The biology and taxonomic status of an estuarine population of *Pranesus pinguis* (Lacépède) (Teleostei: Atherinidae) in south east Africa

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The biology and taxonomic status of *Pranesus pinguis* in the subtropical Kosi estuary in south east Africa were investigated. Data from Kosi specimens support the view that *P. pinguis* is a highly variable species in terms of fin, spines, rays and body ratios. Nearly all the variations reported for *P. pinguis* by Smith (1965) occurred within the Kosi population. Criteria used to distinguish *P. capricornensis, P. ogilbyi* and *P. insularum* fall within the range of variation of *P. pinguis* from Kosi and must therefore be considered synonyms. The diet of *P. pinguis* in Kosi consisted chiefly of Calanoida and feeding took place at night. The fish congregated in shoals around a reef during daylight. The structure and dimensions of the gill rakers related to the diet indicate that, although *P. pinguis* feeds mainly by capturing individual prey, it is also a facultative filter feeder. All stages of the reproductive cycle were recorded from *P. pinguis* in the Kosi estuary. The eggs have a covering of filaments which may allow for demersal attachment. Although no direct evidence was available, spawning within the estuary may occur.

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Die biologie en taksomoniese status van *Pranesus pinguis* in die subtropiese Kosi-strandmeer in Noord-Natal is ondersoek. Die gegewens wat uit hierdie ondersoek spruit dui daarop dat *P. pinguis*, selfs in die omskrewe gebied van die Kosi-strandmeer, 'n hoogs veranderlike spesies is wat betref finstekels, finstrale en ligaamsverhoudings. Byna al die variasies wat Smith (1965) vir *P. pinguis* beskryf kom in die Kosibevolking voor. Die maatstawwe wat gebruik is om *P. capricornensis, P. ogilbyi* en *P. insularum* te onderskei val almal binne die variasiebreedte van die Kosi *P. pinguis*, en moet dus as sinonieme aanvaar word. Die dieet van *P. pinguis* in die Kosi-strandmeer bestaan hoofsaaklik uit Calanoida. Hulle vreet gedurende die nag, en trek gedurende die dag saam in skole om 'n rif. Die struktuur en afmetings van die kiefkamme stem ooreen met die grootte van die prooi, en dit dui daarop dat, alhoewel *P. pinguis* gewoonlik enkelprooi vang, dit ook 'n fakultatiewe filtreervoerder is. Alle stadia van die voortplantingssiklus is onder die *P. pinguis* van die Kosi-strandmeer gevind. Die eiers is bedek deur filamente wat miskien kan dien om hulle aan die bodem te heg. Dit is moontlik dat kuitskiet in die strandmeer voorkom, maar daar is tot dusver nog geen bewyse hiervoor nie.

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Pranesus pinguis is a common atherinid found throughout the subtropical and tropical Indo-Pacific. It is most abundant in sub-littoral areas around coral reefs where it forms vast shoals (Smith 1965). Large numbers occur in Kosi estuary (26°54'S/32°53'E) in northern Zululand (Blaber 1978). A study of *P. pinguis* in Kosi estuary was undertaken for two reasons; first, as part of a wider investigation into the biology and ecology of the fishes of Kosi and secondly, because the Kosi population occurs in an unusual habitat and the taxonomic status of its members was uncertain.

Taxonomic characters such as fin spines, rays and body ratios normally used to separate fish species are highly variable in *Pranesus pinguis* (silverside). Smith (1965) recognized the problem as follows: 'An intensive study of these fishes shows that especially the wide ranging forms are troublesome, resembling the related Mugilidae in the complexity of their relationships. Some exhibit a high degree of variation in fin count, so that basing a new species on a single or only a few fish is venturesome, as is shown in the widespread *P. pinguis*'. Referring to the genus *Pranesus* Smith (1965) further states: 'A moderate number of closely related species, larger and more robust than most others in the subfamily, are spread over a great part of the tropical Indo-west-central-Pacific, at times found in great shoals. Only one rather variable species is here recognized in the Red Sea and the Western Indian Ocean. As at present known, it appears to be most widespread, extending over not only the whole tropical Indian Ocean, but probably also to the central Pacific, where it is possibly divisible into regional subspecies. While the problem requires further investigation, some of the puzzling variations observed in fishes of the Red Sea and Western Indian Ocean may be partially resolved by recognizing three subspecies, two in the Red Sea and the other in the Western Indian Ocean, and beyond'. In this study *P. pinguis pinguis* from Kosi Estuary are compared with those described by Smith (1965) from other areas of the Indo-Pacific region.

Pranesus has been investigated by Hobson & Chess (1973) and Major (1977) in the Pacific, but it was not known how its biology in an estuarine environment differed, particularly with reference to the feeding ecology and reproductive cycle.

Materials and methods

Sampling

Silversides were collected at Kosi estuary in Zululand from January 1977 to July 1980, using seine nets, throw nets and a dip net. The technique used depended largely on the time of day. Daylight sampling required the shoals to be located before netting because of the localized shoaling behaviour of the silversides. Once located, silversides were either seined or throw netted. Night sampling presented different problems due to the dispersal of shoals and spacing of individuals feeding on the surface in quiet shallow waters. These silversides were located with a flashlight by wading in shallow water and captured individually with a dip net. All fish were immediately preserved in 10% formalin. The samples taken during July 1980 were caught over a period of three days at times designed to make up a 24-hour cycle.

