Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters of South Africa

M.J. Smale and M.N. Bruton

Port Elizabeth Museum, Port Elizabeth, and J.L.B. Smith Institute of Ichthyology, Grahamstown

Argyrosomus hololepidotus (kob) is a top predator in the shallow marine environment of the south-eastern Cape. There is considerable change in prey taken over the size range of predators examined (256 – 1701 mm). Young *A. hololepidotus* are planktivorous taking swarming mysids, but as they grow they become piscivorous, feeding on both pelagic and demersal prey associated with soft sediments. The pelagic cephalopod *Loligo reynaudi* is also taken by large specimens. Prey selection varies with locality and time of year. A field experiment in which the prey were compared with fish caught in a small-mesh net revealed a preference for some slow-moving demersal species. The length distributions of dominant prey species are given and these clearly show that larger prey are preferred by larger predators.
S. Afr. J. Zool. 1985, 20: 97 – 108

Argyrosomus hololepidotus (kabeljou) is 'n vername predator in die vlak mariene omgewing van die suidoostelike Kaap. Daar is 'n aansienlike variasie in die prooi wat gevang is in die grootteklasse wat ondersoek is (256 – 1701 mm). Jong *A. hololepidotus* is aanvanklik planktivore wat op swermende Mysidae leef. Later word dit visvretend en benut pelagiese sowel as bodembewonende spesies wat met sagte sedimente geassosieer is. Groot visse voed ook op die pelagiese sefalopood *Loligo reynaudi*. Prooiseleksie varieer met 'n lokaliteit en tyd van die jaar. In 'n veldeksperiment waar prooi vergelyk is met vis wat in 'n kleinmaastreknet gevang is, word 'n positiewe seleksie vir sommige stadigbewegende, bodembewonende spesies getoon. Die lengteverspreiding van belangrike prooisoorte word gegee en dit toon duidelik dat groter predatore groter prooi verkies.
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M.J. Smale*
Port Elizabeth Museum, P.O. Box 13147, Humewood, 6013
Republic of South Africa

M.N. Bruton
J.L.B. Smith Institute of Ichthyology, Grahamstown, 6140
Republic of South Africa

*To whom correspondence should be addressed

Argyrosomus hololepidotus (Lacépède 1802) is a marine and estuarine sciaenid fish which is found south of the equator from the west African coast to Natal, Madagascar, western Indian Ocean off Kathiawar (Seshappa) and off the Australian coast, at least from Brisbane southwards to the Bass Straight (Trewavas 1977).

In the south-eastern Cape *A. hololepidotus* is caught throughout the year by the line-fishery, with highest catches recorded between September and February (Smale 1985). It is common in this area and is the principal species caught by ski-boats over sandy areas. *A. hololepidotus* is frequently recorded in the inshore sole-directed trawl fishery as a by-catch (Hecht 1976; Smale 1985). Juveniles and adults are found in estuaries in Natal and the Cape (Wallace & van der Elst 1975; Wallace 1975; Winter 1979; Marais & Baird 1980a, b). Larvae have occasionally been recorded in the Swartkops estuary (Melville-Smith & Baird 1980).

Large marine nursery areas for *A. hololepidotus* have recently been found in the eastern Cape, particularly in the shallows (< 10 m) of Algoa Bay (Smale 1984). Estuaries are marginal nursery areas for this species, which is far more common in the sea from the surf zone of sandy beaches (Lasiak 1982) to about 150 m (Chao & Trewavas 1981). Both inshore/offshore and longshore movements have been postulated from field sampling (Wallace 1975; Smale 1984, 1985).

This paper reports on a five-year feeding study of *A. hololepidotus* in the marine environment. Feeding preferences are examined by comparing prey taken with inshore small-mesh trawl catches with prey recovered from the stomach contents of the predator.

Materials and Methods

This study was initiated in February 1978 and continued to May 1982, and was run concurrently with an investigation of the biology of the fishes caught by ski-boat anglers in the south-eastern Cape. From the beginning of 1978 to the end of 1980 the important ski-boat launching sites were visited every weekend that weather permitted fishing. Most material was collected from the Port Elizabeth Deep Sea Angling Club, although other clubs as far north as East London (33°02'S/27°55'E) and as far west as Mossel Bay (34°10'S/22°08'E) were visited occasionally between 1979 and 1981. After 1980 line-caught fish were sampled less frequently. Supplementary data on seven large *A. hololepidotus* were collected from trawl samples during 1980 (Smale 1984).

Ski-boats travel as far as 40 km from the launching site but inshore angling (< 8 km from shore) is most common.

Most *A. hololepidotus* were caught using hooks with cut and whole baitfish and squid. Fish caught from various areas and depths were sampled in this way.

As many ski-boat catches as possible were examined each day. All fish were measured, and a subsample was weighed. Stomachs which had not been everted were labelled and kept on ice until processed in the laboratory later that day. Neither formalin nor alcohol was used for field storage of stomach contents as otoliths are etched or made brittle, providing inaccurate measurements or material which is too damaged for accurate identification. Most predators (92%) had either been gutted or had empty or everted stomachs, resulting from capture stress or barotrauma. Regurgitation was accentuated beyond 20 – 30 m, therefore the material best reflects feeding in shallow (< 30 m) marine areas.

In the laboratory stomach contents were sorted, counted, drained and weighed to the nearest 0,1 g. Bait was easily recognized and discarded. Otoliths were removed from fish skulls and cephalopod beaks were removed from buccal masses. The stomach wall and prey remains were thoroughly rinsed in water, causing free otoliths to settle at the bottom of the bowl while free beaks were collected by sieving the fluid. Small invertebrates were removed before washing and, except for cephalopods, all invertebrates were preserved in 10% formalin for later counting and identification. Otoliths were stored dry in labelled vials and cephalopod beaks were preserved in 10% formalin.

Otoliths were examined under a binocular microscope and compared with material held in the otolith collection of the Port Elizabeth Museum. Owing to the complexity of otolith morphology and variations within families, direct comparison with identified material was found to be the best method of identification. The identity of even slightly digested prey was confirmed using otoliths. Otoliths were paired when possible and the highest number of either left or right otoliths counted. Measurements of undigested otoliths were to the nearest 0,01 mm. Digested otoliths were recognized by their chalky eroded appearance and these were not measured. Cephalopod beaks were paired and the highest number of either upper or lower beaks was counted. These were identified by comparison with reference material held in the collection of the Port Elizabeth Museum and by reference to the literature (Clarke 1962; Pinkas, Oliphant & Iverson 1971). Beaks were measured following Clarke (1962) using measuring calipers for those larger than 2 mm and a micrometer eyepiece on a binocular microscope for smaller specimens. Regressions between otolith or beak length against length of whole prey were calculated to obtain estimates of prey size (Smale 1983).

Crustaceans were counted and weighed. In most cases no problems were encountered as species and individuals could be recognized and counted using carapaces or chelae. Mysids and euphausids were counted using the number of eye pairs and, when very large samples were encountered, a subsample was weighed and counted, and the total number in the entire sample was calculated.

Total lenghts (TL) of both *A. hololepidotus* and teleost prey are used throughout. Dorsal mantle lengths (DML) were used for cephalopods, except that ventral mantle lenghts (VML) were used for *Loligo reynaudi*. Total body length was used for mysids.

Stomach contents were analysed using three methods: frequency of occurrence (%F), the numerical method (%N) and the gravimetric method (%M). The use of these three methods largely overcomes the disadvantages of using any one of them alone (Hynes 1950; Windell 1971; Hyslop 1980). Combinations of these measures were not used, as indices of relative importance (IRI) values may compound sources of error (Hyslop 1980).

