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The metazoan ecto- and endoparasites of the rabbitfish, *Siganus sutor* (Cuvier & Valenciennes, 1835) of the Kenyan coast. I.

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Summary

In a survey of the metazoan ecto- and endoparasites of *Siganus sutor* (Cuvier & Valenciennes, 1835), a commercially important herbivorous fish from the Kenyan coast, sixteen species of parasites are found. The gill parasites include Monogenea (*Tetrancistrum sigani* Goto & Kikuchi, 1917; *Microcotyle mouwoi* Ishii & Sawada, 1938; *Pseudohaliotrema* sp. 1 and sp. 2, and an unidentified Microcotylidae species); Copepoda (*Caligus* sp. and *Hatschekia* sp.); and Isopoda (one Gnathiidae species). The intestinal parasites found are Digenea (*Opisthogonoporoides* cf. *hanumanthai* Madhavi, 1972; *Gyliauchen papillatus* Goto & Matsudaira, 1918; *Hexangium sigani* Goto & Ozaki, 1929; and three other unidentified digeneans); Acanthocephala (*Sclerocollum rubrimaris* Schmidt & Paperna, 1978); and Nematoda (*Procamallanus sigani* Yamaguti, 1935). The species listed are first records for the Kenyan coast.

Infection prevalence, mean intensity and site specificity are determined for the different parasite species. The parasites have an aggregated frequency distribution in the host population: some individuals of the siganid population are more heavily infected than expected in a random distribution, while others are very little or not at all infected.

Key words: ecology, ectoparasites, endoparasites, marine, *Siganus*

Résumé

On a découvert seize espèces de parasites lors d'une étude des métazoaires ecto- et endoparasites de *Siganus sutor* (Cuvier & Valenciennes, 1985), un poisson herbivore commercialement important de la côte kéyane. Les parasites des branchies comprennent des Monogeneae (*Tetrancistrum sigani* Goto & Kikuchi, 1917; *Microcotyle mouwoi* Ishii & Sawada, 1938; *Pseudohaliotrema* sp.1 & sp.2, et une espèce non identifiée de Microcotylideae); des Copépodes (*Caligus* sp. et *Hatschekia* sp.) et un Icopode (une espèce de Gnathiideae). Les parasites intestinaux trouvés appartenaient aux Digeneae (*Opisthogonoporoides* cf. *hanumanthai* Madhavi, 1972; *Gyliauchen papillatus* Goto & Matsudaira, 1918; *Hexangium sigani* Goto & Ozaki, 1929; et trois autres Digenaeae non identifiés); aux Acanthocephaleae (*Sclerocollum rubrimaris* Schmidt & Paperna, 1978), et aux Nématodes (*Procamallanus sigani* Yamaguti 1935). Ces espèces sont rapportées pour la première fois sur la côte kényane. Le degré, l'intensité

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moyenne et le site spécifique des infestations sont déterminées pour chaque espèce de parasite. Les parasites présentent une distribution de fréquence en agrégats dans la population-hôte; certains individus de la population des siganidés sont plus infestés qu'une distribution au hasard le laisserait prévoir, alors que d'autres ne le sont pas ou seulement très peu.

Introduction

It has often been indicated that parasites play an important role in the ecology of coastal and marine ecosystems as well as in mariculture. Apparently the origin of most diseases in mariculture is likely to be the wild-caught fingerlings or juvenile fish. Parasite species found to cause no or limited pathological damage in wild fish may, under conditions of mariculture, become pathogenic (Diamant & Paperna, 1986; Paperna, Diamant & Overstreet, 1984). Research dealing with parasitic infections of economically important marine fish species is therefore receiving increasing interest. However, very little is known about the parasitic fauna of marine fishes of the Eastern African coast in comparison with the information available for Northern Hemisphere species. For the Kenyan coast only four Monogenea of marine fish have been described so far (Paperna, 1972; Olliver & Paperna, 1984). Other records for the region are for Digenea: fifteen species for Mozambique (Reimer, 1981, 1983; Paruchin, 1983), eleven species for the Seychelles (Toman, 1977, 1989), and four species for Madagascar (Razarihelisoa, 1960).

An initial survey of ecto- and endoparasites of fishes from the Kenyan coast was conducted in 1991–92. *Siganus sutor* (Cuvier & Valenciennes, 1835) (rabbit-fish) was chosen as host species for this study both because it is a commercially important food fish for local consumption and because of the interest in siganids as possible species for extensive mariculture. Although considerable progress in rearing siganids has been achieved, mariculture still depends on wild-caught juvenile fishes or fish fry (Lam, 1974; Okoth, 1992).

