The ecology of *Sphyraena barracuda* (Osteichthyes: Perciformes) in the Kosi system with notes on the Sphyraenidae of other Natal estuaries

S.J.M. Blaber
Department of Zoology, University of Natal, Pietermaritzburg

The ecology of *Sphyraena barracuda* was studied in the Kosi estuary system of Natal. Fry enter from the sea at a length of 20 mm and live in shallow marginal weed-beds until a length of 80 mm when they move to fringing *Phragmites* reed-beds. After reaching 300 mm they move to open water areas. No specimens longer than 500 mm were recorded and none were mature. Growth is rapid, they attain 180 mm in the first six months and after two years measure 400 – 500 mm. They leave the estuary after about two years. Their significance in the estuarine fish community is due to their predation, at all sizes, on a variety of estuarine-dependent juvenile fishes (e.g. *Rhabdosargus* spp., Mugilidae) and adults of estuarine species (e.g. *Ambassis* spp.). *S. barracuda* was recorded at salinities between 4‰ and 35‰, only in very clear water and at temperatures from 14,4 °C to 37 °C. *Sphyraena bleekeri* and *S. qenie*, which are also clear-water species, were found at Kosi in salinities from 0,5 to 35‰. They are also piscivorous on a range of small teleosts. *Sphyraena jello* is the most widespread barracuda in Natal estuaries, but only juveniles were recorded. This species is tolerant of a wide range of turbidities and salinities which enables it to live under most estuarine conditions. The distribution, ecology and interspecific interactions among Sphyraenidae in Natal estuaries are discussed in relation to their feeding biology, habitat preferenda and physical tolerances.

S. Afr. J. Zool. 1982, 17: 171 – 176

Die ekologie van *Sphyraena barracuda* is in die Kosi-estuariumsisteem bestudeer. Klein vissies van hierdie spesies, met 'n gemiddelde lengte van 20 mm, kom die sisteem vanaf die see binne, en vertoef daar in die vlak rand-wierbeddings totdat hulle 'n lengte van 80 mm bereik, waarna hulle hul tussen die aangrensende *Phragmites*-riete vestig. Hulle trek na die oopwater van die estuarium wanneer hulle 'n lengte van 300 mm behaal. Geen eksemplare langer as 500 mm kom in die sisteem voor nie, en selfs visse van hierdie grootte is nog nie volwasse nie. Die groeitempo van hierdie spesies is vinnig: die jong visse behaal 'n lengte van 180 mm in ses maande, en na ongeveer twee jaar, wanneer hulle die estuarium verlaat, is hulle tussen 400 en 500 mm lank. Die belang van die jong *S. barracuda* in die visbevolking van estuaria is dat alle ouderdomme op jong estuarium-afhanklike visse (bv. *Rhabdosargus*-spp., Mugilidae) sowel as volwasse estuariese vissoorte (bv. *Ambassis*-spp.) voed. *S. barracuda* is in soutgehaltes tussen 4 en 35‰ gevind, maar slegs in baie helder water met temperature tussen 14,4 en 37 °C. *Sphyraena bleekeri* en *S. qenie*, wat ook helderwaterspesies is, is in soutgehaltes tussen 0,5 en 35‰ in die Kosi-sisteem aangetref. Hulle is ook visvretend en vreet 'n verskeidenheid klein vissies. *Sphyraena jello* is die wydste verspreide barrakuda in Natalse estuaria, maar van hierdie spesies is ook slegs die onvolwasse ouderdomsgroepe aangetref. Hulle verdra troebel water sowel as 'n verskeidenheid soutgehaltes, en kan dus by meeste estuariese toestande aanpas. Die verspreiding, ekologie en interspesiewisselwerking onder die Natalse Sphyraenidae in estuaria word bespreek in die lig van hulle voedsel, habitatvoorkeur en fisiese verdraagsaamheid.