Original wet mass was used, despite the shortcomings caused by differential digestion rates of prey (Hyslop 1980). As this was primarily a field study, it was beyond the scope of the programme to overcome this problem with experimental digestion studies. Although reconstituted stomach content mass could have been calculated, digestion rates were complicated by large otoliths (e.g. those of Sciaenidae and Sparidae) resisting erosion while small otoliths were digested rapidly once exposed. Cephalopod beaks were also retained in the stomachs and this compounds errors when using reconstituted mass.

An index of food similarity was calculated for each size group, using the method of Field, Clarke & Warwick (1982).

An examination of prey selectivity was possible as an independent assessment of prey availability was provided by an inshore small-mesh trawling survey in the south-eastern Cape in 1980 (Wallace, Kok, Buxton & Bennet 1984; Buxton, Smale, Wallace & Cockcroft 1984; Smale 1984). The research vessel *Thomas B. Davie* was commissioned by the Port Elizabeth Museum to investigate the occurrence of juvenile estuarine-associated species in inshore waters. The principal sampling gear used was a 20 m otter trawl of 50 mm stretch-mesh. The 3 m cod end was lined with 12 mm stretch-mesh knotless anchovy netting. Wooden otter boards of 1,7 × 0,88 m were used. Only catches made in Algoa Bay (Figure 1) were used in this study. Trawls were confined to soft substrata to avoid damage to gear. Stations deeper than 30 m were excluded, as this is the maximum depth from which stomach contents were collected. Of the four quarterly surveys, catches made in February and May were combined and compared with prey of *A. hololepidotus* caught by line fishermen in the same area. The two trawl surveys at the beginning of the year coincided with large feeding samples of *A. hololepidotus* in Algoa Bay and reduced the effect of seasonal variability in the trawl catches and stomach contents. Trawling depths and times varied and a total of 184 min was spent at depths less than 30 m. The net retained the teleost and cephalopod components of the fauna best. To reduce the effect of prey size selection by *A. hololepidotus*, predators of 501 – 1000 mm were used. The maximum prey size taken by predators of this size is similar, about 300 mm. Animals larger than this are unavailable to these predators so they were subtracted from the trawl catch.

The study sample therefore consisted of 90 *A. hololepidotus* of 501 – 1000 mm caught by line fishermen between the Port Elizabeth harbour wall and Bird Island in Algoa Bay from January to June of 1978 to 1981. The predators had taken 250 fish and cephalopod prey. This prey material was compared with 13 550 fish and cephalopods smaller than 300 mm taken by trawling in Febuary and May 1980.

Selectivity was calculated using a modification of the Shorigin index proposed by Berg (1979). The formula is:

$$Sel = \log_{10} \frac{\% \text{ Ni in the ingested food}}{\% \text{ Ni in the potentially available food}}$$

where Sel = food selectivity and % Ni = the numerical percentage of food component i. This modification overcomes the weighting of food preference over food avoidance (Berg 1979). Conversion of this logarithmic food selection index to the original Shorigin index 'k' is performed using the formula:

$$k = 10^{Sel}$$

The scale varies from $-\infty$ for complete avoidance to $+\infty$ for prey consumed which was not sampled by the net. 'Random' feeding scores 0 in the centre of the scale (Berg 1979).
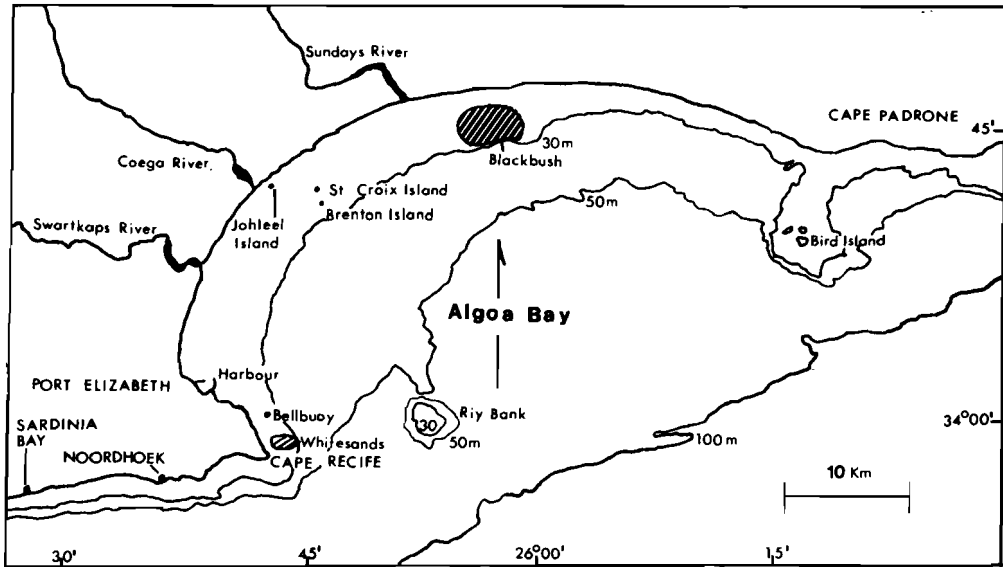
Figure 1 Algoa Bay and environs showing places mentioned in the text.

Results

A total of 6323 *A. hololepidotus* was examined, of which 509 fish had stomach contents. They ranged in size from 226 to 1701 mm and stomachs were collected from specimens ranging from 256 to 1701 mm (Figure 2). The maximum stomach fullness recorded was 8,6% of body mass.
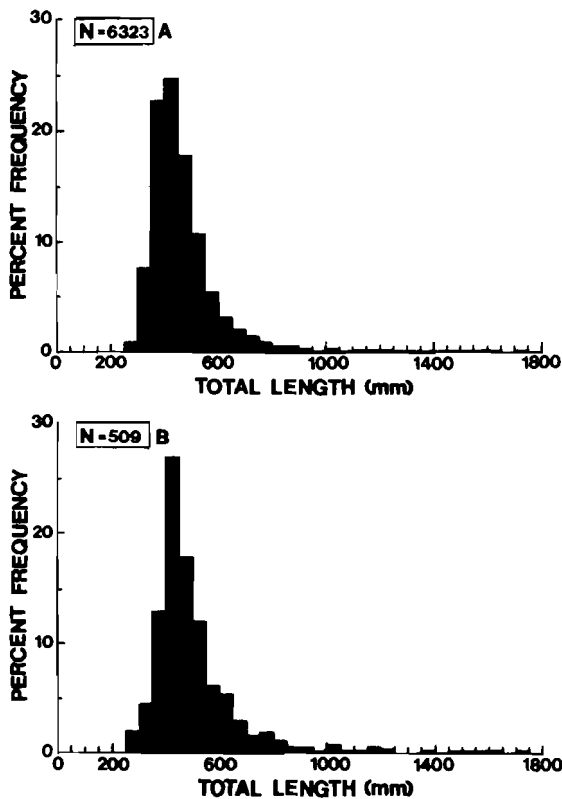

Figure 2 Histograms of the length frequencies of the entire sample of *Argyrosomus hololepidotus* (A) and those with stomach contents (B).

