The diets of littoral fish from the Cape Peninsula

B. Bennett, C.L. Griffiths and Mary-Louise Penrith

Zoology Department, University of Cape Town, and South African Museum, Cape Town

Intertidal fish communities in the south-western Cape have a high density and biomass, implying that the fish are important consumers in the intertidal zone. Stomach content analyses of 20 species were undertaken to ascertain which food resources are most heavily exploited and the extent to which the co-existing fish compete for the same food resources. Three prey types, amphipods, isopods and polychaetes, occur in the diets of almost all the species examined and together comprise more than half the total volume consumed by 14 of the species. Despite the overlap in food types consumed, there was considerable subdivision of the resource, much of which may be explained in terms of horizontal and vertical distribution patterns of the various fish species, their habitat preferences, mouth sizes and changes in diet during growth. The standing stock of food in the pools is thought to be too low to support the resident fish populations, suggesting that some food, at least, is obtained outside the pools while the tide is in. For this reason, the fish are considered to be concentrated in the pools at low tide, indicating that the availability of suitable pool habitats may be important in controlling the densities of intertidal fish communities.

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Visbevolkings van die getysones van die suidwestelike Kaap het hoë digthede en biomassas, wat aandui dat die visse belangrike roofdiere van die sone is. Maaginhoudanalises van 20 spesies is onderneem om vas te stel watter voedselbronne die meeste benut word en die mate van kompetisie tussen simpatriese vissoorte vir dieselfde voedselsoorte. Drie prooi-kategorieë, nl. Amphipoda, Isopoda en Polychaeta kom voor in al die spesies wat ondersoek is en vorm saam meer as die helfte van die totale volume wat deur 14 spesies geëet is. Ten spyte van die oorvleueling van voedselkategorieë, was daar heelwat verdeling van die bron, wat grotendeels verklaar kan word deur die horisontale en vertikale verspreidingspatrone van die onderskeie visspesies se habitatvoorkeure, mondgroottes en verandering van dieet gedurende groei. Die gedagte bestaan dat die biomassa van die voedsel te laag is om die plaaslike visbevolking te onderhou, wat daarop dui dat ten minste 'n gedeelte van die voedsel ver buite die poele gedurende hooggety verkry word. Daar word dus aangeneem dat die visse gedurende laaggety in die poele gekonsentreer is, wat aandui dat die beskikbaarheid van geskikte poelhabitatte belangrik kan wees ten opsigte van die beheer van die digtheid van die visbevolkings van die getysones.

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B. Bennett* and C.L. Griffiths
Zoology Department, University of Cape Town, Rondebosch, 7700
Republic of South Africa
Mary-Louise Penrith
Present address: Transvaal Museum, Pretoria
*To whom correspondence should be addressed

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Little information on the feeding ecology of South African littoral fish has been published. In 1945 Smith made the observation that clinids, the most abundant group, were carnivorous. Since then, data on the diets of eight species sampled from the intertidal zone have been published, all by people working in the eastern Cape. Christensen examined the dietes of *Clinus cottoides* (1978a), *Pavoclinus graminis* and *P. laurentii* (1978b), and three sparid species (1978c). Stobbs (1980) provided information on the feeding of *Chorisochismus dentex* and Butler (1982) attempted to relate the feeding of *Caffrogobius caffer* with the tidal cycle and time of day.

Despite the paucity of published works, a considerable body of unpublished information is available on the feeding ecology of intertidal fishes, particularly in the south-western Cape. Penrith's (1965) doctoral thesis includes a detailed analysis of the diets of six common clinid species and notes on several others; Pitt-Kennedy (1964), in an honours project, examined the diets of the two most abundant gobiid species; Jackson (1950) in his unpublished M.Sc. thesis, provides brief notes on the diets of six clinid species, a goby and *Chorisochismus dentex*; Hutchings (1968) described the diet of the sparid *Sarpa salpa*; and Branch (unpublished) has accumulated a considerable amount of fish feeding data during his extensive studies of intertidal communities.

Further information has recently been collected by Bennett & Griffiths (unpubl.) in the course of an analysis of distribution patterns of littoral fish on the Cape Peninsula. For the purposes of the present analysis data from these sources have been pooled to give an overall sample of 1 938 stomachs from twenty different species representing six genera. The data of Hutchings (1968) are not included as *Sarpa salpa* is not usually resident in the intertidal zone and those of Jackson (1950) were presented in insufficient detail to be included in the analysis.

It is hoped that this comparative information will help to indicate which food items are most heavily exploited by littoral fish communities as a whole and show to what extent co-existing species may compete for the same food resources.

Material and Methods

A list of fish species treated in this study, and of the sources of all material referred to, is given in Table 1. The fish were collected at low tide from intertidal rock pools and gulleys, mainly by poisoning with rotenone dissolved in acetone, but hand nets and baited hooks were also used on occasion. All fish were killed by placing in formalin or alcohol, after which they were transferred to formalin for storage.

Only the stomach contents were analysed, food elsewhere

Table 1 Sources of the data on which this study is based

Species	Number of guts examined				
	M-L. Penrith (1965 unpubl.)	G.M. Branch (unpubl.)	S. Pitt-Kennedy (1964 unpubl.)	Present study	Totals
Clinidae					
Clinus acuminatus	30	32		3	65
C. agilis	106			3	109
C. anguillaris		2		15	17
C. berrisfordi				7	7
C. brevicristatus	7				7
C. capensis	8	5		14	27
C. cottoides	169	178		19	366
C. dorsalis	25	18		12	55
C. heterodon	9			50	59
C. superciliosus	312	313		20	645
C. taurus				3	3
C. venustris				18	18
Pavoclinus graminis	9				9
P. mus	109				109
P. pavo	7	2			9
Blennioclinus brachycephalus	47			4	51
Gobiidae					
Caffrogobius caffer		162	96		258
C. nudiceps		5	41	9	55
Gobiesocidae					
Chorisochismus dentex				50	50
Congrogadidae					
Halidesmus scapularis				19	19

in the digestive tract was usually in an advanced stage of digestion and its inclusion in analyses would have prejudiced results in favour of less digestible food items. Sample sizes for each species (Tables 1 and 2) reflect only the number of stomachs examined that actually contained food. Unless otherwise stated, all fish length measurements are standard length (SL).

