The diet, food selectivity and niche of *Rhabdosargus sarba* (Teleostei: Sparidae) in Natal estuaries

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The juveniles and subadults of *Rhabdosargus sarba* are one of the most common components of the benthic fish community of Natal estuaries. The diet consists mainly of aquatic macrophytes and filamentous algae although a significant proportion is made up of bivalves and the amphipod *Grandidierella lignorum*. The last two taxa are positively selected when little plant material is consumed. *R. sarba* feeds during daylight with a peak in the early afternoon. The relationship between *R. sarba* and the very similar sympatric *R. holubi* and *R. auriventris* are discussed in relation to their diet, divergence and distribution. Resource partitioning in Natal estuaries between *R. sarba*, the Gerreidae and *Pomadasys commersonii* is also discussed.

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Vingerlinge en onvolwasse *Rhabdosargus sarba* is een van die algemeenste komponente van die bentiese visgemeenskap in Natalse getyriviere. Die visse se dieet bestaan hoofsaaklik uit waterlewende makrofiete en veselagtige alge. Tweekleppiges en *Grandidierella lignorum* (Amfipoda), word ook in groot hoeveelhede ingeneem. Laasgenoemde diergroepe word positief geselekteer wanneer min plantmateriaal ingeneem word. *R. sarba* vreet gedurende dagligure met 'n hoogtepunt in die vroeë middag. Die verwantskap tussen *R. sarba* en die soortgelyke simpatriese *R. holubi* en *R. auriventris*, word bespreek wat betref dieet, divergensie en verspreiding. Hulpbronverdeling in Natalse getyriviere tussen *R. sarba*, die Gerreidae en *Pomadasys commersonii*, word ook bespreek.

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Rhabdosargus sarba is a sparid bream which is common in subtropical and tropical inshore waters and estuaries throughout the Indo-Pacific (Smith 1965). It is abundant in Natal waters where juveniles and subadults are conspicuous members of the estuarine fish fauna.

A study of the feeding ecology of *R. sarba* formed part of an overall investigation into the community structure and functioning of the fish component of Natal estuaries. Iliophagous, planktivorous and piscivorous species have been studied (Blaber 1976; 1979; Whitfield & Blaber 1978; Blaber & Cyrus 1983) but with the exception of the Gerreidae (Cyrus & Blaber 1983) and *Pomadasys commersonii* (Hay & Blaber, in press) few details are available on the common benthic feeding species. This major group, of which *R. sarba* is one, is the last component of the fish community to receive attention.

In order to assess the importance of the availability of various benthic foods it was necessary to conduct a benthic invertebrate sampling programme concurrently with the present study. The results of the invertebrate study have been published separately (Blaber, Kure, Jackson & Cyrus 1983) and have allowed the selectivity of *R. sarba* for various foods to be estimated. Particular attention has also been paid to resource partitioning, both between *R. sarba* and two other *Rhabdosargus* species with which it is sympatric, the Gerreidae and *Pomadasys commersonii*. No data were available on the feeding of *R. auriventris* (syn. *thorpei*) and hence its diet was also analysed in this study to allow comparison with *R. sarba*.

Materials and Methods

Field

Fish were collected from the Kosi system (26°50′S/32°38′E), South Lake, St Lucia (28°00′S/32°25′E), Mlalazi estuary (28°57′S/31°48′E) and Durban Bay (29°54′S/31°01′E) at approximately three-monthly intervals from October 1981 to December 1982 using seine and gill-nets. Stomachs of all fish were removed and preserved in 10% formalin.

Laboratory

Stomach contents were analysed by three methods: (a) the percentage frequency of occurrence of each taxon; (b) the percentage 'points' method of Ricker (1968) (volumetric) and (c) percentage dry weight. Plant material was excluded from the gravimetric analyses. Molluscs were weighed shell-free after decalcification with dilute nitric acid. The use of dry weight for animal material allowed direct comparison with benthic survey data from St Lucia (Blaber *et al.* 1983) and hence facilitated prey selectivity analyses using the Electivity Index

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of Ivlev (1961). Selectivity for plant material could not be calculated as its abundance in the environment was not quantified. Feeding periodicity was calculated using volumetric data from 'points' analyses.

