S. Afr. J. Zool. 1989, 24(3)

The diets of fish in three south-western Cape estuarine systems

B.A. Bennett

Zoology Department and Marine Biology Research Institute, University of Cape Town, Rondebosch, 7700 Republic of South Africa

Received 26 September 1988; accepted 28 November 1988

The stomach contents of 2756 fish of 14 species taken by seine and gill netting in the Bot River, Kleinmond and Palmiet estuaries on the south-western Cape coast of South Africa were examined. The small juveniles of all species consumed primarily zooplankton before switching to their adult diets. Seven of the species, *Atherina breviceps, Caffrogobius multifasciatus, Clinus spatulatus, Galeichthys feliceps, Gilchristella aestuaria, Monodactylus falciformis, Psammogobius knysnaensis* and *Syngnathus acus* were carnivores which fed primarily on invertebrates; two, *Hyporhamphus capensis* and *Sarpa salpa,* were herbivores; three, *Lithganathus lithognathus, Rhabdosargus globiceps* and *R. holubi* were omnivores and two, *Lichia amia* and *Pomatomus saltatrix* were piscivores. Within these trophic groupings variations in the diets of fish from the different estuaries were noted as were changes in diet with season. Differences between estuaries were ascribed primarily to food availability and differences in the size ranges of the fish species sampled in them. Differences in the diet between size classes were primarily due to an increasing ability to handle larger food items. The few seasonal differences in diet that occurred appeared not to conform to any observable pattern. Twelve food categories provided > 1% of food consumed by at least one species and each of these categories was represented in the guts of between 9 and 14 of the fish species examined. Six of the prey categories, Isopoda, Amphipoda, Decapoda, Teleostei, Algae and Spermatophyta each provided > 10% of the food consumed by all 14 species combined.

Die maaginhoude van 2756 individue van 14 visspesies wat deur middel van trek- en kiefnette in die Botrivier-, Kleinmond- en Palmiet-estuariums aan die suidwes-Kaapse kus van Suid-Afrika versamel is, is ondersoek. Die klein onvolwassenes van alle spesies het hoofsaaklik soöplankton ingeneem voor oorskakeling na 'n volwasse dieet. Sewe van die spesies, *Atherina breviceps, Caffrogobius multifasciatus, Clinus spatulatus, Galeichthys feliceps, Gilchristella aestuaria, Monodactylus falciformis, Psammogobius knysnaensis* en *Syngnathus acus* was karnivore wat hoofsaaklik ongewerweldes vreet; twee, *Hyporhamphus capensis* en *Sarpa salpa* was herbivore; drie, *Lithognathus lithognathus, Rhabdosargus globiceps* en *R. holubi* was omnivore en twee, *Lichia amia* en *Pomatomus saltatrix* was visvretend. Variasies in die dieet van visse van die onderskeie estuariums, asook die seisoenale dieetverskille, is binne hierdie trofiese klasse aangeteken. Dieetverskille tussen die estuariums word hoofsaaklik toegeskryf aan beskikbaarheid van voedsel en aan die verskille in grootteklasse van die versamelde vissoorte. Dieetverskille tussen vis-grootteklasse was hoofsaaklik 'n gevolg van 'n toenemende vermoë om groter voedselitems te hanteer. Die enkele seisoenale dieetverskille kon aan geen ooglopende patroon gekoppel word nie. Twaalf voedselklasse het meer as 1% van die voedselinname van ten minste een spesie uitgemaak, en elkeen van hierdie klasse is in die maaginhoud van tussen 9 en 14 vissoorte verteenwoordig. Ses van die prooiklasse, Isopoda, Amphipoda, Decapoda, Teleostei, Algae en Spermatophyta het elk meer as 10% van die gesamentlike voedselinname van al 14 spesies uitgemaak.

A considerable amount of information concerning the diets of fish in South African estuaries is available. Published studies include descriptions of the diets of individual species (e.g. Blaber 1974, 1984; Whitfield & Blaber 1978a; Coetzee 1981, 1982a; Coetzee & Pool 1985), taxonomic groups (Masson & Marais 1975; Blaber 1976; Cyrus & Blaber 1983) and guilds (Whitfield & Blaber 1978b; Blaber 1979; Marais 1984). Also included are descriptions of the morphological and ecological inter-relationships between the fish and their food resources (Whitfield 1980; Blaber, Cyrus & Whitfield 1981; Cyrus & Blaber 1982; White & Bruton 1983; Whitfield 1984). All the work mentioned above was conducted on fish in estuaries on the eastern, south-eastern and southern coasts of South Africa and, with the exception of the data provided on *Rhabdosargus globiceps* in the Hermanus lagoon (Talbot 1955), there is no published information on the diets of fish in south-western Cape estuaries.

The data presented in this paper were obtained from fish sampled in three south-western Cape estuaries, namely the Palmiet, Kleinmond and Bot River estuaries (Figure 1). General information on the physical and biological characteristics of these estuaries are provided by Koop (1982); Koop, Bally & McQuaid (1983) and Branch & Day (1984). The main difference between these estuaries is that the Palmiet is usually permanently open to the sea, the Kleinmond is open periodically each year and the Bot River estuary is usually only in contact with the sea for brief periods every 2–4 years after artificial opening. Details of many aspects of the biology and life histories of the fishes inhabiting these estuaries are provided by Bennett (1985, 1989) and Bennett, Hamman, Branch & Thorne (1985).

Methods

Fish were obtained from the Palmiet, Kleinmond and Bot River estuaries with seine and gill nets as described by Bennett *et al.* (1985) and Bennett (1989). Following capture, subsamples were preserved in 10% formalin for analysis of stomach contents. For this purpose fish were either preserved whole if small (< ± 50 mm), or after

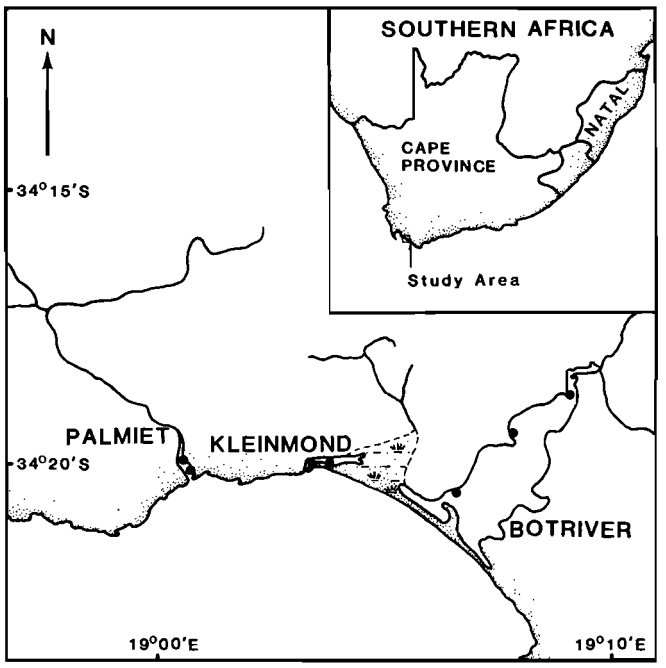

Figure 1 A map of southern Africa showing the locations of the Bot River, Kleinmond and Palmiet estuaries which were sampled to obtain fish specimens for stomach content analysis.

having a midventral abdominal incision made (fish of 50–150 mm), or, in the case of larger fish (> ± 150 mm), stomachs were removed and preserved separately. Stomachs were selected to represent the full size range of each species in each estuary throughout the year.

In the laboratory each stomach was emptied separately into a glass container under a dissecting microscope where the food items that it contained were identified to the lowest possible taxon. The amount of each prey species was measured as the volume displaced in a measuring cylinder, unless the volumes were small (< ± 0,1 cm^3), when estimates were made by flattening the prey items to a thickness of 1 mm using microscope slides and then counting the number of 1-mm squares of a grid placed under the container that were obscured.

Data on stomach contents were recorded separately for each fish together with the species, total length (mm), locality and date of capture of that specimen. Summaries of the percentage volume (%V) and frequency of occurrence (%O) (Hynes 1950; Berg 1979) of each prey species (or of the prey species grouped into higher taxa), were prepared to show differences in diet between each fish species, between the different size classes of each species, for each species in the three different estuaries and at different times of the year.