The prey of *A. hololepidotus* are presented according to size of predator in Table 1 and the principal prey (those items which make up more than 4% by two methods of analysis) are shown in Figure 3. The prey of specimens of 200 – 300 mm consisted principally of crustaceans (99,7% by number, 89%
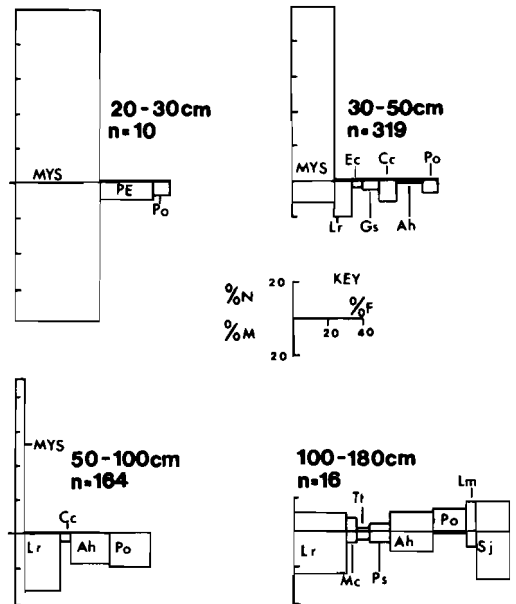

Figure 3 The principal prey of *Argyrosomus hololepidotus*. The size range of each group and the number of stomachs is shown. Ah: *Argyrosomus hololepidotus*, Cc: *Cynoglossus capensis*, Ec: *Engraulis capensis*, Gs: *Galeichthys* sp., Lm: *Lithognathus mormyrus*, Lr: *Loligo reynaudi*, Mc: *Merluccius capensis*, MYS: Mysidacea, PE: Penaeidae, Po: *Pomadasys olivaceum*, Ps: *Pomatomus saltatrix*, Sj: *Scomber japonicus*, Tt: *Trachurus trachurus*.

by mass), and mysids were the most important prey group. Demersal fishes (*Ammodytes capensis*, *Pomadasys olivaceum* and Gobiidae) and unidentified fish remains made up the balance (0,4 %N, 11 %M).

The 301 – 500 mm group took a wide variety of prey (41 taxa), which was in part a result of the large number of fish in this group (319). Crustaceans made up 99% by number and 14% by mass of prey taken. Cephalopods were not important by number (0,1%) but were important by mass (22%) and *Loligo reynaudi* was the most important species. Fishes made up 1% of the number and 64% of the mass of prey. Pelagic schooling teleosts such as *Etrumeus teres* and *Sardinops ocellata* made up 0,1% of the number and 14% of the mass of prey taken. Demersal species, especially those

Table 1 The prey of *Argyrosomus hololepidotus*, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g

Prey	Predator length											
	200 – 300 mm			301 – 500 mm			501 – 1000 mm			1000 – 1800 mm		
	%F	%N	%M	%F	%N	%M	%F	%N	%M	%F	%N	%M
Crustacea												
Unidentified crustaceans	10,0	0,1	2,8	1,6	< 0,1	0,1						
Copepoda				0,6	< 0,1	< 0,1						
Mysidacea	50,0	99,4	76,9	25,7	98,4	11,8	4,9	90,3	0,6			
Caridea				0,3	< 0,1	0,1						
Penaeidae	30,0	0,2	9,2	8,8	0,1	0,9	7,3	0,5	0,2			
Brachyura				0,6	< 0,1	0,1				6,3	2,1	< 0,1
Megalopae				1,3	< 0,1	< 0,1	0,6	0,1	< 0,1			
Anomura				2,5	0,1	1,0						
Callianassa sp.				0,9	< 0,1	0,2						
Mollusca												
Sepiidae				1,6	< 0,1	0,5				6,3	2,1	< 0,1
Loliginidae				0,3	< 0,1	< 0,1						
Loligo reynaudi				11,3	0,1	20,0	22,0	1,0	33,4	31,3	12,7	24,9
Octopoda (Benthic)				0,6	< 0,1	0,2						
Octopus vulgaris				0,3	< 0,1	1,4	1,2	< 0,1	0,7			
Chondrichthyes												
Unidentified elasmobranchs										6,3	2,1	0,9
Osteichthyes												
Unidentified fish	20,0	0,1	1,7	8,8	0,1	3,1	10,4	0,5	1,1			
Etrumeus teres				1,6	< 0,1	1,0	1,8	0,1	0,2	6,3	2,1	0,9
Sardinops ocellata				3,8	< 0,1	4,6	4,3	0,2	4,7	6,3	2,1	1,4
Engraulidae				0,3	< 0,1	< 0,1						
Engraulis capensis				5,6	0,1	4,3	2,4	0,2	0,8			
Galeichthys sp.				10,0	0,4	4,8	14,0	3,5	1,7			
Bregmaceros sp.				1,6	< 0,1	0,1	0,6	0,2	< 0,1			
Merluccius capensis				0,3	< 0,1	< 0,1	0,6	< 0,1	0,5	6,3	8,5	5,8
Bothidae				0,3	< 0,1	0,5						
Soleidae				0,3	< 0,1	< 0,1						
Austroglossus pectoralis							0,6	< 0,1	0,9			
Cynoglossidae				1,3	< 0,1	0,2	0,6	< 0,1	0,1			
Cynoglossus capensis				10,3	0,1	12,0	7,9	0,4	4,2	6,3	2,1	0,3
Cynoglossus zanzibarensis				2,5	< 0,1	2,4						
Ammodytes capensis	10,0	0,1	1,1	0,3	< 0,1	< 0,1	0,6	< 0,1	0,2			
Cheilodactylus pixi				0,6	< 0,1	0,2	0,6	< 0,1	0,2			
Chirodactylus brachydactylus				0,3	< 0,1	< 0,1						
Acanthistius sebastoides							1,2	< 0,1	0,7	6,3	2,1	2,1
Trachurus trachurus				1,9	< 0,1	2,0	0,6	< 0,1	1,3	6,3	2,1	4,8
Pomatomus saltatrix				0,6	< 0,1	1,0	0,6	< 0,1	0,6	12,5	4,3	6,4
Scombrops dubius							0,6	< 0,1	0,8			
Argyrosomus hololepidotus				15,0	0,2	16,5	22,0	1,2	18,8	25,0	10,6	12,0
Umbrina canariensis				0,3	< 0,1	1,3	0,6	< 0,1	0,1			
Pomadasys olivaceum	10,0	0,1	6,6	8,5	0,1	7,0	23,8	1,1	20,6	18,8	12,8	2,4
Rhonciscus striatus				0,3	< 0,1	0,2						
Lithognathus mormyrus										6,3	17,0	9,3
Pagellus natalensis				0,3	< 0,1	< 0,1	1,2	0,1	2,6			
Rhabdosargus holubi							0,6	< 0,1	0,5			
Sarpa salpa							0,6	0,1	0,4			
Scomber japonicus				0,3	< 0,1	0,6	2,4	0,1	4,0	18,8	17,0	28,8
Atherina breviceps				0,3	< 0,1	0,6						
Gobiidae	10,0	0,1	1,7	1,3	< 0,1	0,1						
Chelidonichthys queketti							0,6	< 0,1	0,1			
Chatrabus melanurus				0,3	< 0,1	1,3						
Totals	10	1801	18,1	319	35623	2376,0	164	4167	4653,7	16	47	2353,5

associated with soft sediments, were the most important teleost prey (1 %N, 47 %M). *Cynoglossus capensis, Argyrosomus hololepidotus* and *Pomadasys olivaceum* were particularly important.

A. hololepidotus of 501 – 1000 mm took 29 categories of prey. Crustaceans accounted for 91% by number and 1% by mass. Mysids were again the dominant group, and although they were taken far less frequently (5%) and accounted for a small proportion of the prey mass (1%), they occurred in very large numbers (90 %N). The largest specimen with mysid prey measured 656 mm. Cephalopods were important, comprising only 1% by number but 34% by mass of prey taken. *Loligo reynaudi* dominated this group. Fishes made up the balance of the prey taken, and comprised pelagic schooling species (1 %N, 12 %M) and demersal species, usually associated with sandy substrata (7 %N, 52 %M). The principal teleost prey were all demersal species (*Cynoglossus capensis, A. hololepidotus* and *Pomadasys olivaceum*).