The stomachs were opened into water in a watch glass or petri-dish under a dissecting microscope and all contents removed. Food items were identified to species wherever possible and then grouped into higher taxa, usually orders. The displacement volume of each category was then measured in 25 or 10-ml measuring cylinders. Where volumes were small (<0,1 ml), volumes were estimated with the aid of an eyepiece micrometer or a 1,0-mm^2 grid placed under the petri-dish.

Several methods have been devised for assessing the relative importance of different food organisms in the diets of fishes. Most of these methods can be criticized on various grounds (see Hynes 1950, Berg 1979). For the purposes of the present study, the volumetric and frequency of occurrence methods were used. Volumes of each prey category are expressed as a percentage of the total volume consumed by each fish species and occurrence is the proportion of stomachs containing a particular food category, expressed as a percentage of total number of stomachs examined.

Results

Twenty species of fish were recovered in sufficient numbers to permit a meaningful analysis of stomach contents. The most abundant group were the Clinidae (klipfishes) with sixteen species (12 *Clinus,* 3 *Pavoclinus* and 1 *Blennioclinus*), which together made up over 70% of the fish caught. The remaining fish consisted of Gobiidae (gobies) with two species, of which one (*Caffrogobius caffer*) was very common, one species of sucker fish *Chorisochismus dentex* (family Gobiesocidae) and the eel-like *Halidesmus scapularis* (Congrogadidae).

The numbers of each species of fish examined, their size ranges and the composition of the stomach contents, by volume and percentage occurrence, are given in Table 2. The percentage occurrence of individual prey species in the stomachs of each fish is shown in Table 3. The feeding habits and diets of each species of fish analysed are discussed individually below.

(1) *Clinus acuminatus* was recorded almost exclusively near the top of the shore in barren rocky pools. It occurs on both the west and south-west coasts but is more abundant west of Cape Point. This species seldom attains more than 120 mm (Penrith 1965).

Sixty-five specimens between 34 mm and 127 mm were found to have food in their stomachs. Decapods (32%), molluscs (19%) and goose barnacles (15%) were the most important food items by volume, although all three categories occurred infrequently. The most frequently occurring food categories were amphipods (62%), isopods (53%) and polychaetes (16%).

Clinus acuminatus changes its diet with increasing size. Fish less than 50 mm rely almost exclusively on amphipods, isopods and polychaetes, while for individuals longer than 80 mm decapods and molluscs are of primary importance, although the other taxa continue to be taken.

No prey species had a particularly high frequency of occurrence in the sample examined (Table 3). Eight species occurred in more than 5% of the fish examined, the amphipods *Paramoera capensis* (12%) and *Hyale* spp. (11%) occurring most often. The occurrence of goose barnacles in the stomachs indicates that *C. acuminatus* will feed opportunistically on any suitable food that becomes available.

(2) *Clinus agilis* is abundant on the west coast, but becomes considerably less common east of Cape Point. This species inhabits weedy pools in the middle and lower areas of the intertidal zone. The species is small, seldom exceeding 100 mm (Penrith 1965).

The stomachs of 109 specimens ranging between 32 mm and 95 mm were examined. In comparison with other clinids, *C. agilis* has a restricted diet, prey from only three categories being consumed in appreciable amounts. Amphipods were the most important constituent with 44% by volume and 84% occurrence. Isopods (23% volume, 46% occurrence) and polychaetes (26% and 34%) were next in importance. Other items such as small gastropods, tanaids and copepods occurred in up to 10% of the stomachs, but did not contribute significantly to volume.

Nine prey species occurred in more than 5% of the fish examined, the more important species were the amphipod *Paramoera capensis*, which occurred in 58% of the fish examined, the isopod *Ianiropsis palpalis* (21%) and the polychaete *Platynereis dumerilii* (25%).

There are no pronounced changes in, or additions to, the diet of this species with increasing size.

(3) *Clinus aguillaris* is an elongate species occurring along both the western and southern Cape coasts at all but the

Table 2 The diets of 20 littoral fish species in the south-western Cape (– indicates <0,5% contribution to volume)