Laboratory analyses

Taxonomic measurements

Five samples were analysed for the following characters: fin spines and rays, standard length (S.L.), depth (D), length of head, diameter of eye and width of head. Depth was measured midway between the pectoral and pelvic fins. Length of head was taken from the snout to the posterior edge of the membranous opercular flap. Since Smith (1965) does not give details concerning his measurements, it is possible that they were to the edge of the opercular bone. The diameter of the eye was taken parallel to the long axis of the body and width of head as the distance between the outermost curves of the eye.

A further sample of a S.L. size range was analysed to illustrate the change in depth with increasing S.L.

Diet

Pranesus pinguis does not have a true stomach (Al-Hussaini, 1947) but an intestinal swelling. Gut contents are recognizable in the intestinal swelling and from this region the contents were identified, counted, total fullness of swelling estimated and the percentage that each food item contributed to the total fullness was estimated. The remainder of the intestinal tract was considered as one, and only the total fullness of this region was estimated. The diet was analysed by three different methods: percentage numerical frequency, percentage frequency of occurrence of food items and the 'points' method (Ricker 1968).

Five silversides with standard lengths of 30 mm, 60 mm, 70 mm, and 110 mm were selected to determine whether the gill rakers were used as a filtering apparatus and whether changes in structure during growth were related to changes in methods of feeding. The first gill arch on each side of the gill apparatus was removed and cleaned of all tissue using a Bransonic 12 ultrasonic cleaner. The gill arches were photographed using a Scanning Electron Microscope (Jeol J.S.M. T200). Measurements of the denticle heights and gaps between the denticles were taken from photographs. Measurements of the gap between gill rakers and the lengths of gill rakers were taken using a dissecting microscope fitted with an eyepiece micrometer.

Gonads

Pranesus pinguis used for reproductive studies were the same individuals used for the taxonomic and feeding studies. The gonads of these fish were classified into the following maturity stages after Nikolsky (1963). The macroscopic maturity stages were classified as follows: (i) Immature, young individuals which have not yet engaged in reproduction; gonads of small size; (ii) Resting stage, sexual products have not begun to develop; gonads of small size; eggs not distinguishable to the naked eye; (iii) Maturation, eggs distinguishable to the naked eye; a rapid increase in weight of the gonads is in progress; testes change from a transparent to a pale rose colour; (iv) Mature (Ripe), sexual products ripe; gonads have achieved their maximum weight, but the sexual products are not extruded when light pressure is applied; (v) Reproduction (Ripe running), sexual products are extruded in response to very light pressure on the belly; (vi) Spent, the sexual products have been discharged; genital aperture inflamed; gonads have the appearance of deflated sacs, ovaries usually contain a few left over eggs from stage (v).

Gonads from female fish representative of the maturity stages were removed and, following routine paraffin embedding, sectioned at 7 μm and stained using Mallory's Triple Stain (Pantin 1964).

Results

Taxonomy

Taxonomic data from the silversides of Kosi estuary have been compiled in Table 1, together with data from Smith (1965). Standard lengths of Smith's (1965) silversides (84 – 120 mm) were generally greater than the samples from Kosi estuary (47 – 102 mm), but there is some overlap.

Smith's (1965) depth ratio shows an increase correlated with increase in S.L. (Table 1). Data from Kosi estuary show a relatively uniform ratio, despite changes in S.L. (Table 1). In contrast Smith's (1965) head width in S.L. measurements show a uniform ratio at all S.L., while the data from Kosi are highly variable (Table 1). The measurement of this body ratio depends, however, on whether the eye is damaged during preservation. In many of the Kosi specimens the eyes were flattened or pushed out of shape. Smith's (1965) eye in head ratios are also uniform and the data from Kosi variable (Table 1).

The dorsal spine and ray counts in Smith's (1965) data show great variability and no two are the same (Table 1). Data from Kosi show an even greater variability. The count combinations for Kosi are ranked in Table 1 according to frequency of occurrence. Smith's (1965) dorsal count V + 1 11 occurred in 14 fish from three of the Kosi samples. The dorsal count of VI + 1 10 occurred in seven fish in all Kosi samples. The dorsal count V + 1 10 was found in seven fish but only from one Kosi sample. Dorsal counts VII + 1 10 and V + 1 9 were not found in any Kosi sample. Smith's (1965) anal ray counts show variability from 14 to 17 and, except for 17 which only occurred once, the counts 14, 15 and 16 were found in each Kosi sample.

Table 2 shows depth and eye ratios from silversides with standard lengths from 44 – 122 mm. The depth in S.L. ratios show that depth increases linearly with S.L.

Table 1 Body measurements and fin counts of *Pranesus pinguis*

Locality	Durban[a]	Durban[a]	Durban[a]	Tongaland[a]	Seychelles[a]	Kosi Estuary 31/1/77 $n = 6$	 3/4/79 $n = 22$	 10/4/80 $n = 30$	 16/7/80 $n = 10$
S.L. mm	98	104	106	120	84	47 – 57	99 – 102	52 – 66	89 – 99
Depth in S.L.	4,65	4,7	5,1	5,2	4,7	$\bar{x}$ = 4,99 S = 0,54	$\bar{x}$ = 4,89 S = 0,10	$\bar{x}$ = 4,82 S = 0,23	$\bar{x}$ = 4,86 S = 0,23
Head width in S.L.	6,8	6,6	6,5	6,5	6,5	$\bar{x}$ = 7,49 S = 0,51	$\bar{x}$ = 6,85 S = 0,22	$\bar{x}$ = 5,75 S = 0,23	$\bar{x}$ = 6,71 S = 0,53
Eye in head	2,65	2,65	2,65	2,65	2,5	$\bar{x}$ = 2,35 S = 0,25	$\bar{x}$ = 2,51 S = 0,22	$\bar{x}$ = 2,26 S = 0,10	$\bar{x}$ = 2,48 S = 0,19
Dorsal	V + 1 11	VI + 1 10	V + 1 10	VII + 1 10	V + 1 9	VI + 1 11(4) IV + 1 10(1) VI + 1 10(1)	VI + 1 11(9) V + 1 11(6) VI + 1 10(2) IV + 1 11(1) XV + 1 11(1) V + 1 12(1)	VI + 1 11(9) V + 1 10(7) VI + 1 10(3) V + 1 11(3) V + 1 12(2) VII + 1 11(1) VI + 1 9(1)	V + 1 11(5) VI + 1 11(3) VI + 1 10(1) V + 1 4(1)
Anal 1 +	16	17	14	15	14	17(2) 16(2) 15(1) 14(1)	16(9) 15(8) 14(5)	15(18) 16 (7) 14 (5)	15(5) 16(4) 14(1)