Results and Discussion

Seventeen species of fish are listed by Bennett (1989) as being either abundant or common in south-western Cape estuaries. Of the 14 species examined in this study, 12 appear on this list and provided > 99% of fish sampled in the Palmiet, Kleinmond and Bot River estuaries. Two rare species (*S. salpa* and *H. capensis*) were included because they are the only species which were primarily herbivorous. The five common or abundant species not included were *Liza richardsoni, Mugil cephalus, Myxus*

Table 1 The total number of fish examined for stomach contents from three south-western Cape estuaries sampled in 1980 and 1981. For each estuary the species composition and size range of fish sampled and the number of stomachs that contained food are shown

	Total No. of guts	Palmiet		Kleinmond		Bot River		Total No. with food
		No.	Size	No.	Size	No.	Size	
Atherina breviceps	768	76	28–75	144	23–96	273	21–97	493
Caffrogobius multifasciatus	136	88	31–165			28	28–148	116
Clinus spatulatus	50					47	23–132	47
Galeichthys feliceps	129	11	120–295			102	170–402	113
Gilchristella aestuaria	94	25	43–78			63	22–61	88
Hyporhamphus capensis	6					6	110–182	6
Lichia amia	73	3	71–460	12	95–495	39	443–820	54
Lithognathus lithognathus	346	72	20–294	100	22–268	138	252–660	310
Pomatomus saltatrix	53	5	43–125	5	82–122	31	453–632	41
Psammogobius knysnaensis	871	191	22–60	222	18–69	191	21–61	604
Rhabdosargus globiceps	78	19	28–192	26	27–134	22	208–340	67
R. holubi	65	14	20–195	33	22–155	12	271–368	59
Sarpa salpa	6					6	257–275	6
Syngnathus acus	81					77	41–158	77
Totals	2773	504		542		1035		2081

Table 2 The diets of fourteen fish species from the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape. Only prey categories that contributed >0,5%V consumed by at least one species are included (– indicates < 0,5% contribution to occurrence or volume)

	Food category																							
	Polychaeta		Copepoda		Ostracoda		Isopoda		Amphipoda		Tanaidacea		Decapoda		Insecta		Mollusca		Teleostei		Algae		Spermato-phyta	
Species	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V	%O	%V
Atherina breviceps	3	1	39	6	31	11	8	10	43	35	2	–	7	3	32	26	6	2	6	2	3	1	1	–
Caffrogobius multifasciatus	34	3	9	–	3	–	43	12	97	20	55	3	12	34	27	2			10	20				
Clinus spatulatus	4	–	21	–	19	1	64	37	94	32					51	4	13	23	4	2	2	–	6	–
Galeichthys feliceps	4	–			1	–	58	6	37	9			83	79	15	4	8	–	13	2				
Gilchristella aestuaria	1	1	67	22	60	33	3	–	33	10	7	3			31	12	16	5	14	5	8	2	1	–
Hyporhamphus capensis			17	–	17	–							17	–	100	5			50	1			50	93
Lichia amia													6	–					100	100				
Lithognathus lithognathus	20	–	14	–	14	–	45	5	55	9	14	–	19	21	54	1	36	23	4	1	46	29	16	9
Pomatomus saltatrix						5	–						10	–					100	100				
Psammogobius knysnaensis	26	11	25	2	27	6	10	4	66	47	6	1	3	2	45	22	3	–	3	2	2	–	–	
Rhabdosargus globiceps	18	–	16	–	27	–	60	–	66	–	16	–	58	20	30	–	76	23	7	8	47	46	21	2
R. holubi			22	–			36	–	71	1	10	–	54	18	61	1	54	20			73	29	37	31
Sarpa salpa															50	1	17	–			100	53	83	46
Syngnathus acus			81	43	8	–	22	13	44	42	1	–			19	2	6	–						

capensis, Liza dumerilii and *Oreochromis mossambicus*. Preliminary examinations of the stomach contents of these five species revealed diets similar to those recorded in the literature i.e. fry of $< \pm 30$ mm consumed zooplankton and larger fish contained a mixture of sediment, detritus and benthic diatoms (Blaber 1976, 1977; Blaber & Whitfield 1977; Masson & Marais 1975; Whitfield 1980; Whitfield & Blaber 1978c). The decision not to include detailed analyses of the diets of these species was taken partly because of practical difficulties in the identification, separation and quantification of their stomach contents but more particularly because the published information adequately reflects their diets in the south-western Cape.

A total of 2756 stomachs from 14 species of fish were examined during the course of this study, 2081 of which contained food, 504 of them from 10 species captured in the Palmiet estuary, 542 from seven species from the Kleinmond estuary and 1035 in 14 species in the Bot River estuary (Table 1). The percentage occurrence and composition of each of the 12 major prey categories found in the guts of each species from all three estuaries combined are presented in Table 2. From this table it is apparent that the majority of species consume a wide variety of prey but that in all cases only one or two categories provide the bulk of the diet. Of the 14 species investigated, seven (*Atherina breviceps, Psammogobius knysnaensis, Gilchristella aestuaria* and *Caffrogobius multifasciatus* being most abundant) fed primarily on small invertebrates, two (*Hyporhamphus capensis* and *Sarpa salpa*) were herbivorous; two (*Lichia amia* and *Pomatomus saltatrix*) were piscivorous and three (*Lithognathus lithognathus, Rhabdosargus globiceps* and *R. holubi*) were omnivorous (Table 3). Despite the generality of these trophic groupings the food items consumed often differed quite markedly between fish species within a particular group, and between the same fish species in the three different estuaries (Table 4). Intraspecific differences in diet were also observed, both seasonally and between different size classes, as outlined for each of the following species.

Atherina breviceps

A total of 768 *A. breviceps* stomachs was examined of which 275 were empty or nearly so. Of the 493 stomachs included in this analysis 76 were of fish from the Palmiet, 144 from the Kleinmond and 273 from the Bot River estuaries. The stomachs containing food all came from fish of between 21 and 97 mm in length (Table 1).

Invertebrates provided the bulk of the diet of this species in the three estuaries with amphipods (43%O, 35%V), insects (32%O, 26%V — primarily aquatic chironomid and odonatan larvae), ostracods (31%O, 11%V) and isopods (8%O, 10%V) being the most important prey categories (Table 4). The prey species contributing the greatest amount to the diet were the amphipods *Corophium triaenonyx, Grandidierella bonnieroides* and *Melita zeylanica* (Table 4).

Differences in the composition of the diet of fish taken from the three estuaries were evident (Table 2).

Table 3 The relative importance of invertebrates, weed and fish in the diets of fish from the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape

	Invertebrates		Fish		Weed	
	%O	%V	%O	%V	%O	%V
Carnivores						
Syngnathus acus	100,0	99,8	–	–	–	–
Galeichthys feliceps	100,0	98,0	13,3	2,1	–	–
Clinus spatulatus	100,0	97,0	4,3	2,1	8,5	0,5
Atherina breviceps	99,8	95,9	6,5	1,6	4,3	0,8
Psammogobius knysnaensis	100,0	94,2	3,5	2,0	2,3	0,3
Gilchristella aestuaria	100,0	85,3	13,6	5,3	11,4	2,4
Caffrogobius multifasciatus	100,0	74,9	10,3	19,7	–	–
Piscivores						
Pomatomus saltatrix	14,6	–	100,0	100,0	–	–
Lichia amia	5,6	0,1	100,0	99,9	–	–
Herbivores						
Sarpa salpa	66,7	0,8	–	–	100,0	99,2
Hyporhamphus capensis	100,0	6,2	5,0	0,6	50,0	93,2
Omnivores						
Lithognathus lithognathus	99,7	59,3	3,9	0,5	53,2	38,0
Rhabdosargus globiceps	100,0	44,8	7,5	7,5	77,6	47,6
R. holubi	100,0	40,9	–	–	88,1	59,1

Copepods provided 19% of the total volume consumed by fish in the Palmiet but only 4% and 2% of samples taken in the Kleinmond and Bot River estuaries. Ostracods were, on the other hand, more important in the diets of *A. breviceps* from the Kleinmond (22%V) than either the Palmiet (9%V) or Bot River (5%V) estuaries. Similarly, isopods provided 17% of the volume consumed in the Bot River estuary but less than 3% in the other two estuaries, amphipods provided more than 45% in Palmiet and Bot River estuaries but only 10% in the Kleinmond estuary, and insect larvae provided 46% in the Kleinmond but only 12% and 3% in the Bot River and Palmiet estuaries respectively.