					Food category																									
	Number of	Length range		Mouth size	Amphipods		Isopods		Polychaetes		Tanaids		Molluscs		Copepods		Ostracods		Insects		Decapods		Barnacles		Fish		Algae		Echinoderms		Other	
Species	stomachs	min.	max.	(% SL)	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.	%occ.	%vol.
Clinus acuminatus	65	34	127	12	62	10	53	12	16	7	5	–	5	19	8	–			5	1	11	32	3	15	6	1					11	3
C. agilis	109	32	95	11	84	44	46	23	34	26	9	4	10	–	9	–			1	–	1	–									7	2
C. anguillaris	17	59	186	8	82	18	53	30	6	12			41	2	12	–	6	–			29	38										
C. berrisfordi	7	63	109	12	14	7	71	23	14	1											57	26	86	43								
C. brevicristatus	7	50	61	11	71	50	14				14		28		14																	
C. capensis	27	56	121	11	100	79	11	9	11	7					7	–					7	3							4	–	11	2
C. cottoides	366	33	122	13	65	24	67	30	26	12	4	–	19	2			3	–	2	1	9	14	34	10	2	4					8	3
C. dorsalis	55	36	70	9	82	52	33	24	8	16					2	–			9	2	2	–									16	6
C. heterodon	59	32	108	12	28	21	28	28	22	22	6	2	10	3	8	3			14	15			10	5			2	1				
C. superciliosus	645	25	262	11	82	21	50	9	19	7	10	–	19	18	34	–	18	–	9	–	9	21	3	–	2	8	1	–	1	–	24	16
C. taurus	3	78	231	12	100	75	67	5	67	5			100	5							33	15										
C. venustris	18	32	69	10	73	25	60	20	7	–	7	2	27	2	33	3	13	–			7	9							53	34	13	5
Pavoclinus graminis	9	83	111	8	89	52	11						11		33						22											
P. mus	109	30	96	7	97	48	22	23	9	4			23	6	45	4	11	–			2	14										
P. pavo	9	42	84	8	100		33		11				11																			
Blennioclinus brachycephalus	51	30	92	8	92	51	60	17	26	18	43	12	6	–	9	–	10	–	17	–												
Caffrogobius caffer	258	27	133	11	23	1	19	3	11	1	4	–	19	29	23	–	13	–	9	1	2	3			4	–	51	60				
C. nudiceps	55	35	100	–	41	4	53	73	7	7	6	–	6	11	44	3	16	2	2	–					4	1					12	2
Chorisochismus dentex	50	15	225	16	86	10	86	11	38	6			76	52	4	–	6	–	8	–			10	4			10	8			14	9
Halidesmus scapularis	19	63	145	5	89	52	57	21			31	6	4	–			12	3	4	–							6	1			31	17

Table 3 Percentage occurrence of the prey species most frequently consumed by littoral fish in the south-western Cape. Only those species which occurred in five or more percent of stomachs are considered

	C. acuminatus	*C. agilis*	*C. anguillaris*	*C. berrisfordi*	*C. brevicristatus*	*C. capensis*	*C. cottoides*	*C. dorsalis*	*C. heterodon*	*C. superciliosus*	*C. taurus*	*C. venustris*	*P. graminis*	*P. mus*	*P. pavo*	*B. brachycephalus*	*C. caffer*	*C. nudiceps*	*C. dentex*	*H. scapularis*
Amphiphoda																				
Ampithoe sp.	–	–	6	–	–	–	–	–	–	–	–	–	11	–	–	30	–	–	–	–
Aora typica	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	19	–	–	–	–
Caprella scaura	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	23	–	–	–	–
Ceradocus rubromaculatus	–	–	–	–	–	16	–	–	–	–	33	6	11	–	–	–	–	–	–	–
Gitanopsis pusilla	–	–	–	–	14	–	–	–	–	–	–	–	22	–	–	13	–	–	–	–
Hyale sp.	11	9	18	–	14	16	5	10	22	11	33	11	33	19	22	–	5	–	30	11
Ischyrocerus anguipes	–	5	–	–	43	–	–	–	–	7	–	–	11	75	11	–	–	5	–	–
Jassa falcata	–	6	–	–	–	–	–	–	–	–	–	6	–	–	–	13	–	–	–	–
Lembos sp.	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	13	–	30	–	–
Lysianassa ceratina	–	6	–	–	–	–	–	–	–	7	–	6	–	–	–	13	–	–	–	–
Maera sp.	–	5	–	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–
Melita sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	–	–	–	–	–
Paramoera capensis	12	58	29	–	14	58	18	20	8	38	100	28	56	24	89	–	–	13	12	21
Podocerus africanus	–	–	–	–	43	–	–	–	–	–	–	–	–	19	–	6	–	–	–	–
P. cristatus	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–	9	–	–	–	–
Probaloides rotunda	–	–	–	–	–	26	–	–	–	–	–	11	–	–	–	–	–	–	–	32
Temnophlias capensis	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–
Isopoda																				
Cymodocella sp.	–	–	–	–	–	–	5	–	8	–	–	–	–	–	–	–	–	–	–	–
Dynamenella huttoni	–	–	–	–	–	–	6	–	12	–	–	6	–	–	–	–	–	–	–	–
Exosphaeroma sp.	5	6	18	14	–	–	5	5	6	5	33	11	–	–	22	–	12	36	40	11
E. truncatitelson	8	6	–	–	14	–	8	–	–	–	–	6	–	–	–	–	6	15	8	–
Gnathia sp.	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	5	6	–
Jaeropsis curvicornis	–	–	–	–	–	–	–	–	–	–	33	–	–	–	22	23	–	–	–	–
Ianiropsis palpalis	5	21	12	14	–	–	5	8	–	13	–	–	11	–	–	42	5	–	6	–
Notacellus capensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21
Paridotea ungulata	–	7	–	–	–	–	–	–	–	5	–	–	–	12	–	–	–	–	–	–
Parisocladus perforatus	–	–	–	–	–	–	5	–	6	–	33	–	–	–	–	–	–	–	10	–
P. stimpsoni	6	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	10	–
Stenetrium bartholomei	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Insecta																				
Telmatogeton minor (larvae)	5	–	–	–	–	–	–	8	12	9	–	–	–	–	–	17	9	–	14	–
Tanaidacea																				
Anatanais gracilis	–	8	–	–	14	–	–	–	–	–	–	–	–	–	–	40	–	–	–	–
Leptochelia barnadi	–	–	–	–	–	–	5	–	–	9	–	–	–	–	–	–	–	5	–	11
Polychaeta																				
Gunnarea capensis	–	–	–	–	–	–	–	–	–	–	67	–	–	–	–	13	–	–	38	–
Platynereis dumerilii	–	25	–	–	–	–	9	–	12	7	–	–	–	–	–	9	–	–	–	–
Pomatoleios kraussii	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–
Mollusca																				
Aetoniella nigra	–	8	–	–	29	–	9	–	8	12	67	–	11	5	11	6	–	–	–	–
Fissurella sp.	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–
Gibbula rosea	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helcion pectunculus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
H. pruinosis	–	–	12	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	18	–
Marginella capensis	–	–	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxystele spp.	–	–	6	–	–	–	6	–	6	–	–	–	–	–	–	–	12	–	6	–
Patella barbara	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	–
P. granatina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–
P. granularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–
Siphonaria sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–
Tricolia sp.											67	–	–	11						