[a]Smith (1965); number of observations in parentheses; S = standard error; n = number of fish.

Table 2 Depth in standard length and eye in head ratios of *Pranesus pinguis* from Kosi estuary

Standard length (mm)	Depth in S.L.	Eye in head
122	5,13	2,70
110	4,88	2,63
106	4,85	2,49
106	4,96	2,40
105	4,78	2,63
105	4,99	2,60
104	4,73	2,60
102	4,66	2,58
100	4,62	2,32
98	4,69	2,45
93	4,75	2,46
77	4,90	2,35
73	5,42	2,69
63	4,76	2,25
58	4,77	2,28
54	4,84	2,06
49	3,94	1,89
49	5,45	2,62
47	5,15	2,39
44	5,95	2,20

Table 3 Localities and data from specimens of *Pranesus pinguis* and two Red Sea species. (Reproduced from Smith 1965)

	Spines in First Dorsal V	 VI	 VII	Soft Rays in Second Dorsal 9	 10	 11
Red Sea[a]	3	7	–	6	4	–
E. Africa north of S. Africa	7	5	–	1	11	–
S. Africa	13	4	1	5	9	4
Seychelles, Aldabra, Madagascar, Mauritius	7	10	–	6	11	–
Total	27	19	1	12	31	4
Including Red Sea	30	26	1	18	35	4
capricornensis (Austr.)	1	1	1[b]	1	1[b]	–
insularum (Samoa, Hawaii)	–	X	–	X	X	X

[a]Includes all Ruppell's types; [b]Full range not known; X = recorded.

	Anal Soft Rays 12	 13	 14	 15	 16	 17
Red Sea[a]	4	4	2	–	–	–
E. Africa north of South Africa	–	–	8	3	1	–
Natal, South Africa	–	2	8	5	1	1
Seychelles, Aldabra, Madagascar, Mauritius	–	2	13	1	1	–
Western Indian Ocean total	–	4	29	9	3	1
W. Indian Ocean specimens with black pectoral blotch	–	2	10	5	1	1
capricornensis (Austr.)	–	1	1	1	–	–
insularum (Samoa, Hawaii)	–	–	X	X	X	X

[a]Includes all Ruppell's types; X = recorded.

above about 50 mm (D = 0,21 S.L. + 0,01; r = 0,98; $P > 0{,}001$; n = 18). Smaller animals (S.L. < 48 mm) have less depth. Ratios from such small fish are, however, less accurate due to measurement difficulties. The eye in head ratios show a definite linear increase from small to large fish (Eye in head = 0,13 S.L. + 1,99; r = 0,63; n = 22; $P > 0{,}005$). Thus the eye of *P. pinguis* becomes relatively larger with increasing length.

Table 3 is reproduced from Smith (1965) to allow comparison with data from Kosi specimens. Smith's (1965) data were prepared from *P. Pinguis* specimens caught at localities along the east African coast and data on two *Pranesus* species considered by some authors (Smith 1965) as distinct from *Pranesus pinguis*. Several species closely related to *P. pinguis* are considered by Smith (1965) to fall within the variation known for *P. pinguis*. They are: *Hepsetia pinguis mineri* Nichols and Roemhild, 1951. It is stated to have D V + 1 10. Al 15. Gill Rakers 22. Depth 4,9. Eye 2,5 in head. Pectoral with blotch.

Pranesus capricornensis Woodland, 1961. The description states D V – VII + 1 9 – 10. Al 13 – 15. Gill Rakers 5 – 6 + 1 + 19 – 22 Depth 4,8 – 5,1; head 4,0 – 4,2 in S.L. Pectoral distally dusky.

Pranesus ogilbyi Whitley, 1930. It has the pectoral blotch, appears to be identical with Smith's (1965) specimens, but has gill rakers 6 – 7 + 24 – 27.

Pranesus insularum Jordan and Evermann, 1902. It is stated to have D VI + 1 11. Al 16, depth 4,7; head 4 in S.L.; eye 3,0 in head, the pectoral without the blotch.

Smith's (1965) description of *P. pinguis pinguis* is D V – VII + 1 9 – 11. Al 12 – 17. Gill Rakers 5 – 6 + 1 + 18 – 21. Depth 4,5 – 5,5. Head 3,8 – 4,2 in standard length. Eye 2,4 – 2,9 in head. The blotch on the pectoral fin grades from a distinct black to an immaculate fin. In this study the pectoral blotch was found to vary from a distinct blotch to a clear fin. No correlation could be found between the condition of the fish and the presence of the pectoral blotch.

