S. Afr. J. mar. Sci. 18: 249–264
1997

FEEDING ECOLOGY OF SOUTH AFRICAN *ARGYROSOMUS JAPONICUS* (PISCES: SCIAENIDAE), WITH EMPHASIS ON THE EASTERN CAPE SURF ZONE

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The feeding ecology of dusky kob *A. japonicus* was determined from the stomach contents of line-caught specimens from several estuarine, surf zone and nearshore localities in KwaZulu-Natal and the Eastern and Western Cape. The accuracy of dietary descriptions for dusky kob depends on sample size, sampling frequency and sampling period. *A. japonicus* in the marine environment fed on a wide variety of organisms, including benthic, epibenthic and pelagic crustaceans, cephalopods and teleosts. Teleosts were by far the most important taxon, but at the species level the principal items varied with environment. There was a general increase in the importance of squid and teleosts, and a concomitant decrease in the importance of crustacea with growth. Feeding frequency and intensity were generally higher in the surf zone than in nearby estuaries, which demonstrates the importance of the former as a foraging area. Dusky kob from surf zones with mixed reef/sand substrata fed more regularly, ate larger meals and consumed a wider variety of organisms (38 v. 28) than did those from predominantly sandy substrata. It is concluded that *A. japonicus* is a top predator that influences the pelagic and demersal food chains of estuaries, the surf zone and the nearshore environment, and that its currently depleted condition has almost certainly had an impact on the foodwebs of all three of those habitats.

The dusky kob *Argyrosomus japonicus* is a large sciaenid (maximum size 1.8 m and 75 kg) which occurs in both northern and southern hemispheres. It is found on the southern African coast from the Cape of Good Hope to Moçambique (Griffiths and Heemstra 1995), along the entire southern seaboard of Australia from North West Cape to the Burnette River (Kailola *et al*. 1993, Starling 1993), and from Hong Kong northwards along the Chinese coast to southern Korea and Japan (Trewavas 1977). Until recently, *A. japonicus* was misidentified as *A. hololepidotus* both in southern Africa and in Australia, and in South Africa it was also confused with a new species, *A. inodorus* (Griffiths and Heemstra 1995).

A. japonicus is an important commercial and recreational linefish in South Africa (Griffiths and Heemstra 1995). The adults (>107 cm total length, *TL*) frequent estuaries and the surf zone, but are found mainly nearshore (beyond the surf) to depths of approximately 100 m (Griffiths 1996). Early juveniles (<15 cm *TL*) are found exclusively in estuaries, predominantly in the head regions, whereas older juveniles (15–107 cm *TL*) are found in both estuaries and the surrounding surf zone, but not farther offshore (Griffiths 1996). Essentially, the function of nursery areas is to provide immature fish with adequate food and protection from predators. Although the surf zone and estuaries are generally free of the numerous, large nearshore predators that feed on small sciaenids (Cliff *et al*. 1989, 1990, Cliff and Dudley 1991a, b, Smale 1991, Dudley and Cliff 1993), the relative importance of these two habitats as foraging areas for dusky kob is yet to be established. The nursery functions of the estuarine and surf-zone environments for dusky kobs are, therefore, not well understood.

Medium and high energy surf zones (as are typical off South Africa) are semi-closed ecosystems with well developed pelagic and demersal food chains (McLachlan and Romer 1990, Cockcroft and McLachlan 1993). Given that juvenile *A. japonicus* are important estuarine predators (Marais 1984), and that they are abundant in the surf, it is plausible that they play a significant role in the foodwebs and trophodynamics of the surf-zone ecosystem. The large size of adults also suggests that *A. japonicus* might be an important predator of the nearshore zone. A recent stock assessment indicates that the biomass of South African dusky kob has been reduced to <10% of its pristine level (Griffiths 1997a), suggesting a situation of ecosystem overfishing (*sensu* Bohnsack and Ault 1996). In order to understand the environmental implications of a depleted dusky kob population, a knowledge of their primary prey organisms is necessary. Such information is also useful for formulating diets for captive breeding programmes, and can assist in the understanding of distribution patterns (spatial and temporal).

Although the feeding of dusky kob has been studied in at least seven South African estuaries (Whitfield

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Manuscript received: July 1997

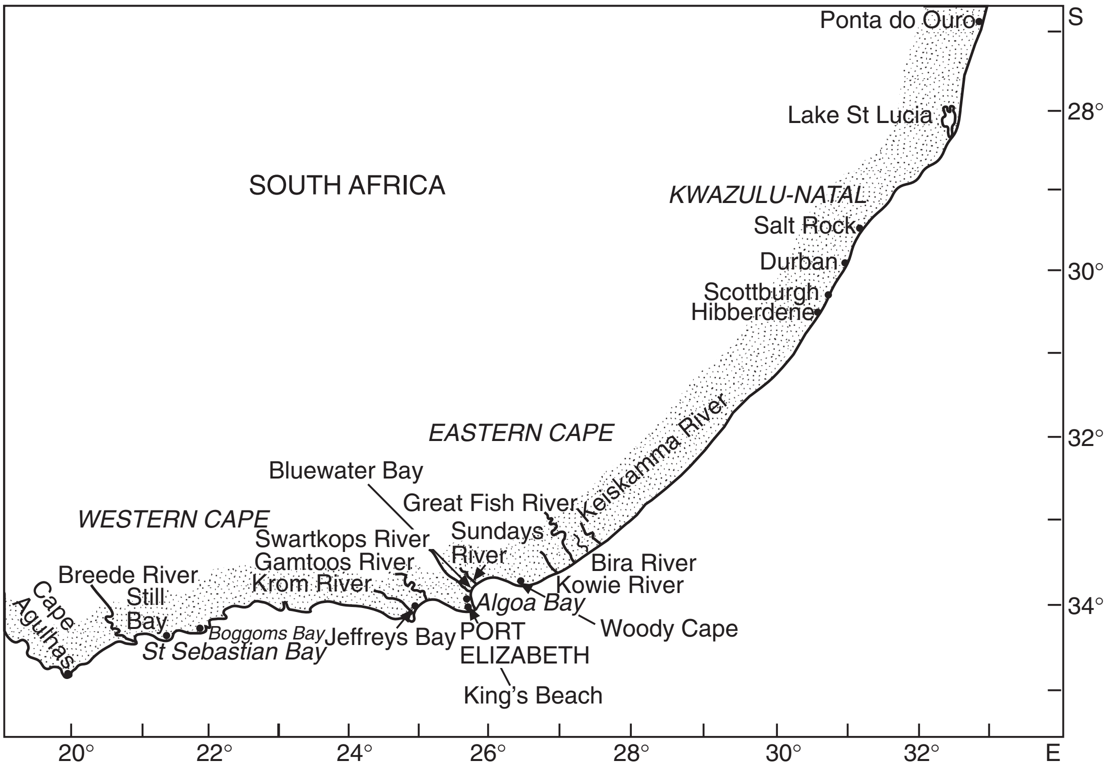

Fig. 1: Map of South Africa, showing sampling sites and localities mentioned in the text

and Blaber 1978, Marais 1984, Coetzee and Pool 1991, Griffiths 1997b), the diet of juveniles in the surf zone and of adults in the nearshore environment has been largely neglected. Lasiak (1982) examined the stomach contents of 136 small (mostly 16–40 cm *TL*) juveniles from the surf zone of Algoa Bay, and Schleyer and Wallace (1986) analysed the stomach contents of 18 specimens from the surf zone of KwaZulu-Natal using broad taxonomic categories and a "subjective method". In both of those studies teleost prey was analysed as a single category. Smale and Bruton (1985) investigated the feeding of "*A. hololepidotus*" in the nearshore environment of the Eastern Cape, but according to voucher material (otoliths) and predator size (97% <100 cm *TL*), their study was based predominantly on *A. inodorus*. An earlier study on trawled specimens (Smale 1984) was also based on this species.