Siagnids contribute 50% of the total catches of the artisanal fisheries, with *Siganus sutor* being the most common species (Ntiba, 1986). The existing literature on the specific parasites of rabbitfish consists mainly of taxonomic and descriptive accounts of various helminths (Yamaguti, 1935, 1958, 1963; Young, 1967; Paperna, 1972; Velasquez, 1975; Toman, 1977, 1989; Schmidt & Paperna, 1978). For siganids of the Kenyan coast, only one monogenean has so far been described (Paperna, 1972). The relevance of siganid parasites as potential pathogens for mariculture has been studied for *Siganus* spp. of the Red Sea (Paperna *et al.*, 1984; Diamant & Paperna, 1986). These studies indicate that the most important disease encountered in mariculture of siganids and causing mortalities of fishes is due to infestation of gills by Monogenea.

A preliminary study of the gill and intestinal parasites of *Siganus sutor* was conducted on fish from one of the local fish markets which included only adult fishes (22 fishes, mean total length=24·5 cm) (Geets & Martens, 1992). The study reported in the present paper was more elaborate and gives data on the metazoan parasites of siganids from fresh fish of all sizes caught from the Nyali beach area (North of Mombasa, Kenya). Infection prevalence, mean intensity and site specificity are discussed for the different parasite species. Taxonomic description of the parasites found and their geographical distribution will be published in the next paper (Martens & Moens, in prep.).

Material and methods

Fish were sampled with fish traps and seine nets from the lagoon at the Nyali beach area in April and May, 1993. The gills and intestinal tract were examined from 34 fishes with total length ranging from 7 to 21 cm (mean total length = 15·5 cm).

For taxonomic study, the parasites were collected from fresh fish. Monogeneans and digeneans were fixed in FAA for whole mounts, in Steve and Bouin solution for light microscopy sections; nematodes were fixed in Berland's GAA/formalin solution, cleared in lactophenol or glycerol; acanthocephalans were rinsed with tapwater to make them extrude their proboscis, fixed in 4% formalin and cleared in glycerol or lactophenol; and crustaceans were fixed in 4% formalin. The numbers of the parasites and their distribution in the host were separately recorded as follows: for the gill parasites on left and right gill numbers 1 to 5, and for the gastrointestinal parasites in stomach and intestine part 1 (including pyloric caeca) to 4.

Statistical analyses of the data were performed using SPSS/PC Statistical Package.

Results

Species diversity

Representatives of the different parasite groups found in *Siganus sutor* are given in Table 1. Sixteen species of parasites were found: eight species occurred on the gills, and eight species in the gastrointestinal tract. Taxonomic descriptions of the parasites and their geographical distributions will be published in the next paper (Martens & Moens, in prep.).

Prevalence and intensity of infection

Prevalence and mean intensity of infection are given in Table 2. As identification of the monogeneans (*Tetrancistrum sigani* Goto & Kikuchi, 1917; *Pseudohaliotrema* spp. and *Microcotyle mouwoi* (Ishii & Sawada, 1938), on formolized gills was excluded due to their small size and contraction, they were counted as one group. The unidentified monogenean, Microcotylidae sp., is larger and readily distinguished from the other monogenean species. Chalimus larvae of *Caligus* sp. were found in only one fish on the outer surface of the operculum and the scales around it, but these data were not taken into account for the statistical analyses.

Prevalence of infection (% fishes infected with a particular parasite species) for the gill parasites ranged from 11·8% for Microcotylidae sp. to 100% for the other monogeneans. For the intestinal parasites the prevalence ranged from 11·8% for Digenea type 3 to 88·2% for *Gyliauchen papillatus* (Goto & Matsudaira, 1918).

The mean intensity of infection (mean number of a particular parasite species per infected host) was lowest for *Sclerocollum rubrimaris* (Schmidt & Paperna, 1978) (2·3) and highest for the grouped monogeneans (62·0). Regression analyses between parasite numbers and fish length (Fig. 1) indicate a positive correlation for the gill parasites as well as for the gastrointestinal parasites.

Table 1. Gill and intestinal parasites found in *Siganus sutor* from Nyali beach area (North of Mombasa, Kenya)

On the gills	
Monogenea:	
Dactylogyridae:	*Tetrancistrum sigani* Goto & Kikuchi, 1917
	Pseudohaliotrema sps 1 and 2
Microcotylidae:	*Microcotyle mouwoi* Ishii & Sawada, 1938
	Microcotylidae sp.
Copepoda:	*Caligus* sp.
	Hatschekia sp.
Isopoda:	Gnathiidae sp. (praniza larvae)
In the intestine	
Digenea:	
Allocreadiidae:	*Opisthogonoporoides* cf. *hanumanthai* Madhavi, 1972
Gyliauchenidae:	*Gyliauchen papillatus* Goto & Matsudaira, 1918
Microschaphidiidae:	*Hexangium sigani* Goto & Ozaki, 1929
Digenea sps 1, 2 and 3	
Acanthocephala:	
Rhadinorhynchidae:	*Sclerocollum rubrimaris* Schmidt & Paperna, 1978
Nematoda:	
Camallanidae:	Yamaguti, 1935

Distribution and site preference

Distribution of the parasites on the gills and in the intestinal tract are given in Tables 3 and 4, respectively.