Results

The diet in four estuarine systems

Juvenile *Rhabdosargus sarba* (30 – 265 mm S.L.) feed on plant material and a wide selection of invertebrate benthos. No differences in feeding preferences with increase in size were noted. The proportion of plant material consumed by volume at each sampling site, together with the predominant animal prey are shown in Table 1. All the plant material consumed appeared broken up and well digested in the rectum. There is considerable variation in diet according to locality and brief descriptions of the food in each estuary follow.

Durban Bay

The chief prey were littorinid gastropods followed by filamentous algae (*Chaetomorpha* sp.) and the amphipod *Grandidierella lignorum* (Table 2). The littorinids are probably taken from the harbour walls and pilings where they are abundant. These artificial structures provide the only hard substrata and no littorinids occur on the soft substrata. Filamentous algae and *G. lignorum* are however common on the intertidal mudflats of the bay. During their ecological survey of Durban Bay in the early 1950s when the influences of industrial and harbour development were less, Day & Morgans (1956) recorded a wide range of Crustacea and bivalves in the diet of *R. sarba* but very little plant material.

Table 1 Summary of the percentage ('points' method) of plant material in the diet of *Rhabdosargus sarba* at various sampling sites. The chief animal prey are also indicated

Sample site	% Plant	Animal prey
Kosi		
Estuary	87	Penaeidae & fish fry
Channel into 1st Lake	29	Chironomid larvae & bivalves
1st Lake	47	Bivalves & chironomid larvae
2nd Lake	73	Bivalves
St Lucia		
Nkazana	14	Bivalves
Game Guard Camp	37	Bivalves
Makakatana	83	*Grandidierella* & bivalves
Gilly's Point	30	*Grandidierella* & bivalves
Off Charters Creek	77	Bivalves
Mlalazi	58	Bivalves & Crustacea
Durban Bay	23	Littorinids & *Grandidierella*

Table 2 The diet of *Rhabdosargus sarba* in Durban Bay. (% F = percentage frequency; % Pts = percentage 'points'; % Wt = percentage dry weight; *n* = 52)

Taxa	% F	% Pts	% Wt
Filamentous algae	44	21	–
Aquatic macrophytes	4	0,4	–
Grandidierella lignorum	21	5	0,1
Hymenosoma orbiculare	2	1	0,4
Copepodids	2	1	<0,1
Cirripedia	2	1	<0,1
Bivalve siphons	4	1	–
Littorinids	85	60	99
Fish scales	20	4	–
Unidentified remains	35	5	–

Mlalazi estuary

The diet was dominated by filamentous algae (mainly *Chaetomorpha* spp.) and *Ruppia* in almost equal proportions (Table 3). Bivalves, bivalve siphons and various Crustacea were eaten in relatively small amounts.

Table 3 The diet of *Rhabdosargus sarba* in Mlalazi estuary. (% F = percentage frequency; % Pts = percentage 'points'; % Wt = percentage dry weight; *n* = 52)

Taxa	% F	% Pts	% Wt
Filamentous algae	35	29	–
Aquatic macrophytes	40	29	–
Grandidierella lignorum	20	4	9
Rhynchoplax bovis	5	0,2	42
Cirripedia	5	0,4	–
Penaeidae	15	6	21
Dosinia hepatica	25	4	28
Bivalve siphons	20	15	–
Gastropoda	5	2	–
Unidentified remains	35	10	–

South Lake, St Lucia

The diets for $1\frac{1}{2}$ years sampling combined at five sites (Figure 1) are shown in Table 4. The quantity of plant material, a mixture of *Ruppia* spp. and *Enteromorpha* spp., varied from 14% at Nkazana to 77% at Makakatana and Charters Creek. The proportions of plant material in the diet also varied seasonally, and at the Game Guard Camp site (Figure 1), for example, the percentages eaten by volume were 26% in November/December 1981, 77% in March 1982 and nil in June 1982. During June 1982 the most important food item was the siphons of the bivalve *Solen cylindraceus* (68% by volume). Similarly at Nkazana (Figure 1) where 41% of the diet was plant material in November/December 1981, it only constituted 1% in March and June 1982. In the latter months the main prey were the bivalve *Eumarcia paupercula* and the amphipod *G. lignorum*.