The composition of the diets of three size classes of fish from one locality in the Bot River estuary is shown in Table 5 and indicates that the diet of *A. breviceps* changes with size. Small individuals (< 25 mm) consumed primarily copepods (56%V) and molluscan larvae (18%V) whereas fish of intermediate size (25–50 mm) fed largely on amphipods (47%V) and insect larvae (12%). Larger fish (> 50 mm)consumed a wider variety of prey with amphipods (24%V), isopods (17%V), gastropods (10%V) and decapods (10%V) all being important. These changes, which primarily involved a decrease in the proportion of small planktonic organisms

Table 4 The composition (%V) of the diets of 14 fish species from the Bot River (B), Kleinmond (K) and Palmiet (P) estuaries. Only prey species that constituted > 5%V in at least one species from at least one estuary are included (– indicates < 0,5%V)

	Atherina breviceps			*Caffrogobius multifasciatus*		*Clinus spatulatus*	*Galeichthys feliceps*		*Gilchristella aestuaria*		*Hyporhamphus capensis*	*Lichia amia*			*Lithognathus lithognathus*			*Pomatomus saltatrix*			*Psammogobius knysnaensis*			*Rhabdosargus globiceps*			*R. holubi*			*Sarpa salpa*	*Syngnathus acus*
	B	K	P	B	P	B	B	P	B	P	B	B	K	P	B	K	P	B	K	P	B	K	P	B	K	P	B	K	P	B	B
Polychaeta																															
Ceratonereis erythraeensis		–	1	3											–	2	–				3	6	3								
Crustacea																															
Copepoda																															
Pseudodiaptomus hessi	1	–	2			–			4							15	–				1	1	–							27	
Calanoidea	–	2	12						9	20																				8	
Ostracoda	5	22	9			1	–		30	43	–				–	–					7	5	7		1	1		2	3	–	
Isopoda																															
Cyathura estuaria	–		1	8	5	1	3	–							2		–		4		–	–	4	–		2		1	1		
Exosphaeroma hylecoetes	1	3	15	4	–	30	3								4	1					2	–	–						.	8	
Amphipoda																															
Corophium triaenonyx	22		–	9	–	4			4						–	–	–				14	–	–		–		–	–		14	
Grandidierella bonnieroides	5	7	30	–	20			63	1	3						2	7				2	14	73		–	3	–	1	2		
Melita zeylanica	17	1	9	8		28	4		7						8	68					15	12	–	–	2	1	–	1	1	27	
Talorchestia sp.		–	6																												
Decapoda																															
Callianassa kraussi	–		3	6	6		83	6							7		6		4		4		–	17	18	19	17	10	20		
Cleistosoma edwardsii					1		–																–		9	5			–		
Hymenosoma orbiculare	4	–	5	12	29						–						61				–		–	1	5	11	2	5	4		
Palaemon pacificus													1			–			10			–									
Insecta																															
Aquatic larvae																															
Chironomidae	9	22	2	14	–	3	4	2	14	2					1	1	–				34	35	1	–	1	1	–	2	1	11	
Odonata	2	23									3					4						–									
Adults																															
Diptera	2	9	3			–			–		–						–				–	–	–								
Mollusca																															
Gastropoda																															
Hydrobia sp.	4		–			2	–		4						1		–			–	–		–	23	22	11	19	20	22	–	–
Tomichia sp.						21									–						–			–			1				
Pelecypoda																															
Arcuatula sp.							–								20									1			–				
Teleostei																															
Whole fish																															
Atherina breviceps				16		2	–				–	5	6		–			20	13	7				8							
Caffrogobius multifasciatus					4							5	8		–			2													
Clinus spatulatus				6			–					59			–			16													
Liza richardsoni												26	60			–		4													
Mugil cephalus													22																		
Mugilidae																			31	36											
Pomadasys olivaceum												5						8													
Psammogobius knysnaensis					11								1																		
Rhabdosargus holubi																		5													
Sarpa salpa																		12													
Syngnathus acus															–			14													
Eggs																															
Psammogobius knysnaensis																					–	5									
Algae																															
Cladophora sp.						–									24	–	1				–	–	–	47	38	20	26	32	18	38	
Enteromorpha sp.															7	1	22				–	–				15	–	8	20	10	
Spermatophyta																															
Potamogeton sp.											93				–									–			23	9		
Ruppia sp.	1					–			1						8						–			1			9	6		46	

Table 5 The diets (%V) of three different size classes of *Atherina breviceps* sampled at one locality in the Bot River estuary. Only prey categories which provided more than 5%V in at least one of the size classes are included

	Size class		
Prey category	< 25 mm	25–50 mm	> 50 mm
Copepoda	56	6	1
Ostracoda	–	5	2
Isopoda	–	6	17
Annphipoda	7	47	24
Decapoda	–	–	10
Insect larvae	3	12	9
Adult insects	–	2	5
Gastropoda	–	–	10
Molluscan larvae	18	–	–

and an increase in larger benthic and weed-dwelling forms with increasing fish size, were apparent in all three estuaries.

Sufficient numbers of guts were examined on a monthly basis in the Bot River and Kleinmond estuaries to investigate seasonal changes in diet (Table 6). The majority of the important prey groups occurred throughout the year. Although these quantities varied, there were no strong seasonal patterns. Only *G. bonnieroides* in the Bot River and odonatan larvae in the Kleinmond estuary showed any seasonal pattern, both occurring almost exclusively during the late autumn and winter months.

Previous references to the diet of *A. breviceps* have been made by Blaber (1979), Day, Blaber & Wallace (1981) and Coetzee (1982b). Blaber (1979) examined the guts of 30 fish from lake St Lucia and found that 99% of their calorific consumption was accounted for by the copepod *Pseudodiaptomus stuhlmanni* which was taken by filter feeding. Day *et al.* (1981) stated that *A. breviceps* is a zooplankton feeder but provided no details of the diet. Coetzee (1982b) provided considerably more information from his analysis of stomach contents from fish caught in Groenvlei and Swartvlei. He identified amphipods, isopods and ostracods as the most important food categories but pointed out differences in diet between his two sampling localities which he ascribed to food availability. He also described a change in diet from filter feeding amongst small fish to the active capture of selected organisms by larger fish. In all these respects his observations are similar to the present results obtained for this species.

Caffrogobius multifasciatus

A total of 136 stomachs from this species were examined

Table 6 The monthly contribution (%V) of important prey species in the diet of *Atherina breviceps* in the Bot River and Kleinmond estuaries. Species represented are those which contributed > 5% to overall volume

	Month											
Prey species	J	F	M	A	M	J	J	A	S	O	N	D
Bot River												
Corophium triaenonyx	63	–	62	19	3	–	9	26	3	10	16	7
Exosphaeroma hylecoetes	6	16	–	–	5	31	11	8	–	13	49	15
Melita zeylanica	8	3	18	39	27	–	4	12	1	–	–	9
Grandidierella bonnieroides	–	–	–	11	16	5	6	8	–	–	–	–
Ostracoda	3	12	6	–	–	26	–	4	10	13	–	–
Chironomid larvae	6	–	–	10	4	3	2	6	15	9	8	5
Kleinmond												
Ostracoda	75	1	10	2	2	3	4	2	24	52	1	–
Chironomid larvae	7	17	34	36	–	1	23	4	54	1	3	5
Grandidierella bonnieroides	–	5	–	–	6	–	16	–	–	–	12	17
Odonatan larvae	–	–	–	–	70	5	14	–	–	–	–	–
Dipteran adults	–	4	–	–	11	3	–	–	5	35	9	15

of which 116 (85%) contained food, 88 from fish taken in the Palmiet estuary and 28 from the Bot River estuary (Table 1). This species was not common in the Kleinmond estuary and guts from the few individuals taken there were not examined.