The present study provides detailed information on the diets of a wide size range (40–140 cm *TL*) of *A. japonicus* from surf-zone and nearshore localities throughout the Eastern Cape, and it includes a comparison of predominantly sandy, and mixed rock and sand surf-zone substrata. Analyses based on smaller sample sizes from the Western Cape and KwaZulu-Natal are included for comparative purposes. The surf zone is also evaluated as a foraging area for juvenile dusky kob, by comparing the feeding intensities and the proportions of specimens containing food in this environment with those from nearby estuaries.

MATERIAL AND METHODS

Dusky kob caught by rock-and-surf anglers and skiboat fishermen at several localities in KwaZulu-Natal and the Eastern and Western Cape were opportunistically sampled between October 1990 and December 1993 (Table I, Fig. 1). Because of the minimum size limit imposed on linefishermen, all specimens were >40 cm *TL*. Total length of each specimen was measured (to the nearest mm) and the

Table I: Dates, localities and number (*n*) of *A. japonicus* sampled during this study

Location	Date	*n*
KWAZULU-NATAL		
Surf zone		
St Lucia – Mapelane	August 1991	8
Salt Rock	August 1990	1
Scottburgh – Hibberdene	March 1990	8
	September 1991	13
	November 1991	6
	October 1992	9
Nearshore environment		
Durban – Salt Rock	August 1991	27
	September 1991	10
	August 1992	38
Durban – Scottburgh	August 1990	24
	August 1991	73
	September 1991	89
EASTERN CAPE		
Surf zone		
Keiskamma – Bira Rivers (Ciskei surf)	November 1990	39
	December 1990	23
	February 1991	38
	November 1991	38
Great Fish Estuary – Kowie Rivers (Kowie surf)	October 1990	12
	November 1990	6
	February 1991	2
	April 1991	11
	October 1991	14
	November 1991	2
Sundays River – Woody Cape (Sundays surf)	October 1990	12
	November 1990	5
	January 1991	46
	February 1991	29
	March 1991	99
	November 1991	8
	December 1991	7
Estuaries		
Keiskamma Estuary	November 1990	27
	January 1991	21
	February 1991	46
	November 1991	13
Great Fish Estuary	October 1990	31
	December 1990	26
	February 1991	37
	February 1991	11
	April 1991	24
	May 1991	4
	October 1991	19
Nearshore environment		
Algoa Bay	October 1991	28
	December 1991	3
	January 1992	10
Jeffreys Bay	November 1990	5
	October 1991	6

(Continued)

Table I: *(continued)*

Location	Date	*n*
WESTERN CAPE		
Surf-zone		
Boggoms Bay	March 1993	11
Still Bay	March 1993	42
Estuary		
Breede Estuary	December 1990	38
	January 1991	27
	February 1991	29
	October 1991	10
	December 1991	10
Nearshore		
Still Bay	December 1992	22
St Sebastian Bay	December 1990	11
	February 1991	5
	October 1991	15

stomach contents were analysed while still fresh. Prey items were identified to the lowest possible taxon and counted and weighed (wet) to the nearest 0.01 g. Bait was recognized easily and discarded. Teleosts were identified whole, or by comparing sagittal otoliths (stored dry) with a reference collection. Cephalopods were identified by their beaks (preserved in 10% formalin). Crustaceans not identified immediately were preserved in 10% formalin for further examination.

Prey importance was assessed by percentage frequency of occurrence (%*F*), which provides an indication of how often a particular prey item is selected within a population (Hynes 1950), and by percentage by mass (%*M*), which gives a measure of the energy contribution of that item (Windell and Bowen 1978, Macdonald and Green 1983). As a result of potential biases, the importance of certain prey items can be anomolously elevated when each of these methods is applied separately. For example, an infrequently consumed large item (especially if fortuitously undigested) may result in a high %*M*, and a frequently eaten small item would generate a high %*F*. An index of relative prey importance (*IRI*) was therefore calculated for each prey category *i* as the product of $\%M_i$ and $\%F_i$. In order to facilitate comparisons of prey importance between analyses (temporally or spatially separated), this was expressed as a percentage (Cortés 1997), where

$$\%IRI_i = 100\, IRI_i / \sum_{i=1}^{n} IRI_i$$

and *n* is the total number of food categories considered

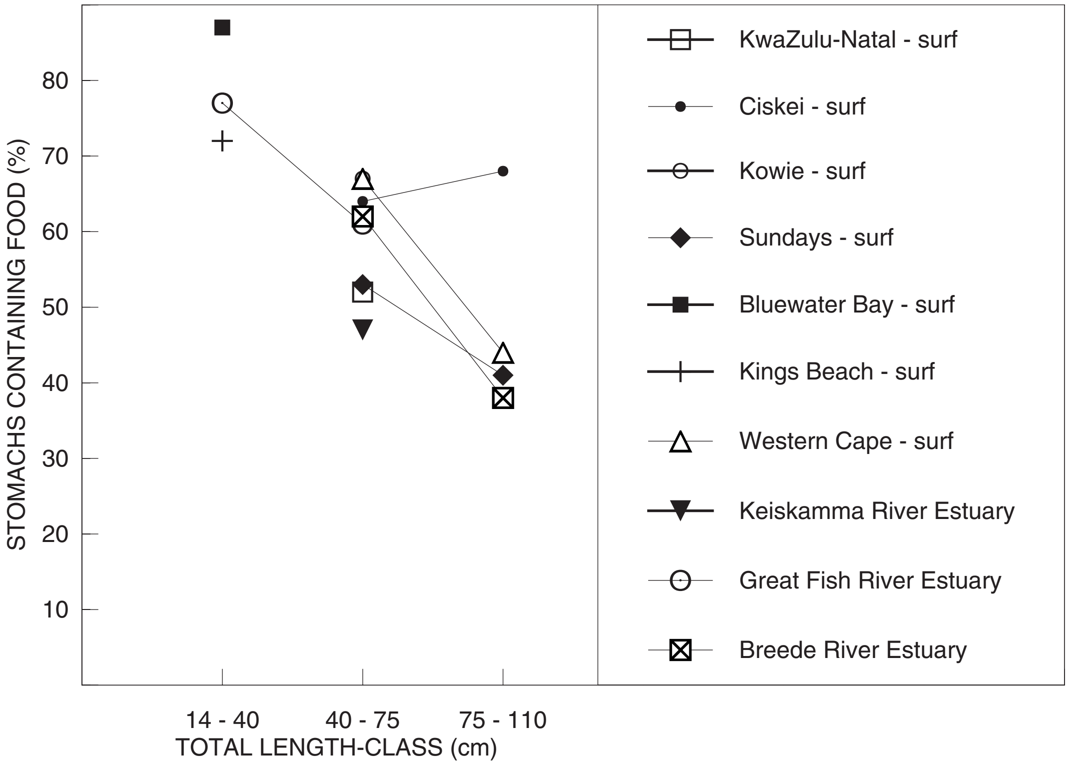

Fig. 2: The proportions of *A. japonicus* stomachs containing food in each of three size-classes for various surf-zone and estuarine localities. Fish <40 cm were seine-netted and those >40 cm were line-caught. Data for Kings Beach and Bluewater Bay after Lasiak (1982)

at a given taxonomic level. Numerical percentage contribution (Pillay 1952) was excluded because, although it may impart information on the feeding behaviour of individuals (Macdonald and Green 1983), it is biased towards small prey items (e.g. mysids and isopods) and provides little information on the importance of a food item to the population as a whole.

All surf-zone localities sampled, except that associated with the Sundays River, consisted of mixed sand/reef substrata. The Sundays River surf zone (adjacent to a 40 km stretch of sandy beach) has a predominantly sandy substratum with limited areas of subtidal, low-profile sandstone reef, which are often sanded over (A. C. Cockroft, Sea Fisheries Research Institute [SFRI], pers. comm.). Data for the Eastern Cape sampling areas, with mixed rock/sand substrata, were pooled and compared with those from the sandy Sundays River surf. To determine whether sufficient specimens had been sampled to adequately describe the diet of *A. japonicus* in each of the two substratum types, the cumulative number of prey types was plotted against the number of randomly pooled stomachs. The asymptotic stabilization of the curve indicates the minimum number of stomachs required (Cortés 1997). As a result of small sample sizes and low sampling frequencies (see below), the data collected from the surf zones of the Western Cape and KwaZulu-Natal and from the nearshore environment of all areas were not regarded as comprehensive. These data were therefore not subjected to precision analyses. Given the small nearshore sample sizes (mainly because of the affects of barotrauma, see below) and the similarity of the nearshore fauna of the Eastern and Western Cape (east of Cape Agulhas), the diet data for these two regions were combined.

