Turbidity-induced changes in feeding strategies of fish in estuaries

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The aim of this study was to determine the effect of turbidity on the feeding strategies of fish in estuaries. Three species representing different feeding guilds were selected for the investigation. These were *Elops machnata* (representative piscivore), *Pomadasys commersonnii* (a macrobenthivore) and *Atherina breviceps* (a planktivore). The stomach contents of these fish were examined from a clear and a turbid estuary and some experimental work was carried out on *A. breviceps* to test the hypothesis that turbidity affects feeding behaviour. Turbidity was found to have no effect on size selection of prey, but feeding rate, particularly of visual predators, was reduced at higher turbidity levels. This was caused by a decrease in the reactive distance of the fish. It would appear that in order to optimize the aquisition of food under different turbidity conditions fishes have the ability to change their feeding strategies. Visual predators are more affected by turbidity than are macrobenthic feeders.

Die doel van hierdie ondersoek was om die invloed van watertroebelheid op die voedingstrategie van vis in getyriviere te ondersoek. Drie spesies met verskillende voedingsgewoontes is gekies vir die ondersoek, naamlik *Elops machnata* (verteenwoordigende visvreter), *Pomadasys commersonnii* (makrobentiese vreter) en *Atherina breviceps* (planktonvreter). Die maaginhoud van hierdie vissoorte vanaf 'n helder en 'n baie troebel getyrivier is ondersoek en ontleed. Sekere eksperimentele werk is ook onderneem om die hipotese te toets dat watertroebelheid 'n verandering in die vreetgewoontes van vis teweeg bring. Die resultate het gewys dat troebelheid geen effek het op die grootte van die prooi wat geselekteer word, maar dat voedingskoers verlaag, hoofsaaklik by visuele roofvisse as gevolg van 'n afname in die reaktiewe afstand van die vis. Visuele roofvisse word tot 'n groter mate as makrobentiese vreters deur watertroebelheid geaffekteer.

Turbidity is defined as: 'the optical property of a suspension with reference to the extent to which the penetration of light is inhibited by the presence of insoluble material' (US Geological Survey 1964). Turbidity is thus a function of both concentration and particle size of the suspended material. Kirk (1983) on the other hand defines turbidity as 'the optical property of a liquid which causes light to be scattered and absorbed rather than transmitted in straight lines'. Thus both suspensoid load (solid or colloidal particles) and the properties of such suspensoids contribute towards turbidity (Bruton 1985), which has long been recognized as affecting aquatic life and fishes in particular. Bruton (*op cit.*) reviewed the effects of turbidity on fish, and concluded that the most important effects are: reduction in light penetration and consequent photosynthesis resulting in reduced food availability and plant biomass, reduced visibility of pelagic prey, reduced availability of benthic food owing to smothering, clogging of gillrakers and gill filaments and reduced areal predation risk.

High turbidity has also been shown to effect a reduction in hatching success (Rosenthal & Alderdice 1976), egg survival (Cambray 1983; Wilber 1983), feeding efficiency (Moore & Moore 1976; Vinyard & O'Brien 1976; Brusven & Rose 1981; Gardner 1981), growth rate (Crouse, Callahan & Malweg 1981), and population size (Wilber 1983). However, the effects of turbidity on the feeding strategies of fish in estuaries are not well understood. Many studies have been undertaken on the feeding ecology of South African estuarine fishes, in clear and in turbid estuaries (van der Westhuizen & Marais 1977; Whitfield & Blaber 1978; Whitfield 1980; Coetzee 1982; Blaber 1983; Marais 1984). None of the above, however, have been specifically concerned with the effects of turbidity on feeding strategies.

The estuaries of the South African east coast, as elsewhere, are important nursery grounds for several fish species (Cyrus 1984). Wallace, Kok, Beckley, Bennett, Blaber & Whitfield (1984) showed that estuaries are utilized by approximately 100 species. Of these, eight are dependent upon estuaries for their entire life, 22 are dependent on estuaries for the juvenile phase of their life and a further 19 occur mainly in estuaries but also in the sea. The importance of estuaries in the life histories of South African marine fishes emphasizes the need for investigations to establish the relationship between turbidity and aspects of the biology of fish and other organisms, especially since seasonal rainfall and agricultural malpractice results in heavy sediment loads in rivers (Day 1981).