Four categories of prey each provided more than 10% of the total volume consumed by the sample, namely decapods (34%), amphipods (20%), fish (20%) and isopods (12%). Two of these categories occurred in a large proportion of the guts examined (amphipods 97%, isopods 43%), whereas decapods (12%) and fish (10%) occurred less frequently (Table 2).

Some differences in the composition of the diet were evident between samples from the Bot River and Palmiet estuaries (Table 4). In the Bot River estuary *C. triaenonyx* and *M. zeylanica* provided most of the amphipod category whereas in the Palmiet *G. bonnieroides* was the most important species. Chironomid larvae provided 14%V in the Bot River estuary but < 0,5%V in the Palmiet, and the decapod *H. orbiculare* provided 29%V in the Palmiet but less than half that (12%) in the Bot River estuary. The main fish species consumed also differed between the two estuaries. In the Bot River *A. breviceps* was an important source of food (16%V) while in the Palmiet estuary *P. knysnaensis* was more significant (11%V).

Sufficiently large samples were obtained from the Palmiet estuary to examine whether there were any changes in diet with fish size (Table 7). Copepods were found only in fish < 40 mm and tanaids and insect larvae decreased in importance with increasing fish size. Decapods and fish were most important in the diet of the larger fish (> 100 mm) but absent from those < 40 mm.

Clinus spatulatus

Fifty guts of this species were examined of which 47 contained food (Table 1). The sample was obtained entirely from the Bot River estuary as this species is very rare in the Kleinmond and absent from the Palmiet.

All guts contained small invertebrates which provided 97% of the volume of food consumed (Table 3). Isopods (64%O, 37%V), amphipods (94%O, 32%V) and gastropod molluscs (13%O, 23%V) were the most important prey categories (Table 2) and *Exosphaeroma hylecoetes* (30%V), *M. zeylanica* (28%V) and *Tomichia* sp. (21%V) were the most important species (Table 4).

Ostracods and insect larvae provided 29% and 21 % of the total volume consumed by fish of < 30 mm and less than 3% in the larger size classes (Table 8). Amphipods were important throughout the size range sampled, providing approximately 30% of the total volume of food consumed. Isopods and gastropods were more important in the diets of fish of more than 30 mm in length and small fish were consumed only by *C. spatulatus* of over 100 mm in length.

A less detailed report on the diet of this species is provided by Bennett (1983).

Galeichthys feliceps

The stomachs of 129 *G. feliceps* were examined. Of these 113, contained food: 11 from the Palmiet estuary and 102 from the Bot River estuary (Table 1).

Invertebrates provided 98% of the total volume of food consumed by this species with decapods (79%V) the most important prey category and *Callianassa kraussi* (78%V) the most important prey species. This description of the diet is heavily influenced by the large sample obtained from the Bot River estuary. In the Palmiet estuary where fewer, smaller, fish were collected, amphipods, especially *G. bonneroides* (63%V), were most important with decapods (19%V), fish (10%V) and isopods (6%V) all contributing significantly (Tables 2 and 4).

Stomach contents of *G. feliceps* from five other estuaries in the eastern and south-eastern Cape have been reported by Marais (1984) and Coetzee & Pool (1985). There are minor differences in diet between these estuaries but decapod crustaceans (usually *Upogebia africana* and *H. orbiculare*) were the most important food in almost all samples.

Gilchristella aestuaria

Eighty-eight of the 94 stomachs examined contained food and these were from fish of between 22 and 78 mm in length. Most of the fish with food in their stomachs

Table 7 The percentage composition (%V) of the major prey categories in the diet of three different size classes of *Caffrogobius multifasciatus* in the Palmiet estuary

	Size class		
Prey category	< 40 mm	40–100 mm	> 100 mm
Polychaeta	2	1	2
Copepoda	6	–	–
Isopoda	17	13	10
Amphipoda	31	33	13
Tanaidacea	15	9	–
Decapoda	–	28	43
Insect larvae	29	1	–
Teleostei	–	10	24

Table 8 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Clinus spatulatus* from the Bot River estuary

	Size class		
Prey category	< 30 mm	30–100 mm	< 100 mm
Ostracoda	29	–	–
Isopoda	10	31	44
Amphipoda	32	35	29
Mollusca	3	29	18
Insect larvae	21	3	3
Teleostei	–	–	4

were from the Bot River estuary (63), the remainder coming from the Palmiet (Table 1).

Ostracods (60%O, 330%V), copepods (67%O, 22%V), insects (31%O, 12%V) and amphipods (33%O, 10%V) were the most important prey categories (Table 2). A large proportion of the prey consumed by *G. aestuaria* was of larval or juvenile stages from the aforementioned groups which, because of their small size and the degree of digestion, could not be identified to species. Adults of larger prey species that were identified included *Pseudodiaptomous hessi* (3,3%V), *C. triaenonyx* (2,9%V), *M. zeylanica* (5,1%V) and *Hydrobia* sp. (3,1%V). Also of some importance was detritus (3,9%V) (Table 4).

The diet of fish from the Palmiet contained 13% more ostracods and 24% more copepods than fish from the Bot River estuary. This difference was compensated for by the inclusion of more chironomid larvae, amphipods, tanaids and gastropods in the diets of Bot River fish (Table 4).

The diets of small (< 30 mm), intermediate (30–50 mm) and large (> 50 mm) *G. aestuaria* from the Bot River estuary are shown in Table 9. In the small size class copepods (38,7%V), diatoms (17%V) and detritus (11,7%V) provided a substantial proportion of the total amount of food consumed but their importance decreased markedly in fish > 30 mm in length. Ostracods (44,1%V) were the dominant food category in fish of intermediate size although three other categories, amphipods, copepods and insect larvae all contributed between 12 and 14% to the volume consumed. The largest fish (> 50 mm) had more diverse diets. Insect larvae were the main contributors by volume (19,9%) but larger organisms such as polychaetes, gastropods and fish larvae, which were not found in smaller fish, constituted almost a quarter of their diet. Small *G. aestuaria* rely primarily on small invertebrates which they may obtain by filter feeding, whereas larger individuals consume a higher proportion of benthic organisms , suggesting an increasing reliance on prey that are probably selected individually.

Table 9 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Gilchristella aestuaria* in the Bot River estuary

Prey category	Size class		
	< 30 mm	30–50 mm	> 50 mm
Polychaeta	–	–	3
Ostracoda	7	44	18
Copepoda	39	12	14
Tanaidacea	–	4	4
Insect larvae	6	12	20
Gastropoda	2	2	12
Fish eggs	–	2	4
Fish larvae	–	–	7
Diatoms	17	1	–
Detritus	12	4	3

Analyses of the stomach contents of *G. aestuaria* from nine different estuarine, coastal lake and freshwater localities have been reported (Blaber 1979, Blaber *et al.* 1981; Coetzee 1982b; Talbot 1982; White & Bruton 1983). Considerable differences in the major prey categories between localities are evident. In St Lucia, for example, 68% of the calorific contribution to their diet was the copepod *Pseudodiaptomus stuhlmanni* (Blaber 1979), in Lake Nlange chironomid larvae contributed 47% and *P. stuhlmanni* 26% and in the adjacent Lake Makhawulani macruran zoae contributed 87% (Blaber *et al.* 1981). In Swartvlei copepod nauplii and detritus were the major stomach contents and in Groenvlei *Grandidierella lignorum* was most important (Coetzee 1982). Diatoms were found to be the most important food category in the Bloukrans River (White & Bruton 1983). These results show that *G. aestuaria* are capable of consuming a wide variety of food organisms which they obtain either by filtering or by selecting individual larger prey. The relative importance of these two modes of feeding probably varies according to the size spectrum and abundance of available food.

Hyporhamphus capensis

The stomachs of six *H. capensis* (110–182 mm) from the Bot River estuary were examined, all of which contained food. The aquatic macrophyte *Potamogeton pectinatus* provided the bulk of the gut contents (93%V) but it occurred in only half the fish examined. Insects, both aquatic larvae and terrestrial adults, occurred in all stomachs but provided only 5%V (Table 2).