Kosi system

Plant material consumed varied from 87% by volume at the estuary to 29% at the entrance to 1st Lake (Table 5). Bivalves and chironomid larvae were the main invertebrate prey, although at the estuary, where most plants were eaten, penaeid prawns and fish fry were the chief animal foods. The diets varied according to season and site but these differences were not as marked as at St Lucia and the main food items remained the same.

The diet of *R. auriventris* was investigated at Kosi where the species is common. In contrast with *R. sarba* very little plant material was found in the diet (Table 6) and the most important prey item was the bivalve *Brachidontes virgiliae*,

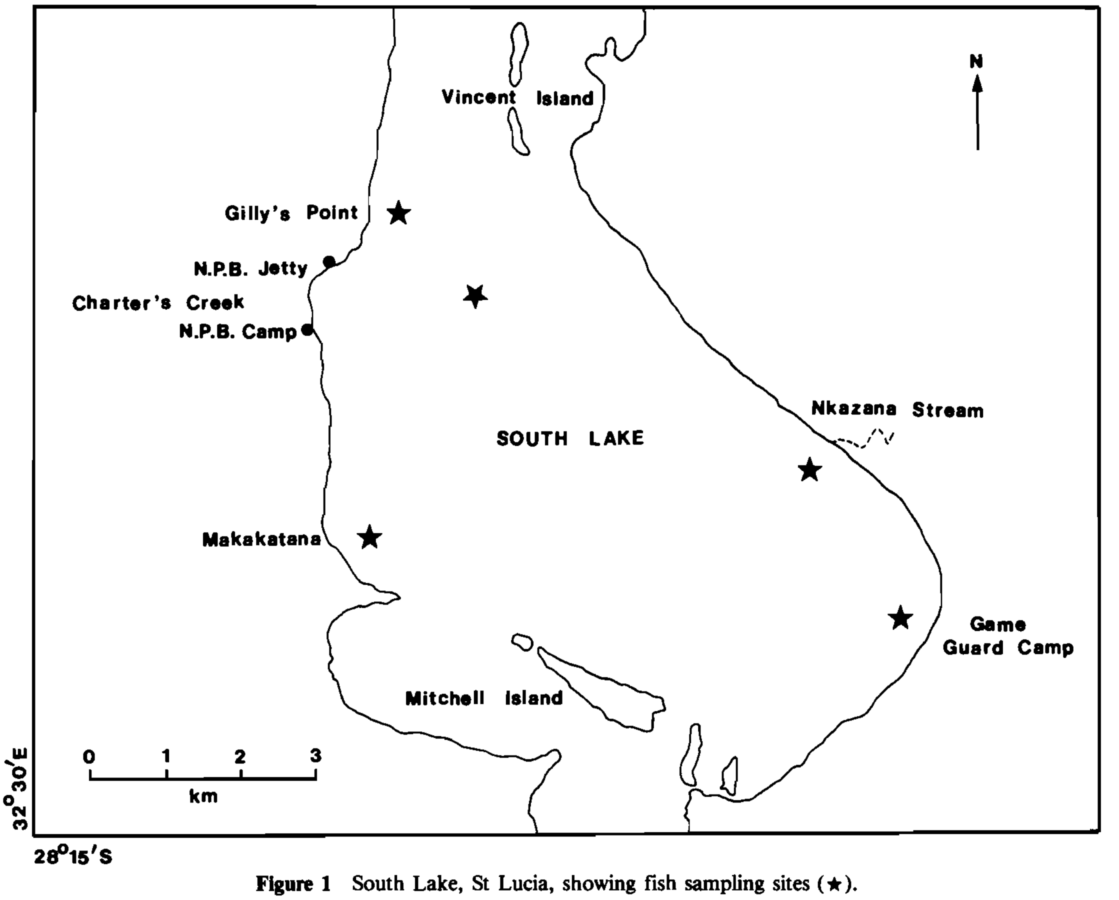

Figure 1 South Lake, St Lucia, showing fish sampling sites (★).