A. hololepidotus larger than 1000 mm took few crustaceans; brachyuran remains occurred in 6% of the stomachs examined and made up 2% by number but < 0,1% by mass of the prey. Cephalopods made up 15% of the number and 25% by mass of the prey. Fishes made up the bulk of the diet (83 %N, 75 %M), and included both pelagic (28 %N, 42 %M) and demersal (53 %N, 32 %M) species. *Scomber japonicus* was a principal prey and dominated other teleosts by mass. Other major prey were *A. hololepidotus,*

Lithognathus mormyrus and *P. olivaceum.*

Similarities in the prey taken by these predator size groupings are shown in Figure 4, according to prey mass. It is evident that the smallest group is least similar to the others, while the middle-sized groups show most similarity.

The length relationship between *A. hololepidotus* and all prey is given in Figure 5. There is a point of inflection at about 500 mm. The highest ratio between calculated prey length and predator length was 57% and the smallest 2%. If mysids and other small crustaceans are included, the minimum drops to about 1%. A rapid increase in prey maximum lengths occurs as kob double in length between 250 and 500 mm. The prey length maxima show an increment approximately to the power of 10 (26 – 290 mm). The relative prey size taken is greater over this range than with large specimens. Kob larger than 520 mm took prey which were relatively smaller. Beyond this size there was a notable lack of very small prey.

Dominant prey taken by different size groups of *A. hololepidotus* are plotted in Figures 6 & 7. The larger predators take larger prey than the smaller specimens, although there is considerable overlap in prey sizes taken by predators of different length groups. This trend is shown most clearly with *Pomadasys olivaceum* and *A. hololepidotus* as prey. With *Loligo reynaudi, Cynoglossus capensis* and *Galeichthys* species the trend is less obvious.

Prey selection and locality

A. hololepidotus were divided according to size and area caught (Table 2). Area A is from the harbour around the edge of Algoa Bay to just beyond the Sundays River mouth, but including St Croix, Jahleel and Brenton Islands. Area B includes Riy Bank, Cape Recife, Noordhoek and Sardinia Bay. These are more exposed areas of Algoa Bay and environs, where fish are often caught close to reefs. Area C includes Port Alfred and East London. Area D stretches from Jeffreys Bay to Mossel Bay, where few fish were collected. Only two size groups were used as few small (< 300 mm) or large (> 1000 mm) specimens were sampled.

In Area A, the prey of both the small and large individuals are similar. They took mysids, *Loligo reynaudi, Galeichthys* species, *A. hololepidotus* and *Pomadasys olivaceum* in diffe-
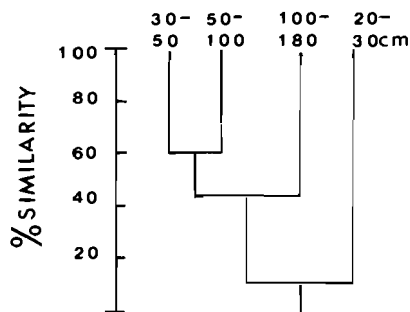

Figure 4 Similarity dendrograms of diets of *Argyrosomus hololepidotus* size groups, according to prey mass.
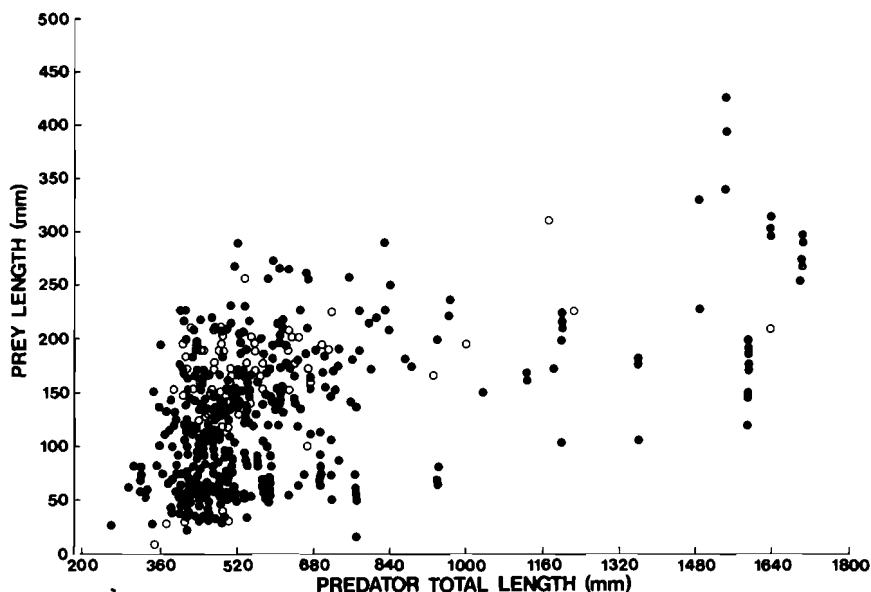

Figure 5 Scatter diagram of prey length against total length of *Argyrosomus hololepidotus*. Cephalopods are shown by open circles and fishes by closed circles.
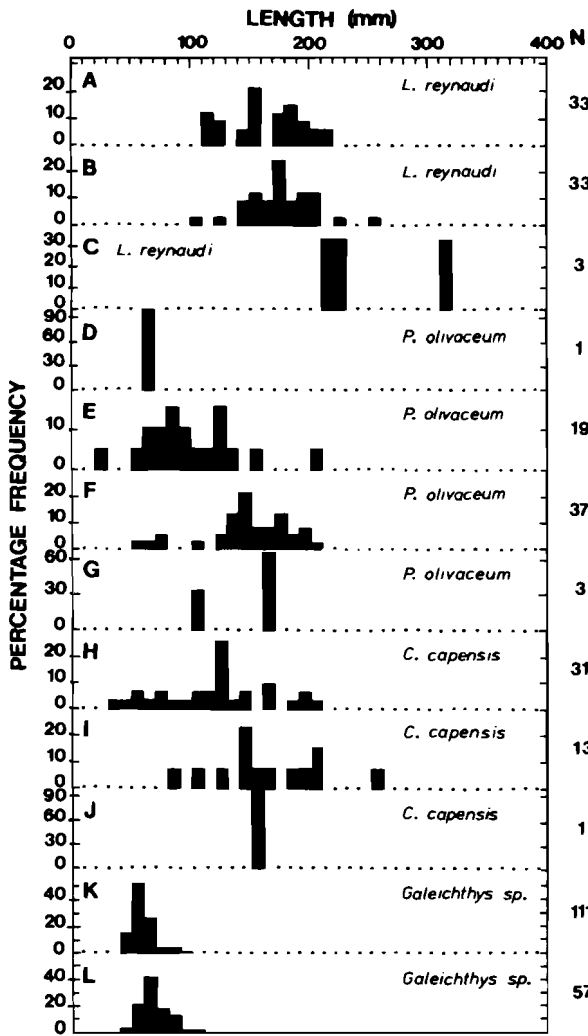
Figure 6 Histograms of the length frequencies of *Loligo reynaudi* (A,B,C); *Pomadasys olivaceum* (D,E,F,G); *Cynoglossus capensis* (H,I,J); *Galeichthys* sp. (K,L); taken by *Argyrosomus hololepidotus* of 201–300 mm (D); 301–500 mm (A,E,H,K); 501–1000 mm (B,F,I,L) and > 1000 mm (C,G,J). Mantle length was measured for *Loligo reynaudi* and total length for fishes.

Figure 7 Histograms of the length frequencies (TL) of *Argyrosomus hololepidotus* cannibalized by fish of 301 – 500 mm (A); 501 – 1000 mm (B) and > 1000 mm (C).

rent proportions, although the large group took more squid and fishes.