Coetzee (1981) provided a detailed description of the gut contents of *H. capensis* from Rondevlei in the southern Cape. He showed that their diet varied with size, animal material forming the bulk of the gut contents in small (< 9 cm) and large (> 17 cm) fish, with plant material being most important in the intermediate size class. He also showed that the diet of the intermediate sized fish varied seasonally, with plant material being most important in the summer and least important during the spring months.

Lichia amia

The stomachs of 73 *L. amia* were examined and 54 found to contain food. Most of the sample was obtained from the Bot River estuary (39 fish) with only 12 and three from the Kleinmond and Palmiet estuaries respectively. The fish from the latter two estuaries were also considerably smaller (71–495 mm) than those from the Bot River estuary (443–820 mm).

More than 99% of the food consumed by *L. amia* was fish, the only other prey species being the decapod *Palaemon pacificus* which occurred in the stomachs of two small individuals (95–135 mm) from Kleinmond. *A. breviceps* and *C. multifasciatus* occurred in the diets from all three estuaries but provided < 10%V in each case. *Liza richardsoni* was the most important species in the Palmiet (53%V) and Kleinmond (60%V) estuaries whereas *C. spatulatus*, a species rare or absent in these

estuaries, was most important (59%V) in the Bot River estuary.

The stomach contents of *L. amia* have previously been described by Whitfield & Blaber (1978b), Coetzee (1982a), Smale & Kok (1983) and Marais (1984). In all cases the main prey types were similar to those reported above, crustacea and fish being of importance in smaller specimens (< ± 200 mm) whereas larger fish are almost exclusively piscivorous.

Lithognathus lithognathus

Three hundred and forty-six *L. lithognathus* stomachs were examined and 310 were found to contain food; 72 from the Palmiet estuary, 100 from the Kleinmond and 138 from the Bot River estuary. There was only partial overlap in the size of fish sampled from the estuaries. In the Palmiet and Kleinmond estuaries the size range was 20–294 mm and in the Bot River estuary it was 252–660 mm (Table 1).

Table 3 shows that when the data from the three estuaries are combined approximately 60%V of the diet of *L. lithognathus* was invertebrates and 40%V was aquatic plants, so that this species may be considered omnivorous. In the Palmiet estuary the main items consumed were decapods (67%V) and algae (24%V); *H. obiculare,* (61%V) and *Enteromorpha* sp. (22%V) contributing substantially to these respective categories. The diet of this species from the Kleinmond estuary was quite different, amphipods providing the bulk of the diet (69%V) with one species, *M. zeylanica* contributing 68%V. Also important were copepods, almost entirely represented by *P. hessi* (15%V). In the Bot River estuary *L. lithognathus* consumed a wider variety of food. Algae (32%V) were the major category but molluscs (25%V), decapods (21%V), amphipods (9%V) and spermatophytes (9%V) were also important.

The diet of *L. lithognathus* in the Palmiet and Kleinmond estuaries changed as the fish increased in size but the important food categories differed in the two estuaries (Table 10). In the Kleinmond estuary copepods (56%V) and ostracods (38%V) were the most important prey items in fish of less than 30 mm whereas amphipods (46%V) and copepods (34%V) were important in the intermediate class (30–100 mm), and the larger class (> 100 mm) consumed primarily amphipods (76%V). Polychaetes and insect larvae provided between 5 and 11%V in the larger two size classes. In the Palmiet estuary copepods were consumed only by small fish and the proportion of amphipods decreased with increasing fish size from 86%V to 6%V. Decapods and algae, on the other hand, were absent from the stomachs of the smallest size class but of major importance in the largest class where they provided 68%V and 24%V respectively. In the Bot River estuary where no small fish were sampled plant material provided 41%V and a bivalve species 28%V.

Table 10 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Lithognathus lithognathus* in the Kleinmond and Palmiet estuaries

	Size class		
Prey category	< 30 mm	30–100 mm	> 100 mm
Kleinmond			
Polychaeta	–	11	6
Copepoda	56	34	10
Ostracoda	38	1	–
Amphipoda	3	46	76
Insecta	–	6	5
Palmiet			
Copepoda	5	–	–
Amphipoda	86	79	6
Decapoda	–	7	68
Algae	–	1	24

Mehl (1973) found that in the Heuningnes estuary *L. lithognathus* had a varied diet, the composition of which was fairly constant throughout the year. The most commonly consumed prey items were decapods, amphipods, aquatic plants, gastropods and polychaetes. Whitfield (1985) reported that *L. lithognathus* of < 30 mm in Swartvlei consumed primarily amphipods and copepods. Marine samples examined by Lasiak (1984) contained mainly the swimming prawn *Macropetasma africana,* bivalves (*Donax* spp.) and polychaetes.

Pomatomus saltatrix

The stomachs of 53 *P. saltatrix* were examined, 41 of which contained food, five each from the Palmiet and Kleinmond estuaries, where the size range was 43–225 mm, and 31 of between 435 and 623 mm from the Bot River estuary (Table 1).

This species was almost exclusively piscivorous. All guts contained fish, which provided 99,97%V of their diet. The remaining 0,03%V was crustaceans which were found in the smallest fish from the Palmiet and Kleinmond estuaries. Only *A. breviceps* was identified in the diets of fish from the three estuaries and it provided 20%V overall. A major proportion of the diet in all three estuaries was unidentified pieces of fish. This shows that *P. saltatrix,* which has sharp interlocking teeth, can bite pieces off their prey, an ability which allows the consumption of prey items which would otherwise be too large to handle.

Previous descriptions of the stomach contents of *P. saltatrix* include those by van der Elst (1976), Smale & Kok (1983), Marais (1984) and Smale (1984). From these studies it is apparent that the diet of this species is similar in both the estuarine and marine environments with the general pattern as described above, i.e. smaller fish (< ± 200 mm) consume both crustaceans and fish but larger individuals consume almost entirely fish with cephalopods occasionally being important.

Psammogobius knysnaensis

Eight hundred and seventy-one guts of this species were examined of which 604 (69%) contained recognizable

food items, 222 from the Kleinmond and 191 each from the Bot River and Palmiet estuaries. The size range was 18–69 mm (Table 1).

This species is carnivorous with small invertebrates occurring in all the guts analysed and providing 94% of the total volume consumed (Table 3). Amphipods (66%O, 47%V), insects (45%O, 22%V) and polychaetes (26%O, 11%V) were the most important prey categories (Table 2).

The major difference in diet between samples in the three estuaries was that amphipods provided 74%V in the guts of the Palmiet sample but only approximately 30% in the other two estuaries. Almost all the amphipods consumed in the Palmiet were *G. bonnieroides* whereas in the Kleinmond *G. bonnieroides* and *M. zeylanica* were consumed and in the Bot River estuary *M. zeylanica* and *C. triaenonyx* were almost equally important species. The other notable difference in diets between the estuaries was that aquatic insect larvae (primarily chironomids) provided 37% and 35% of the volume consumed in the Kleinmond and Bot River but < 1% in the Palmiet estuary.

A summary of the diets of three size classes of *P. knysnaensis* from a single Bot River estuary sampling locality is given in Table 11. From this table it is evident that small invertebrates such as copepods (24%V) and ostracods (36%V) predominate in the small size class (< 30 mm) but are relatively unimportant to larger fish. The intermediate size class (30–50 mm) relied primarily on amphipods (40%V) and insect larvae (39%V) and larger fish (> 50 mm) on amphipods (42%V), decapods (22%V), insect larvae (16%V) and isopods (11%V).