Two-sample analysis of variance indicates that there was no difference in infection intensity between the left and right gills ($P \leqslant 0{\cdot}01$). Therefore, the data for left and right gills were pooled for further analyses.

On gill no. 1 no parasites were found. The monogenean group showed a significantly high preference for gill no 3 and a lower one for gill no 2. They were found mainly on the distal half of the filaments. The Microcotylidae sp. showed a preference for gill no. 4, in the middle part of the gill and mainly near the tips of the filaments. *Hatschekia* sp. had a distinct preference for gill nos 2 and 3. *Caligus* sp. and the Gnathiidae praniza larvae were not found on gill no. 5, but showed no significant preference for any of the other gills. *Hatschekia* sp. and the praniza larvae were mainly found on the basal zone of the gill filaments, their head near the base and their body pointing upwards, while *Caligus* sp. did not show a preference for a specific gill area.

The stomach contained only a few Digenea sp. 1, *Sclerocollum rubrimaris* (Schmidt & Paperna, 1978) and *Procamallanus sigani* (Yamaguti, 1935). *Opisthogonoporoides* cf. *hanumanthai* (Madhavi, 1972) showed a significant preference for intestine part 3, while there was no significant difference between their

Table 2. Prevalence % fishes infected with a particular parasite species and mean intensity of infection (mean number of parasites per infected fish) in *Siganus sutor* ($N=34$, mean total length = 15·5 cm)

Parasite	Prevalence (%)	Mean intensity
Tetrancistrum sigani *Pseudohaliotrema* spp. *Microcotyle mouwoi*	100	62·0
Microcotylidae sp.	11·8	4·3
Caligus sp.	14·7	5·6
Hatschekia sp.	32·4	6·4
Gnathiidae sp.	29·4	3·8
Opisthogonoporoides cf. *hanumanthai*	73·5	51·0
Gyliauchen papillatus	88·2	66·2
Hexangium sigani	50·0	9·8
Digenea		
sp. 1	70·6	7·3
sp. 2	44·1	3·3
sp. 3	11·8	3·2
Sclerocollum rubrimaris	32·4	2·3
Procamallanus sigani	55·9	5·7

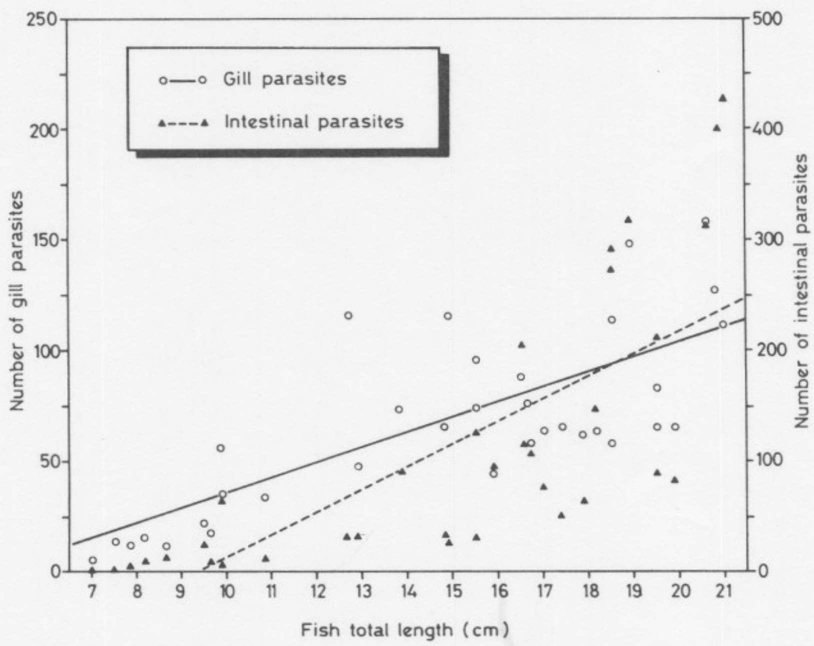

Fig. 1. Infection intensity in relation to host size. Regression analyses between parasite infection intensity (P) and fish total length (L), and results of analyses of variance. For gill parasites the regression equation is $P = -35{\cdot}098 + 6{\cdot}879L$ ($r=0{\cdot}76$, $P<0{\cdot}001$), for intestinal parasites $P = -191{\cdot}007 + 20{\cdot}504L$ ($r=0{\cdot}74$, $P<0{\cdot}001$).