Table 4 The diet of *Rhabdosargus sarba* in South Lake, St Lucia (%F = percentage frequency; %Pts = percentage points; %Wt = percentage dry weight; *n* = 273)

	Game Guard Camp *n* = 120			Nkazana *n* = 55			Makakatana *n* = 62			Off Charters Creek *n* = 11			Gilly's Point *n* = 25		
Taxa	%F	%Pts	%Wt	%F	%Pts	%Wt	%F	%Pts	%Wt	%F	%Pts	%Wt	%F	%Pts	%Wt
Filamentous algae	41,7	31,3	–	36,4	13,4	–	83,9	44,1	–	18,2	19,9	–	44,0	27,7	–
Aquatic macrophytes	15,8	6,1	–	1,8	0,6	–	41,9	38,5	–	63,6	56,8	–	12,0	3,0	–
Synedra (diatom)	–	–	–	1,8	–	–	–	–	–	–	–	–	–	–	–
Plant seeds	–	–	–	1,8	–	–	–	–	–	–	–	–	–	–	–
Nematoda	1,7	0,1	–	–	–	–	–	–	–	–	–	–	–	–	–
Polychaeta	10,0	3,7	0,2	10,9	1,2	<0,1	9,7	3,0	–	9,1	0,6	0,6	8,0	5,2	–
Pseudodiaptomus stuhlmanni	6,7	1,6	0,3	1,8	0,1	<0,1	8,1	2,1	23,2	–	–	–	16,0	0,4	0,1
Oithona sp.	0,8	0,1	–	–	–	–	–	–	–	–	–	–	–	–	–
Cumacea	13,3	0,9	0,1	3,6	0,2	<0,1	–	–	–	–	–	–	4,0	0,1	<0,1
Argulus sp.	–	–	–	–	–	–	1,6	0,1	–	–	–	–	–	–	–
Grandidierella lignorum	20,8	5,2	0,3	30,9	7,1	0,1	51,6	10,1	72,7	18,2	1,1	0,7	84,0	33,0	14,6
Apseudes digitalis	3,3	1,0	<0,1	–	–	–	–	–	–	–	–	–	–	–	–
Hymenosoma orbiculare	12,5	1,7	4,0	23,6	4,0	5,4	–	–	–	9,1	1,7	28,3	20,0	11,1	72,0
Crustacean remains	16,7	5,3	–	32,7	16,1	–	8,1	0,9	–	–	–	–	24,0	6,6	–
Assiminea sp.	8,3	1,1	<0,1	25,5	9,2	<0,1	1,6	0,1	0,3	–	–	–	16,0	0,5	0,1
Haminea petersi	2,4	0,1	–	1,8	0,1	–	–	–	–	–	–	–	–	–	–
Brachidontes virgiliae	2,5	0,2	<0,1	–	–	–	–	–	–	9,1	0,6	3,1	–	–	–
Dosinia hepatica	5,0	1,2	0,5	1,8	0,1	<0,1	–	–	–	27,3	13,6	38,0	–	–	–
Eumarcia paupercula	4,2	2,3	<0,1	23,6	20,0	3,3	–	–	–	18,2	4,5	29,3	4,0	5,3	13,0
Siliqua sp.	1,7	1,2	1,6	1,8	0,1	0,5	–	–	–	–	–	–	–	–	–
Solen cylindraceus	3,3	1,3	93,6	7,3	4,1	91,0	–	–	–	–	–	–	–	–	–
Solen siphons	23,2	19,2	–	1,8	0,2	–	–	–	–	–	–	–	4,0	1,3	–
Bivalve siphons	27,5	15,2	–	30,9	12,5	–	9,7	3,0	–	9,1	0,6	–	8,0	5,3	–
Insecta	3,3	0,1	–	1,8	0,1	–	–	–	–	–	–	–	–	–	–
Fish remains	7,5	0,6	<0,1	14,6	2,9	–	–	–	–	–	–	–	8,0	5,6	–
Unidentified remains	2,5	0,5	–	16,4	6,1	–	–	–	–	–	–	–	–	–	–