Table 3 (continued)

	C. acuminatus	*C. agilis*	*C. anguillaris*	*C. berrisfordi*	*C. brevicristatus*	*C. capensis*	*C. cottoides*	*C. dorsalis*	*C. heterodon*	*C. superciliosus*	*C. taurus*	*C. venustris*	*P. graminis*	*P. mus*	*P. pavo*	*B. brachycephalus*	*C. caffer*	*C. nudiceps*	*C. dentex*	*H. scapularis*
Pycnogonida																				
Tanystylum brevipes	–	–	–	–	29	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–
Ophiuroidea	–	–	–	–	–	–	–	–	–	–	–	53	–	–	–	–	–	–	–	5
Decapoda																				
Cyclograpsus sp.	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plagusia chabrus	5	–	24	43	–	5	7	–	–	–	33	6	22	–	–	–	–	–	–	–
Copepoda																				
Harpacticoidea	–	8	6	–	14	–	–	–	8	–	–	22	33	43	9	–	5	30	–	–

highest intertidal levels. Larger individuals are found lower on the shore than juveniles. The largest recorded specimen is 278 mm (Penrith 1969).

Seventeen specimens between 59 mm and 186 mm long were examined. Amphipods (82%), mainly *Paramoera capensis* and *Hyale* spp., and isopods (53%), mainly *Ianiropsis palpalis* and *Exosphaeroma* spp. occurred most frequently and provided 18% and 30% of the volume respectively. Decapods, mainly *Plagusia chabrus*, were the single most important food category, providing 38% of the volume consumed and occurring in 29% of the stomachs examined. Small molluscs occurred in 41% of the stomachs, but provided very little volume, the two most common species being *Marginella capensis* and *Helcion pruinosus*.

Although sample size was small there was definite evidence that diet changed with size. Small prey items such as amphipods, isopods and polychaetes were important to smaller individuals, whereas decapods and, to a lesser extent, molluscs became important in larger fish.

(4) *Clinus berrisfordi* is a little-known south-coast species. It occurs in rocky pools at the bottom of the intertidal zone. The largest recorded specimen is 109 mm long.

The seven specimens examined, ranging between 63 mm and 109 mm, all contained food. Barnacle cirri occurred in six of the individuals and constituted 43% of the total stomach content volume. The other apparently important food categories were decapods (*Plagusia chabrus*), which occurred in four of the specimens (26% by volume) and the isopods *Exosphaeroma* spp., *Gnathia* spp. and *Ianiropsis palpalis*, which occurred in five of the fish, making up 23% of the volume.

(5) *Clinus brevicristatus*. This is a rare species found in weedy pools in the lower intertidal zone from False Bay westwards. It seldom attains more than 100 mm in length (Penrith 1965).

The seven specimens examined ranged between 50 mm and 61 mm long. Amphipods were the only important diet category, occurring in five of the stomachs and accounting for half the volume. Eleven prey species were identified in the stomach contents, *Ischyrocerus anguipes* and *Podocerus africanus* being the most frequently occurring. Five other categories were present, each only represented by one identified species.

(6) *Clinus capensis* is a moderately elongate species with an acutely pointed snout and is the only species recorded here that bears barbels on its chin and snout. It is common in rocky pools low on the shore and subtidally from False Bay eastwards, but rare along the west coast, and attains 246 mm (Penrith 1969).

Twenty-seven specimens between 56 mm and 121 mm in length had food in their stomachs. Every individual contained amphipods which made up 79% of the volume consumed. Isopods and polychaetes were found in three fish and constituted nine and seven percent of the total volume respectively.

Four amphipod species and one isopod were identified. *Paramoera capensis* was found in 58% of stomachs, *Probaloides rotunda* in 26%, *Ceradocus rubromaculatus* and *Hyale* spp. in 16%. The isopod was *Stenetrium bartholomei*.

Decapod larvae, which were considerably larger than all the other prey items consumed by *C. capensis*, were found in two individuals of moderate size. There is, however, no evidence to suggest that a change in diet occurs with increasing size, since the major food of all species was small items even though mouth size of small individuals would have allowed the consumption of larger prey species.

(7) *Clinus cottoides* was the most abundant intertidal species from Cape Point eastwards. It is also very abundant on the west coast, though ranking second to *C. superciliosus*. *Clinus cottoides* occurs at all levels of the shore, but is most common in rocky pools at mid-tide levels. It is a smaller species than *C. superciliosus*, specimens over 115 mm being unusual (Penrith 1965).

A total of 366 guts from individuals ranging between 33 and 122 mm in length were analysed. Volumetrically isopods (30%) and amphipods (24%) were the most important food categories, but decapods (14%), polychaetes (12%) and barnacle cirri (10%) were also important. The most frequently occurring categories were isopods (67%), amphipods (65%) and barnacle cirri (34%).

Christensen (1978a) examined the stomachs of 82 *C. cottoides* from the eastern Cape, and the results of this study are similar to those presented here, although in his sample, isopods and polychaetes occurred more frequently and barnacle cirri less frequently.