infection levels in the other parts of the intestine. A similar distribution was found for Digenea sp. 1. *Gyliauchen papillatus* (Goto & Matsudaira, 1918) and Digenea sp. 3 showed a distinct preference for intestine part 4, while *Hexangium sigani* (Goto & Ozaki, 1929) and Digenea sp. 2 were almost equally distributed in intestine parts 3 and 4. *Sclerocollum rubrimaris* was principally found in intestine part 1, while their infection levels in stomach, and intestine parts 2 and 3 were not significantly different. The *P. sigani* infection intensities in intestine parts 1, 2 and 3 were almost equal and significantly different from the intensities in the stomach.

Frequency distribution

Frequency histograms (Figs 2 and 3) indicate an aggregated distribution in the fish population for the Monogenea, *Opisthogonoporoides* cf. *hanumanthai*, *G. papillatus*, *H. sigani*, *P. sigani* and Digenea spp. 1 and 2. For the other parasite species samples were too small to show a specific distribution pattern.

Discussion

Species diversity

Comparison of the parasites found in *S. sutor* from the Kenyan coast with reports on *Siganus* species from other regions such as the Red Sea (Diamant & Paperna, 1986), Australia (Beumer *et al.*, 1982), Pacific (Velasquez, 1975; Yamaguti, 1935, 1958, 1963) shows that the parasite faunas are nearly identical in the genera present. Even according to the species identified so far some of the parasite species found are identical (such as *T. sigani*, *H. sigani*, *G. papillatus* and *P. sigani*) and can apparently be seen as typical siganid parasites.

The ecto- and endoparasites found in the young siganids are the same species as the ones encountered in the adult fishes. When the parasite species in young hosts are different from the species in the adults, the apparent reasons are migration of the fish with corresponding change of diet. Having the same parasites indicates that young siganids have similar herbivore food habits as the adult stages, and occupy similar habitats in the inshore waters. These findings support the observations on feeding habits of other siganid species (Lam, 1974; Von Westernhagen, 1973, 1974; Woodland, 1983). Siganid larvae are pelagic and planktivorous, while both juveniles and adults are mainly restricted to the shallow littoral and sublittoral zone and are herbivores, feeding principally on seaweeds (Woodland, 1983). This is also reflected in the morphology of the intestinal tract of the fishes: stomach thick-walled, intestine broad, extremely long and coiled (3 to 4 times total fish length). Although herbivorous fish may be quite selective about which algae species they eat, their diets depend largely on the relative abundance of the algae species (Von Westernhagen, 1974), which will be the same for juveniles and adults occurring in the Nyali beach lagoon. During feeding on benthic algae they ingest accidentally the infective stages of parasites together with the plant material. Residuals of invertebrates (amphipods, copepods, fish and crustacean larvae) which may be intermediate parasite hosts, have been found repeatedly in stomach and gut contents of the fish.

Prevalence and intensity of infection

The prevalence and infection intensity was much lower in this study than that for the sample of adult fishes in the preliminary study. In the preliminary study the

Table 3. Distribution of parasites on the gills. Data listed are: for each site the numbers, percentages, mean intensity ± SD; results of analyses of variance. Bold values indicate significant preferences at 5% level (Tukey Multiple Range Test)

Parasite species	Total number	Gill 1	Gill 2	Gill 3	Gill 4	Gill 5	*F*-ratio	Significance
Monogenea spp.	2108	0	**565**	**1263**	212	68		
			22·0%	68·6%	7·3%	2·2%	43·95	*P*<0·001
			16·61 ± 11·80	37·15 ± 24·03	6·24 ± 6·29	2·00 ± 2·15		
Microcotylidae sp.	17	0	0	1	**12**	4		
				5·9%	70·6%	23·4%	8·31	*P*<0·005
				0·25 ± 0·50	3·00 ± 1·41	1·00 ± 0·82		
Caligus sp.	28	0	9	12	7	0		
			32·1%	42·9%	25·0%		0·60	*P*<0·1
			1·80 ± 1·09	2·40 ± 1·82	1·40 ± 1·34			
Hatschekia sp.	70	0	**31**	22	14	3		
			44·3%	31·4%	20·0%	4·3%	13·57	*P*<0·001
			2·82 ± 1·47	2·00 ± 0·78	1·27 ± 1·08	0·27 ± 0·46		
Gnathiidae sp.	38	0	9	11	18	0		
			23·7%	28·9%	47·4%		2·20	*P*<0·1
			0·90 ± 0·87	1·10 ± 0·99	1·80 ± 1·13			

prevalence ranged between 43·7% and 100% for gill parasites, and between 68·2% and 100% for intestinal parasites; the mean intensities were 5·3 to 97·4 and 2·7 to 201·6, respectively (Geets & Martens, 1992).