The aim of this study was to test the hypothesis that turbidity affects the feeding strategies of fish. The hypothesis was tested by two different methods. Firstly, the stomach contents of selected species, belonging to three different feeding guilds, from a clear and a turbid estuary were analysed and compared. Secondly, laboratory experiments were conducted to assess the effect of turbidity on various aspects of the feeding biology of a filter-feeding planktivore, common to both estuaries. A valid criticism which could be levelled at this study is that we did not sample prey density at the same time as sampling fish for stomach content analysis. We therefore had to rely on the available published and unpublished information.

Materials and Methods

Field studies

Fish were sampled from the Kariega estuary and the Great Fish estuary along the Eastern Cape coast of South Africa

(Figure 1). Turbidity was measured in Nephelometric Turbidity Units (NTU). During the study period turbidities in the Kariega ranged from 3,2 to 6,8 NTU, and in the Great Fish estuary from 68,0 to 91,0 NTU (Table 1). These two estuaries were thus good examples of a clear (< 10 NTU) and a turbid (> 80 NTU) estuary (Cyrus 1984). Other physical and chemical parameters that were monitored included salinity in ppt, temperature in degrees Celsius, pH and dissolved oxygen in ppm (see Table 1). Water samples for these analyses were taken from the middle of the water column.

Three species were chosen for stomach content analysis, on the basis of their known dietary habits. The ten pounder or skipjack, *Elops machnata* (Elopidae) was chosen as a representative piscivore (van der Elst 1981), the spotted grunter, *Pomadasys commersonnii* (Haemulidae) as a representative macrobenthic feeder (van der Elst *op cit.*), and the silverside, *Atherina breviceps* (Atherinidae) as a filter feeding pelagic planktivore (Blaber 1979).

Sampling sites in the two estuaries are shown in Figure 1. Quarterly sampling trips were undertaken, corresponding roughly to summer, autumn, winter and spring. Fish were captured using a 400 m fleet of gill nets, with mesh sizes ranging from 40 to 150 mm stretch mesh, set overnight. A 60 m monofilament seine net (40 mm stretch mesh) and a

Table 1 Mean physical and chemical characteristics of the Kariega (K) and Great Fish (GF) estuaries during the quarterly sampling trips

Parameter	Summer 22/2–24/2 K	GF	Autumn 3/5–5/5 K	GF	Winter 28/6–30/6 K	GF	Spring 6/9–8/9 K	GF
Turbidity (NTU)	5,4	90,2	6,8	68,0	3,2	91,0	4,9	77,0
Salinity (ppt)	33,5	34,0	35,0	34,0	35,0	35,0	34,0	35,0
Temperature (°C)	19,2	20,2	17,8	17,3	15,0	14,9	16,3	16,7
pH	8,16	7,14	8,04	7,10	7,63	6,69	8,12	7,18
Dissolved O₂ (ppm)	10,0	7,8	8,5	8,4	9,1	8,2	10,4	8,9

15 m anchovy seine net (10 mm stretch mesh) were also used. Incidental samples of *E. machnata* were also obtained from the Kowie estuary during the winter using gill nets. This estuary is also a clear estuary (11 NTU), although slightly more turbid than the Kariega.

The fish were measured for standard length (SL) in mm and weighed to the nearest gram i.e. *E. machnata* and *P. commersonnii*, and *A. breviceps* to the nearest 0,1 g. Immediately after measuring the fish for length and weight they were killed and 50% formalin was injected into the body cavity of the larger fish (> 100 mm SL), whereafter they were fixed in 10% formalin. The smaller fish were killed and fixed directly in 10% formalin. Individual items were identified to species level were possible and the methods used to analyse the stomach contents included the gravimetric methods, the numerical method and the frequency of occurrence method (Hynes 1950). An index of relative importance (IRI) (Pinkas, Oliphant & Iverson 1971) was calculated using the results of the above three methods, in the form of IRI = (%N + %W) × %FO, where %N = percentage number, %W = percentage weight and %FO = percentage frequency of occurrence. Feeding intensity was assessed by expressing the total weight of prey as a percentage of body weight of each fish.

An index of diet similarity was also calculated for each species in the systems using the method of Bray & Curtis (1957, in Field, Clarke & Warwick 1982), which has the following form:

$$D_{jk} = \frac{\sum\limits_{i=1}^{s} [Y_{ij} - Y_{ik}]}{\sum\limits_{i=1}^{s} [Y_{ij} + Y_{ik}]}$$

where Y_{ij} = score for the i th diet item in the j th sample; Y_{ik} = score for the i th diet item in the k th sample; D_{jk} = dissimilarity between the j th and the k th samples summed over all s diet items. D_{jk} ranges from 0 (identical score for all dietary items) to 1 (no diet items are common), and is the complement of S_{jk} (similarity) = $1 - D_{jk}$.