Some evidence of seasonal differences in diet were apparent in all three estuaries sampled (Table 12). In the Bot River estuary six species provided more than 5% of

Table 11 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Psammogobius knysnaensis* in the Bot River estuary

	Size class		
Prey category	< 30 mm	30–50 mm	> 50 mm
Polychaeta	5	5	6
Copepoda	24	2	–
Ostracoda	36	4	–
Isopoda	3	1	11
Amphipoda	27	40	42
Decapoda	–	1	22
Insect larvae	3	39	16

Table 12 The monthly contribution (%V) of important prey species in the diet of *Psammogobius knysnaensis* in the Bot River, Kleinmond and Palmiet estuaries. Species represented are those which contributed > 5% to overall volume

	Month											
Prey species	J	F	M	A	M	J	J	A	S	O	N	D
Bot River												
Ostracoda	7	1	2	1	–	14	–	12	9	9	2	6
Corophium triaenonyx	12	11	36	40	–	–	–	17	23	–	16	22
Melita zeylanica	31	55	18	32	–	4	–	23	20	10	6	16
Polychaeta	–	–	5	–	–	45	–	16	14	2	6	–
Chironomid larvae	12	10	14	12	–	11	–	5	25	68	25	18
Grandidierella bonnieroides	13	1	1	–	–	–	–	2	1	1	11	10
Kleinmond												
Ostracoda	1	–	1	2	2	7	2	45	24	2	1	2
Melita zeylanica	1	1	–	35	28	18	42	10	1	3	1	–
Polychaeta	26	17	10	–	41	15	8	47	26	1	31	28
Chironomid larvae	68	40	40	26	10	16	32	1	10	85	9	50
Grandidierella bonnieroides	3	22	38	8	9	40	2	1	3	2	55	10
Palmiet												
Ostracoda	–	–	2	2	40	26	20	1	2	–	–	–
Polychaeta	1	–	–	17	23	18	27	8	3	–	–	–
Grandidierella bonnieroides	93	96	95	73	9	25	9	68	88	79	91	97

the total volume of food consumed throughout the year. Most polychaetes were taken between June and September, most chironomid larvae between September and November and most *G. bonnieroides* between November and January. *M. zeylanica* formed a substantial proportion of the diet between February and April but it was also important in other months. The contribution to the diet of the other two important categories, ostracods and *C. triaenonyx*, varied throughout the year. In the Kleinmond estuary the contribution of *M. zeylanica* was greatest from April to July and that of ostracods in August and September. The three other important prey categories (polychaetes, chironomid larvae and *G. bonnieroides*) showed no clear seasonal pattern. Only three categories provided > 5% of the total volume consumed in the Palmiet estuary. Ostracods and polychaetes provided their greatest contributions between April and July, and *G. bonnieroides* was overwhelmingly dominant for the remainder of the year.

Hanekom & Baird (1984) reported that *P. knysnaensis* in the Kromme River estuary fed on copepods, ostracods, isopods, amphipods, tanaids, cumaceans and annelid worms, a diet very similar to that reported above.

Rhabdosargus globiceps

Seventy-eight guts of *R. globiceps* were examined and 67 of them contained food, 19 from the Palmiet, 26 from the Kleinmond and 22 from the Bot River estuary. The size range of fish containing food was 28–192 mm in the Palmiet, 27–134 mm in the Kleinmond and 208–340 mm in the Bot River (Table 1).

Combined samples from the three estuaries indicated that algae (46%V), molluscs (23%V), decapods (20%V) and fish (8%V) were the main diet of this species (Table 2). There were, however, some differences in diet between the three estuaries. Isopods and amphipods, for example, provided approximately 5%V in the Palmiet but only 1–2%V in the Kleinmond and < 0,5%V in the Bot River estuary. Decapods which provided 38%V and 32%V in the Palmiet and Kleinmond estuaries provided only 18%V in the Bot River estuary. The opposite trend was true for molluscs, fish and algae, all of which were more important in the diet of the Bot River sample.

Sample sizes were too small to detect dietary changes with size or season but superficial examination of the data indicated that very small prey items such as copepods and ostracods were only present in fish of < 50 mm.

A detailed examination of the diet of juvenile *R. globiceps* in the Hermanus lagoon was provided by Talbot (1955). He found that this species consumed a wide variety of both 'hard' and 'soft' foods with filamentous algae occurring most frequently. Other common food items were amphipods, isopods and small gastropods. He also showed that very small fish (20–40 mm) fed primarily on planktonic organisms before diversifying to a wider variety of small invertebrate prey. Only when in excess of 100 mm did they start consuming 'hard' prey such as gastropods. No major changes in diet with season were reported.

Samples of guts of adult *R. globiceps* from the marine environment have been examined by Talbot (1955) and Buxton & Kok (1983). These authors show that small crustacea, bivalves, echinoids and polychaetes are the most important dietary components and that plant material is seldom consumed.

Rhabdosargus holubi

Sixty-five guts of *R. holubi* were examined of which 59 contained food, 14, 33 and 12 from the Palmiet, Kleinmond and Bot River estuaries respectively. The size ranges were 20–195 mm (Palmiet), 22–155 mm (Kleinmond) and 271–368 mm in the Bot River estuary (Table 1).

Approximately 59% of the volume of food consumed by *R. holubi* in the three estuaries was aquatic plant material and 41% invertebrates. The plant component comprised algae (primarily *Cladophora* sp. 26%V) and spermatophytes (primarily *Potamogeton* sp. 21%V). The invertebrate categories were molluscs, primarily *Hydrobia* sp. (20%V), and decapods, of which *C. kraussi* (16%V) was the most important species (Table 4). There was very little variation in diet between the three estuaries despite the large discrepancy in the size of the fish sampled. The four major food categories mentioned above provided 88–99% of the total amount of food consumed in the three estuaries and the only variation between them was that the contribution of vascular plants was smaller in the Palmiet estuary.

The diet of *R. holubi* has previously been examined by a number of authors. Blaber (1974) analysed guts from four eastern Cape estuaries and found that macrophytes and green algae provided an average of 81% of the diet with invertebrates, primarily amphipods, isopods and decapods, making up the remainder. Whitfield (1984) examined the guts of a similar size range (approx. 60–170 mm) in Swartvlei and showed that plants made up 55–72% of the diet, with *Musculus virgiliae* and *H. orbiculare* the only two important invertebrate species. The gut contents of smaller fish were examined from the Kromme estuary (Hanekom & Baird 1984), the Mhlanga estuary and Swartvlei (Whitfield 1985). In the Kromme estuary where the size range of fish examined was (20–60 mm) plants dominated the diet, whereas in the Mhlanga estuary and Swartvlei where fish of < 35 mm were examined there was no plant material and copepods, crustacean larvae, chironomid larvae and amphipods provided the bulk of the diet. Large individuals (> 150 mm) both in estuaries (Blaber 1974) and in the marine environment (Buxton & Kok 1983) consume primarily invertebrates with bivalves, polychaetes and decapods being the most important categories.

Sarpa salpa

The guts of six individuals of this species from the Bot River estuary were examined and all contained food. Algae, primarily *Cladophora* sp. and vascular plant material (primarily *Ruppia* sp.) occurred in all guts in approximately equal quantities and together provided over 99% of the contents. Very small amounts of insect

Table 13 The percentage composition (%V) of the major prey categories in the diets of three size classes of *Syngnathus acus* in the Bot River estuary

	Size class		
Prey category	< 70 mm	70–120 mm	> 120 mm
Copepoda	72	42	39
Isopoda	5	9	19
Amphipoda	21	46	39
Insect larvae	2	2	2

larvae and gastropods were also present.

The diet of this species in both the estuarine and marine environments has been described by a number of authors. Post larvae and small juveniles (< ± 20 mm) consume primarily copepods (Christensen 1978; Whitfield 1985) but larger fish feed almost exclusively on aquatic plants (Christensen 1978; Joubert & Hanekom 1980; Gerking 1984).

Syngnathus acus

This species was rare in the Palmiet and Kleinmond estuaries, consequently the entire sample for stomach content analysis was obtained from the Bot River estuary.

Small Crustacea were the only prey consumed (Table 3) and copepods (91%O, 43%V), amphipods (44%O, 42%V) and isopods (22%O, 13%V) were the only important prey categories. Within these categories *P. hessi* (27%V), *M. zeylanica* (27%V), *C. triaenonyx* (14%V) and *Exosphaeroma* sp. (8%V) were the most important species (Table 4).

Changes in diet with size were evident (Table 13). Copepods provided 71% of the volume consumed by the small size class (< 70 mm) but were less important in the diet of larger fish. Amphipods, on the other hand, although providing 21% of volume in the smaller size class, were twice as important to larger fish. The proportion of isopods increased with increasing fish size but insect larvae remained unchanged.