The role of the surf zone as a nursery area for *A. japonicus*, particularly with regards to the provision of food, was also investigated. To this end, feeding data were collected from line-caught specimens from three important (for dusky kob) estuaries, the Keiskamma and Great Fish systems in the Eastern

Cape and the Breede Estuary in the Western Cape (Table I). Feeding intensity (i.e. mass of food in each non-empty stomach divided by body mass) and the proportions of dusky kob with food from surf-zone and estuarine localities were then compared.

RESULTS

Surf-zone environment

The proportion of dusky kob with stomach contents varied according to both fish size and sampling locality. The percentage of stomachs containing food generally declined with fish length (Fig. 2). The exception to this pattern was in the Ciskei surf, where a slightly higher proportion of the 75–110 cm size-class contained food than did the 40–75 cm size-class. However, this may be an artifact of the small sample size of the larger group (n = 25). Although dusky kob of <40 cm were caught with beach-seine nets and those >40 cm with hook and line, it has been demonstrated (Griffiths 1997b) that there is no difference in the proportion of fish with food between line- and seine-caught individuals of comparable size in the Great Fish Estuary. These results suggest that larger dusky kob feed less frequently than smaller individuals, possibly because smaller fish generally have higher rates of growth and food consumption than do larger specimens of the same species (Palomares and Pauly 1989). An inverse relationship between predator length and the proportions with stomach contents was also established for dusky kob of 3–80 cm in the Great Fish Estuary (Griffiths in 1997b).

The proportions of 40–75 cm *A. japonicus* with stomach contents from the Ciskei (64%) and Kowie (67%) surf zones of the Eastern Cape, and of the Western Cape (67%) surf zone were similar; and in all cases were higher than those of the nearby estuaries, i.e. Keiskamma (47%), Great Fish (61%) and Breede (62%) systems (Fig. 2). The proportion of *A. japonicus* (40–75 cm) containing food in the sandy Sundays River surf (53%) was lower than in the sand/reef Eastern Cape surf zones (i.e. Ciskei and Kowie), but

Table II: Feeding intensity, expressed as food mass as a percentage of body mass, and the percentage of *A. japonicus* with stomach containing food from various surf-zone and estuarine localities. The feeding intensity values were based on all fish >40 cm *TL*

Locality	Size range (cm, *TL*)	% with food	*n*	Feeding intensity		Source
				Range	Mean	
Surf zone						
KwaZulu-Natal[L]	40–75	52	12	0.005–2.206	0.372	This study
Ciskei[L]	40–75	64	72	0.005–8.800	0.757	This study
	75–110	68	17			
Kowie[L]	40–75	67	29	0.006–3.160	0.605	This study
Sundays[L]	40–75	53	85	0.001–7.600	0.331	This study
	75–110	41	26			
Bluewater Bay[S]	14–40	87	35	0.01–4.31	1.37	Lasiak (1982)
Kings Beach[S]	14–40	72	106	0.01–5.39	0.67	Lasiak (1982)
Southern Cape[L]	40–75	67	18	0.008–2.458	0.615	This study
	75–140	44	12			
Estuaries						
St Lucia[G]	27–111	53	217	–	–	Whitfield and Blaber (1978)
Keiskamma[L]	40–75	47	44	0.004–4.324	0.400	This study
Great Fish[L, S]	14–40	77	50			Griffiths (1997b) and this study
	40–75	61	83	0.002–1.852	0.234	
Sundays[G]	21–129	33	69	?–3.2	0.8	Marais (1984)
Swartkops[G]	21–66	46	51	?–6.5	1.2	Marais (1984)
Krom[G]	22–89	40	50	?–6.3	1.2	Marais (1984)
Gamtoos[G]	22–90	52	222	?–6.7	1.0	Marais (1984)
Breede[L]	40–75	62	48	0.005–1.729	0.182	This study
	75–120	38	18			

[L] Line-caught
[G] Gill-netted
[S] Beach-seined
n = number of stomachs containing food

Table III: Stomach contents of *A. japonicus* from the Ciskei and Kowie surf zones (combined), expressed as the percentage frequency of occurrence (%*F*) and mass (%*M*) of each prey taxon. Totals represent number of stomachs (*F*) and mass of prey (*M*). %*IRI* is the percentage index of relative prey importance at the species and at a higher (bold) taxonomic level.

Prey	Value per predator total length-class					
	40–75 cm			75–110 cm		
	%*M*	%*F*	%*IRI*	%*M*	%*F*	%*IRI*
Crustacea						
Macrura	5.1	48.5	4.78	0.3	6.9	0.04
Macropetasma africana[P]	4.7	33.7	10.88	0.3	6.9	0.18
Palaemon pacificus[B]	0.1	4.0	0.03			
Ogyrides saldanhae[B]	0.1	1.0	<0.01			
Macruran remains	0.2	9.9	0.14			
Brachyura	4.5	32.6	2.83	1.9	6.9	0.24
Ovalipes trimaculatus[B]	0.9	2.0	0.12			
Plagusia chabrus[B]	2.0	7.9	1.09	1.9	6.9	1.13
Unidentified Portunidae[B]	0.6	5.0	0.21			
Megalopae[P]	0.8	14.9	0.82			
Brachyuran remains	0.1	4.0	0.03			
Anomura	0.1	2.0	<0.01			
Upogebia africana[B]	0.1	2.0	0.2			
Isopoda	0.6	12.9	0.15			
Paridotea ungulata[B]	0.2	5.0	0.07			
P. rubra[B]	0.1	3.0	0.02			
Cirolana sp.[B]	0.1	3.0	0.02			
Synidotea[B]	0.1	1.0	0.02			
Exosphaeroma[B]	<0.1	2.0	<0.01			
Aegidae[B]	<0.1	1.0	<0.01			
Unidentified isopod	<0.1	2.0	<0.01			
Amphipoda	0.1	4.0	<0.01			
Lysianassa ceratina[B]	0.1	4.0	0.03			
Mollusca						
Gastropoda	0.2	1.0	<0.01			
Bullia digitalus[B]	0.2	1.0	0.01			
Cephalopoda	20.9	23.8	9.60	22.4	34.5	14.44
Octopus vulgaris[B]	7.4	4.0	2.03	1.4	6.9	0.83
Octopus sp.[B]	3.6	10.9	2.69	0.4	6.9	0.24
Loligo vulgaris reynaudii[P]	9.8	10.9	7.34	20.5	24.1	42.45
Teleostei	68.6	62.4	82.63	75.4	58.6	85.28
Pomatomus saltatrix[P]	6.2	7.9	3.37	6.6	3.4	1.92
Pomadasys olivaceum	3.3	10.8	2.45	2.4	20.7	4.27
Sardinops sagax[P]	48.0	19.8	65.3	46.0	10.3	40.71
Etrumeus whiteheadi[P]	2.8	1.0	0.19	5.5	6.9	3.27
Liza spp.[P]	1.6	3.0	0.33	2.2	3.4	0.64
Argyrosomus inodorus[S]	1.9	2.0	0.26			
Sarpa salpa[S]	3.0	6.9	1.42	3.4	13.8	4.03
Diplodus sargus capensis[S]	0.9	5.9	0.36	0.3	3.5	0.09
Diplodus cervinus hottentotus[S]	0.2	2.0	0.03			
Chirodactylus brachydactylus[B]	0.1	2.0	0.01			
Lithognathus mormyrus[S]	0.1	3.0	0.02			
Pervager melanocephalus[S]	0.2	3.0	0.04			
Austroglossus pectoralis[B]	0.3	3.5	0.09			
Boopsoidea inornata[E]	0.1	1.0	<0.01			
Rhabdosargus holubi[E]	<0.1	1.0	<0.01			
Clinidae[B]	0.1	3.5	0.03			
Triglidae[B]	<0.1	1.0	<0.01			
Unidentified teleosts	0.6	8.9	0.61	0.1	3.5	0.03
Total	1 349.3	101		1 387	29	

[P] Pelagic species
[B] Benthic species
[E] Epibenthic species

greater than in the Sundays River Estuary (33%). It was marginally greater than recorded previously in the Swartkops (46%), Krom (40%) and Gamtoos (52%) estuaries (Marais 1984). Although the data from that study were based on a wide size range of fish (Table II), the samples may have been biased towards smaller individuals (mean sizes 27–56 cm). Consequently, the proportions of estuarine fish with food may have been even lower for comparable size-classes (i.e. 40–75 cm) than the cited values. The proportion of *A. japonicus* with stomach contents in the KwaZulu-Natal surf zone (52%) was similar to that calculated by Whitfield and Blaber (1978) for the Lake St Lucia Estuary (53%).