Table 5 The diet of *Rhabdosargus sarba* in the Kosi system (%F = percentage frequency; %Pts = percentage points; %Wt = percentage dry weight; *n* = 353)

	Kosi estuary n = 21			Channel into 1st Lake n = 14			1st Lake n = 198			2nd Lake n = 120		
Taxa	%F	%Pts	%Wt	%F	%Pts	%Wt	%F	%Pts	%Wt	%F	%Pts	%Wt
Filamentous algae	71,0	54,1	–	50,0	27,8	–	70,7	45,7	–	64,2	71,9	–
Rhodophyta	–	–	–	–	–	–	–	–	–	2,5	2,1	
Centric diatoms	38,0	–	–	–	–	–	1,0	–	–	–	–	–
Aquatic macrophytes	76,2	33,4	–	7,1	1,4	–	8,1	1,4	–	2,5	0,6	–
Nemertea	–	–	–	–	–	–	0,5	<0,1	0,1	–	–	–
Nematoda	–	–	–	–	–	–	3,0	<0,1	0,1	–	–	–
Polychaeta	–	–	–	–	–	–	12,0	2,9	<0,1	2,5	0,5	<0,1
Pseudodiaptomus stuhlmanni	–	–	–	–	–	–	4,0	0,1	<0,1	0,8	0,1	<0,1
Harpacticoida	–	–	–	–	–	–	1,0	<0,1	<0,1	–	–	–
Ostracoda	–	–	–	–	–	–	0,5	–	–	–	–	–
Cumacea	–	–	–	–	–	–	2,0	1,0	<0,1	–	–	–
Cladocera	4,8	–	<0,1	–	–	–	3,0	0,6	9,8	–	–	–
Afrochiltonia capensis	4,8	–	5,2	–	–	–	0,5	0,1	0,1	–	–	–
Grandidierella lignorum	4,8	–	0,5	28,6	5,7	2,7	35,9	11,7	1,9	2,5	0,1	<0,1
Apseudes digitalis	4,8	–	0,6	–	–	–	–	–	–	–	–	–
Isopoda	–	–	–	–	–	–	1,5	<0,1	0,4	–	–	–
Alpheus sp.	–	–	–	–	–	–	–	–	–	0,8	0,2	78,9
Macrobrachium sp.	–	–	–	–	–	–	0,5	0,1	–	–	–	–
Penaeidae	19,0	7,1	79,3	–	–	–	–	–	–	–	–	–
Hymenosoma orbiculare	–	–	–	–	–	–	4,5	0,5	8,7	–	–	–
Rhynchoplax bovis	–	–	–	–	–	–	1,0	0,1	0,8	2,5	0,3	0,4
Brachyura (adults)	4,8	–	0,8	–	–	–	–	–	–	–	–	–
Crustacean remains	19,0	1,2	–	14,3	22,0	–	14,6	1,5	–	17,5	2,5	–
Assiminea sp.	4,8	–	<0,1	–	–	–	–	–	–	–	–	–
Brachidontes virgiliae	–	–	–	57,1	9,6	40,0	68,7	22,5	58,5	90,0	19,9	20,2
Hiatula lunulata	–	–	–	–	–	–	3,5	0,1	5,3	–	–	–
Bivalve siphons	–	–	–	–	–	–	0,5	0,1	–	0,8	0,7	–
Insecta	14,3	–	6,4	71,4	25,4	57,7	37,0	9,7	7,5	18,3	0,8	0,1
Fish remains	19,0	4,7	–	–	–	–	1,5	1,5	2,5	6,8	0,3	–

Table 6 The diet of *Rhabdosargus auriventris* in the Kosi system (% F = percentage frequency; % Pts = percentage 'points'; % Wt = percentage dry weight; *n* = 77)

Taxa	% F	% Pts	% Wt
Filamentous algae	37	7	–
Nemertea	2	0,4	2
Nematoda	5	0,1	<0,1
Polychaeta	7	7	0,3
Ostracoda	2	<0,1	–
Cumacea	2	<0,1	<0,1
Cladocera	2	<0,1	0,5
Grandidierella lignorum	21	4	0,7
Penaeidae	2	5	0,5
Hymenosoma orbiculare	2	2	3
Isopoda	2	0,1	–
Crustacean remains	9	3	–
Chironomid pupae/larvae	26	6	1,5
Zygopteran larvae	2	4	–
Assiminea sp.	2	0,7	0,1
Brachidontes virgiliae	93	50	91
Bivalve siphons	2	5	–
Fish remains	2	6	–

followed by a wide variety of benthic invertebrates.