Diet

The food items found in *P. pinguis* are shown in Tables 4 and 5. Figure 1 shows the fullness estimates of the intestinal swelling and the remainder of the intestine at intervals during a 24-h period at Kosi estuary in July, 1980. Silversides clearly feed only at night. The morning sample was partially empty but by late morning all silversides were empty. Table 4 shows the percentage frequency of food items in the gut of silversides at different seasons. Only summer, autumn and winter samples are represented. Unfortunately the results from different seasons in Table 4 are not strictly comparable, due to the bias in the sampling procedure caused by daylight sampling in summer and autumn. The exceptionally low percentage frequencies of food items in the autumn (April) sample were a result of all the fish being caught in the late morning and afternoon. The winter (July) samples were caught at night.

Despite this bias, the diversity and order of importance of food items are comparable. The importance of insects as a food item in summer was probably due to their abundance at this season. The autumn sample shows no clear dominance. In the winter sample Copepoda and Isopoda were the dominant food items. Mysidaceae, fish eggs and megalopa larvae have percentage frequencies similar to the commonest food items in the summer and autumn samples. This is probably a bias caused by day versus night sampling. In all three samples small floating prey such as Foraminifera, bivalve spat and fish eggs were significant.

Table 5 shows the data obtained from three night samples of *P. pinguis*. The gut contents were analysed by percentage frequency, percentage numerical frequency and percentage points of estimated volume. The significance of each food item can be established by using all three methods of analysis. According to all three

Table 4 Diet of *Pranesus pinguis* during three seasons at Kosi estuary analysed by frequency of occurrence (*n* = number of fish)

Summer November/January/February		Autumn April		Winter July	
n = 70		*n* = 62		*n* = 68	
Food item	% F.	Food item	% F.	Food item	% F.
Insecta	31,43	Megalopa larvae	16,13	Copepoda	79,41
Isopoda	8,57	Bivalve spat	14,52	Isopoda	64,71
Foraminifera	5,71	Copepoda	12,90	Mysidaceae	41,18
Isopoda	5,71	Penaeidae	12,90	Fish eggs	33,82
Ostracoda	5,71	Isopoda	11,29	Megalopa larvae	30,88
Araneida	4,29	Gastropoda	11,29	Mysis larvae	22,06
Gastropoda	2,86	Insecta	9,68	Amphipoda	19,12
Penaeidae	2,86	Polychaeta (Sedentaria)	8,06	Ostracoda	14,71
Megalopa larvae	2,86	Ostracoda	6,45	Insecta	14,71
Whelk eggs	1,43	Foraminifera	6,45	Oligochaete larvae	10,29
Empty *n* = 41		Mysidaceae	3,23	Fish	8,82
		Empty *n* = 56		Gastropoda	7,35
				Penaeidae	7,35
				Polychaeta	5,88
				Bivalve spat	4,41
				Zoae larvae	4,41
				Foraminifera	1,47
				Empty *n* = 0	

Table 5 Food items in the intestinal swelling of *Pranesus pinguis* from three night samples at Kosi estuary (L = larvae, *n* = number of fish)

Sample	19h00/20h00 *n* = 29				22h00 *n* = 20				02h00 *n* = 13		
Food item	% Freq.	% Num. freq.	% Points	Food item	% Freq.	% Num. freq.	% Points	Food item	% Freq.	% Num. freq.	% Points
Copepoda	72,41	41,23	16,27	Copepoda	100	79,27	79,65	Copepoda	100	70,70	72,13
Isopoda	51,72	21,73	19,65	Isopoda	85	2,29	4,34	Isopoda	76,9	7,12	12,77
Megalopa L	37,93	8,36	9,60	Mysidaceae	75	1,41	3,20	Mysidaceae	69,2	1,31	4,65
Amphipoda	27,59	5,85	4,94	Fish eggs	60	13,76	7,03	Fish eggs	69,2	18,37	2,84
Insecta	27,59	1,95	2,10	Mysis L	50	0,42	0,57	Megalopa L	15,4	0,29	1,16
Ostracoda	13,79	1,11	0,82	Megalopa L	35	0,44	1,30	Gastropoda	15,4	0,28	0,90
Mysidaceae	13,79	1,67	1,74	Oligochaeta	30	0,31	0,30	Mysis L	15,4	1,31	0,65
Penaeidae	10,34	0,84	0,82	Ostracoda	25	0,21	0,24	Amphipoda	15,4	0,58	0,58
Fish	10,34	0,56	3,66	Gastropoda	20	0,13	0,11	Ostracoda	7,7	0,15	0,26
Mysis L	10,34	0,84	0,18	Fish	15	0,08	1,57	Polychaeta	7,7	0,15	0,26
Fish eggs	6,90	3,90	0,64	Amphipoda	15	0,08	0,16	Insecta	7,7	0,15	1,03
Bivalve spat	6,90	0,56	0,18	Polychaeta	10	0,08	0,65	Remains	–	–	2,52
Zoae L	6,90	0,56	2,01	Foraminifera	10	1,57	0,11				
Gastropoda	3,45	0,28	0,09	Penaeidae	5	0,03	0,11				
Polychaeta	3,45	0,28	1,37	Zoae L	5	0,03	0,05				
Oligochaeta	3,45	0,28	0,37	Bivalve spat	5	0,03	0,05				
Remains	–	–	35,74	Insecta	5	0,03	0,05				