S.-Afr. Tydskr. Dierk. 1982, 17: 171 – 176

S.J.M. Blaber
Department of Zoology, University of Natal, P.O. Box 375,
Pietermaritzburg 3200, Republic of South Africa

Received 11 February 1982; accepted 14 June 1982

Sphyraena barracuda occurs throughout the tropical and subtropical Indo-Pacific and Atlantic Oceans where adult fish are solitary and subadults form shoals, usually in the vicinity of coral reefs. The biology and systematics of *S. barracuda* are discussed extensively by de Sylva (1963, 1973) and Williams (1959, 1965). The fry and juveniles penetrate shallow estuaries and coastal waters (de Sylva 1963) but little is known of their ecology in estuaries of the Indian Ocean.

This paper reports on a study from 1977 to 1981 on *S. barracuda* in the Kosi estuary system of northern Zululand (Figure 1) where the species is one of the more common

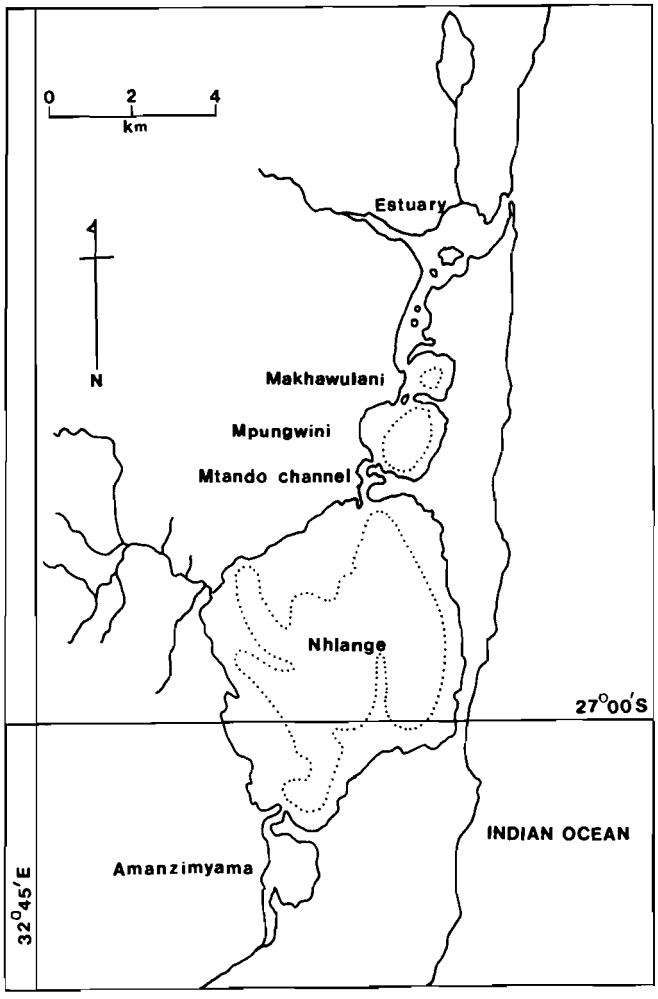


Figure 1 The Kosi system showing main basins and 5 m depth contour.

piscivores. The investigation forms part of a study of the ecology of the fish community of Kosi (Blaber 1978; Blaber & Cyrus 1981) as well as contributing to an overall study of the trophic structure of the fish communities of Natal estuaries.

Notes on the occurrence and ecology of other *Sphyraena* species which occur in the estuaries of Natal are included for comparison with *S. barracuda*. Sphyraenidae are mainly voracious piscivores and when present in an estuary may exert a significant influence on fish community structure and play an important role in the population dynamics of estuarine fishes.

Study areas

The following estuarine systems of Natal, from south to north, were sampled: Mtamvuna (open tidal estuary; 31°04'S/30°11'E), Tongati (closed estuary; 29°33'S/31°11'E), Mlalazi (open tidal estuary; 28°57'S/31°48'E), St Lucia (coastal lake estuary system; 28°00'S/32°25'E) and Kosi (coastal lake estuary system; 26°50'S/32°38'E). *S. barracuda* was captured only at Kosi which consists of a series of coastal lakes connected to the sea through a usually permanently open estuary (Figure 1). Details of the bathymetry, physics and chemistry, and factors of importance to the fish populations of Kosi are given in Hill (1975), Allanson & Van Wyk (1969) and Blaber (1978) respectively. The Kosi system is characterized by very clear water and sandy substrates.