In Area B mysids were considerably less important for the small group and were not taken at all by the larger fish. *Loligo reynaudi* was more important here to both groups, but especially to large predators. Schooling pelagic fish, especially *Sardinops ocellata* and *Engraulis capensis*, were the major

prey of the small group but not of large specimens which took mainly demersal fish such as *Pomadasys olivaceum*, *Pagellus natalensis*, *Sarpa salpa* and *Acanthistius sebastoides*. It is noteworthy that the latter two species occur on reefs.

In Area C mysids were again dominant prey for small fish but were not recorded for larger specimens, which took crab megalopae. *Loligo reynaudi* was one of several important prey of small *A. hololepidotus*, and the single most important prey of those over 500 mm. *Engraulis capensis*, *Bregmaceros* sp., Bothidae, and *Cynoglossus zanzibarensis* (a warm water cynoglossid) were the more important fish prey of small kob. The large size group also took *E. capensis*, *Bregmaceros* sp., *Merluccius capensis* and *Scombrops dubius*, although teleosts were of secondary importance to cephalopods by mass.

In Area D only large *A. hololepidotus* were sampled. These had taken *Merluccius capensis*, *Pomatomus saltatrix*, *Lithognathus mormyrus* and *Scomber japonicus*. Fish made up the entire diet in this area.

It appears from the above results that the prey of *A. hololepidotus* differs markedly according to locality and predator size.

Seasonality of prey selection

A bi-monthly analysis of prey taken is shown in Figure 8. Only two size groups were used as few very small (< 300 mm) or very large (> 1000 mm) specimens were taken. Mysids were preyed on by small fish (< 500 mm) throughout the year, but were particularly dominant in March – April. Mysids were rarely taken by large *A. hololepidotus*. *Galeichthys* sp. was most commonly recorded as prey in the first half of the year. *Loligo reynaudi* was most dominant in July – August and November – December in small *A. hololepidotus*. Large specimens took squid throughout the year although this prey dominated in the latter half of the year. Although *Engraulis capensis* was taken throughout the year either by large or small *A. hololepidotus*, their contribution by mass was small. *Cynoglossus capensis* was taken almost throughout the year. Both small and large *A. hololepidotus* were cannibalistic almost throughout the year. *Pomadasys olivaceum* was taken by small *A. hololepidotus* throughout the year except in September – October. This prey was taken by the large fish throughout the year.

The seasonal variation in prey taken may result from the varying relative abundance of the major prey species on account of movements of both predator and prey populations between habitats.

Annual variation

Large fluctuations in important prey were found, probably because of the proportion of material collected in different areas. However, it was notable that *Sardinops ocellata* decreased in importance between 1978 and 1980, while *Engraulis capensis* was a more dominant prey after 1978. This finding agrees with information collected from pelagic predators and suggests a change in relative abundance of these two species during the study period (Smale 1983).

Feeding selectivity

The results of the trawling experiment are shown in Figure 9A. Fourteen species (*Solea bleekeri*, *Cheilodactylus pixi*, *Chirodactylus brachydactylus*, *Priacanthus hamrur*, *Cheimerius nufar*, *Rhabdosargus globiceps*, *Spondyliosoma emarginatum*, *Atractoscion aequidens*, *Amblyrhynchotes honckenii*, *Sphyraena africanum*, *Chelidonichthyes capensis*, *Chelidonichthyes kumu*, *Trichiurus lepturus*, *Sygnathus acus*)

Table 2a The prey of *Argyrosomus hololepidotus*, of 200 – 500 mm taken in three localities — see text for details. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g

Prey	Area A			Area B			Area C		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
Crustacea									
Unidentified crustaceans	1,1	< 0,1	< 0,1	6,7	1,7	0,9			
Copepoda	0,4	< 0,1	< 0,1				5,6	0,3	< 0,1
Mysidacea	30,5	98,8	13,8	6,7	60,0	0,8	16,7	87,9	3,8
Caridea	0,4	< 0,1	0,1						
Penaeidae	7,5	0,1	0,8	22,2	5,5	1,8	5,6	0,6	0,6
Brachyura	0,8	< 0,1	0,1						
Megalopae	0,4	< 0,1	< 0,1	6,7	1,7	0,3			
Anomura	0,8	< 0,1	0,8	11,1	8,1	1,8	5,6	0,6	2,5
Callianassa sp.				6,7	1,3	1,8			
Mollusca									
Sepiidae				11,1	2,1	5,2			
Loliginidae	0,4	< 0,1	< 0,1						
Loligo reynaudi	10,5	0,1	18,9	13,3	3,0	29,4	11,1	0,6	18,9
Octopoda (Benthic)	0,8	< 0,1	0,2						
Octopus vulgaris	0,4	< 0,1	1,6						
Osteichthyes									
Unidentified fish remains	7,9	< 0,1	2,7	11,1	2,6	5,0	22,2	1,8	5,7
Etrumeus teres	1,5	< 0,1	1,0				5,6	0,3	2,5
Sardinops ocellata	3,4	< 0,1	4,5	6,7	1,7	6,8			
Engraulidae	0,4	< 0,1	< 0,1						
Engraulis capensis	3,4	< 0,1	1,4	15,6	6,4	29,2	11,1	0,6	10,1
Galeichthys sp.	11,7	0,4	5,3	2,2	0,4	0,9			
Bregmaceros sp.							27,8	4,1	3,9
Merluccius capensis							5,6	0,3	0,8
Bothidae							5,6	0,6	15,1
Soleidae	0,4	< 0,1	< 0,1						
Cynoglossidae	0,4	< 0,1	< 0,1	2,2	0,4	0,2	11,1	0,6	6,3
Cynoglossus capensis	11,3	0,1	13,3	6,7	1,3	3,4			
Cynoglossus zanzibarensis	1,9	< 0,1	1,8				16,7	1,2	24,3
Ammodytes capensis	0,4	< 0,1	< 0,1				5,6	0,3	1,0
Cheilodactylus pixi	0,8	< 0,1	0,2						
Chirodactylus brachydactylus				2,2	0,4	0,2			
Trachurus trachurus	2,3	< 0,1	2,2						
Pomatomus saltatrix	0,8	< 0,1	1,1						
Argyrosomus hololepidotus	17,7	0,2	18,2	2,2	0,4	4,1			
Umbrina canariensis	0,4	< 0,1	1,5						
Pomadasys olivaceum	10,2	0,1	7,8	2,2	0,4	1,4			
Rhonciscus striatus							5,6	0,3	4,5
Pagellus natalensis	0,4	< 0,1	< 0,1						
Scomber japonicus	0,4	< 0,1	0,7						
Atherina breviceps				2,2	2,1	5,9			
Gobiidae	1,5	< 0,1	< 0,1	2,2	0,4	0,9			
Chatrabus melanurus	0,4	< 0,1	1,5						
Totals	266	36849	2095,4	45	235	219,3	18	340	79,5

contributed < 0,1 %N of the trawl catch. They are not shown in the figure as they were not taken by *A. hololepidotus*.

The difference in the numbers under consideration (13 550 trawled specimens against 250 taken by *A. hololepidotus*) suggests that rarely caught fishes would not be found in predators' stomachs unless they were highly preferred. As *A. hololepidotus* shows no evidence of a preference for them, their absence in stomachs is probably attributable to differences in sample sizes so they are not considered further.

Figure 9B shows that among the four species commonly caught in the trawl, *A. hololepidotus* prefers *Galeichthys* species, *A. hololepidotus* and *Pomadasys olivaceum* but did not prey on *Pomatomus saltatrix*. There is a strong preference for *Austroglossus pectoralis* and *Cynoglossus capensis* but slight avoidance of *Umbrina canariensis*. There is a very high preference for *Acanthistius sebastoides, Rhabdosargus holubi* and *Loligo reynaudi* and slight preference for *Etrumeus teres* and *Engraulis capensis*. *Sardinops ocellata* and *Scomber japonicus* were not taken by trawling while *Trachurus trachurus* was caught by the trawl but not recorded in *A. hololepidotus* stomachs. *Pagellus natalensis* was not taken by *A. hololepidotus* in this sample.

