered in our study were also collected on the siganid species investigated by DIAMANT & PAPERNA (1986), except for *H. sigani* on *S. luridus* and *P. elatensis* on *S. argenteus*. Infection levels were marked by DIAMANT & PAPERNA (1986) on a nominal scale from “not found” to “rare”, “fairly common” and “abundant”. Heavy infections with *O. hanumanthai* and *Gyuliauchen papillatus* were not noted in the Red Sea siganids. *H. sigani* and *G. papillatus* were also found in *Siganus* spp. (probably *S. oramin* and *S. fluvescens* resp.) from the Seychelles (TOMAN, 1977; 1989).

The mean intensities of digenean trematodes found in *S. sutor* are remarkably high. Stomach analysis only occasionally revealed remains of small crustaceans and gastropods, which could have served as intermediate hosts (pers. obs.). VON WESTERNHAGEN (1973) also reported small invertebrates to occur as part of the food of *S. oramin* and *S. striolata*. The life cycles of the three digenean species, *O. hanumanthai*, *G. papillatus* and *H. sigani* have not yet been elucidated. Since *S. sutor* does not feed selectively on invertebrate prey, infection probably occurs by incidental ingestion of either encysted metacercariae on the plant material or small epiphytic invertebrates which are intermediate hosts. For digenean-dominated communities, (such as in *S. sutor*), the molluscan fauna determines which lifecycles will be possible in the ecosystem (KØIE, 1983, ESCH *et al.*, 1990). Those potential intermediate host species found in the stomach of *S. sutor* could be examined for metacercariae as a first step to elucidating some of the life cycles of the digeneans found as adults in the whitespotted rabbitfish.

The acanthocephalan *Sclerocollum rubrimaris* was described by SCHMIDT & PAPERNA in 1978 from *Siganus rivulatus* and *S. rostratus*. DIAMANT (1989) studied the infection of the species in *S. argenteus*, *S. rivulatus* and *S. luridus*. Although the prevalence of *S. rubrimaris* in *S. sutor* (81.8 %) was higher than in any of the three *Siganus* species investigated by DIAMANT (1989), the mean intensity noted in *S. sutor* was lower (2.72 ± 0.12). DIAMANT (1989) also suggested that the infection route would be by accidental ingestion of the infected intermediate host (mostly crustaceans).

The nematode *Procamallanus elatensis*, previously recorded in *S. luridus* and *S. rivulatus* from the Gulf of Eilat (FUSCO & OVERSTREET, 1979) is also presumably acquired through the ingestion of infective larvae in crustaceans.

All five endoparasites displayed an aggregated distribution in the host population. CROFTON (1971) pointed out that the infection process of parasites tends to lead to an overdispersed distribution, with heavily infected hosts often killed by the parasites. An overdispersed distribution ensures that the infection is kept at a low level with only a few hosts becoming heavily infected. In fact, the parasite species acts as a regulator of the host population, the degree of the regulatory function being related to both host and parasite population densities. The dynamic equilibrium of host and parasite populations is essential to the continuous association between both. DIAMANT (1989) found an overdispersion of *Sclerocollum rubrimaris* in both *Siganus rivulatus* and *S. argenteus* populations and the frequency distribution could be fitted to the negative binomial function. Several other examples of overdispersed trematode distribution patterns have been recorded (CANNON, 1972, WANSTALL *et al.*, 1990).

Although an overdispersed distribution is noted, the negative binomial is not always the right theoretical function to be fitted. HINE & KENNEDY (1974) noticed this for *Pomphorhynchus laevis* in dace (*Leuciscus leuciscus*). In our study, the frequency distribution of the nematode *P. elatensis*, although clumped according to the variance to mean ratio, could not be described by the negative binomial function. The distribution seemed to be bimodal.

Changes in the abundance of parasites with host size is a well known phenomenon. DIAMANT (1989) noted increasing numbers of *Sclerocollum rubrimaris* with total length of *Siganus rivulatus*, but a decreasing trend in *S. argenteus*. He suggested that the acantho-