Methods

Field

Fish were captured using a large seine net (70 m × 2 m × 12 mm bar mesh), a small seine net (10 m × 1,5 m × 4 mm bar mesh) and a fleet of monofilament gill nets (50, 56, 75, 100, 144 mm stretch mesh). At Kosi, fish were also caught by trolling and catches from native fish traps were examined. Stomach contents were removed from all fish and preserved in 10% formalin. All fish were measured to standard length (SL). Water turbidity was measured with a Hach 16800 nephelometer calibrated against formazin standards and the results expressed as nephelometric turbidity units (NTU). Salinity was measured with a Goldberg optical salinometer and temperatures with a standard thermometer.

Laboratory

Stomach contents were identified as far as possible and counted. Fish prey digested beyond visual recognition were identified from otoliths using a reference collection of otoliths. The energy values (J/mg) of all prey species were determined using a Gallenkamp Ballistic Bomb Calorimeter. Length — dry mass regressions were calculated for the prey species to enable the energy value of any length of prey to be estimated. The diet is expressed in terms of the percentage energy contribution and the percentage frequency of occurrence of each prey category. The percentage fullness of each stomach was assessed by the 'points' method.

Identification

After consultation with Dr P.C. Heemstra of the J.L.B. Smith Institute of Ichthyology and Professor D.P. de Sylva of the University of Miami, concerning possible confusion of species, the Sphyraenidae were identified using the keys of de Sylva (1973) and Williams (1959).

Results

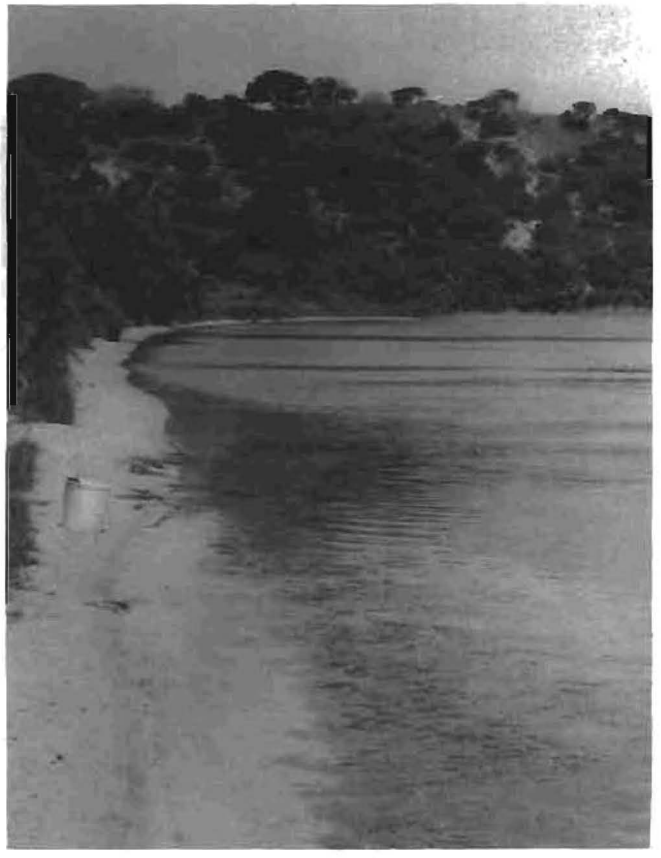
Sphyraena barracuda

This species was captured only in the Kosi system where it was restricted to the estuary and Lakes Makhawulani and Mpungwini (Figure 1). It was found in specific habitat types according to length (Figure 2). Fry occurred in marginal weed-beds of *Potamogeton pectinatus* and *Chaetomorpha* sp. within 3 m of the shore; juveniles from 80 to 300 mm SL were found among fringing *Phragmites* reed-beds and adjacent roots of *Hibiscus tiliaceus, Barringtonia racemosa* and *Avicennia marina*, while fish of 300 to 500 mm SL occurred in open-water areas.