Day *et al.* (1981) reported that *S. acus* feeds on zooplankton, primarily copepods and amphipods. Hanekom & Baird (1984) reported that two specimens from the Kromme river estuary contained only macrurans.

Conclusions

The diets of some species varied between the three south-western Cape estuaries and between these estuaries and others elsewhere in South Africa. These differences were, however, usually quite small and involved changes only in the relative contribution of particular prey species or categories. For example the amphipod *G. bonnieroides* was common in the diets of carnivores in the Palmiet estuary but only occurred infrequently in samples from the Bot River estuary. The converse was true for *C. triaenonyx*. Omnivores consumed quantities of *Ruppia* sp. and *Potamogeton* sp. in the Bot River estuary but *Enteromorpha* sp., a species seldom found in the guts of fish from the Bot River estuary, was the only frequently consumed weed in the Palmiet estuary. These observed differences in diet between estuaries were never large enough to cause any doubt about the allocation of a particular species to a trophic category and there is evidence that they are attributable to differences in food availability. Branch & Day (1984) provide data that shows *G. bonnieroides* and *Enteromorpha* sp. to be common and *C. triaenonyx, Ruppia* sp. and *Potamogeton* sp. to be rare or absent from the Palmiet estuary whereas Koop *et al.* (1983) and de Decker & Bally (1985) who sampled the Bot River estuary show the opposite.

A striking feature of the dietary data presented here is that fish of < ± 30 mm, regardless of species, all consume minute invertebrates, primarily zooplankton. The importance of zooplankton in the diets of postlarval fish has been examined by Whitfield (1985). He reviews literature that shows zooplankton to be the major nutritional resource of larval and postlarval fish in most aquatic environments and suggests that this is due to the higher energy value of zooplankton relative to other organisms of equivalent size. He considered that consumption of alternative food by fry would occur only where zooplankton stocks are low relative to other detritus based food resources, a situation common in South African estuaries.

When larger than ± 30 mm the fish developed considerably more diverse diets and most of the species specialized to some extent. Two of the species became primarily herbivorous, five became detritivorous, seven remained carnivorous, three became omnivorous and two became piscivorous. When these categories of food are compared with available resources (from data provided by Koop 1982; Koop *et al.* 1983; Branch & Day 1984; de Decker & Bally 1985) it is apparent that the whole spectrum of available food is utilized by the fish fauna.

If Whitfield (1985) is correct in arguing that fry will benefit from eating only zooplankton, then the consumption of less energy rich invertebrates (such as amphipods) by the fish species sampled in this study suggests that zooplankton may be in short supply. A similar line of thought could also be used to explain the consumption of large quantities of plants by the three omnivores, *R. globiceps, R. holubi* and *L. lithognathus*. The diets of these species change from zooplankton in fry (< 30 mm) to primarily small invertebrates (when the fish are 30–100 mm) and then to a mixture of small invertebrates, larger invertebrates and weed. In the marine environment these species eat almost entirely invertebrates (Talbot 1955; Mehl 1973; Buxton & Kok 1983). When one considers that plant material is less digestible and energy rich than invertebrates (Brett & Groves 1979) this might suggest that the consumption of weed in estuaries occurs because the larger size classes of invertebrates are not available in sufficient quantities.

The existence or intensity of competition between fish species, and whether or not food is in any way limiting, cannot be ascertained from the data presented in this

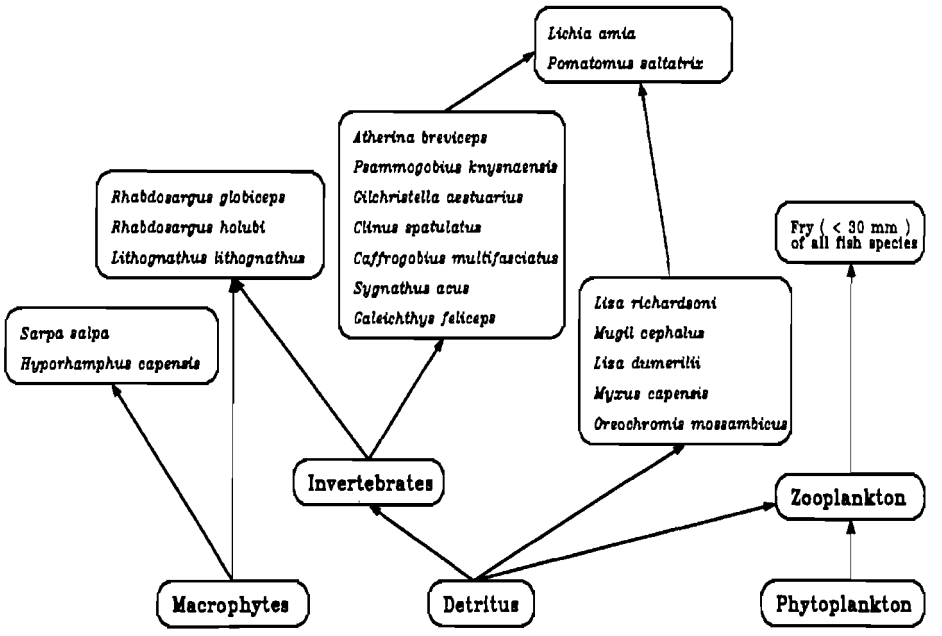

Figure 2 A summary of the most important trophic links betwen fish species common in the Bot River, Kleinmond and Palmiet estuaries in the south-western Cape.

paper. Only when details of the mechanisms of resource partitioning between species have been elucidated and when the total annual production of the food resources and consumption by the fish community are available, will a greater understanding of the trophic interrelationships within south-western Cape estuaries be possible.

Trophic relationships between the fish species examined in this study are summarized in Figure 2. There were three primary sources of food; phytoplankton, aquatic macrophytes and detritus. None of the fish species examined consumed significant amounts of phytoplankton although this food source may have been of some importance in supporting the fry of all species via zooplankton. Macrophytes were consumed directly by the two herbivores and formed a significant proportion of the diets of the three omnivores. The major proportion of the south-western Cape fish population, however, relied either directly or indirectly on detritus, a feature that it has in common with estuarine fish populations elsewhere in South Africa (Day *et al.* 1981) and worldwide (Odum, Zieman & Heald 1972; Carr & Adams 1973; Fagade & Olaniyan 1973).

Acknowledgements

I thank the South African Nature Foundation (affilated to the World Wildlife Fund) and the Estuaries Programme of the South African National Committee for Oceanographic Research for funding this work, Prof. G.M. Branch of the University of Cape Town for his enthusiastic support and the people, too numerous to name here, who assisted me in the field and laboratory.

References

BENNETT, B.A. 1983. *Clinus spatulatus,* a new species of clinid fish (Perciformes: Blennoidei) from South Africa, with a modified definition of the genus *Clinus*. *Spec. Publ. J.L.B. Smith Inst. Ichthyol.* 29: 1–9.

BENNETT, B.A. 1985. A mass mortality of fish associated with low salinity conditions in the Bot River estuary. *Trans. Roy. Soc. S. Afr.* 45: 437–447.

BENNETT, B.A. 1989. A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the southwestern Cape, South Africa. *S. Afr. J. Mar. Sci.* 8: in press.

BENNETT, B.A., HAMMAN, K.C.D., BRANCH, G.M. & THORNE, S.C. 1985. Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Trans. Roy. Soc. S. Afr.* 45: 449–464.

BERG, J. 1979. Discussion of the methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavenscus* (Gobiidae). *Mar. Biol.* 50: 263–273.

BLABER, S.J.M. 1974. Field studies of the diet of *Rhabdosargus holubi* (Pisces: Sparidae). *J. Zool. Lond.* 173: 407–417.

BLABER, S.J.M. 1976. The food and feeding ecology of Mugilidae in the St Lucia lake system. *Biol. J. Linn. Soc.* 8: 267–277.

BLABER, S.J.M. 1977. The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biol. J. Linn. Soc.* 9: 259–275.

BLABER, S.J.M. 1979. The biology of filter-feeding teleosts in Lake St Lucia, Zululand. *J. Fish. Biol.* 15: 37–59.