Small *C. cottoides* feed mainly on amphipods and isopods, but when over 50 mm long a wider range of food items become important. Barnacle cirri occur most frequently in fish between 50 mm and 70 mm, decapods and polychaetes being most important in fish more than 80 mm long.

Seventeen prey species occurred in 5% or more of the guts examined. The barnacle cirri were mainly those of *Tetraclita serrata* and *Octomeris angulosa*, but cirri from other species were also taken. The only other species to occur in more than 10% of stomachs was the amphipod *Paramoera capensis*.

(8) *Clinus dorsalis* is a small elongate species seldom exceeding 70 mm (Penrith 1965). Common on both the western and southern Cape coasts, it is found at all except the very highest intertidal levels.

The stomach contents of 55 specimens ranging between 36 mm and 70 mm were analysed. The most important food category was amphipods which occurred in 82% of the sample constituting 52% of the total volume. Isopods were the second most important group, occurring in 33% of stomachs, and providing 24% of the volume. The only other major food category was polychaetes with 16% volume and 8% occurrence.

Five prey species occurred in 75% of stomachs examined, with *Paramoera capensis* and *Hyale* spp. being the most commonly consumed amphipods, and *Exosphaeroma* spp. and *Ianiropsis palpalis* the important isopods. The larvae of *Telmatogeton minor* occurred in 8% of stomachs.

There was no evidence for a shift in diet composition with increasing size.

(9) *Clinus heterodon* is common on the west coast but very rare in False Bay. It occurs in rocky and weedy pools mainly in the mid- and lower intertidal zone.

Fifty-nine specimens between 32 and 108 mm long were examined. Amphipods, isopods and polychaetes each provided approximately a quarter of the volume consumed and occurred in between 22% and 28% of the fish. Contributions of lesser importance were made by barnacle cirri and insect larvae. Important prey species were *Hyale* spp. and *Dynamenella huttoni* and *Telmatogeton minor*.

Changes in diet with size were apparent. Copepods and tanaids were taken only by fish less than 55 mm long. Isopods became less important with increasing size, although they did occur throughout the size range. Gastropods and chironomid larvae were relatively more important in fish over 80 mm long. The above trends should be treated with some caution since they may represent local food availability, the larger fish analysed all being captured in one area.

(10) *Clinus superciliosus* was the largest and most abundant species examined. It occurs at all intertidal levels and subtidally. Size segregation is apparent with smaller individuals predominating at higher intertidal levels.

A total of 645 stomachs from fish ranging between 25 and 262 mm were analysed. Volumetrically the most important food categories were amphipods (21%), decapods (21%), and molluscs (18%). In terms of occurrence amphipods (82%), isopods (50%) and copepods (34%), dominated the samples.

Changes in the relative importance of the different food categories did occur, larger food items becoming more important in the diets of larger fish. Amphipods, isopods, copepods and polychaetes became less important with increasing size whereas molluscs, decapods and fish are rarely taken by *C. superciliosus* less than 60 mm long and become increasingly more important in the diets of larger individuals.

One hundred and twenty two prey species were identified in the stomachs of *C. superciliosus*, with 11 species occurring in more than 5% of the sample. *Paramoera capensis* (38%) and *Hyale* spp. (11%) are the most commonly occurring amphipods, the isopod *Ianiropsis palpalis* was found in 13%, and the gastropod *Aetoniella nigra* in 12% of the stomachs examined.

(11) *Clinus taurus*. This is a rare species occurring at the bottom of the intertidal zone and subtidally around the entire Cape coast.

Three specimens, 78, 140 and 231 mm were examined and all had food in their stomachs. *Paramoera capensis* occurred in all stomachs and together with two other amphipod species, constituted 75% of the volume. Small molluscs also occurred in all three stomachs, but supplied only 5% of volume. A single crab, *Plagusia chabrus*, made up 15% of the volume.

(12) *Clinus venustris* occurs on the west and south coasts, but is rare east of Cape Point. A small species, it seldom exceeds 110 mm and is found only in low and mid-shore pools (Penrith 1965).

The stomachs of 18 individuals between 32 and 69 mm in length were analysed. Volumetrically the most important food was ophiuroids (34%) which occurred in 53% of stomachs. Six amphipod species, the most common being *Paramoera capensis*, occurred in 73% of the stomachs supplying a quarter of the volume, and isopods, mainly *Exosphaeroma* spp., occurred in 60% of the sample, providing 24% of the volume consumed.

The smallest individuals of this species contained only amphipods, isopods and copepods; whereas in those over 40 mm ophiuroids became important. The largest individual contained a decapod larva.

(13) *Pavoclinus graminis*. Known from False Bay eastwards, found in weedy pools and weedbeds in the lower intertidal zone. Attains approximately 140 mm (Penrith 1965).

The stomachs of nine specimens between 83 mm and 111 mm long were analysed. Amphipods formed 52% of the food volume and occurred in eight of the nine fish. A wide variety of prey species were taken (Table 3), with *Paramoera capensis* and *Hyale* spp. occurring most frequently. Two megalopae of *Plagusia chabrus* were present in the two largest fish and contributed considerably to the stomach contents volume. Christensen (1978b) examined the guts of 66 specimens collected in the eastern Cape and he also found amphipods to be the major food category.

(14) *Pavoclinus mus*. This was the only member of this weed-dwelling genus which was obtained in sufficient numbers to be used for a detailed study of feeding. It is one of the more highly modified weed-dwellers and is always taken amongst algae. *Pavoclinus mus* is a small species, not attaining more than 100 mm (Penrith 1965). It has not been found on the west coast.