Feeding periodicity

The diel feeding periodicity of *R. sarba* at two estuaries according to the percentage fullness of the stomach is shown in Figure 2. The results are drawn from 380 fish caught at Kosi and 286 fish caught at St Lucia during all seasons. The feeding patterns at Kosi and St Lucia are similar, with maximum fullness during the early afternoon and least fullness early in the morning. Although no samples were collected during the night, the absence of food in fish caught at dawn suggests a cessation of feeding during darkness.

Prey selection

The concurrent survey of the benthos of South Lake, St Lucia has permitted an analysis of how selective *R. sarba* is for prey in relation to prey abundance, using the Ivlev (1961) Index. The Ivlev indices for six taxa at four sample sites during various months are shown in Figure 3. The results are very variable, particularly with regard to the bivalves *Eumarcia* and *Solen*. On some occasions they are positively selected and at others negatively. In this respect it appears that a greater positive selection was exhibited for *Eumarcia* and *Solen* when least plant material was consumed (Table 4, Figure 3). A strong positive selection is evident at nearly all times for the amphipod *G. lignorum* and strong negative selection for the tanaid *Apseudes*

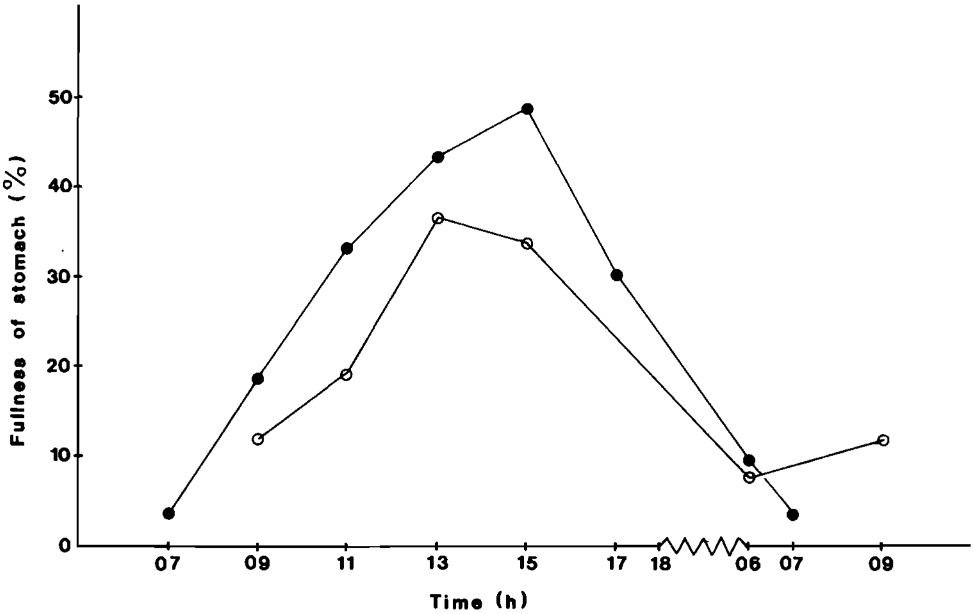

Figure 2 The feeding periodicity of *Rhabdosargus sarba* at St Lucia (● – ●) and Kosi (○ – ○).