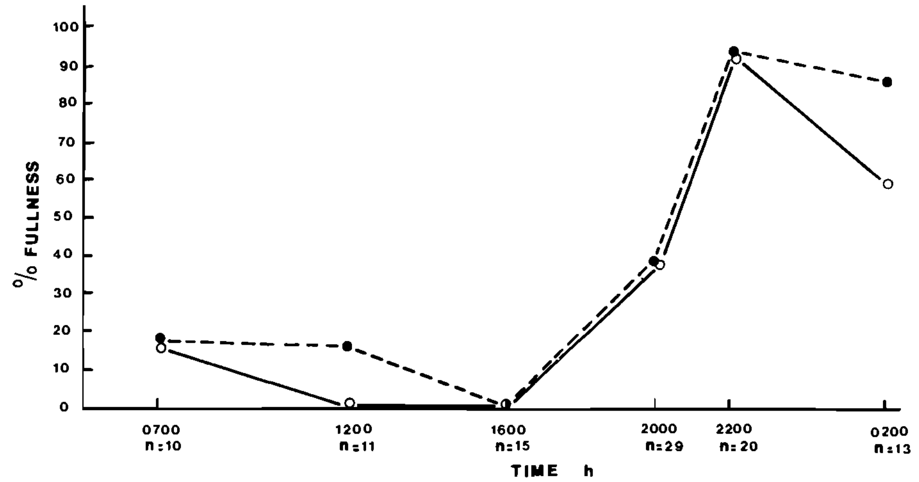

Figure 1 Feeding periodicity of *Pranesus pinguis* in Kosi estuary (●---●: intestine and rectum, o——o: intestinal swelling).

analysis methods, Copepoda form the dominant food item of *P. pinguis*. The next most important food items in order of importance were Isopoda and fish eggs. In the 22h00 sample Mysidaceae are ranked according to percentage frequency above fish eggs, yet, according to percentage numerical frequency and percentage points, (estimated volume), fish eggs were more significant. Thus fish eggs occurred in fewer fish than Mysidaceae but were found in higher numbers and formed a greater part of the gut volume.

The measurements from gill rakers of a size range of silversides are shown in Table 6. The gill raker gap and the gill raker length increased slightly with increasing S.L. The raker length was divided by the S.L. and an almost identical ratio was obtained from three specimens (0,044; 0,047; 0,046), indicating that these gill raker parameters increase in a linear fashion, related to body length. Denticle gap and denticle length measurements were taken, but probably have little significance as they are highly variable (Table 6). Figures 2a and 2b show the pharyngeal teeth on the ascending arms of the gill arches and interlocking gill rakers. The gill rakers are long with

Table 6 Gill raker measurements of *Pranesus pinguis* from Kosi estuary

	Gill raker gap μm		Raker length μm		Denticle gap μm		Denticle length μm	
S.L.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
120	190	30	5260	630				
100					80	40	80	10
68	100	30	3250	190	50	10	50	10
55	80	30	2540	200	70	30	80	10
29	80	20			70	30	60	10

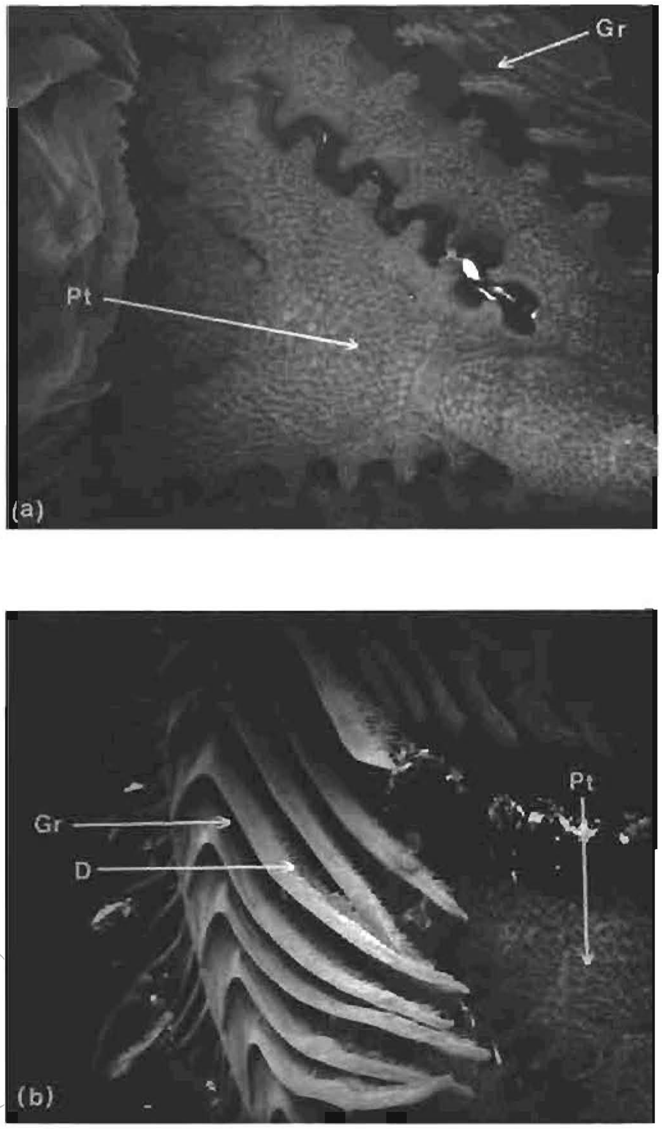

Figure 2 (a) Dorsal view of the floor of the pharynx of *Pranesus pinguis* showing pharyngeal teeth. (b) Gill rakers of *Pranesus pinguis* (D : denticles; Gr: gill raker; Pt: pharyngeal teeth).

denticles facing into the buccal cavity. These structures suggest a masticating function for the pharyngeal complex of gill arches, gill rakers and associated denticles and teeth.