The positive correlation between the fish length and the degree of parasitic infestation suggests that higher infection may simply be due to a chance accumulation of parasites over time. Parasite infections change with age (fish length) and an increase of infection is more common than a decrease (Rohde, 1984). Larger siganids have lower assimilation rates and compensate by having high ingestion rates (Bryan, 1975). This increased feeding activity may result in increased ingestion of infective stages and build up of parasite numbers. Adult fish also have larger available microhabitats for parasites (Rhode, 1984).

The data, as well as the regression curve of the numbers of monogenean gill parasites as a function of fish length, show that all the juvenile fishes were also infected. Most monogeneans have a direct life cycle and infection may be by contact transfer of free larvae or juveniles. By living in large schools the fish allow monogenean larvae to have readily accessible hosts, which may promote infection dispersion. The regression curve of the numbers of intestinal parasites as a function of fish length indicates that the smallest fish have zero to only a few parasites. This may suggest that the juveniles of *S. sutor* start feeding on benthic algae and begin accidentally accumulating infective stages when they reach about 7–8 cm total length. This behaviour would be in accordance with that of juveniles of *S. vermiculatus* (Cuvier & Valenciennes) and *S. rivulatus* (Forskal) which, after migrating to shallow coastal waters, first start feeding on epiphytic algae before moving to deeper lagoon areas to graze on benthic algae (Gunderman, Popper & Lichatowich, 1983; Popper & Gunderman, 1975).

Table 4. Distribution of parasites in the intestinal tract. Data listed are: for each site the numbers, percentages, mean intensity ± SD; results of analyses of variance. Bold values indicate significant preferences at 5% level (Tukey Multiple Range Test)

Parasite species	Total number	Stomach	I1	I2	I3	I4	*F*-ratio	Significance
Opisthogonoporoides cf. *hanumanthai*	1275	0	11 0·9% 0·44 ± 0·96	247 19·4% 9·88 ± 14·92	954 74·8% 38·16 ± 57·89	63 4·9% 2·52 ± 3·02	8·45	*P*<0·001
Gyliauchen papillatus	1985	0	0	6 0·3% 0·20 ± 0·66	133 6·7% 4·43 ± 4·39	**1846** 93·0% 61·53 ± 50·89	15·70	*P*<0·001
Hexangium sigani	167	0	0	4 2·4% 0·24 ± 0·52	**80** 47·9% 4·71 ± 3·06	83 49·7% 4·89 ± 3·14	29·28	*P*<0·001
Digenea sp. 1	176	5 2·8% 0·21 ± 0·10	9 5·1% 0·38 ± 0·32	38 21·6% 1·58 ± 1·07	**124** 70·5% 5·17 ± 4·51	0	22·44	*P*<0·001
Digenea sp. 2	50	0	0	7 14·0% 0·47 ± 0·63	**21** 42·0% 1·40 ± 0·82	22 44·0% 1·47 ± 1·12	5·32	*P*<0·005
Digenea sp. 3	13	0	0	1 7·7% 0·25 ± 0·50	2 15·4% 0·50 ± 0·47	**10** 76·9% 2·50 ± 0·57	19·91	*P*<0·001
Sclerocollum rubrimaris	25	3 12·0% 0·27 ± 0·41	**19** 76·0% 1·73 ± 1·00	2 8·0% 0·18 ± 0·40	1 4·0· 0·09 ± 0·13	0	17·78	*P*<0·001
Procamallanus sigani	109	4 3·6% 0·21 ± 0·35	**27** 24·8% 1·42 ± 1·01	40 36·7% 2·10 ± 1·16	38 34·9% 2·00 ± 1·05	0	14·33	*P*<0·001