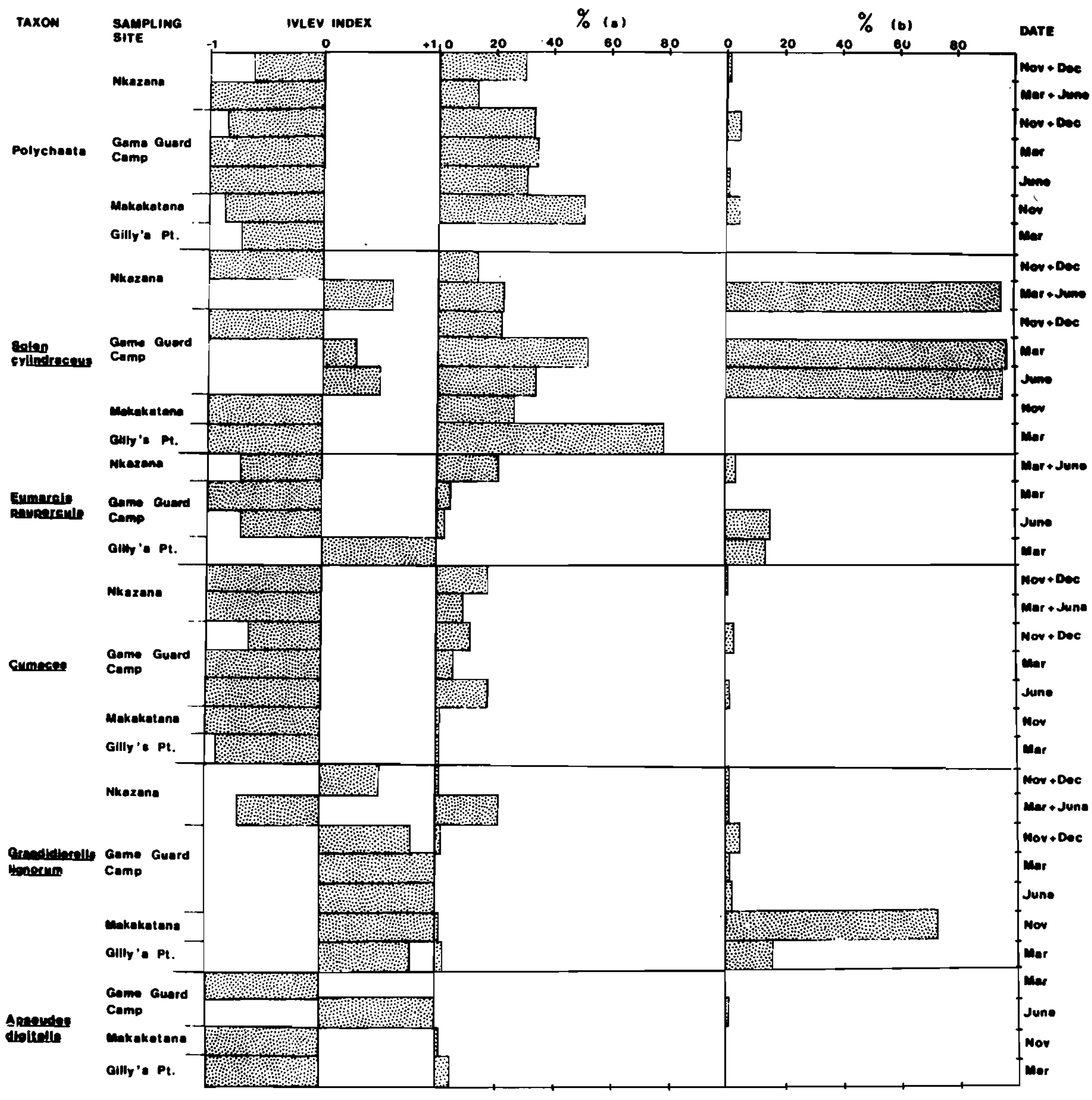

Figure 3 The selectivity of *Rhabdosargus sarba* for six prey items in St Lucia according to the Ivlev Electivity Index (+ = positive selection; – = negative selection) and the relative abundance (% dry weight) of each taxon in the benthos (a) and stomach contents (b). See Figure 1 for sampling sites.

digitalis, polychaetes and cumaceans. Although selectivity for bivalve siphons could not be estimated it is apparent from Tables 2 to 5 that low numbers are eaten in Kosi and Durban Bay while relatively large quantities are consumed in St Lucia and Mlalazi.