Trends in mean feeding intensity were similar to those depicted by the proportions of fish with food (Table II). Feeding intensity was highest in the sand/reef surf zones of the Cape regions (Ciskei surf – 0.757%, Kowie surf – 0.605% and Western Cape - 0.615%). Values for estuarine habitats were 0.400, 0.234 and 0.182% for the Keiskamma, Great Fish and Breede systems respectively. Mean feeding intensity in the KwaZulu-Natal (0.372%) and sandy Sundays River (0.331%) surf zones was substantially lower than in the sand/reef surf zones of the Cape regions and slightly lower than in the Keiskamma Estuary (0.40%), but were greater than in the other two estuarine systems.

The size composition of surf-zone *A. japonicus* with stomach contents (Fig. 3) was representative of fish >40 cm found in each region (Griffiths 1996). Dusky kob in the Eastern Cape consumed a wide variety of prey organisms, including benthic, epibenthic and pelagic species (Tables III, IV). Totals of 28 and 38 prey species were respectively recorded from fish in sandy (Sundays River) and mixed sand/reef (Ciskei and Kowie) surf-zone substrata. Precision analyses indicated that sufficient stomachs were examined to describe accurately the diet of *A. japonicus* in both of the Eastern Cape surf-zone habitats (Fig. 4). Asymptotic stabilization was attained at 91 stomachs (70% of those examined) for the sand/reef substratum and at 60 stomachs (54% of those examined) for the sandy substratum. Important prey taxa of the Eastern Cape surf zone included surf shrimps (macrura), crabs (brachyurans), cephalopods (octopus and squid) and fish (teleosts), with the latter being the most important prey taxon (Tables III, IV). By including data from Lasiak (1982) for fish of 16–40 cm, an ontogenetic dietary shift is demonstrated for surf-zone dusky kob in the Eastern Cape (Fig. 5). Although teleosts were the most important taxon of all kob size-classes between 16 and 110 cm, the importance of this group increased with size. The dietary importance of cephalopods also increased with growth, whereas that of crustaceans decreased.

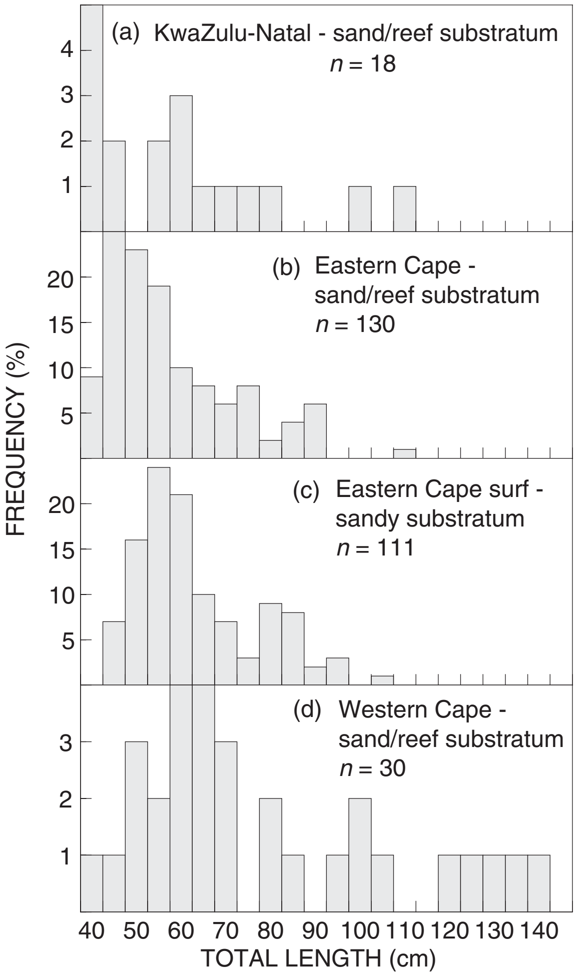

Fig. 3: Total length frequency distributions of surf-zone *A. japonicus* with stomachs containing food in (a) KwaZulu-Natal, (b and c) the Eastern Cape and (d) the Western Cape

In order of priority, the three most important prey species of dusky kob between 40 and 75 cm *TL* in the sand/reef surf zone were sardine *Sardinops sagax*, surf shrimp *Macropetasma africana* and chokka squid *Loligo vulgaris reynaudii*. Sardine, chokka squid and pinky *Pomadasys olivaceum* were most important for dusky kob between 75 and 110 cm (Table III). Other important species included elf *Pomatomus saltatrix*, *Octopus* sp. and strepie *Sarpa salpa*. In descending order of importance, prey items of kob <75 cm in the Sundays River surf were elf,

Table IV: Stomach contents of *A. japonicus* from the Sundays River surf zone, expressed as the percentage frequency of occurrence (%*F*) and mass (%*M*). Of each prey taxon. %*IRI* is the percentage index of relative prey importance at the species and at a higher (bold) taxonomic level

Prey	Value per predator total length-class					
	40–75 cm			75–110 cm		
	%*M*	%*F*	%*IRI*	%*M*	%*F*	%*IRI*
Crustacea						
Macrura	10.3	60.0	11.95	1.4	38.5	1.06
Macropetasma africana[P]	8.9	41.2	16.70	0.9	19.2	1.81
Palaemon pacificus[B]	0.2	4.7	0.04	<0.1	3.8	0.04
Ogyrides saldanhae[B]			0.1	3.8	0.04	
Macruran remains	1.2	14.1	0.78	0.4	15.3	0.60
Mysidacea						
Mesopodopsis slabberi[P]	1.2	3.5	0.08			
	1.2	3.5	0.19			
Brachyura	4.6	32.9	2.93	1.1	11.5	0.25
Ovalipes trimaculatus[B]	1.0	3.8	0.04			
Ocypode ryderi[B]	1.8	1.2	0.10			
Megalopae[P]	2.6	28.2	3.37	0.1	7.7	0.08
brachyuran remains	0.2	3.5	0.03			
Anomura	0.2	2.4	<0.01			
Upogebia africana[B]	0.1	1.2	<0.01			
Callianassa sp.[B]	0.1	1.2	<0.01			
Isopoda	0.5	12.9	0.13			
Paridotea ungulata[B]	0.1	2.4	0.01			
Cirolana sp.[B]	0.2	5.9	0.06			
Pontegeloides latipes[B]	<0.1	1.2	<0.01			
Isopod remains	0.1	3.5	0.02			
Mollusca						
Gastropoda	<0.1	1.2	<0.01			
Bullia digitalus[B]	<0.1	1.2	<0.01			
Cephalopoda	20.1	18.8	7.30	31.6	23.0	14.20
Octopus vulgaris[B]	<0.1	3.8	0.04			
Octopus sp.[B]	19.8	17.6	11.43	2.3	11.5	2.77
Loligo vulgaris reynaudii[P]	0.2	2.4	0.02	29.2	15.4	47.06
Polychaeta[B]				0.1	3.8	0.01
Teleostei	63.2	63.5	77.60	66.0	65.4	87.46
Pomatomus saltatrix[P]	39.9	27.1	46.84	9.3	11.5	11.20
Pomadasys olivaceum[E]	6.8	36.5	17.12	0.2	15.4	0.32
Pomadasys commersonnii[E]	1.4	1.2	0.08			
Engraulis capensis[P]	2.2	2.4	0.78			
Sardinops sagax[P]	2.2	2.4	0.24	0.1	3.8	0.04
Liza spp.[P]	0.5	1.2	0.03	16.9	7.8	13.79
Argyrosomus inodorus[E]	0.5	1.2	0.03	17.0	3.8	6.76
Diplodus sargus capensis[E]	0.4	4.7	0.09	17.7	3.8	7.04
Sarpa salpa[E]	0.8	3.8	0.31			
Juvenile *Caranx*[P]	0.4	1.2	0.02			
Juvenile Triglidae[B]	0.1	1.2	<0.01			
Teleost remains	0.5	7.1	0.17	4.0	19.2	7.95
Totals	489.1	85		454.5	26	