Table 2b The prey of *Argyrosomus hololepidotus* of 501 – 1800 mm taken in four localities — see text for details. The totals are number of stomachs (F), number of items (N) and prey wet mass (M), g

Prey	Area A %F	Area A %N	Area A %M	Area B %F	Area B %N	Area B %M	Area C %F	Area C %N	Area C %M	Area D %F	Area D %N	Area D %M
Crustacea												
Mysidacea	5,4	90,9	0,5									
Penaeidae	7,4	0,5	0,1	8,3	3,4	< 0,1						
Brachyura	0,7	< 0,1	< 0,1									
Megalopae							6,3	9,7	0,1			
Mollusca												
Sepiidae	0,7	< 0,1	< 0,1									
Loligo reynaudi	19,5	0,9	25,6	41,7	20,7	59,8	43,8	22,6	77,6			
Octopus vulgaris	0,7	< 0,1	0,5	8,3	3,4	1,1						
Chondrichthyes												
Unidentified elasmobranchs				8,3	3,4	3,8						
Osteichthyes												
Unidentified fish	7,4	0,4	0,2	25,0	13,8	5,3	18,8	9,7	1,8			
Etrumeus teres	2,7	0,1	0,5									
Sardinops ocellata	5,4	0,2	4,5									
Engraulis capensis	2,0	0,1	0,2				6,3	12,9	6,0			
Galeichthys sp.	14,8	3,4	1,4	8,3	20,7	0,1						
Bregmaceros sp.							6,3	22,6	0,1			
Merluccius capensis							6,3	3,2	4,3	33,3	28,6	34,6
Austroglossus pectoralis	0,7	< 0,1	0,8									
Cynoglossidae	0,7	< 0,1	0,1									
Cynoglossus capensis	8,7	0,4	3,6				6,3	3,2	< 0,1			
Ammodytes capensis	0,7	< 0,1	0,1									
Cheilodactylus pixi							6,3	3,2	1,6			
Acanthistius sebastoides	1,3	< 0,1	0,6	8,3	3,4	9,5						
Trachurus trachurus	1,3	< 0,1	3,1									
Pomatomus saltatrix	1,3	< 0,1	2,7							33,3	7,1	7,6
Scombrops dubius							6,3	3,2	7,0			
Argyrosomus hololepidotus	26,8	1,4	20,8									
Umbrina canariensis	0,7	< 0,1	0,1									
Pomadasys olivaceum	26,2	1,1	18,0	16,7	13,8	2,9	6,3	6,5	0,5			
Lithognathus mormyrus										33,3	57,1	55,4
Pagellus natalensis	0,7	< 0,1	0,9	8,3	6,9	13,7						
Rhabdosargus holubi	0,7	< 0,1	0,4									
Sarpa salpa				8,3	10,3	3,8						
Scomber japonicus	4,0	0,3	15,3							33,3	7,1	2,5
Chelidonichthys queketti							6,3	3,2	1,0			
Totals	149	4140	5568,8	12	29	526,1	16	31	515,3	3	14	397

Discussion

The deep body, truncate tail and relatively deep caudal peduncle of *A. hololepidotus* suggest that this is a relatively slow-moving species (Norman & Greenwood 1963; Whitfield & Blaber 1978). However, the copious production of mucus through the skin, which is evident when one handles specimens, may partially off-set this. In addition to other functions, mucus is known to reduce drag as fish swim (Lagler, Bardach, Miller & Passino 1977). Drag reduction is particularly important during hunting, when bursts of speed are necessary for the predator to outswim the prey. *A. hololepidotus* usually occurs in schools, especially when small, and probably benefits by hunting schooled prey; many of the prey species identified in this study were schooling demersal species. The predator's silvery to dark body colouration acts as camouflage by counter-shading and darker colouration occurs most frequently in specimens found in turbid water. The function of the silver spots along the lateral line is not clear but their close association with the lateral line suggests that they may be specialized pressure receptors which may be used to detect prey and avoid predators in turbid water. Its preference for turbid water is also evident in estuaries (Wallace & van der Elst 1975; Whitfield & Blaber 1978). Davis & Miller (1967) found that minnows inhabiting turbid water have a large number of cutaneous taste buds, reduced optic lobes and several features which would aid non-visual prey location. On the other hand, those fish living in clear water locate food visually and have few taste buds. *A. hololepidotus* is likely to be similarly adapted to low-visibility hunting.

There is some evidence that *A. hololepidotus* exhibits size segregation according to depth. Wallace & van der Elst (1975) and Whitfield & Blaber (1978) found that large *A. hololepidotus* remained in the deeper waters of Lake St Lucia while smaller specimens entered the shallows more readily. However, this estuarine system is very shallow throughout (< 2 m). Whitfield & Blaber (1978) attributed the depth preferences of this fish to the threat of attack by fish eagles, prevention of cannibalism, prevention of over-exploitation of prey and the distribution of aquatic macrophytes. In addition, the threat of stranding must be great in such a shallow system. The
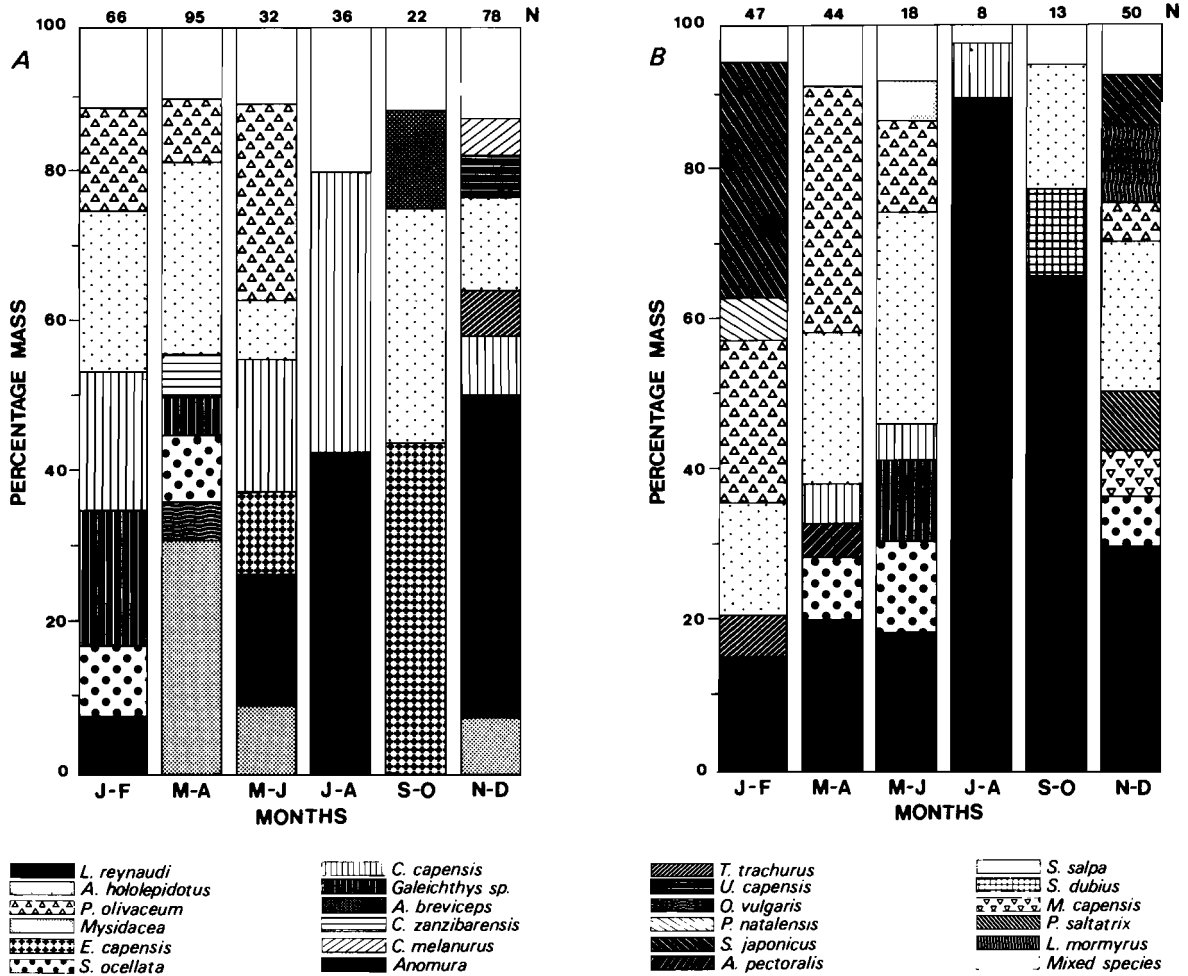
Figure 8 The percentage composition by mass of prey of *Argyrosomus hololepidotus* of 200 – 500 mm (A) and > 500 mm (B) in bi-monthly periods, all years combined. N is the sample size.
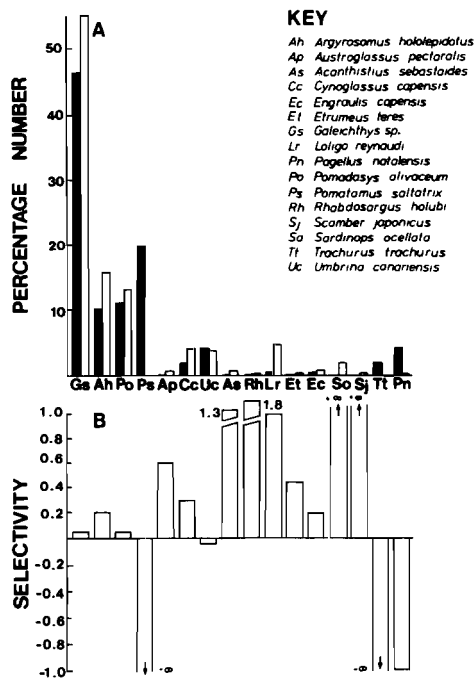