Discussion

Although there is considerable variation in the proportions of different food items consumed by *R. sarba* in Natal estuaries the constituents remain relatively constant. Plants in the form of filamentous algae and aquatic macrophytes, such as *Ruppia* and *Potamogeton*, which are macerated by the strong molariform teeth and hence well digested, form the bulk of the food. Various bivalves which can also be crushed by the strong teeth form the most important animal food, followed by the amphipod *G. lignorum* and in Kosi, chironomid larvae. The diet of *R. sarba* is similar throughout its Indo-Pacific range as juveniles in Lake Macquarie, New South Wales, feed on algae and a wide range of invertebrates (Thomson 1959) and in Lake Chilka, India, a similar diet has been reported (Patnaik 1973).

The diet of *R. sarba* differs from that of the very similar *R. holubi* and *R. auriventris* with which it is sympatric, mainly with regard to the importance of plant material. *R. holubi* ingests large quantities of plant material but this is not digested as the major food is the associated epiphytic diatoms (Blaber 1974). Small numbers of amphipods and polychaetes are also taken. *R. auriventris* is almost entirely carnivorous with only small, probably incidental, amounts of plant material in the diet. The main prey of this species are bivalves but a wide variety of Crustacea are also eaten. Therefore, despite occurring in mixed species shoals, the three *Rhabdosargus* species exhibit differences in feeding ecology. Both *R. sarba* and *R. holubi* consume plants but treat them differently, the former gaining nutriment from the plants and their epiphytes and the latter only from the epiphytes. *R. holubi* consume fewer of the bivalves which form the main invertebrate food of *R. auriventris*. The diets of adults in the sea off Natal are not well known but bivalves form an important part of the diet of all three species (Van der Elst 1981). The diet of larger *R. holubi* in the sea between Mossel Bay and Algoa Bay was studied by Buxton & Kok (1983) and found to consist chiefly of *Echinocardium cordatum*, polychaetes and isopods.

It is possible that in the divergence of these three closely related species there has been evolution in the juveniles either towards herbivory (*R. sarba*) or towards bivalve feeding (*R. auriventris*). However, *R. sarba* juveniles can be considered true omnivores and therefore perhaps ancestral to the more localized *R. holubi* (herbivorous, adapted for taking advantage of epiphytic diatoms in estuaries) and *R. auriventris* (carnivorous mainly on bivalves) which have become more specialized in their juvenile feeding ecology. *R. holubi* and *R. auriventris* are both African endemics, the former on the south-east coast and the latter on the east coast, while *R. sarba* occurs throughout the Indo-Pacific.

Juveniles of all three species nevertheless retain the opportunistic and flexible feeding ecology necessary for living in estuaries. This is evidenced by their consumption of a wide range of invertebrate benthic fauna.

In terms of the position of juvenile and subadult *R. sarba* in the fish community of Natal estuaries, apart from the relationships with its congeners, the diet overlaps to a limited extent with that of Gerreidae (Cyrus & Blaber 1983) and *Pomadasys commersonii* (Hay & Blaber, in press) all of which consume bivalves and bivalve siphons. The Gerreidae are apparently dependent on bivalve siphons in the Kosi system where some competitive exclusion is reported with *P. commersonii* (Hay & Blaber, in press). The degree of overlap with *R. sarba* is probably insignificant as few bivalve siphons are eaten by *R. sarba* in Kosi although they are a common feature of the diet in St Lucia where Gerreidae are scarce. The partially herbivorous habit of *R. sarba* appears to give it a unique niche among the common benthic fish of Natal estuaries. An interesting case of resource partitioning is evident in St Lucia where *P. commersonii* and *R. sarba* are the dominant benthic fish; the former consumes large quantities of the tanaid *A. digitalis* and very few of the amphipod *G. lignorum* (Hay & Blaber, in press), while *R. sarba* shows a definite selection for *G. lignorum* (Figure 3) and almost ignores *A. digitalis*. The feeding periodicities of the two fish are also different. *P. commersonii* feeds mainly early in the morning and at dusk (Hay & Blaber, in press) with a low in the middle of the day when *R. sarba* shows peak fullness.

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