cephalan infection is associated with feeding on deeper, adjoining algal patches where red sea weeds are abundant. *S. rubrimaris* infection showed a slight, but not significant, negative correlation with the size of *S. sutor*. In a study on the incidence of trematode parasites of long rough dab (= American plaice) (*Hippoglossoides platessoides*) in relation to fish length, SCOTT (1975) pointed out that changes in the fish's diet were the main cause for the observed differences (increasing as well as decreasing numbers of parasites with increasing host size). CANNON (1972) came to the same conclusions for intestinal trematodes of perch (*Perca flavescens*). The observed negative correlations between the intensities of the digeneans *O. hanumanthai* and *H. sigani* and total length of *S. sutor* might be caused by a change in the fish's diet, but a preliminary analysis of the food content of the stomachs did not show remarkable differences between smaller or bigger specimens (pers.obs.). DIAMANT (1989) relates the increasing spring abundance of *S. rubrimaris* with the accelerated feeding rates of *S. rivulatus* and *S. argenteus* during gonadal development and maturation. In our study, all *S. sutor* which were screened for parasites were adult and ready for spawning in January - February (NTIBA & JACCARINI, 1990). Migration movements associated with spawning behaviour and possible temporal changes in feeding habits of the adult fish have not yet been investigated for *S. sutor*, but they may provide valuable information to explain the observed differences in parasite load.

Mass infections of parasites can negatively influence the host condition and growth (ROHDE, 1984). This may provide an alternative explanation for the observed differences in length and weight of lightly and heavily parasitized rabbitfish. The high infections of *S. sutor* with both endo- and ectoparasites (Monogenea, Isopoda, Copepoda) (GEETS, in prep.) and the lack of knowledge on their life cycles and impact on their hosts, make the interpretation and detection of causative agents for this phenomenon impossible at this stage.

Analysis of interspecific relationships between the five endoparasites demonstrated that only the three digenean species significantly occurred together and that their infection intensities were positively correlated. Positive associations were found between a number of intestinal helminths in brown trout (*Salmo trutta*) (THOMAS, 1964). HINE & FRANCIS (1980) studied interspecific associations between three digeneans and two nematodes of New Zealand freshwater eels (*Anguilla dieffenbachii* and *A. australis*) and attributed the positive association between two of the digeneans to their use of the same intermediate host. To explain positive associations, THOMAS (1964) suggested two hypotheses. The association could be of mutual benefit for both parasites, or the observed association could be the result of ecological factors outside the host. HINE & FRANCIS (1980) stated that positive associations are unusual and that they rather result from the distribution of the infectious larval stages of the helminths in relation to feeding habits of the host than from any cooperation between the helminths. The importance of the intermediate host was also emphasized by SOUSA (1994). Helminth parasites which share the same intermediate host will often co-occur in individual vertebrate hosts since they are acquired simultaneously when the final host feeds on this intermediate host.

The correlated response of different parasites to certain heterogenous qualities of the host eg. age, sex, host size, was also suggested to result in positive associations of parasites. For *O. hanumanthai* and *H. sigani* infections in *S. sutor*, this last assumption could be

true. Intensities of infection of both species are negatively correlated with host size. Hence, their apparent interspecific interaction might be a result of independent negative correlation with host size. Since *G. papillatus* infections are independent of host size (within the examined range), the positive association between *O. hanumanthai* or *H. sigani* and *G. papillatus* is not explained by this hypothesis. It is striking, however, that positive associations were only found between the three digenean species and no associations involved the acanthocephalan or the nematode species. A detailed study of *S. sutor*'s feeding habits would probably provide a suitable explanation.

The relationship between interspecific interaction and site selection by parasites has been widely discussed (HOLMES, 1973; 1990b). Assemblages of parasites consist of varying numbers of potentially interacting species (SOUSA, 1994). BUSH & HOLMES (1986) defined a parasite infracommunity as being all parasites species in a single host individual, and the component community (ESCH *et al.*, 1990, SOUSA, 1994) as all parasite species in a population of a certain host species. Parasite infracommunities are classified as interactive or isolationist (HOLMES & PRICE, 1986). Most infracommunities will be situated somewhere in between these two extremes. The parasite infracommunity of *Siganus sutor* tends to be more interactive than isolationist. Characteristics are: high colonization rates, high average densities of parasite infrapopulations and high species diversities (SOUSA, 1994). In an interactive parasite infracommunity, as in *S. sutor*, frequent interspecific interactions amongst the parasites will occur, which will eventually lead to a reduced spatial overlap and a tendency towards site specificity. Site selection is an active and continuing process on the part of the parasite (HOLMES, 1973). The presence of other parasites may modify the microhabitat selected by a particular species. It is a generally accepted rule in ecology that species which coexist in the same habitat, at the same time, will either compete or interact to specialize and hence segregate their niches. HOLMES (1973) hypothesized that interactive segregation, in which the realized niche of a species is reduced by the presence of another species, would gradually be replaced by (genetically based) selective segregation, in which the realized microhabitat does not change in the presence or absence of another species.