Table 7 shows the dimension of food items found in a size range of silversides. The relatively large food items indicate that *P. pinguis* can feed on individual food items. It is also significant that no item, food or otherwise, found in the gut was smaller than the gill raker gap. There is probably no change in function of the gill rakers with increasing length.

Reproduction

Seasonal gonadal changes based on gross morphology

The percentage of fish at each stage of maturity is plotted against months of the year in Figure 3. They represent only adult fish and include macroscopic stages III to VI. Fish longer than 100 mm were considered adult, although individuals less than 100 mm, but showing gonadal maturity, were also classed as adults.

The main features of male and female cycles (Figure 3) were sufficiently similar to allow both to be considered together. Only in November did *P. pinguis* show ripe gonads. One November individual was ripe-running (V), maturation stage (III) showed a peak in September, two months before ripe stage (IV). In males the high percentage of Stage III individuals in November indicated that a number of the November male population had still to spawn. Similarly the high percentage of spent (VI) females in November indicated that spawning had occurred before November. From Figure 4 it is evident that spawning occurs over a period of several months in summer, probably from October to January. In both sexes a peak of spent individuals occurred in April.

Histological stages in maturation seen in female Pranesus pinguis and the development of oocyte filaments

All seven stages of oogenesis (Dipper & Pullin 1979) were recorded in *P. pinguis* from Kosi estuary.

Davis (1977) describes fish eggs at the pre-vitellogenic stage as, 'having a thin follicle layer enveloping the oocyte. In the late pre-vitellogenic stage a non-cellular membrane forms between the follicle layer and the developing oocyte. This is the zona radiata. In the stage of vitellogenesis the follicle becomes thickened and forms a single layer of distinctly nucleated cells called the granulosa. The theca, a thin layer of connective tissue, surrounds the granulosa'. The formation of these three membranes in *P. pinguis* does not follow the above pattern. Filaments which form the granulosa begin development first in the yolk precursor oocytes (Figure 4a). The zona radiata begins to form in the secondary yolk oocytes and reaches full development only when the secondary yolk has excluded the primary yolk. Figure 4b shows the wall of ripe oocyte. The granulosa has a distinct filamentous appearance.

Discussion

Taxonomy

The taxonomic data will be discussed in two parts.

(i) Morphometric measurements and body ratios

Depth in standard length. Smith (1965) describes *P.*

Table 7 Size of food items in the gut of a size range of *Pranesus pinguis* from Kosi estuary

S.L. mm	Fish eggs µm	Copepoda µm	Isopoda µm	Mysidaceae µm	Foraminifera µm	Sand grains µm
85	–	250 – 330	1700	3400	500	–
70	720 – 800	520 – 1800	2400	–	260	200 – 440
69	–	400 – 2500	–	2800 – 3400	300	–
59	–	830 – 2100	1250 – 3750	2500	–	

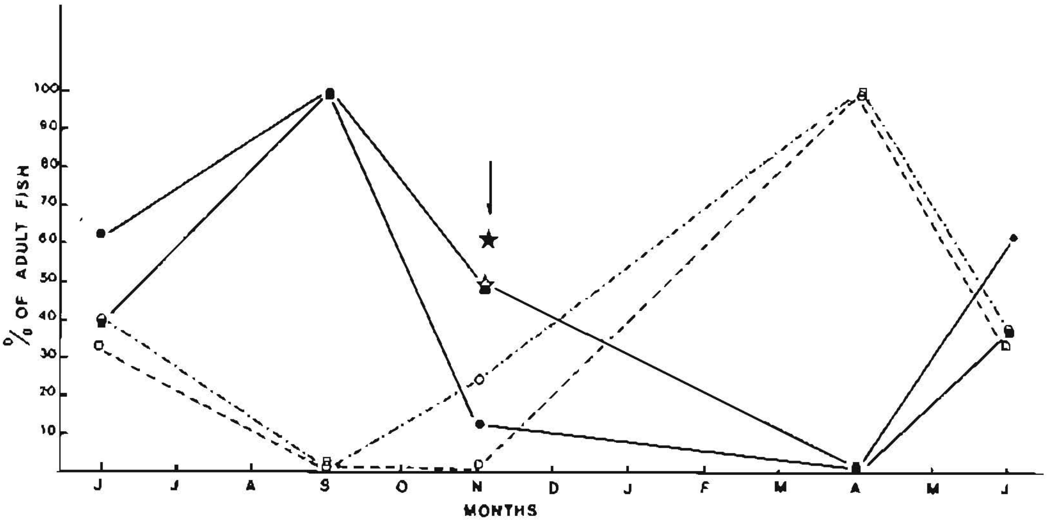

Figure 3 Reproductive cycle of *Pranesus pinguis* in Kosi estuary according to gonad stages (■——■: male stage III; ●——●: female stage III; ☆: male stages IV/V (ripe/ripe running); ★: female stages IV/V (ripe/ripe running); □---□: male stage VI (spent); o·····o: female stage VI (spent); ↓: spawning).