S. barracuda was not recorded at salinities of less than 4‰ such as occur in Lakes Nhlange and Amanzimnyama (Figure 1). Turbidities throughout the Kosi system are low (0,2 – 8,6 NTU) and *S. barracuda* were recorded at values between 0,3 and 2,2 NTU. Fry were recorded at temperatures from about 20 °C to 37 °C in shallow water during summer but larger fish which occurred throughout the year in the system were found in temperatures from 14,4 °C to 28 °C.

Fry of 20 – 40 mm SL were recorded in Kosi from October to April indicating a protracted spawning and recruitment cycle, similar to that of *S. barracuda* in the west Atlantic (de Sylva 1963). Insufficient numbers of each size class could be captured to permit accurate polymodal growth analyses. However, fry of 20 – 30 mm SL, which were present in summer (Dec. – Jan.) in marginal weed-beds, were very uncommon in April, when fish of 80 – 90 mm SL became common in *Phragmites* areas, and were absent in July, at which time the modal size of *Phragmites* fish had reached 200 mm SL. If these figures reflect a movement of the same age group then they indicate a relatively rapid growth of ± 180 mm in the first six months in the estuary. No fish longer than 500 mm SL were captured and most open-water *S. barracuda* measured between 300 and 450 mm SL. It is likely therefore that the rapid growth rate is maintained in the second year and that *S. barracuda* leave the estuary after about two years. No reproductively mature fish were captured.

The diets of the three habitat groups (Figure 2) of *S. barracuda* are shown in Table 1. At all sizes they are almost exclusively piscivorous. Fry feed chiefly on the fry of Mugilidae and the cichlid *Sarotherodom mossambicus* which are abundant in and adjacent to marginal weed-beds. The mugilid fry were mainly larger (10 mm) than the cichlids (mostly less than 10 mm) hence their greater contribution to energy intake. It is significant that *S. barracuda* of 20 mm SL frequently consume prey of half their own length. Fish between 80 and 300 mm SL feed on a wide variety of species which occur in *Phragmites* and mangrove areas, particularly *Ambassis* and *Rhabdosargus* species. The filter-feeding clupeid, *Gilchristella aestuarius* is probably captured in adjacent open-water areas. The length ranges (SL) of prey species are shown in Table 1. Of the larger fish longer than 300 mm SL, only those captured in shallow areas (less than 2 m), both during the day and night, contained food. They apparently move onto the shallow sandy shelf areas to prey on the common *Gerres*,



Fry 20 – 79 mm
Marginal weed beds of *Potamogeton pectinatus* and *Chaetomorpha* sp. within 3 m of shore, not >0.5 m deep

80 – 300 mm
Phragmites beds and adjacent roots of *Hibiscus*, *Barringtonia* and *Avicennia*, <2 m deep

Enter estuary from sea at 20 mm

300 – 500 mm
Open water; but venturing into open shallow areas for feeding

Figure 2 The life cycle and habitats of *Sphyraena barracuda* in the Kosi system.

Table 1 The diet of three length groups of *Sphyraena barracuda* in the Kosi system (% E = % of energy intake; % F = % frequency of occurrence; *n* = number of stomachs analysed)

	20–79 mm (*n* = 27)			80–300 mm (*n* = 77)			300–500 mm (*n* = 18)		
Prey	%E	%F	(SL mm)	%E	%F	(SL mm)	%E	%F	(SL mm)
Ambassis natalensis	–	–	–	24	15	(20–50)	–	–	–
Ambassis productus	–	–	–	20	3	(30–60)	17	36	(40–60)
Croilia mossambica	–	–	–	5	9	(20–40)	–	–	–
Gerres acinaces	–	–	–	<1	2	(20–50)	43	18	(110)
Gilchristella aestuarius	–	–	–	12	14	(20–60)	–	–	–
Glossogobius giuris	–	–	–	6	7	(10–50)	–	–	–
Hyporhamphus sp	–	–	–	<1	2	(50)	–	–	–
Mugilidae (fry)	51	12	(10)	2	7	(10–20)	–	–	–
Pranesus pinguis	–	–	–	–	–	–	6	9	(80)
Rhabdosargus holubi	2	4	(10)	4	2	(40)	13	9	(70)
Rhabdosargus sarba	–	–	–	18	9	(10–50)	22	9	(90)
Sarotherodon mossambicus	36	33	(<10–10)	5	3	(10–30)	–	–	–
Unidentified fish	10	50	(<10–10)	–	24	–	–	18	–
Total fish	–	100	–	–	95	–	–	95	–
Amphipoda	–	–	–	<1	2	–	–	–	–
Penaeidae	–	–	–	5	14	–	–	9	–
Empty	–	12,5	–	–	24	–	–	39	–