[P] Pelagic species
[B] Benthic species
[E] Epibenthic species

surf shrimp, pinky and *Octopus* sp., whereas chokka squid, mullet *Liza* sp. and elf were most important for fish >75 cm (Table IV). As expected, reef associated species, such as rock crab *Plagusia chabrus* and teleosts, e.g. *Sarpa salpa*, *Diplodus cervinus hottentotus* and *Chirodactylus brachydactylus,* were almost entirely absent from dusky kob diets in the Sundays River surf. The presence of grazing isopods (e.g.

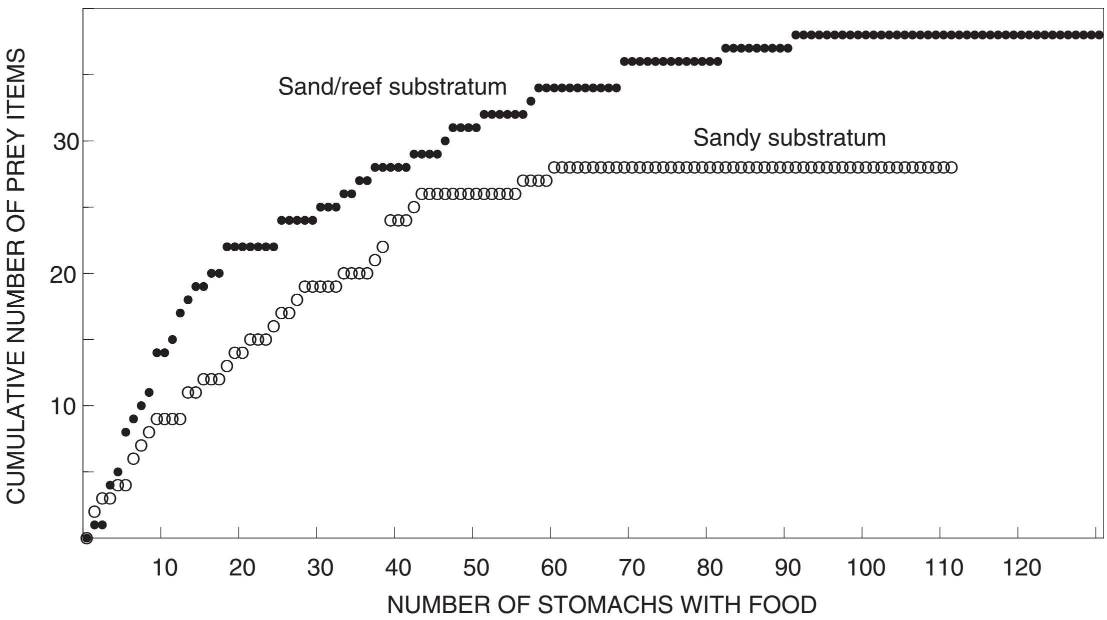

Fig. 4: Cumulative prey curves for *A. japonicus* from the Eastern Cape surf zone

Paridotea ungulata) in the Sundays River surf-zone diet is probably the result of imported macroalgae and associated organisms from the western areas of Algoa Bay (A. C. Cockcroft , pers. comm.). The importance of *Octopus* sp. was unexpected, but is possibly attributable to the fact that the limited reef of the Sundays River surf represents the only area where paralarvae transported into this area might settle, and juvenile concentrations may therefore at times be high. The *Octopus* sp. eaten in that area were generally small, ranging in dorsal length from 3 to 8 cm (n = 12). Tagging studies indicate that juvenile dusky kob generally do not move large distances (Griffiths 1996), and it is therefore unlikely that the octopus were eaten farther afield.

The occurrence of specific prey items and the proportion of dusky kob with stomach contents from both the sandy and sand/reef surf-zone substrata varied widely with sampling date (Fig. 6). Although prey abundance was not measured during the present study, the diet of *A. japonicus* in Lake St Lucia reflected temporally the relative abundance of prey species in that system (Whitfield and Blaber 1978). Temporal variation in the surf-zone diet of dusky kob in the Eastern Cape is probably also related to changes in prey availability. This indicates that, aside from the number of stomachs examined, the accuracy with which dietary descriptions reflect the diet of

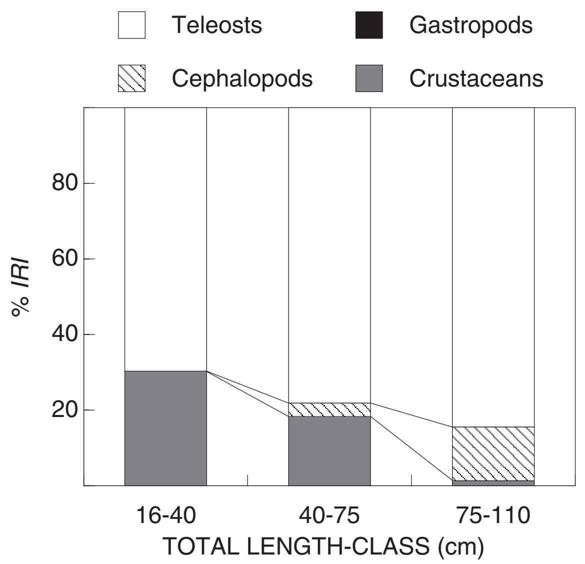

Fig. 5: Percentage index of relative importance (%*IRI*) of major prey taxa in three size-classes of *A. japonicus* from the Eastern Cape surf zone (all areas combined). Data for the 16–40 cm size-class were calculated from %*F* and %*M* values presented in Lasiak (1982)