Figure 9 (A) The percentage number of the species caught by trawling in Algoa Bay at 7 – 30 m in February and May 1980 (closed bars) and the percentage number of the species taken by *Argyrosomus hololepidotus* of 501 – 1000 mm in Algoa Bay (Area 1) in the months of January to June in the years 1978 to 1981. (B) Selectivity of *A. hololepidotus* of 501 – 1000 mm TL.

length distribution of *A. hololepidotus* trawled in Algoa Bay showed a similar pattern. Smaller fish were abundant in the shallows (Smale 1984) and the modal size increased with depth. The increase in the size of prey such as *Pomadasys olivaceum* and *A. hololepidotus* taken by larger predators suggests that the predator may hunt in the depth range where the most suitably sized prey occur, as there is some evidence that the depth inhabited varies with size in many of these prey species (Buxton *et al.* 1984; Smale 1984). Depth is one of several factors affecting the distribution of juvenile teleosts (Blaber & Blaber 1980), and many prey species migrate between microhabitats diurnally (Clarke 1966; Hobson 1968; Hobson & Chess 1976; Major 1977; Bruton 1979; Lasiak 1982).

Many predatory fishes move inshore at twilight and at night. Examples are sharks (Wallett 1978), freshwater catfish (Bruton 1979) and several tropical reef predators, although Hobson (1973) notes that relatively few tropical predators are active at night. It is quite likely that factors affecting predation by tropical reef fishes are very different in the turbid, and spatially less complex, warm temperate seas. Nevertheless, some behavioural patterns will be common to both. Examples are prey schooling to avoid predation (Starck & Davis 1966; Hobson 1968; Potts 1969, 1970; Hobson 1978; Radakov 1973; Bruton 1979; Potts 1980, 1981; Smale 1983) and movement within their habitat (e.g. Hobson 1968, 1973; Lasiak 1982). Evidence that *A. hololepidotus* moves inshore in the evening is provided by beach anglers who catch more by night than by day (personal observations). Lasiak (1982) also found that

they move into the surf zone at night. These specimens may be very large. B.E. Trow (Department of Ichthyology and Fisheries Science, Rhodes University, pers.comm.1982) has made the following observations: A large specimen estimated at 2 m long was observed swimming in water 1 m deep on a moonless night in the summer of 1979/80 at Coffee Bay, Transkei. On another occasion a kob of about 2 m was found in a closed tidal pool at night, feeding on a trapped school of *Sarpa salpa*. These observations suggest that *A. hololepidotus* does enter shallow water and feeds there, especially at night. This may explain the occurrence of juvenile *Galeichthys* species, which appear to be confined to shallow water (Buxton *et al.* 1984), in the diet of this predator. Furthermore, the occurrence of large fish in estuaries (Day & Morgans 1956; Wallace 1975; Whitfield & Blaber 1978) clearly shows that depth preferences are not rigid and may depend on prey distribution. The relatively low number of kob from surf-zone samples suggests that deeper areas are preferred. Lasiak (1982) found that they made up about 4% of the total surf-zone catch.

A. hololepidotus takes a wide range of prey species, varying from small crustaceans to demersal and pelagic fish. Small crustaceans, especially penaeids and mysids, dominated the prey of small kob (200 – 300 mm TL). An independent study of predation by small, trawl-caught *A. hololepidotus* (< 200 mm) (Smale 1984) found that mysids, especially *Mesopedopsis slabberi*, were the most dominant prey. *M. slabberi* is a common inshore species found over a wide variety of substrata and even enters estuaries (Tattersall & Tattersall 1951; Wittmann 1977; Wooldridge 1983). It occurs in extremely large swarms in Algoa Bay and is an important prey of several other juvenile fish species (Smale 1984; Buxton *et al.* 1984). Mysids were found in the stomachs of *A. hololepidotus* as large as 656 mm TL, probably because *M. slabberi* characteristically forms dense swarms (Wittman 1977). Rather than being a plankton picker, *A. hololepidotus* is probably an active planktivore which takes large mouthfuls of the swarms, making mysids energetically rewarding, despite their small size.

The occurrence of crustaceans in the diet of *A. hololepidotus* has also been observed in other studies. Thirteen kob (207 – 384 mm) caught in Durban harbour had taken penaeid prawns, crown crabs (*Hymenosoma* species) and fish (Day & Morgans 1956). Whitfield & Blaber (1978) recorded that crustaceans made up 17,6% of the number and 6,3% of the mass of prey taken in Lake St Lucia estuary. Lasiak (1982) found that crustaceans constituted 20,3% of the prey wet mass taken from Kings Beach, Algoa Bay, although here mysids were minor components (0,04%). The prawn *Macropetasma africanum* was more dominant, making up 19,2% of the wet mass and occurring in 48,1% of the stomachs examined. At Bluewater Bay near the Swartkops River, Lasiak (1982) found that crustaceans made up 30,7% of the wet mass of prey and that *M. slabberi* was more important, making up 7,7% of the wet mass (predator size range, 148 – 452 mm).