Stomachs of 109 specimens between 30 and 96 mm were analysed. Amphipods were the most important food category, occurring in almost all the specimens examined and constituting approximately half of the total volume

of food taken. Isopods were fairly important both in terms of volume (23%) and occurrence (22%). Copepods occurred in a high percentage of fish, but even a large number of harpacticoid copepods occupy only a very small volume.

Polychaetes were not found in fish smaller than 50 mm and their consumption increased in fish over this size. Isopods and molluscs, although present in small fish, become increasingly important in larger individuals. Copepods showed the reverse trend, occurring more frequently in smaller fish. Amphipods had a consistently high occurrence, but their contribution to volume decreased with increasing fish size.

Ten prey species were identified as having occurred in more than 5% of the *P. mus* stomachs examined. The tube-dwelling amphipod *Ischyrocerus anguipes* was by far the most commonly occurring species, being present in 75% of stomachs. Other amphipods, *Paramoera capensis, Podocerus africanus* and *Hyale* spp. were also frequently taken.

(15) *Pavoclinus pavo* occurs in weedy low-shore pools on the west and south coasts, but is nowhere very common. It is a relatively small species rarely reaching 110 mm in length (Penrith 1965).

Nine specimens, 42 mm to 84 mm, were examined. Amphipods formed the dominant food category in all the stomachs. *Paramoera capensis* occurred in eight of the specimens; *Ischyrocerus anguipes, Hyale* spp. and *Melita subchaelata* were also recorded. Small individuals of *Exosphaeroma* sp. and *Jaeropsis curvicornis* and the minute gastropod *Aetoniella nigra* were also recorded in one or more stomachs.

(16) *Blennioclinus brachycephalus* is locally common in low-shore pools east of Cape Point and less common along the west coast, where it is found only in sheltered areas. It is a small species apparently not attaining more than 100 mm (Penrith 1965).

Fifty-one stomachs from fish ranging between 30 and 92 mm in length were examined. Amphipods were the most important food category by both occurrence (92%) and volume (51%). Polychaetes occupied a relatively large volume (18%) and occurred in 26% of the sample. Isopods and tanaids occurred frequently (60% and 43% respectively), but occupied only small volumes.

Eighteen food species occurred in more than 5% of the stomachs examined. The amphipods *Caprella scaura, Aora typica* and *Ampithoe* spp. occurred in more than 20%, as did the isopods *Ianiropsis palpalis* and *Jaeropsis curvicornis* and the tanaid *Anatanais gracilis.*

Changes in diet composition with growth in this species appear to be negligible, no new categories or species becoming important as the fish increase in size.

(17) *Caffrogobius caffer* is the dominant species in barren high-shore pools east of Cape Point. It becomes progressively less abundant down the shore.

The stomachs of 258 fish between 27 and 133 mm long were examined. In terms of both volume and occurrence algae were the most important food category, comprising 61% and 51% respectively. *Ulva* spp. were the main algal species consumed but *Enteromorpha* sp., *Sargassum* sp. and *Cladophora* sp. were also taken. The only other important food category was molluscs (29% volume and 19% occurrence), *Oxystele* sp. being the most commonly consumed species. Amphipods (23%), isopods (19%), copepods (23%) and polychaetes (11%) all occurred frequently but, relative to the algae, their volume was very small.

Caffrogobius caffer exhibits a change in diet with size, small specimens being predominantly carnivorous whereas larger individuals are omnivorous, consuming large amounts of algae. The change-over occurs between 50 and 70 mm.

This species does appear to gain nutritional benefit from the algae it consumes, for Hamerton (1982) has shown that the energy content of faecal algae is lower than that ingested and, in addition, demonstrated destruction of the algal cells during passage through the gut.

(18) *Caffrogobius nudiceps* occurs in high amd midshore pools both east and west of Cape Point, but is more abundant on the west coast.

The stomachs of 55 specimens between 35 and 100 mm were analysed. This species was found to be entirely carnivorous with isopods of the genus *Exosphaeroma* dominating the diet (73% volume and 53% occurrence). Amphipods (41%), copepods (44%) and ostracods (16%) occurred frequently but together comprised only 9% of the volume.

There is some evidence of a change of diet with size, larger individuals taking larger food items such as fish and chitons, but the smaller prey categories continued to be important throughout the size range.

(19) *Chorisochismus dentex* is a relatively large species abundant on both the east and west coasts in rock pools from midshore downwards. Large individuals occur only near the low-water mark and subtidally. The species attains a total length of at least 300 mm (Smith 1965) and has a relatively very large mouth. It is the only species among those studied with large, strong incisors.

Fifty specimens 15 – 225 mm were examined. Amphipods and isopods occurred in 86% of the sample, but each made up only 10% of the volume of food consumed. The most important food category was molluscs, mainly limpets, which occurred in 76% of the stomachs examined and provided half of the volume. Polychaetes, sea urchins, chitons and barnacle cirri occurred in varying numbers of stomachs and provided between 4% and 8% of the volume.

Marked size-related trends in feeding were observed. Fish less than 25 mm long consumed only small crustaceans, mainly amphipods and isopods, although ostracods and copepods were important in the smallest fish. Crustaceans continued to be taken in decreasing amounts up to 150 mm after which they were virtually absent from the diet. Molluscs became increasingly important with fish size, occurring in all fish more than 180 mm long. Sea urchins occurred in a few of the largest fish. The heads of *Gunnarea capensis* and barnacle cirri were frequently taken by fish of intermediate size, being absent in all individuals less than 30 mm and more than 160 mm long.

The diet of *C. dentex* has previously been studied by Stobbs (1980) who examined 55 individuals from the eastern Cape. His findings concerning the relative contributions of the different food categories and changes in diet with size are very similar to those described above.