BLABER, S.J.M. 1984. The diet, food selectivity and niche of *Rhabdosargus sarba* (Teleostei: Sparidae) in Natal estuaries. *S. Afr. J. Zool.* 19: 241–246.

BLABER, S.J.M., CYRUS, D.P. & WHITFIELD, A.K. 1981. The influence of zooplankton food resources on the morphology of the estuarine clupeid *Gilchristella aestuaria* (Gilchrist, 1914). *Env. Biol. Fish.* 6: 351–355.

BLABER, S.J.M. & WHITFIELD, A.K. 1977. The feeding of juvenile mullet (Mugilidae) in south-east African estuaries. *Biol. J. Linn. Soc.* 9: 277–284.

BRANCH, G.M. & DAY, J.A. 1984. Ecology of South African estuaries: Part XIII. The Palmiet River estuary in the south-western Cape. *S. Afr. J. Zool.* 19: 63–77.

BRETT, J.R. & GROVES, T.D.D. 1979. Physiological energetics. In: Fish physiology, (eds) Hoar, W.S., Randall, D.J. & Brett, J.R. Academic Press, New York.

BUXTON, C.D. & KOK, H.M. 1983. Notes on the diet of *Rhabdosargus holubi* (Steindachner) and *Rhabdosargus globiceps* (Cuvier) in the marine environment. *S. Afr. J. Zool.* 18: 406–408.

CARR, W.E.S. & ADAMS, C.A. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102: 511–540.

CHRISTENSEN, M.S. 1978. Trophic relationships in three species of sparid fish in the South African marine littoral. *Fish. Bull. U. S.* 76: 389–401.

COETZEE, D.J. 1981. Analysis of the gut contents of the needlefish, *Hyporhamphus capensis* (Smith) from Rondevlei, southern Cape. *S. Afr. J. Zool.* 16: 14–20.

COETZEE, D.J. 1982a. Stomach content analysis of the leervis *Lichia amia* (L.), from the Swartvlei system, southern Cape. *S. Afr. J. Zool.* 17: 177–181.

COETZEE, D.J. 1982b. Stomach content analyses of *Gilchristella aestuaria* and *Hepsetia breviceps* from the Swartvlei system and Groenvlei, southern Cape. *S. Afr. J. Zool.* 17: 59–66.

COETZEE, D.J. & POOL, R.C. 1985. Stomach content analysis of the sea barbel *Galeichthyes feliceps* (Valenciennes in C & V), from the Swartvlei system, southern Cape. *S. Afr. J. Zool.* 20: 33–37.

CYRUS, D.P. & BLABER, S.J.M. 1982. Mouthpart structure and function and the feeding mechanism of *Gerres* (Teleostei). *S. Afr. J. Zool.* 17: 117–121.

CYRUS, D.P. & BLABER, S.J.M. 1983. The food and feeding ecology of Gerreidae, Bleeker 1859, in the estuaries of Natal. *J. Fish. Biol.* 22: 373–393.

DAY, J.H., BLABER, S.J.M. & WALLACE, J.M. 1981. Estuarine fishes. In: Estuarine ecology with particular reference to southern Africa, (ed.) Day, J.H. Balkema, Cape Town. pp. 197–221.

DE DECKER, H.P. & BALLY, R. 1985. The benthic macrofauna of the Bot River estuary, South Africa, with a note on its meiofauna. *Trans. Roy. Soc. S. Afr.* 45: 379–396.

FAGADE, S. O. & OLANIYAN, I.O. 1973. The food and feeding interrelationship of the fishes in the Lagos Lagoon. *J. Fish. Biol.* 5: 205–225.

GERKING, S.D. 1984. Assimilation and maintenence ration of an herbivorous fish, *Sarpa salpa,* feeding on a green alga. *Trans. Am. Fish. Soc.* 113: 378–387.

HANEKOM, N. & BAIRD, D. 1984. Fish community structures in *Zostera* and non-*Zostera* regions of the Kromme estuary, St Francis Bay. *S. Afr. J. Zool.* 19: 295–301.

HYNES, H.B.N. 1950. The food of freshwater sticklebacks. *J. Anim. Ecol.* 19: 36–58.

JOUBERT, C.S.W. & HANEKOM, P.B. 1980. A study of feeding in some inshore reef fish of the Natal coast, South Africa. *S. Afr. J. Zool.* 15: 262–274.

KOOP, K. 1982. Bot/Kleinmond system (CSW 13). In: Estuaries of the Cape Part II: Synopses of available information on individual systems. (Eds) Heydorn, A.E.F. & Grindley, J.R. Report No. 18. *Res. Rep. S. Afr. Coun. sci. ind. Res.* 417: 1–62.

KOOP, K., BALLY, R. & McQUAID, C.D. 1983. The ecology of South African estuaries part XII: The Bot River, a closed estuary in the south-western Cape. *S. Afr. J. Zool.* 18: 1–10.

LASIAK, T.A. 1984. Aspects of the biology of three benthic-feeding teleosts from King's Beach, Algoa Bay. *S. Afr. J. Zool.* 19: 51–56.

MARAIS, J.F.K. 1984. Feeding ecology of major carnivorous fish from four eastern Cape estuaries. *S. Afr. J. Zool.* 19: 210–223.

MASSON, H. & MARAIS, J.F.K. 1975. Stomach content analysis of mullet from the Swartkops estuary. *Zool. Afr.* 10: 193–207.

MEHL, J.A.P. 1973. Ecology, osmoregulation, and reproductive biology of the white steenbras, *Lithognathus lithognathus* (Teleostei: Sparidae). *Zool. Afr.* 8: 157–230.

ODUM, W.E., ZIEMAN, J.C. & HEALD, E.J. 1972. The importance of vascular plant detritus to estuaries. In: Coastal marsh and estuary management, (ed) Chabreck, R.H. Louisiana State University, Baton Rouge.

SMALE, M.J. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 3. The occurrence and feeding of *Argyrosomus hololepidotus, Pomatomus saltatrix* and *Merluccius capensis. S. Afr. J. Zool.* 19: 170–179.

SMALE, M.J. & KOK, H.M. 1983. The occurrence and feeding of *Pomatomus saltatrix* and *Lichia amia* juveniles in two Cape south coast estuaries. *S. Afr. J. Zool.* 18: 337–342.

TALBOT, F.M. 1955. Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier) and on the fish fauna of the Klein River estuary. *Trans. Roy. Soc. S. Afr.* 34: 387–407.

TALBOT, M.M. 1982. Aspects of the ecology and biology of *Gilchristella aestuaria* in the Swartkops estuary. Unpubl. M.Sc. thesis, University of Port Elizabeth, Port Elizabeth.

VAN DER ELST, R.P. 1976. Game fish of the east coast of southern Africa. 1. The biology of the elf *Pomatomus saltatrix* (L.) in the coastal waters of Natal. *Investl Rep. oceanoar. Res. Inst.* 44: 1–59.

WHITE, P.N. & BRUTON, M.N. 1983. Food and feeding mechanisms of *Gilchristella aestuarius. S. Afr. J. Zool.* 18: 31–36.

WHITFIELD, A.K. 1980. A quantitative study of the trophic relationships within the fish community of the Mhlanga estuary, South Africa. *Est. coast. Mar. Sci.* 10: 417–435.

WHITFIELD, A.K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. *Estuar. Coastl Shelf Sci.* 18: 315–329.

WHITFIELD, A.K. 1985. The role of zooplankton in the feeding ecology of fish fry from some southern African

estuaries. *S. Afr. J. Zool.* 20: 166–171.

WHITFIELD, A.K. & BLABER, S.J.M. 1978a. Scale eating habits of the marine teleost *Terapon jarbua* (Forskal). *J. Fish Biol.* 12: 61–70.

WHITFIELD, A.K. & BLABER, S. J. M. 1978b. Food and feeding ecology of piscivorous fishes at lake St Lucia, Zululand. *J. Fish Biol.* 13: 675–691.

WHITFIELD, A.K. & BLABER, S.J.M. 1978c. Resource partitioning among iliophagous fish in Lake St Lucia, Zululand. *Env. Biol. Fish.* 3: 293–296.