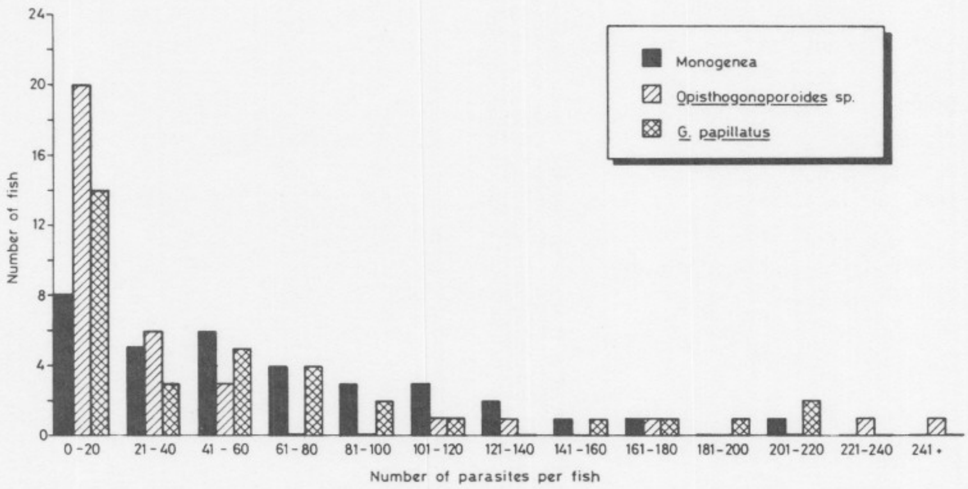

Fig. 2. Frequency histograms for Monogenea, *Opisthogonoporoides* cf. *hanumanthai*, and *Gyliauchen papillatus*.

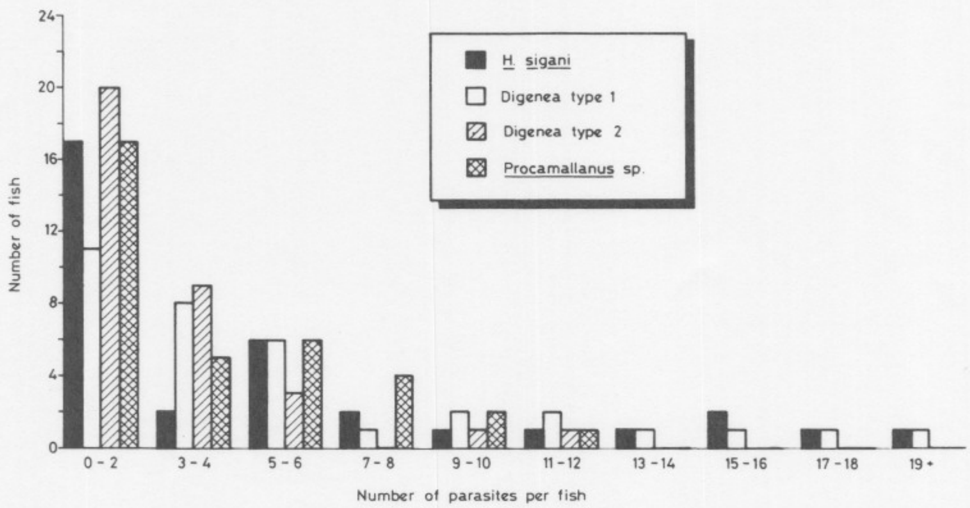

Fig. 3. Frequency histograms for *Hexangium sigani*, *Procamallanus sigani* and *Digenea* spp. 1 and 2.

Distribution and site preference

The data on distribution of the parasites on the different gills and the resultant statistical analyses indicate that most parasite species show distinct site preferences for certain gills. Only *Caligus* sp. and the Gnathiidae larvae showed no clear preference between gill nos 2, 3 and 4. Gill no. 1 on which no parasites were found, is a pseudobranch, much smaller than the other four gills and might not be so accessible for parasites.

The nature of the attachment organs determines the ability of the ectoparasites to move on the gills and thus influences their site restrictions. The monogenean parasites are found mostly in the middle part of the gills and/or distal half of the gill filaments. As each gill has thinner and shorter filaments at the anterior and posterior ends, these filaments obviously have less chance to become infected than the filaments of the middle part. Firmly attached to the gill filaments by their opisthaptor clamps, the monogeneans clearly show how restricted their microhabitats are. The copepod *Caligus* sp. has the best locomotory ability (it was often seen moving along the gill filaments in fresh fish) and an associated larger microhabitat due to the versatility of its attachment apparatus. The fact that chalimus larvae were found on the outer surface of the operculum may indicate that the microhabitat of *Caligus* sp. even extends beyond the gills. Although always firmly attached, the praniza larvae show only a preference for the gill base while *Hatschekia* sp., of which only females were found, has a more restricted microhabitat. Similar site preferences were found for *H. pagrosomi* (Yamaguti, 1939) and Gnathiidae larvae of *Chrysophrys auratus* (Block & Schneider) (Roubal, Armitage & Rohde, 1983); and for Copepoda of *Acanthopagrus australis* (Gunther) (Roubal, 1981). The site restrictions of the parasites on the gills support the hypothesis described by Rhode (1980, 1989), that all parasites have restricted microhabitats; but species with good locomotory ability or large populations and asexual stages have larger microhabitats than sessile or low population species with sexual stages. In most cases, however, there is at least some overlap with other species. Overlap of related species is usually less than that between unrelated species (Rhode, 1989), as seen here for *Microcotyle mouwoi* and the other Microcotylidae species. This could be explained by the supposedly more intense competition between closely related species. However, all gill parasites use the same food resources (blood and/or mucus) and space for attachment on the gills. It seems, therefore, that reinforcement of reproductive barriers, and not interspecific competition, has led to spacial segregation (Rhode, 1984, 1989). Habitat restriction leads to a significant increase in intraspecific contact in order to facilitate cross-fertilization. A further study will be carried out to check the degree of spatial segregation between the two *Pseudohaliotrema* species.