(20) *Halidesmus scapularis* is a small eel-like species, locally common in the lowest intertidal pools east of Cape Point. It attains a total length of approximately 175 mm (Smith 1965).

Nineteen specimens between 63 and 145 mm contained food. Eighty-nine percent of the fish examined contained amphipods, which constituted 52% of the total volume consumed. Isopods occurred in 57% of stomachs providing 21% of the volume. Tanaids and leptostracans occurred frequently, but did not contribute substantially to volume.

The two most important species in the diet of *H. scapularis*, the amphipod *Probaloides rotunda* and the isopod *Notocellus capensis* were species that occurred very seldom in the food of any of the other fish species examined. No change in diet with increasing size was observed, the same small prey species being equally important in all size classes.

Discussion

Species diversity of the rock-pool fish population in the south western Cape is very high, a Shannon-Weiner diversity index of 2,1 being obtained from a recent survey on the east and west coasts of the Cape Peninsula (Bennett & Griffiths, unpubl.). This value is considerably higher than for fish populations sampled in estuaries (1,1), surf zone (1,4) and offshore demersal (1,6) environments in the same area (Bennett, unpubl.). The high diversity of the rock-pool ichthyofauna is remarkable because of the high biomass (49,60 g m^{-2}) and limited range of feeding types inhabiting the pools, all but one species being small, cryptic carnivores.

The co-habitation of numerous, often closely related, species with similar habitat and dietary requirements gives rise to speculation on the possible competitive interactions occurring between them. This question has received attention from workers studying fish assemblages in other parts of the world. Some consider that Gaussian principles do not apply because food is superabundant (Hartley 1948; Larkin 1956). More recently it has been suggested that interspecific and intraspecific differences in ecology serve to reduce competition for food (Gibson 1972; Keast 1970, 1980).

Superficial examination of Table 2 reveals that amphipods, isopods, and to a lesser extent, polychaetes, were the most important food items consumed by intertidal fishes in the south-western Cape. The first two categories occurred in all species examined and the third in 18 of the 20. Together these three groups comprised more than half the total food consumed by 14 of the species.

Despite the large amount of dietary overlap evident from Table 2, not all the species appear to be in direct competition with each other. Many of the species consume food types that are apparently not important in the diets of the rest of the species. For example, molluscs are consumed in varying amounts by 17 of the species but are of special importance in *Chorisochismus dentex*. Decapods are the single most important category in *Clinus anguillaris* and *C. acuminatus*. Barnacle cirri are found in six species, constituting 43% of the volume consumed by *C. berrisfordi*, but were also important to *C. cottoides* and *C. acuminatus*. Ophiuroids were very seldom found in any of the species, but accounted for 34% of the stomach volume of *C. venustris*; algae were important in the diet of *Caffrogobius caffer* but were considered incidental where they occurred in other species. The intensity of competition between the co-habiting species groups is therefore reduced by virtue of the fact that not all species are relying on the same categories for major parts of their diets.

Competition can be further attenuated if fish species feed on different prey species in a category at different intensities. *Blennioclinus brachycephalus*, for example, eats large amounts of the amphipods *Ampithoe* spp., *Aora typica* and *Caprella scaura*, prey species that only occurred in two other fish species. *Halidesmus scapularis* consumes large amounts of *Probaloides rotunda*, a prey species also consumed by only two other species. *Pavoclinus mus* and possibly *C. brevicristatus* rely to a large extent on *Ischyrocerus anguipes*, a prey species unimportant to any other fish examined.

Thus, although all the co-habiting fish species are reliant on the same food categories, the actual species eaten are subdivided between them. Information collected during this study enabled some explanation of how this subdivision may occur.

Differences in distribution

If the species consistently feed in different areas or habitats, competition between them is likely to be reduced or eliminated.

The distribution and type of habitat in which each species is most commonly found has already been given. From this, it is obvious that not all species are found in any particular area. Species such a *Pavoclinus mus, P. graminis* and *Halidesmus scapularis*, for example, are found only to the east of Cape Point, while others, such as *Clinus capensis* and *Caffrogobius caffer*, are considerably more abundant in this area than they are on the west coast. Other species such as *Clinus agilis, C. heterodon* and *C. venustris* are abundant on the west coast but rare on the east coast. These differences in relative abundance will have a direct bearing on the intensity of competition in a particular area.

Vertical differences in relative abundance are also apparent among species that have overlapping horizontal distributions. Some species, for example *Blennioclinus brachycephalus, P. mus* and *H. scapularis*, are restricted to very low shore areas, while others (e.g. *Caffrogobius caffer* and *Clinus acuminatus*) are characteristically high shore forms. Yet another group which includes *C. superciliosus, C. cottoides* and *C. dorsalis* are found at almost all intertidal levels. Most species are, however, most abundant in the middle and lower regions.

Further separation of the species within a specific area of shore is also possible. In the low shore zone, for example, many species may occur together in a pool but *Pavoclinus* species will be absent unless quantities of algae are present. *Clinus agilis* and *C. brevicristatus* are also invariably absent in pools where there is no weed.

Among the species that do occur within a single pool, body shape may allow further sub-division of the habitat. Elongate species such as *C. anguillaris, C. dorsalis* and *H. scapularis* are able to gain access to considerably smaller holes and crevices than those utilized by all but the very smallest individuals of the more conventionally shaped species, and therefore may exploit different food resources. The differences in relative abundances and apparent habitat preferences outlined in the previous section describe the situation only at low tide, when all sampling was conducted. It is likely that the patterns described will change if the fish feed while submerged by the tide.