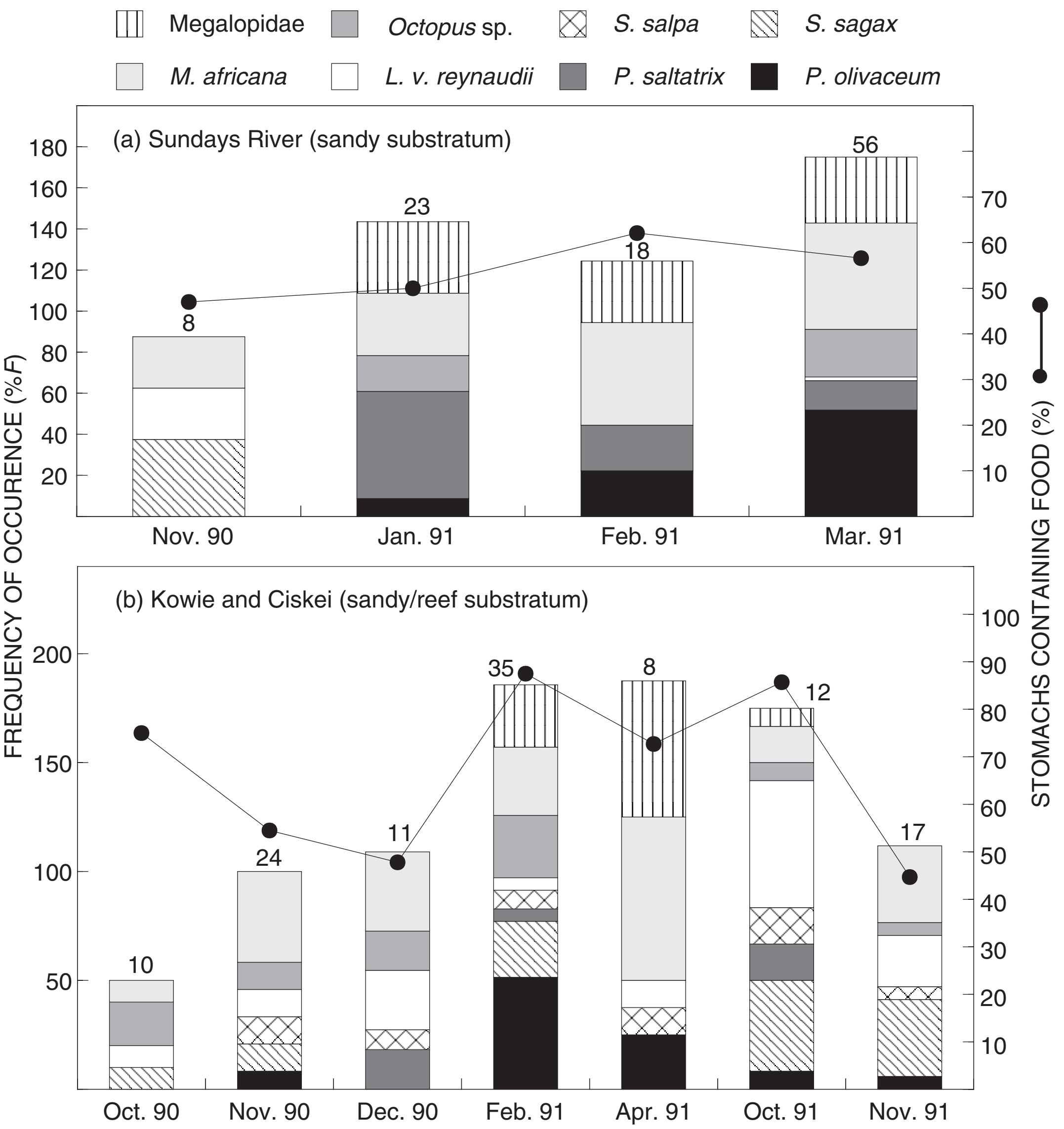

Fig. 6: Proportion of *A. japonicus* stomachs containing food and the frequency of occurrence (%*F*) of the primary prey species for each sampling month in (a) the sandy substratum of the Sundays River surf zone and (b) the sand/reef substratum of the Kowie and Ciskei surf zone of the Eastern Cape. The number of stomachs containing food is given

A. japonicus in a particular system will also depend on both sampling period and frequency.

Because of the small sample sizes and the infrequent nature of sampling in KwaZulu-Natal and the Western Cape (Table I), the surf-zone diets recorded for dusky kob in those regions (Tables V, VI) cannot be regarded as complete. However, they do provide some indication of the taxa consumed and allow for broad comparison with the more comprehensive Eastern Cape analyses. As observed for the Eastern Cape samples, crustaceans were more prevalent in the surf-zone diets of dusky kob <75 cm than in larger fish. Surf shrimp were important food items for fish of 40–75 cm in all sampling regions and, as in the

Table V: Stomach contents of *A. japonicus* from the Western Cape surf zone, expressed as the percentage frequency of occurrence (%*F*) and mass (%*M*) of each prey taxon. Totals represent number of stomachs (*F*) and mass of prey (*M*). %*IRI* is the percentage index of relative prey importance, at the species and at a higher (bold) taxonomic level

Prey	Value per predator total length-class					
	40–75 cm			75–144 cm		
	%*M*	%*F*	%*IRI*	%*M*	%*F*	%*IRI*
Crustacea						
Macrura	14.3	56.0	13.03			
Macropetasma africana[P]	13.2	33.6	13.22			
Macruran remains	1.1	22.2	0.79			
Brachyura	6.2	5.6	0.22			
Plagusia chabrus[B]	6.2	5.6	1.12	<0.1	8.3	<0.01
Crab remains				<0.1	8.3	0.01
Mollusca						
Cephalopoda				0.3	8.3	0.03
Loligo vulgaris reynaudii[P]				0.3	8.3	0.18
Teleostei	79.6	66.7	86.40	99.7	100	99.97
Pomatomus saltatrix[P]	27.9	27.8	25.07	0.9	16.7	1.06
Pomadasys olivaceum[E]	46.8	38.9	58.06	3.9	16.7	4.61
Sardinops sagax[P]				7.6	33.3	17.93
Scomber japonicus[P]				7.8	16.7	9.23
Liza spp.[P]				34.0	16.7	40.22
Diplodus sargus capensis[E]	0.4	5.6	0.07	11.2	8.3	6.59
Sarpa salpa[E]				<0.1	8.3	0.02
Pterogymnus laniarius[E]				0.3	8.3	0.18
Gonorynchus gonorynchus[E]				1.4	8.3	0.82
Acanthistius sebastoides[B]				15.8	8.3	9.29
Clinidae[B]	0.4	11.1	0.14			
Caffrogobius sp[B]	1.1	5.6	0.20			
Cheilodactylus sp[B]	0.4	5.6	0.07			
Cynoglossus capensis[B]	2.5	5.6	0.45			
Synaptura marginata[B]				16.8	8.3	9.88
Totals	184.4	18 1		694.1	12	

[P] Pelagic species
[B] Benthic species
[E] Epibenthic species

Eastern Cape, pinky and elf were important in the diet of this size group in the Western Cape.

Nearshore environment

Dusky kob from the nearshore zone were caught at water depths of 10–50 m. The combination of a large swimbladder and a large mouth (Griffiths and Heemstra 1995) make this species vulnerable to barotrauma, and stomach eversion is a common symptom on capture. As a result, only seven of the 261 fish sampled in KwaZulu-Natal (2.7%) and 32 of the 110 fish from the Cape regions (29%) contained food. The higher proportion of kob with food in the Cape nearshore zone is largely because of a large sample from <20 m deep in Algoa Bay. Despite small sample sizes, the lengths of those fish with stomach contents (Fig. 7) were representative of the population (mostly adults) found in this habitat (Griffiths 1996).

Teleosts were the most important prey taxon of dusky kob from the Cape nearshore zone, followed by cephalopods, and then by several groups of minor importance, including crustaceans, gastropods and chondrichthyans (Table VII). No single teleost species dominated the diet and, as in the surf zone, a wide variety of benthic, epibenthic and pelagic shoaling species were consumed. *L. v. reynaudii* was the most important item at the species level. Pelagic shoaling teleosts constituted the entire diet of the seven nearshore *A. japonicus* sampled in KwaZulu-Natal (Table VII).

DISCUSSION

Estuaries are generally accepted as important nurseries and feeding grounds for fish, because they are usually more productive than the surrounding seas (Whitfield 1997). Studies in the Eastern Cape, however, have revealed that the abundance and biomass of zooplankton in the surf zone are an order of magnitude higher than offshore, and are even higher than recorded in most estuaries (McLachlan 1983, Wooldridge 1983). This indicates that the surf zone is also highly productive and therefore potentially an important foraging area. A comparison of the proportion of *A. japonicus* with stomach contents in seven surf-zone localities and eight estuaries revealed that feeding frequency of specimens of similar-size was usually higher in the surf zone than in the proximal estuaries. Surf-zone dusky kob from mixed (sand/reef) substrata also fed more often than those from predominantly sandy environments. Mean feeding intensities were also higher for fish in the surf zone than in the proximal estuaries of the present study, and were higher in mixed rather than sandy substrata. Surf-zone values ranged from 0.33 to 0.76% and estuarine values from 0.18 to 0.4%. Lasiak (1982) recorded mean feeding intensities of 0.67% for the Kings Beach surf (i.e. similar to the Ciskei, Kowie and Western Cape surf zone values of the present