The distribution of the endoparasites also indicates preferences for particular sites in the gastrointestinal tract. *Opisthogonoporoides* cf. *hanumanthai* displayed a clear preference for the third quarter of the intestine (I3), together with Digenea sp. 1. *Gyliauchen papillatus* and Digenea sp. 3 were mainly found in the last quarter of the intestine I4, while *Hexangium sigani* and Digenea sp. 2 were mainly spread over intestinal parts 3 and 4. As far as the taxonomic study of the parasite species has been performed, it appears that the unidentified Digenea species are juvenile stages or allometric forms of the other species present. Their respective distribution may support this suggestion, but further microscopic studies have to be completed before anything conclusive can be said. The acanthocephalan showed a distinct preference for the first intestine quarter. The same site preference for *S. rubrimaris* was also observed in a siganid species of the Red Sea (Diamant, 1989). The nematodes were distributed over the first three quarters of the intestine.

A similar distribution pattern was found for the intestinal parasites in the adult siganids used for the preliminary study.

Frequency distribution

Aggregated or overdispersed distributions are considered as an inherent characteristic of parasite populations: some individuals of a host population are more heavily infected than expected in a random distribution while others are very lightly infected or not at all infected (Crofton, 1971; Rohde, 1984). The most commonly used description for aggregation in parasites is the negative binomial distribution as described by Crofton (1971). The frequency histograms follow such a distribution pattern, similar also to what had been reported for other helminth infections of fishes (Rohde, 1984, 1988). Factors which may contribute to aggregation in parasite distribution are: (i) heterogeneity in the exposure of fish to infection, generated by non-random distribution of infective stages in the habitat; (ii) the fish are exposed to a series of infections during their life time, each exposure having a different chance of infections; (iii) a single parasite may multiply on or in the host; (iv) an infection may enhance the probability of further infections. However, to indicate the relative importance of the different factors the biology of the parasite species needs to be more fully studied.

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References

BEUMER, J.P., ASHBURNER, L.D., BURBURY, M. E., JETTE, E. & LATHAM, D.J. (1982) A checklist of the parasites of the fishes from Australia and its adjacent Antarctic Territories. *Commonw. Agric. Bur. Techn. Comm.* **48,** 1–99.

BRYAN, P.G. (1975) Food habits, functional digestive morphology, and assimilation efficiency of the rabbitfish *Siganus spinus* (Pisces, Siganidae) on Guam. *Pacif. Sci.* **29,** 269–277.

CROFTON, H.D. (1971) A quantitative approach to parasitism. *Parasitology* **62,** 179–193.

DIAMANT, A. (1989) Ecology of the acanthocephalian *Sclerollum rubrimaris* Schmidt and Paperna, 1978 (Rhadinorhynchidae: Gorgorhynchinae) from wild populations of rabbitfish (genus *Siganus*) in the northern Red Sea. *J. Fish. Biol.* **34,** 387–397.

DIAMANT, A. & PAPERNA, I. (1986) The parasites of wild Red Sea rabbitfish (*Siganus* spp.) (Teleostei: Perciformes) as potential pathogens in mariculture. In: *Pathology in Marine Aquaculture* (Eds C.P. Vivares *et al.*). *Spec. Publ. Eur. Aquacult. Soc.* **9,** 71–83.

GEETS, G. & MARTENS, E. (1992) Parasitological study of *Siganus sutor*, a commercially important fish species of the Kenyan coast. Paper presented at *IZWO Workshop on Marine Research in Kenya, Ostend, Belgium.*

GUNDERMAN, N., POPPER, D.M. & LICHATOWICK, T. (1983) Biology and life cycle of *Siganus vermiculatus* (Siganidae, Pisces). *Pacif. Sci.* **37,** 165–180.

LAM, T.J. (1974) Siganids: their biology and mariculture potential. *Aquaculture* **3,** 325–354.

NTIBA, M. (1986) *The Biology of the Kenya Reef Fish of the genus* Siganus. MSc thesis, University of Nairobi, Kenya.

OKOTH, B. (1992) Research on *Siganus sutor* for the use in mariculture. EC project *Dynamics of Mangrove Ecosystems*. Final Report, KMFRI Mombasa, Kenya.