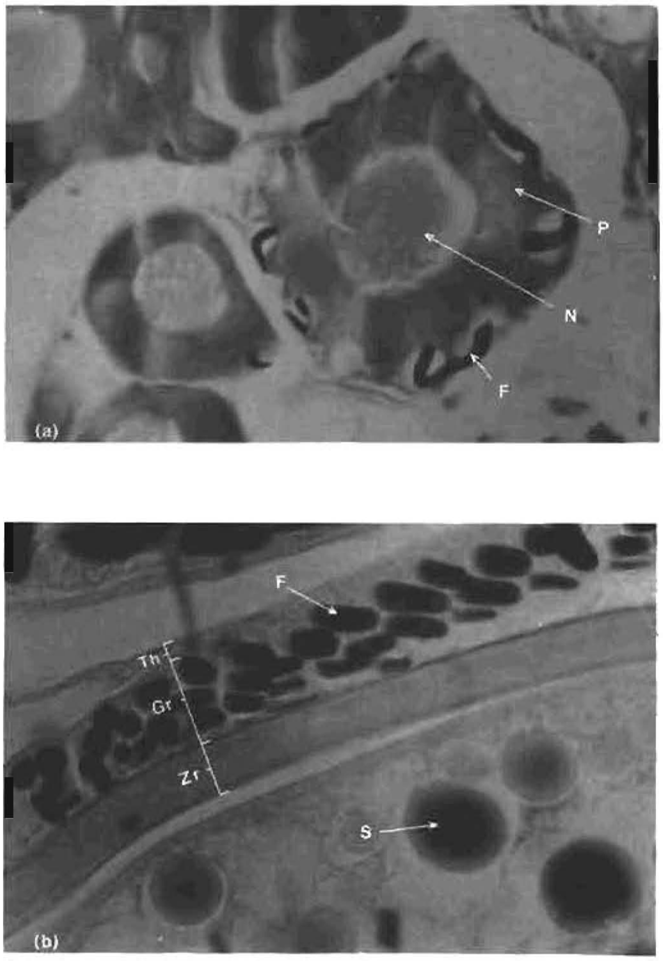

Figure 4 (a) Histological section through yolk precursor oocytes (× 100) of *Pranesus pinguis* showing early development of filaments. (b) Histological section through a ripening oocyte (× 100) of *Pranesus pinguis* showing transverse sections of fully developed filaments forming the granulosa (F: filaments; Gr: granulosa; N: nucleus; P: primary yolk; S: secondary yolk; Th: theca; Zr: zona radiata).

pinguis as having a depth of 4,5 – 5,5, a range greater than shown in Table 1. A wide range such as this renders a character of little taxonomic value. However, Table 2 and the linear regression of depth on S.L. (D = 0,21 S.L. + 0,01) show clearly the reason behind the wide range, namely that, with an increase in S.L., the depth also increases. The linear regression (D = 0,21 S.L. + 0,01) can be used to reduce the possible depth range of *P. pinguis* to a range applicable only to the particular specimen being analysed.

Head width in standard length. Results from Kosi were extremely variable. Smith (1965) does not quote this measurement ratio in his description of *P. pinguis*, yet includes it in his Table III which suggests that he did not consider it a reliable taxonomic character. Width of head ratio results appear to be random, which indicates the error to which this measurement is susceptible, that is, damage to the eyes during preservation.

Eye in head. Smith (1965) describes *P. pinguis* as having eye 2,4 – 2,9 in head. This is a smaller range than that presented in Table 1. However, these data are drawn from a wide length range. Table 2 and the linear regression (Eye in head = 0,13 S.L. + 1,99) show that variation in the eye in head ratio depends on variation in S.L. The linear regression can also be used to cut down the possible eye in head ratio range to maximize its usefulness as an identification characteristic.

(ii) Fin Formula

Although the occurrence of *P. pinguis* in shallow waters along the coastline of the Indo-Pacific, stretching over thousands of kilometres, might favour the formation of a cline, the data presented here discount that possibility. The fin formula for *P. pinguis* from Smith (1965) is D V – VII + I 9 – 11. AI 12 – 17. The data in Table 1 from the Kosi estuary show a variation largely within this range. There are three dorsal spine counts which fall out of the range, one of which is an extreme variant (D XV). There are also three dorsal ray counts which fall outside of the range, one of which is an extreme variation (D V + I 4). The anal ray counts used in Smith (1949) as the basis of his identification key, show greater stability than the dorsal fin. The data in Table 1 show that the Kosi samples have a restricted anal ray variation falling within Smith's (1965) description. (A1 12 – 17).

The data in Table 3 compared with Table 1 show that variations in fin count of silversides from all Smith's (1965) localities occurred *within* the samples from Kosi estuary. Thus the variation does not follow the pattern of a cline in being variable over a range of localities and is a local phenomenon.

Smith (1965) stated that the *Pranesus* species considered distinct from *P. pinguis* represented only one rather variable species and that the original data are from only the type specimens. Examination of larger samples would almost certainly have revealed variation in the data and shown overlap with the Western Indian Ocean specimens. *Pranesus capricornensis, P. ogilbyi* and *P. insularum* have been considered distinct on the basis of differing fin counts, body ratios and the presence or absence of a dark blotch on the pectoral fin. This study has shown that these characteristics are highly variable and a complete range occurs within the *P. pinguis* population of Kosi estuary. To distinguish a taxon by such highly variable characteristics is not acceptable, unless population studies have shown a distinct shift of characteristics outside of Smith's (1965) description. It must be kept in mind while considering variation in silversides, that much of the variation is due to changes of body ratios related to growth.

Biology

The diel cycle of feeding apparent in Figure 1 can be related to the behavioural pattern of silversides, described for fish from the Marshall Islands by Hobson & Chess (1973). Silversides formed a diurnal shoal in which the fish kept close to the shore, remaining relatively inactive. In the late afternoon the fish gradually drew together to form a compact unit just beneath the surface. Shortly after sunset the silversides migrated offshore and spread out just below the surface with 2 to 4 m between each fish, feeding on plankton throughout the night. They returned to their day time shoaling site just before sunrise. The Kosi estuary population has the same diet-related migratory behaviour. Figure 1 shows a fullness peak at 22h00 for both the intestinal swelling, intestine and rectum. The 02h00 sample shows that the intestinal swelling has a fullness less than that for the intestine and rectum. This indicates that the silversides stopped feeding after 22h00.