Rhabdosargus and *Ambassis* species, but return to the surface waters over the deep basins when not feeding. The stomachs of all those captured over deep water were empty. The feeding periodicity of *S. barracuda* from 80–500 mm SL, based on the percentage fullness of the stomach, is shown in Figure 3. Feeding takes place mainly in daylight in the early morning and evening.

Other Sphyraenidae

The occurrence of *Sphyraena bleekeri, S. jello* and *S. qenie* in Natal estuaries is shown in Table 2. Only data from this study are included owing to the previous probable taxonomic confusion between these three species. In this regard de Sylva (1973, p.85) states '*S. bleekeri* has frequently been identified as almost every Indo-Pacific barracuda but usually as *jello*'. *S. bleekeri* and *S. qenie* occurred only in Kosi, including Lake Nhlange, as juveniles and adults in open-water areas but no fry were found. Juvenile *S. jello* were captured in most estuaries although at Kosi were restricted to the *Phragmites* margins of Lake Nhlange and the Mtando channel (Figure 1) with one specimen recorded from the estuary. Fry of *S. jello* were captured at Tongati, Mlalazi and St Lucia but no adults were caught during the study period. The salinity, turbidity and temperature ranges in which each species was found are shown in Table 3. All are euryhaline and occur within similar temperature ranges but *S. jello* occurs in a very wide range of turbidities, while the others have only been recorded from the clear waters of the Kosi system. *S. jello* of 130 to 300 mm SL was particularly common in the mangrove areas of Mlalazi estuary where its most important prey, *Valamugil cunnesius*, is very common. The diets of *S. bleekeri, S. jello* and *S. qenie* are shown in Table 4. All are mainly piscivorous. The diet of *S. jello* is assessed from data from all estuaries. The feeding periodicities, based on the percentage fullness of stomachs, of *S. jello* and *S. qenie* are shown in Figure 3. Although the data are incomplete they suggest a similar feeding regime to that of *S. barracuda*. Not more than one *Sphyraena* species was captured in the same area at the same time and mixed shoals were not encountered.

Table 2 The occurrence of Sphyraenidae in Natal estuaries (TR = turbidity range; + = recorded in this study; – = absent; J = juvenile; A = adult)

		Mtamvuna TR 1,6–86,0	Tongati TR 5,0–464,0	Mlalazi TR 4,4–65,0	St Lucia TR 2,0–1472,0	Kosi TR 0,2–8,6
S. barracuda	J	–	–	–	–	+
	A	–	–	–	–	–
S. bleekeri	J	–	–	–	–	+
	A	–	–	–	–	+
S. jello	J	+	+	+	+	+
	A	–	–	–	–	–
S. qenie	J	–	–	–	–	+
	A	–	–	–	–	+

Table 3 The recorded salinity, turbidity and temperature ranges of Sphyraenidae in Natal estuaries (fry excluded)

	Salinity (‰)	Turbidity (NTU)	Temperature (°C)
S. barracuda	4–35	0,35–2,2	14,4–28
S. bleekeri	0,5–35	1,0–5,8	14,5–28
S. jello	0,5–36	3,25–65,0	14,0–28
S. qenie	0,5–35	0,35–5,8	14,5–28