OLIVER, G. & PAPERNA, I. (1984) Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea), parasites de Perciformes de Mediterranee orientale, de la mer Rouge et de l'ocean Indien. *Bull. Mus. natn. Hist. nat., Paris* **6,** 49–65.

PAPERNA, I. (1972) Monogenea from Red Sea fishes. I. Monogenea of fish of the genus *Siganus. Proc. Helmin. Soc. Wash.* **39,** 33–39.

PAPERNA, I., DIAMANT, A. & OVERSTREET, R.M. (1984) Monogenean infestations and mortality in wild and cultured Red Sea fishes. *Helgolander Meeresunters* **37,** 445–462.

PARUCHIN (1983) New trematode species from the commercial Indian Ocean fishes. *Zool. Zh. (USSR)* **62,** 1106–1110.

POPPER, D. & GUNDERMAN, N. (1975) Some ecological and behavioural aspects of siganid populations in the Red Sea and Mediterranean coast of Israel in relation to their suitability for aquaculture. *Aquaculture* **6,** 127–141.

RAZARIHELISOA, M. (1960) Sur quelques Trematodes digenes de Poissons de Nossibe (Madagascar). *Bull. Soc. Zool. Fr.* **84,** 421–434.

REIMER, L.W. (1981) Lepocradidae (Digenea) aus Fishen der Kuste von Mocambique. *Angew. Parasitol.* **22,** 204–212.

REIMERE, L.W. (1983) Acanthocolpidae (Digenea) aus Fishen der Kuste von Mocambique. *Angew. Parasitol.* **24,** 134–146.

ROHDE, K. (1980) Comparative studies on microhabitat utilization by ectoparasites of some marine fishes from the North Sea and Papua New Guinea. *Zool. Anz., Jena* **204,** 27–63.

ROHDE, K. (1984) Ecology of marine parasites. *Helgolander Meeresunters* **37,** 5–33.

ROHDE, K. (1988) Rarity in marine Monogenea. Does an Allee-effect or parasite-inducted mortality explain truncated frequency distributions? *Biol. Zent. bl.* **107,** 327–338.

ROHDE, K. (1989) Simple ecological systems, simple solutions to complex problems. *Evol. Theory* **8,** 305–350.

ROUBAL, F.R. (1981) The taxonomy and site specificity of the metazoan ectoparasites on the black bream, *Acanthopagrus australis* (Gunther), in northern New South Wales. *Aust. J. Zool., Suppl. Ser.* **84,** 1–100.

ROUBAL, F.R., ARMITAGE, J. & ROHDE, K. (1983) Taxonomy of metazoan ectoparasites of snapper, *Chrysophrys auratus* (Family Sparidae), from southern Australia, eastern Australia and New Zealand. *Aust. J. Zool., Suppl. Ser.* **94,** 1–68.

SCHMIDT, G.D. & PAPERNA, I. (1978) *Sclerocollum rubrimaris* gen. et sp. n. (Rhadinorhynchidae: Gorgorhynchinae), and other Acanthocephala of marine fishes from Israel. *J. Parasit.* **64,** 846–850.

TOMAN, G. (1977) Digenetic trematodes of marine teleost fishes from the Seychelles, Indian Ocean. I. Family Angiodictyidae. *Inst. Biol. Public. Espec.* **4,** 335–341.

TOMAN, G. (1989) Digenetic trematodes of marine teleost fishes from the Seychelles, Indian Ocean. *Acta Parasit. Polonica* **34,** 235–246.

VELASQUEZ, C.C. (1975) *Digenetic Trematodes of Philippine Fishes*. University of Philippines Press, Quezon City.

VON WESTERNHAGEN, H. (1973) The natural food of rabbitfish *Siganus oramin* and *S. striolatus. Mar. Biol.* **22,** 367–370.

VON WESTERNHAGEN, H. (1974) Food preferences in cultured rabbitfishes (Siganidae). *Aquaculture* **3,** 109–117.

WOODLAND, D.J. (1983) Zoogeography of the Siganidae (Pisces): an interpretation of distribution and richness patterns. *Bull. Mar. Sci.* **33,** 713–717.

YAMAGUTI, S. (1935) Studies on the helminth fauna of Japan. Part 9. Nematodes of fishes. *Jap. J. Zool.* **6,** 337–386.

YAMAGUTI, S. (1958) *Systema Helminthum. Vol. 1: Digenetic trematodes of Vertebrates.* Interscience Press, New York.

YAMAGUTI, S. (1963) *Systema Helminthum. Vol. 4: Monogenea and Aspidocotylea.* John Wiley, New York.

YOUNG, P.C. (1967) Some species of the genus *Tetrancistrum* Goto and Kikuchi, 1917 (Monogenoidea: Dactylogyridae). *J. Parasit.* **53,** 1016–1022.

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