Although crustaceans were taken by *A. hololepidotus* in each of the size groups in the present study, cephalopods and fish dominated the diet of individuals larger than 300 mm. Schooling squid (*Loligo reynaudi*) and fish (*Sardinops ocellata, Engraulis capensis, Merluccius capensis, Trachurus trachurus* and *Pomadasys olivaceum*) were important prey. These fish and squid are both pelagic and demersal schoolers which probably would be attacked most successfully by schooling predators (Smale 1983). *A. hololepidotus* usually occurs in schools of similar-sized fish although individuals may be observed on occasion (Whitfield & Blaber 1978; this study).

When alone, individual prey items such as Gobiidae, *Chatrabus melanurus* and cynoglossids may be taken more efficiently.

The large number of teleost species taken by *A. hololepidotus* is partly a reflection of its wide choice of habitats. It was shown earlier that prey preference varies between areas. It is noteworthy that *Lithognathus mormyrus* was taken most frequently by kob west of Algoa Bay, where this sparid is most common (Buxton *et al.* 1984). Similarly, *L. reynaudi* was taken in areas where it is common in the diet of other predators. This implies that prey are taken in proportion to their abundance, as reported by Whitfield & Blaber (1978) who found that *A. hololepidotus* responds to an increase in the abundance of *Gilchristella aestuarius* by feeding on it more frequently. Similarly, they found when penaeid prawns were more abundant during summer, they contributed up to 70% of the diet. Marais (1984) recorded a similar dominance of crustaceans, especially mysids, in the diet of small *A. hololepidotus* (< 430 mm standard length) in an eastern Cape estuary. It is clear that the low similarity of the smallest group of *A. hololepidotus* compared to the larger specimens, which resulted from the preponderance of mysids in the diet of young fish, is borne out by other studies in the sea and estuaries. There is no clear-cut change in the diet at a specific size but rather a gradual change towards piscivory with growth. Choice between these two types of prey is probably strongly influenced by the relative abundance of catchable and energetically rewarding prey.

Cannibalism is a noteworthy feature of *A. hololepidotus*. It was shown that kob of 301 – 500 mm (about 1 – 2 years old) preyed on conspecifics of 36 – 209 mm (0 + years), according to age studies of Wallace & Schleyer (1979). Although these age estimates should be used with caution owing to differences in the sampling areas, they provide some insight into natural mortality. The 501 – 1000 mm group (2 – 6 years) cannibalized fish of 79 – 288 mm (0 + 1 year) while those of 1001 – 1800 mm (6 – > 12 years) took conspecifics of 314 – 425 mm (2 years). About 10% of the *A. hololepidotus* caught by ski-boats were larger than 600 mm TL, suggesting that the greatest predation will be on kob of 0 + years (< 230 mm). At this age mysids and other crustaceans are dominant prey. Cannibalism in *A. hololepidotus* would reduce particularly strong year classes and could decrease the likelihood of intra-specific competition for food by adults. These observations accord with those of previous studies (Davies 1949; Richards 1976; Helfman 1978; Macpherson 1980; Smale 1983). Fox (1975) reviewed cannibalism in natural populations and noted that it is often a response to population density and food availability, but that several factors may interact. As discussed below, it seems that small *A. hololepidotus* may be taken in a density-dependent way (although possibly preferred) and it was noted that Algoa Bay (mainly between the harbour wall and Bird Island) was the principal place where cannibalism was recorded. This finding needs confirmation by more intensive sampling along other areas of the east and south Cape coast, but it suggests that Algoa Bay may be a major nursery area, as has been confirmed during a trawling survey there (Smale 1984). It is interesting to note that the depth preferences postulated by Whitfield & Blaber (1978) to prevent cannibalism in estuaries do not hold in the sea, perhaps because juvenile *A. hololepidotus* apparently do not seek refuge in the shallow surf zone in the sea (Lasiak 1982) in the same way as they use calm shallows of estuaries. This may be a direct result of avoidance of the turbulent surf zone.

Prey selectivity of active piscivores in the sea is difficult

to study and the present work is one of the most quantative attempts to date. The results suggest that the most numerous prey available are taken in a density-dependent manner. This clearly holds for *Galeichthys* sp., *A. hololepidotus* and *Pomadasys olivaceum*. The complete absence of *Pomatomus saltatrix* in stomachs suggests that they are capable of outswimming this relatively slow predator, although they have occasionally been taken by *A. hololepidotus* in other areas during this study. On the other hand, the two flatfish, *Austroglossus pectoralis* and *Cynoglossus capensis*, were probably easily caught. These two species hide by camouflaging themselves on or just under the sand, but *A. hololepidotus* is able to detect and capture them. The apparently strong selection for *Loligo reynaudi, Etrumeus teres, Sardinops ocellata* and *Scomber japonicus* but strong avoidance of *Trachurus trachurus* may in part be artifacts caused by the difficulty of catching these species in demersal trawl nets, even in relatively shallow water. These species school and are patchily distributed, making it unlikely that they would be sampled in proportion to their abundance with limited trawling. Futhermore, *S. ocellata* was commonly recorded in the diets of pelagic fishes during 1978 but they were less commonly recorded in subsequent years (Smale 1983; Batchlor & Ross 1984). The effects of diurnal changes in the distribution of *Loligo reynaudi* is unclear, but may result in the squid not being equally available to trawls and *A. hololepidotus*. Furthermore, it is likely that squid are particularly vulnerable to predation during spawning (Smale 1983). *Pagellus natalensis*, a small demersal schooling species which has been recorded in *A. hololepidotus* stomach contents from other areas, was rarely taken in the selectivity investigation. This may result from a preference for flatfish and *A. hololepidotus* by the predators. Alternatively it may reflect differences in microhabitat selection and thus a low encounter rate, as has been proposed in other systems (Whitfield & Blaber 1978).

The dominant prey species of this predator occur over soft substrates, are usually dark (e.g. *Galeichthys* species), silvery (e.g. *Pomadasys olivaceum* and *A. hololepidotus*) and may have bars (e.g. *Lithognathus mormyrus*). These patterns provide obliterative counter-shading which allows the fish to blend in with the background of scattered light (Edmunds 1974; Lagler *et al.* 1977). The camouflage is enhanced by the fact that water is often turbid in inshore and estuarine habitats and the type of sensory perception used to locate these prey species depends on the predator (Hobson 1963; Lissman 1963; Kalmijn 1966; Davis & Miller 1967; Hodgson & Mathewson 1971). Solitary prey, on the other hand, may bury themselves (tonguefishes and soles) while others have strong spination (Triglidae, Ariidae). Hoogland, Morris & Tinbergen (1956) have demonstrated how a few strong spines protect sticklebacks against predation. The same defence mechanism appears to work with *Galeichthys* species. Of the wide size range present (Buxton *et al.* 1984), only small specimens were taken by *A. hololepidotus*, suggesting that strong spination is an effective defence. The advantages of strong spination, schooling and inhabiting turbid water are apparently optimized by adult *Galeichthys* species which carry the brood in the mouth, then deposit juveniles in shallow marine areas or in estuaries (Buxton *et al.* 1984; pers.obs.) for protection during the vulnerable early growth stages.

Ontogenetically, *A. hololepidotus* initially preys on crustaceans then changes to fishes, many of which take similar prey to young *A. hololepidotus* and which also feed over soft substrata. For example *Pomadasys olivaceum* feeds mainly on crustaceans, with mysids often dominating in the south-eastern

Cape (Lasiak 1982; Buxton *et al.* 1984). Similarly *Pagellus natalensis* preys on small fish such as Gobiidae, as well as polychaetes, small cephalopods and small crustaceans (Buxton *et al.* 1984). Although demersal species are preyed on by *A. hololepidotus*, typically pelagic prey, such as engraulids and loliginids are also taken. It is clear therefore that *A. hololepidotus* is a top predator in the demersal food web over sandy substrata, but it also has an influence on the pelagic food web.

Acknowledgements

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