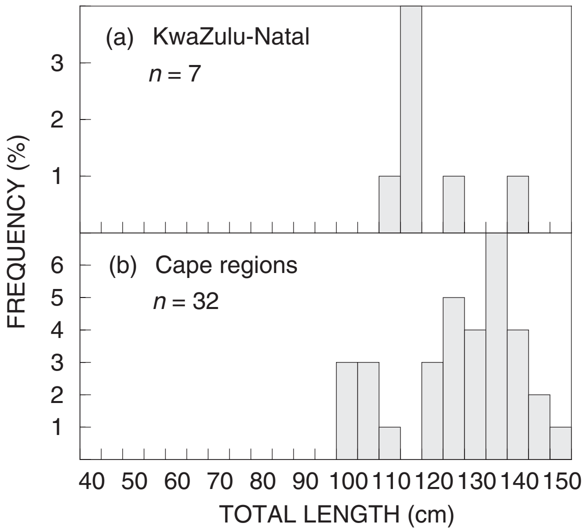

Fig. 7: Total length frequency distribution of nearshore *A. japonicus* with stomachs containing food in (a) KwaZulu-Natal and (b) the Cape regions

Table VI: Stomach contents of *A. japonicus* from the KwaZulu-Natal surf zone, expressed as the percentage frequency of occurrence (%*F*) and mass (%*M*) of each prey taxon. Totals represent number of stomachs (*F*) and mass of prey (*M*). %*IRI* is the percentage index of relative prey importance at the species and at a higher (bold) taxonomic level

Prey	Value per predator total length-class					
	40–75 cm			75–120 cm		
	%*M*	%*F*	%*IRI*	%*M*	%*F*	%*IRI*
Crustacea						
Macrura	53.2	58.3	58.39			
Macropetasma africana[P]	19.1	41.7	39.53			
Penaeus sp.	34.0	16.6	28.01			
Brachyura	7.8	33.3	4.01			
Emerita austroafricana[B]	6.4	8.3	2.64			
Megalopae[P]	0.7	8.3	0.29			
Unidentified crab remains	0.7	16.7	0.58			
Mollusca						
Cephalopoda				31.9	25.0	13.51
Octopus vulgaris[B]				31.9	25.0	18.95
Teleostei	39.0	50.0	36.70	68.1	75.0	86.49
Pomatomus saltatrix[P]	0.3	8.3	0.12			
Liza sp.[P]	30.3	16.7	25.10	17.2	50.0	20.49
Pomadasys olivaceum[E]	2.2	8.3	0.91			
Rhabdosargus sp.[E]				50.5	50.0	60.15
Glossogobius callidus[B]	0.5	16.7	0.42			
Unidentified remains	5.8	8.3	2.39	0.3	50.0	0.36
Totals	140.3	12		672.2	4	

[P] Pelagic species
[B] Benthic species
[E] Epibenthic species

Table VII: Stomach contents of *A. japonicus* (102–151 cm *TL*) from the nearshore area of KwaZulu-Natal and the Cape regions (Eastern and Western Cape combined), expressed as percentage frequency by occurrence (%*F*) and mass (%*M*) of each prey taxon. Totals represent number of stomachs (*F*) and mass of prey (*M*). %*IRI* is the percentage index of relative prey importance at the species and at a higher (bold) taxonomic level

Prey	Value per region					
	Cape Region			KwaZulu-Natal		
	%*M*	%*F*	%*IRI*	%*M*	%*F*	%*IRI*
Crustacea						
Brachyura	0.1	9.4	0.01			
Unidentified remains	0.1	9.4	0.09			
Mollusca						
Gastropoda	0.1	3.1	<0.01			
Bullia annulata[B]	0.1	3.1	0.03			
Cephalopoda	24.0	28.1	9.95			
Loligo vulgaris reynaudii[P]	23.5	25.0	57.92			
Sepia simoniana	0.5	3.1	0.09			
Chondrichthyes	0.8	3.1	0.04			
Unidentified shark	0.8	3.1	0.25			
Teleostei	75.0	81.3	90.0	100	100	100
Etrumeus whiteheadi[P]	2.9	12.5	3.58	8.6	42.9	19.95
Sardinops sagax[P]	2.9	15.6	4.46	6.0	42.9	13.92
Pomatomus saltatrix[P]	2.4	12.5	2.96	40.3	14.3	31.17
Scomber japonicus[P]	1.9	9.4	1.76	29.0	14.3	22.43
Trachurus trachurus capensis[P]	5.4	3.1	16.7	12.3	14.3	9.51
Liza spp.[P]	13.1	3.1	4.00	3.9	14.3	3.00
Trichiurus lepturus[P]	0.9	3.1	0.28			
Pomadasys olivaceum[E]	1.4	12.5	1.73			
Argyrosomus inodorus[E]	2.0	6.3	1.24			
Pagellus bellotti natalensis[E]	0.9	9.4	0.84			
Diplodus sargus capensis[E]	4.9	3.1	1.50			
Sarpa salpa[E]	12.6	6.3	7.83			
Pterogymnus laniarius[E]	0.2	3.1	0.06			
Rhabdosargus holubi[E]	<0.1	3.1	0.01			
Stromateus fiatola[E]	11.6	3.1	3.55			
Galeichthys sp.[B]	<0.1	3.1	0.01			
Conger sp.[E]	1.8	3.1	0.55			
Gonorynchus gonorynchus[E]	0.6	3.1	0.19			
Acanthistius sebastoides[B]	6.9	3.1	2.11			
Cynoglossus capensis[B]	2.0	9.4	1.85			
Unidentified fish remains	0.6	25.0	1.48			
Totals	3 884.6	32		855.9	7	

[P] Pelagic species
[B] Benthic species
[E] Epibenthic species

study) and 1.37% for the Bluewater Bay surf. However, the latter value was based on a small sample size ($n = 35$) and may have been positively biased by an opportunistic incident of intense feeding. Marais (1984) calculated mean feeding intensity values of 0.8–1.2% for dusky kob gill-netted in four Eastern Cape estuaries. These values are 2–7 times the estuarine values of the present study. It is unlikely that the feeding intensities of dusky kob reported by Marais (1984) should be that much greater than those of the present study, and the discrepencies imply a methodological bias. It is tempting to suggest that the hook and line method employed here may either select for fish with empty or partially full stomachs, or result in higher rates of regurgitation. However these arguments are negated by the fact that higher maximum feeding intensity values were recorded for line-caught fish from the Ciskei and Sundays River surf zones than in the estuaries of Marais' (1984) study, and the larger proportions of line-caught than gill-netted dusky kob with food. Alternatively, the omission of very small items or parts of items from otherwise empty stomachs could have positively biased the mean feeding intensity values of the previous study. Unfortunately, Marais (1984) did not present minimum values and this omission precludes further investigation.

Regardless of these disparities, the present study indicates that feeding intensity in surf-zone localities is generally higher than in nearby estuaries which are commonly utilized by dusky kob. Therefore, *A. japonicus* in the surf zone appear to feed more frequently and consume larger meals than those of equivalent size in estuaries. This implies that the surf zone is an important foraging environment for juvenile dusky kob. A lack of overlap in the diet of dusky kob from estuaries and surf zones (see below) indicates that, under normal conditions, fish do not move rapidly between the two environments. It would therefore appear that the habitats do not operate together as a nursery area (i.e. feeding in one and protection in the other), and that the surf-zone and estuarine environments may be important nurseries for dusky kob of 15–107 and 3–107 cm respectively. The dietary importance of species that are not regular visitors to the surf zone (e.g. *S. sagax* and *L. v. reynaudii*) indicates that juvenile dusky kob may also feed beyond the backline of the breakers, but their absence from the catches of skiboats and trawlers, which generally operate at depths >20 m (Griffiths 1996), suggests that they do not move far offshore.