Table 4 shows that the diet of silversides at Kosi estuary changed with season, while Table 5 indicates that diet changed to a lesser extent during the night. Hobson & Chess (1973) state that silversides select their prey from among other organisms of the same size that are not taken. They also indicate that differences in prey composition are reflected in the gut contents of silversides. Both points of view can be shown to be important in the occurrence of insects in the Kosi estuary samples. Insects were the most important food item in the summer samples, (Table 4), and less important in the autumn and winter samples. This was probably related to the changing seasonal abundance of insects, summer being the period of their greatest abundance. Table 5 shows insects to be most important in the silverside diet in the early evening, this coincides with the greatest abundance of flying insects, (Martin, pers. comm.). The night feeding behaviour of *P. pinguis* may be related to the diel migration of Copepoda, their main food source, or to the threat of predation (Major 1977).

The gill raker gap of *P. pinguis* shows little change over a size range (Table 6), indicating that there is no change in diet due to a structural change in the feeding mechanism. Table 7 shows that no item found in silversides was smaller than the gill raker gap. The gill rakers (Figure 2b) may function as a filter but the large size of some prey items indicated that the silversides were eating individual prey and would have little use for a filtering mechanism. However, silversides sampled in February 1977 were feeding mainly on Foraminifera with a diameter of about 260 μm. The fish had a S.L. of 36 – 72 mm, indicating a maximum gill raker gap of 100 μm. Because of the number and size of the Foraminifera (one fish contained more than 3000), it seems probable that these fish were filtering their prey. *P. pinguis* is probably, therefore, a facultative filter feeder. On most occasions in Kosi estuary it feeds on individual zooplankters, but when large concentrations of small zooplankters, such as fish eggs or Foraminifera are available, it is able to filter feed. The gill raker gap of *P. pinguis* can be compared with the gill raker gap of *Gilchristella aestuarius*, a filter feeder in Lake St Lucia (Blaber 1979). *Gilchristella aestuarius* with a S.L. of 40 mm has a gill raker gap of 103 μm. *P. pinguis* with a S.L. of 55 mm has a gill raker gap of 80 μm. Blaber (1979) found that *Pseudodiaptomus stuhlmanni*, with a mean length of 1024 μm, was the dominant food item of *G. aestuarius*. The copepod species found in the gut contents of *P. pinguis* (Table 7) range in length from 400 to 2500 μm. The prey sizes are similar and it is notable that in both fish the dominant prey are larger than the gill raker gap.

The morphology of the gut (Al-Hussaini 1949) can also be related to the food of *P. pinguis*. The crustacean food of silversides was still visible as exoskeletons in the rectum. The triturating of the pharyngeal region (Figure 2a) is probably just sufficient to crack the exoskeleton and allow digestion. When the crustaceans are swallowed, their exoskeletons are still hard and thus a storage space, the intestinal swelling, is required. Once the exoskeletons have softened, their passage into the narrow intestine is possible. Digestion probably occurs in both intestinal swelling and intestine, a brush epithelial border occurs in both regions. Al-Hussaini (1949) proposed that the high incidence of goblet cells in the rectum is required to form faeces. In *P. pinguis* every single epithelial cell is a goblet cell and combined with the fact that crustacean exoskeletons were still visible in this region, the 'gumming' together of the rectal contents by mucus to form faeces appears a distinct possibility.

P. pinguis has been reported occurring in Morrumbene estuary (Day 1974) and Quissico Lake (Hill, Blaber & Boltt 1975), but its distribution points to it being predominantly a sub-littoral species. The question that arises from the presence of silversides in estuaries is: why are they found in estuaries? In the Kosi situation the estuary is merely an extension of the marine environment and the silversides find protection in the estuary. In Quissico Lake, silversides were found 30 km upstream from the estuary mouth. This extension of range is probably opportunistic, stemming from the protection afforded by the estuary. However, there are several lines of evidence which support the possibility of *Pranesus pinguis* breeding in estuaries and fresh water. Grassé (1957) described Atherinid eggs as being demersal. Smith (1965) stated that in the Atherinidae, females of the commoner species in the Western Indian Ocean contain ripe relatively large eggs from about July to October, and nothing is known of their breeding habits in the Western Indian Ocean, but survival rate of eggs and larvae must be high, based on the fact that even the largest female can only shed about 5000 eggs and must have no protective mechanism. In *P. pinguis* filaments formed by the granulosa (Figures 4a & 4b) can however be considered a protective mechanism and allow for the demersal attachment of the eggs. Wallace (1975) reported that '*Hyporhamphus knysnaensis* is able to spawn in estuaries because its eggs are demersal and densely covered with glutinous hair-like filaments which serve to attach the eggs to weeds'. In the present study, silversides were found in an estuary at salinities as low as 10‰. *Hepsetia breviceps* in Lake Sibaya (Bruton 1979) and *Teramulus kieneri* found in the upper reaches of estuaries and coastal swamps in Madagascar (Smith 1965) are both members of the same sub-family (Atherininae) as *P. pinguis*, and both species have adapted to breeding in fresh water.

The above evidence, together with the histological evidence that every stage of oogenesis was found in estuarine *P. pinguis* indicates that it may possibly breed in estuaries, although no direct evidence of spawning was found.

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