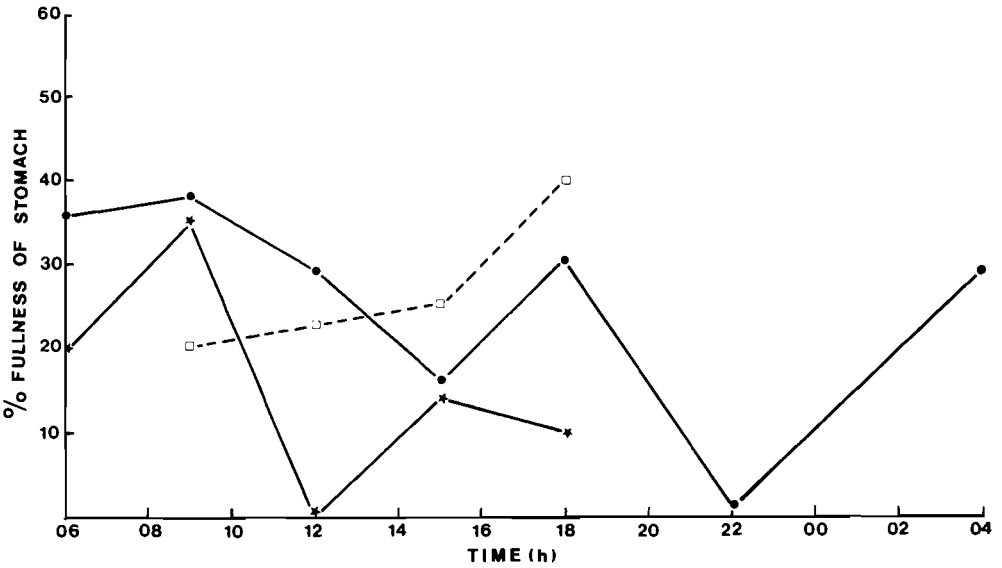


Figure 3 Feeding periodicity of *S. barracuda* (●—●), *S. jello* (□ – – □) and *S. qenie* (★—★)

Table 4 The diet of *Sphyraena bleekeri, S. qenie* and *S. jello* in Natal estuaries (%E = % of energy intake; %F = % frequency of occurrence; *n* = number of stomachs analysed)

	S. bleekeri *n* = 9		*S. qenie* *n* = 31		*S. jello* *n* = 30	
Prey species	%E	%F	%E	%F	%E	%F
Pisces						
Ambassis natalensis	–	–	15	18	28	17
Ambassis productus	52	44	42	36	<1	3
Anguilla sp.	–	–	1	9	–	–
Gerres acinaces	–	–	28	9	–	–
Gerres rappi	32	11	–	–	–	–
Gilchristella aestuarius	–	–	1	5	3	3
Glossogobius giuris	–	–	–	–	13	7
Hyporhamphus sp.	8	11	–	–	–	–
Mugilidae (Unid.)	–	–	–	–	2	3
Pomadasys commersonni	–	–	–	–	–	3
Pranesus pinguis	–	–	–	–	6	3
Rhabdosargus sarba	–	–	13	9	–	–
Sarotherodon mossambicus	8	11	–	–	–	–
Valamugil cunnesius	–	–	–	–	47	7
Unidentified fish	–	–	–	–	<1	10
Crustacea						
Penaeidae	–	–	<1	9	1	7
Amphipoda	–	–	–	–	<1	3
Macrobrachium sp.	–	–	<1	18	–	–
Length ranges (mm)	320–790		94–700		130–370	

Discussion

Williams (1965) states that maturity in *S. barracuda* is reached between 540 and 670 mm SL and this, together with the absence of fish longer than 500 mm SL in Kosi, indicates that this system is used solely during the juvenile phase of the life cycle. The estimated growth rate for Kosi fish corresponds closely to that of *S. barracuda* from the west Atlantic (de Sylva 1963), with fish attaining a length of about 500 mm SL in two years. Further growth to maturity in Natal thus takes place outside the estuary.