Feeding in relation to habitat

Little information on the habitat preferences of prey species is available but it was possible to characterize many of them as weed-dwelling, rock-dwelling or ubiquitous (i.e. likely to be found amongst rock and weed). Differences in the contribution of these three categories to the diet of the different fish species indicate where the majority of feeding takes place.

Clinus acuminatus, C. anguillaris and *Chorisochismus*

dentex all contained high proportions of prey items classified as rock-dwellers and significant amounts of ubiquitous species, but almost no weed-dwellers. The reverse was found to be true for *P. mus* in which weed-dwelling prey species were overwhelmingly important. Many of the fish species, especially the more abundant ones, contained mixtures of prey from all habitats. In *C. cottoides* and *C. superciliosus* approximately half the stomach contents were rock-dwelling species and one third were weed-dwellers. *Clinus brevicristatus, C. heterodon* and *C. agilis* contained reasonably equal mixtures of rock and weed-dwelling species, but in these species weed-dwellers tended to predominate. The proportions of different food organisms consumed did not always reflect the type of habitat that the fish species were observed to occupy. *Pavoclinus pavo* and *P. graminis*, although apparently occurring exclusively in weedy areas, contained large amounts of prey species that were considered to be characteristically rock-dwelling.

Blennioclinus brachycephalus, which was not considered to be primarily a weed-dweller, appears to obtain most of its food from within algal mats.

Mouth size

The upper size limit of prey that can be taken by a fish is determined by its mouth size (Keast 1970; Yasuda 1960). In this study, mouth sizes of the species examined ranged between 5% (*H. scapularis*) and 16% (*Chorisochismus dentex*) of standard length. The mouth-size distribution showed two modes, one at 8% comprised of two *Pavoclinus* species, *B. brachycephalus* and *Clinus anguillaris* and the other between 11% and 12% with eight *Clinus* species and the two gobies.

All species with mouths smaller than 10% of standard length relied on small food items to a large extent, the amphipod, isopod and polychaete categories providing at least 50% of the total volume consumed. Larger food items such as decapods, most molluscs and echinoderms were usually absent or, if present, found only in the largest individuals. Certain species with larger mouths also relied heavily on small food items such as *C. agilis* and *C. capensis* which continued to consume small items even when they were large enough to prey on the larger species. The high percentage (>65%) of small food items in *C. cottoides* and *C. heterodon* is due to the size distribution of the samples, for in both species juveniles less than 70 mm long predominated.

Since mouth size is related to body length, the size ranges of different species competing for a food particle of particular size will not be the same. For example, the largest particle taken by *H. scapularis* of 100 mm length will be the same as that for *B. brachycephalus* of 63 mm, *C. superciliosus* of 45 mm and *Chorisochismus dentex* of 34 mm. When the size distribution of the population is taken into account, it appears that competition is most intense for small food items and the number of species competing for larger items is considerably smaller.

Changes in diet during growth

The preceding sections have been primarily concerned with interspecific relationships whereas here intraspecific dietary differences are considered. The ability to take larger food items as the fish increase in size is reflected in some species by a change in the species composition of the diet. In this study, it was not possible to assess confidently whether or not changes in diet occurred in all species, because sample sizes or size ranges were in some cases too small.

More than 50 individuals of each of 11 species were examined. Eight (73%) showed changes in diet with increasing size and three continued to eat small species throughout their size range. For an additional four species more than 10 specimens were examined, of which two species showed some indication that larger fish were relying on larger prey species.

Two of the species that did not change diet as they grew (*Clinus capensis* and *C. agilis*) had mouths more than 10% of body length and three, *C. dorsalis, B. brachycephalus* and *H. scapularis* were small-mouthed species that failed to attain a size large enough to enable them to take the larger size-categories of prey.

Conclusions

The results presented in this paper show that although there is considerable dietary overlap among the 20 fish species examined, there is also considerable subdivision of the food resources between them. Much of the observed subdivision is explainable in terms of horizontal and vertical distributional patterns, habitat preferences, mouth size and changes in diet during growth, but the extent to which these factors reduce competition for food is unknown.

It has been pointed out (Hess 1961) that the degree of competition for food between co-habiting species can be ascertained only when population sizes and production rates of both predators and prey species, as well as the rates at which the prey species are consumed, are known. Quantitative data of this nature are at present unavailable for the species under consideration. A rough estimate of annual consumption and food standing stock is, however, possible and allows speculation on factors possibly active in controlling rock-pool fish populations in the south-western Cape.

The mean fish biomass was found to be 49,60 g m^{-2} (wet mass). If daily consumption is considered to be 5% body weight per day (Pandian 1967; Carline & Hall 1973; Bennett 1979) it is evident that approximately 1 000 g m^{-2} $year^{-1}$ is consumed by the fish population. If the prey production : biomass ratio is considered to be 2 : 5 (McLachlan 1977; Koop & Griffiths 1982), then the standing stock must be in the region of 400 g m^{-2}. Although no measurements have been made, this value is considered to greatly exceed the amount of food available. From this, it may be assumed that many of the fish forage outside the pools when they are immersed or that considerable reliance is placed on food that is washed into the pools from the surrounding areas. For this reason, the fish may be considered to be 'concentrated' in the pools at low tide. If this is the case, then the number of pools, their physical complexity or the number of habitat types within pools in a particular shore area, may be factors affecting rocky shore fish communities. Marsh, Crowe & Siegfried (1978) have, in fact, shown significant positive correlations between the amount of cover present and the abundance and diversity of clinids in south-western Cape rock pools. Food, however, probably also plays some role in limiting the fish populations since the degree of dietary overlap relative to the degree of subdivision between the species is appreciable, indicating that some food categories, at least, may be in short supply.

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