A study of the diet of *A. japonicus* in the Great Fish Estuary in relation to the distribution patterns of their prey (Griffiths 1997b) suggested that conspecific predator avoidance might be the main factor controlling the distribution of early juveniles (2–15cm) in estuaries, and that it is responsible for the restriction of this life-history phase to the upper reaches of the Great Fish system. Given that cannibalism of early juveniles is common in South African estuaries (Whitfield and Blaber 1978, Marais 1984, Griffiths 1997b), the absence of surfzone cannibalism supports the hypothesis concerning the confinement of early juveniles to estuaries. Lack of cannibalism in the surf zone also indicates that early juvenile recruits (c. 2 cm) do not simply move inshore and then follow the surf zone until they encounter an estuary, but that, as postulated by Griffiths (1996), they are more likely to locate estuaries via offshore olfactory cues of freshwater origin.

The advantages of a dual estuarine/surf-zone habitat for juvenile dusky kob include: 1) a greater collective nursery allowing for larger juvenile populations; 2) lower rates of early juvenile cannibalism as a result of reduced juvenile densities in estuaries; and 3) a buffer mechanism against extreme variation in either environment. Examples of such events include reduced freshwater inflow (natural or anthropogenic), which causes a general decline in the biomass of estuarine prey (Griffiths in prep.), and can result in mouth closure (Whitfield 1997); excessive freshwater inflow into estuaries during flood conditions (Marais 1988) and cold upwelling events in the marine environment during summer (Schumann *et al*. 1982). The utilization of inshore (v. nearshore) nursery areas by dusky kob reduces competition for food resources, both intra-specifically (between juveniles and adults), and inter-specifically (with congeneric species). *A. thorpei* and *A. inodorus* respectively occur in the nearshore environments (seaward of surf zone to 100 m depth) of KwaZulu-Natal and the Cape regions (Griffiths and Heemstra 1995). According to Griffiths (1996), the comparatively predator-free inshore nursery has allowed *A. japonicus* to evolve a larger size and age-at-maturity than either of its two congeneric species, both of which utilize nearshore marine areas.

A comparison of the estuarine and surf-zone diets of juvenile *A. japonicus* in the Eastern Cape indicated that prey species diversity was greater in the latter habitat, particularly where substrata are mixed. Between 13 and 25 prey species were eaten in each of the five estuaries studied (Marais 1984, Griffiths 1997b), whereas 28 and 38 species were recorded in dusky kob from the predominantly sandy and the sand/reef surf zones of the present study respectively. Despite the fairly wide range of prey taken by juveniles in estuaries, one or two principal taxa were dominant in each system. The small, pelagic estuarine round herring *Gilchristella aestuaria* was by far the most important prey item in the Gamtoos, Krom and Swartkops estuaries (Marais 1984). In the Sundays River Estuary, mysids and *G. aestuaria* were the most dominant prey of dusky kob of 22–50 cm, whereas *G. aestuaria* was the most important food item for fish of 50–128 cm (Marais 1984). A recent study in the Great Fish Estuary demonstrated that juveniles of 15–40 cm fed predominantly on mugilids, *G. aestuaria* and mysids, that those of 40–60 cm consumed mainly mysids and *G. aestuaria*, and that fish of 60–80 cm ate mostly the latter (Griffiths 1997b). In Lake St Lucia, KwaZulu-Natal, the primary prey of dusky kob were *G. aestuaria* and a tropical pelagic teleost, *Thryssa vitrirostris* (Whitfield and Blaber 1978). Dusky kob of 15–42 cm in the Algoa Bay surf zone fed mostly on *Macropetasma africana* and a variety of teleosts, unfortunately not analysed at the species level (Lasiak 1982). The present study revealed that the principal prey species of *A. japonicus* (40–110 cm) of the Eastern Cape surf zone were *M. africana*, *P. saltatrix*, *P. olivaceum*, *P. sagax*, *S. salpa*, *Liza* sp., *Octopus* sp. and *L. v. reynaudii*. The occurrence of these items varied with sampling event. Surf shrimp and *Octopus* sp. were not important items of fish >75 cm, and chokka squid, although important for fish of 40–75 and 75–110 cm, were more important to the larger size-group. Despite small sample sizes, *A. japonicus* in the surf zones of KwaZulu-Natal and the Western Cape, and in the nearshore environment of the Cape regions, also appear to feed on a wide variety of organisms. As in the Eastern Cape, *M. africana*, *P. saltatrix*, *P. olivaceum*, *S. sagax* and *Liza* spp. were important prey items in the surf zone of the Western Cape. The prey species most frequently taken in the nearshore environment of the Cape regions was *L. v. reynaudii*, followed by a number of teleosts, including *S. sagax*, *P. saltatrix*, *Etrumeus whiteheadi*, *P. olivaceum*, *Scomber japonicus*, *Pagellus belotti natalensis* and *Cynoglossus capensis*. These results indicate that estuarine dusky kob feed mainly on pelagic shoaling species, particularly teleosts, whereas those in the surf zone and the nearshore environment feed on a wider variety of important prey taxa, including benthic, epibenthic and pelagic representatives of the macrura, cephalopoda and teleostei.

Pelagic shoaling teleosts constituted the entire diet of the seven nearshore *A. japonicus* sampled in KwaZulu-Natal. Despite the small sample size, data were collected over a two-year period and were not biased by a single feeding event. Many of the prey species, e.g. *S. sagax* (Baird 1971, Armstrong *et al*. 1991), *P. saltatrix* (Van der Elst 1981), *S. japonicus* and *Trachurus trachurus capensis* (A. D. Connell, Council for Scientific Research, pers comm.) migrate from the Cape waters to KwaZulu-Natal at the same time as do adult dusky kob (Griffiths 1996). These concurrently migrating prey species may provide an important source of energy for both migration and gonad development, as has been shown for *S. sagax* and the migratory sciaenid *Atractoscion aequidens* (Griffiths and Hecht 1995).

Given the diverse prey of dusky kob in both the surf-zone and nearshore environments, the variable frequency with which the specific prey items were consumed and the fact that they appear to modify their diet in accordance with prey abundance (Whitfield and Blaber 1978), *A. japonicus* may be regarded as a generalist with broad trophic adaptability. They are usually found in turbid water (Griffiths 1996), where they enjoy several sensory advantages over their prey. Mechano-reception is enhanced by well-developed lateral line and auditory (large swimbadder and otoliths) systems (Griffiths and Heemstra 1995), and the capture of several blind dusky kob in Lake St Lucia by hook and line using cut bait (pers. obs.) suggests that chemo-reception is acute. It is therefore postulated that dusky kob locate and stalk their prey using predominantly non-visual cues and that visual contact occurs only in the final stages of the attack. The large, wedge-shaped caudal fin and deep caudal peduncle (Griffiths and Heemstra 1995), which enable rapid acceleration (Pauly 1989), and the large buccal cavity, which allows for effective suction feeding (Gerking 1994), are anatomical adaptations that promote successful attack at close quarters. The consumption of such diverse organisms as swarming mysids and surf shrimp, obligate shoaling pelagic fish and solitary benthic and epibenthic species, imply that dusky kob are further assisted by a high degree of feeding mode plasticity.

It is concluded that *A. japonicus* is a top predator, which may influence the pelagic and demersal food chains of estuaries, the surf zone and the nearshore environment. Stock depletion through recruitment overfishing is likely to have had an impact on the foodwebs of all three habitats. The impact of a substantially reduced predator population is, however, further complicated by concomitant exploitation of several of the important prey species (e.g. *P. saltatrix*, *S. sagax* and *L. reynaudii*), and is possibly best quantified with trophic mass-balance assessments such as ECOPATH modelling (Walters *et al.* 1997). Feeding data, such as those presented in this paper, are essential to an exercise of this nature.

ACKNOWLEDGEMENTS

I thank Prof. C. L. Griffiths (University of Cape Town [UCT]) for identifying the isopods and amphipods, Dr M. R. Lipiński (SFRI) for identifying the cephalopods and Drs B. Cooke (UCT) and M. J. Smale (Port Elizabeth Museum) for assisting in the identification of brachyuran and teleost prey respectively. Drs A. C. Cockcroft and R. L. Tilney (both SFRI) commented on an earlier draft of the manuscript. I also thank all those recreational anglers and commercial fishermen who made their catches available for sampling.

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