The habitat preferences of the juveniles in Kosi differ slightly from those in the west Atlantic where the life cycle is chiefly marine rather than estuarine. In Florida the fry are found in sandy and weedy shore areas, thereafter moving to mangrove and then reef habitats as they grow. The occurrence of *S. barracuda* in the Kosi system is probably a result of the unusual nature of this estuary with its clear, calm waters adjacent to deep oceanic water and reefs (Blaber 1978). The turbulent conditions found along most of the Natal coast are in general unattractive to juvenile fish (Blaber & Blaber 1980) and the high turbidities of most estuaries other than Kosi may exclude *S. barracuda* which was only recorded in the clear waters of Kosi. *S. barracuda* would fall into the category of a 'clear-water' species as defined by Blaber & Blaber (1980). It is possible therefore that offshore stocks of *S. barracuda* in the Natal region may be dependent on the Kosi system as the only suitable area for juveniles along about 800 km of coastline.

The occurrence of *S. barracuda* in Kosi in salinities as low as 4‰ is interesting and differs from the situation in Florida where the fish do not usually live in salinities of less than 24‰ (de Sylva 1963). It is possible that the absence of adult *S. barracuda* from Kosi may be related partly to salinity since de Sylva (1963) states that adult *S. barracuda* are typically oceanic and tend to avoid waters of low salinity. The temperatures in which *S. barracuda* were recorded at Kosi are within the ranges tolerated by this species according to de Sylva (1963) and low temperature 'kills', as reported in Florida at temperatures of about 10 °C, could not occur at subtropical Kosi where the lowest recorded temperature is 13 °C.

Both Williams (1965) and de Sylva (1963) indicate that *S. barracuda* is primarily a fish eater and the diet at Kosi is almost entirely fish (Table 1: 95 – 100% fish). The actual prey eaten probably reflects the different structures

of the various fish communities rather than any strict food preferences by the barracuda. The differences between the diets of barracuda in Florida, east Africa and Kosi can be attributed to contrasts between estuarine and marine communities and zoogeography. The prey species of the different size groups of *S. barracuda* at Kosi are those most common in each habitat (Table 1, Figure 2). De Sylva (1963) suggests that larger barracuda show a preference for two main categories of fishes: comparatively fast-swimming fishes of the surface or mid-depths and sluggish reef-dwelling tetraodontiform fishes. In Kosi the 80 – 300-mm group (Table 1) also feeds on a mixture of surface-swimming species, such as *Gilchristella aestuarius* and relatively sluggish bottom-dwelling Gobiidae such as *Glossogobius giuris* and *Croilia mossambica*. Adults feeding in coral reef areas of the sea in Natal thus may exhibit the same basic feeding behaviour.

The significance of *S. barracuda* in the estuarine fish community of Kosi lies in its role as a predator of all sizes of estuarine-dependent juveniles, including newly recruited fry, of marine genera such as *Rhabdosargus* and of adults of truly estuarine species such as *Ambassis natalensis* and *Gilchristella aestuarius*. No good data are available on the juveniles of *S. bleekeri* and *S. qenie,* since too few were captured or analysed, and other than the work of Williams (1959, 1965), little is known of the biology of the adults.

The few *S. bleekeri* taken in Kosi were reproductively inactive but since Williams (1965) states that maturity in this species is reached between 360 and 450 mm SL, it may be assumed that the length range from Kosi (Table 4) included adult fish. A greater length range of *S. qenie* occurred in Kosi (Table 4) and the sex could be distinguished in fish longer than about 400 mm SL (12 specimens, 400 – 700 mm SL) but all gonads were inactive or at stage II. The absence of fry and small juveniles of *S. bleekeri* and *S. qenie* and the relatively low numbers of both species indicate that they enter the Kosi system opportunistically for feeding. They prey mainly on relatively slow-moving mid-water to benthic fish such as *Ambassis, Gerres* and *Rhabdosargus*. Both species were recorded with full stomachs over deep and shallow-water areas.

S. bleekeri and *S. qenie* are apparently 'clear-water' species similar to *S. barracuda,* but they occur in a wider range of salinities (Table 3). They probably occur in typically oceanic water such as that adjacent to Kosi estuary and their salinity tolerance allows them to utilize the low-turbidity, food-rich waters of Kosi.