When we consider the microhabitat uses of the three digenean parasites found in the intestinal tract of *S. sutor*, more evidence is found for selective than for interactive site segregation. Since no single species infections were recorded in present study, possible shifts in microhabitat use could only be compared in fish with high or low intensities of infection of a certain parasite. *G. papillatus*, in 95 % of the cases found in the last quarter of the intestine (I4), did not change its distribution when it was the only digenean species present (observed in 4 fish). When infections of *G. papillatus* were low and outnumbered by *O. hanumanthai* or by *H. sigani*, no changes in the distribution along the intestine were observed for the last two species, which again is an indication of selective site segregation.

Site segregation along the intestine of fish is well documented (MACKENZIE & GIBSON, 1970, CANNON, 1972, MÖLLER, 1974, HINE, 1980a; 1980b, KENNEDY & MORIARTY, 1987, DIAMANT, 1989, WANSTALL *et al.*, 1990, BUCHMANN, 1991). Our observations on the overall distribution of the five endoparasites of *S. sutor* along the intestinal tract, coincide with

the distributions indicated by DIAMANT & PAPERNA (1986) for the same endoparasites in three other siganid species of the Red Sea.

CROMPTON (1973) stated that the distribution of helminths in the intestine of vertebrates is related to the different conditions in different parts of the tract, to the effect of digestion and to the nature of the diet. Digenean parasites feed mainly on mucosa and epithelial tissue. Therefore, they will be browsing in the intestine in places where the epithelial turnover rate is high (CROMPTON, 1973). The fact that the three digenean parasites in our study were most frequently found in the posterior part of the gut (I3 and I4) could support this hypothesis. HALTON & ARME (1971) pointed out that body surfaces of trematodes are fragile. The intestinal wall of I3 and I4 of *S. sutor* is characterized by dense villi which could act as a protection for the digeneans. When a mixed parasite population is present, the relative size of the parasite bodies is also of importance (CANNON, 1972). Closely related sympatric parasite species (or ecological equivalents) were generally separated by at least a 10 % linear measurement and the smaller species was a more specialized feeder (KEAST, 1968, *vide* CANNON, 1972). *O. hanumanthai* is the smallest of the three digeneans, followed by *G. papillatus* and *H. sigani* is the largest (*pers. obs.*). Both smaller species have a more restricted (specialized?) microhabitat than *H. sigani*. Furthermore, it was noted that the villi in the I3 part were much smaller than in the I4 part. *G. papillatus* (generally found in I4) was immediately noticed when it was present in I3, since its body partly projected into the lumen. *O. hanumanthai* specimens were more frequently found completely enclosed between the small villi of the third part of the intestine.

The microhabitat of the acanthocephalan *Sclerocollum rubrimaris* in *Siganus sutor*, coincides with the distribution reported for the same species in *S. rivulatus* and *S. argenteus*, namely the anterior 5-25 % of the gut (DIAMANT, 1989). Acanthocephalans feed by absorbing nutrient molecules through the trunk. CROMPTON (1973) suggests that the attachment sites of adult acanthocephalans are therefore limited to regions of the intestine which are specialized for the absorption of nutrients.

Nematoda are equipped with an alimentary canal and would thus be more free to roam around the intestine. *Procamallanus elatensis* also seemed to be the least site specific of the five endoparasites of *S. sutor*. Nevertheless, certain sites seem to be preferred by certain nematode species. HINE (1980b) described the distribution of three nematode species in two New Zealand freshwater eels. He noted that *Paraquimperia sp.* and *Spirocamallanus sp.* were mostly found in the anterior or mid intestine, depending on the host species. *Cucullanus sp.* occurred more throughout the intestine. Migrations of this nematode with food was a possible explanation.

SOMMERVILLE (1963, *vide* HOLMES, 1973) stated that "each species of nematode tends to be located about the region of greatest abundance as a normal frequency distribution." This can also be noticed for the distribution of *P. elatensis* in the gut of *S. sutor* (Fig. 3).

The site segregation of the endoparasites of *S. sutor* described in the present study, is probably not the only mechanism of niche restriction involved for the parasites. Since only adult fish of one sampling occasion were investigated, temporal segregation for instance could not be studied. Infection with different parasites at different times of the year was demonstrated in previous studies to be a potential mechanism to avoid competition. Parasites may also utilise different age classes of the host, which is a special kind of tem-

poral niche segregation, or may show a reproductive segregation in time. Furthermore, spatial segregation, as described here within the intestine of a host, is not the only aspect of differential use of 'space'. Geographical segregation (not discussed here) is an other mechanism to avoid niche overlap.

Deeper understanding of the observed infection patterns of *Siganus sutor* endoparasites will have to await studies on the ecology of the fish and elucidation of the life cycles of its parasites.

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