S. jello is the most widely distributed sphyraenid in Natal but only juveniles were recorded in this study. It has wide salinity and turbidity tolerances (Table 3) which allow it to occur in most estuarine situations. However, the relatively low numbers recorded, suggest either that the species is not estuary-dependent during the juvenile phase, or that it is generally uncommon in Natal estuaries. It is interesting that Williams (1965) could obtain no information on juvenile *S. jello* in the sea in east Africa and that the size of *S. jello* at first maturity is unknown. It is possible that the juveniles are dependent on tropical estuaries north of Natal, perhaps in mangrove areas, in which case the juvenile *S. jello* in Natal are close to the limit of their distribution. The juveniles are most common in Natal in the mangrove areas of Mlalazi estuary. Adult *S. jello* are common in the sea off Natal in breeding condition, particularly in the north, but juveniles have not been positively recorded in the sea (van der Elst, pers. comm.). It is likely therefore that *S. jello* populations in Natal are a southern extension of what is essentially a tropical species.

Although their diets are similar, interspecific interactions between the four species of barracuda in Kosi are unlikely, owing firstly, to their habitat preferences and secondly, to a superabundance of suitably sized prey species. *S. barracuda* fry and juveniles occur in the weed-beds and *Phragmites* of Lakes Makhawulani and Mpungwini (Figure 1) whereas juveniles of *S. jello* are found among the *Phragmites* of the lower salinity areas of Lake Nhlange. Larger *S. barracuda, S. bleekeri* and *S. qenie* occur in open-water areas but the first feeds mainly in shallow areas while the last two range more widely. In other Natal estuaries *S. jello* is the only barracuda and since hunting techniques of Sphyraenidae, which involve a combination of stealth and speed (de Sylva 1963), are different from other predators in Kosi (Blaber & Cyrus in press), competition with piscivores may be reduced. The juveniles of both *S. barracuda* and *S. jello* occur in vegetated areas where few other predators venture and where many small prey fish are abundant.

Acknowledgements

I thank the Natal Parks, Game and Fish Preservation Board and the KwaZulu government for permission to work in areas under their control. The South African National Committee for Oceanographic Research and the University of Natal provided financial support. Tessa Blaber, Digby Cyrus, Tim Martin, Duncan Hay and Scotty Kyle assisted at various times with field-work for which I am very grateful.

References

ALLANSON, B.R. & VAN WYK, J.D. 1969. An introduction to the physics and chemistry of some lakes in northern Zululand. *Trans. R. Soc. S. Afr.* 38: 217 – 240.

BLABER, S.J.M. 1978. The fishes of the Kosi system. *Lammergeyer* 24: 28 – 41.

BLABER, S.J.M. & BLABER, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. *J. Fish Biol.* 17: 143 – 162.

BLABER, S.J.M. & CYRUS, D.P. 1981. A revised checklist and further notes on the fishes of the Kosi system. *Lammergeyer* 31: 5 – 14.

BLABER, S.J.M. & CYRUS, D.P. In press. The biology of Carangidae (Teleostei) in Natal estuaries. *J. Fish. Biol.*

DE SYLVA, D.P. 1963. Systematics and life history of the Great Barracuda, *Sphyraena barracuda* (Walbaum). *Stud. trop. Oceanogr.* 1: 1 – 179.

DE SYLVA, D.P. 1973. Barracudas (Pisces: Sphyraenidae) of the Indian Ocean and adjacent seas — A preliminary review of their systematics and ecology. *J. mar. biol. Ass. India* 15: 74 – 94.

HILL, B.J. 1975. The origin of southern African coastal lakes. *Trans. R. Soc. S. Afr.* 41: 225 – 240.

WILLIAMS, F. 1959. The barracudas (Genus *Sphyraena*) in British East African waters. *Ann. Mag. nat. Hist.* (2) 13: 92 – 128.

WILLIAMS, F. 1965. Further notes on the biology of East African pelagic fishes of the families Carangidae and Sphyraenidae. *E. Afr. agric. For. J.* 31: 141 – 168.