The length weight relationship, in the form of $W = aL^b$, was calculated for each species from each estuary in each quarter. The value of the exponent (b) was used as an indicator of condition, since differences in this value between different populations of the same species are presumed to be
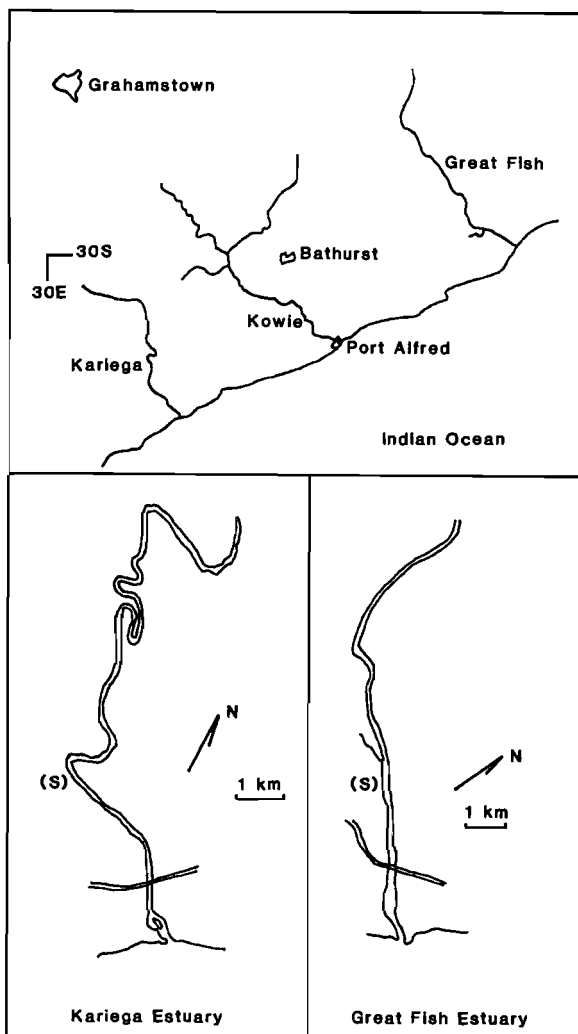

Figure 1 Study area, and sampling sites (S) in the Kariega and Great Fish estuaries.

associated with nutritional condition (Ricker 1975). A comparison of the seasonal condition factors for each of the three species in the two estuaries was undertaken by calculating the 95% confidence limits (CL) of the exponential value 'b'. The length weight relationship is a power function and such curves can be compared in terms of their slopes (b) by using a modified t test, whereby confidence limits are calculated using the equation 95% CL = $t_{(n-2)df}$ × sb, where t is obtained from a t distribution table at a significance level of p = 0,025 and at n–2 degrees of freedom, sb is the standard error of b. Overlap of the 95% CL indicates that there is no significant difference (at the 95% confidence level) between condition factors (McGill, Tukey & Larsen 1978).

Laboratory studies

Experiments were designed to examine the effect of turbidity on various aspects of the feeding biology of the silverside A. breviceps. Firstly, to establish whether turbidity influences size selection of prey organisms, secondly whether turbidity reduces feeding rate and thirdly whether turbidity reduces the reactive distance of the fish.

For these experiments, specimens were captured in a tidal lagoon of the Kowie estuary using a seine net (10 mm stretch mesh) and transported back to the laboratory. In the laboratory the fish were divided into two groups and acclimated for a period of five days in two 100 l holding tanks, one of which contained clear seawater (0 NTU). The water in the other container was made up to 120 NTU using silt from the Great Fish estuary. During the acclimation period the fish were fed on live Daphnia and crushed trout pellets. The daphnids ranged in size from 0,8 to 1,6 mm. While Daphnia did not form part of the natural diet of the fish in the two estuaries, they do occasionally occur in the diet of A. breviceps in brackish coastal lagoons (Coetzee 1982). It was decided to use the cladoceran in the experimental trials for the following reasons. They are of a suitable size, could be easily procured and only began to show osmotic stress after 5 min and succumbed after 8 min.

Size selection and feeding rate experiments

All experiments were carried out in glass tanks (900 × 310 × 380 mm) containing 100 l of either clear (0 NTU) or turbid water (120 NTU). Each tank was fitted with a gauze-net false bottom with which all the fish could be removed from the tank at the same time after the experimental period had elapsed. Recirculating water pumps were used to avoid settlement of suspended sediments and temperature was maintained at 20 ± 1°C. Each run was undertaken with 40 fish. Prior to each of the replicate experimental runs the fish were acclimated to the glass aquaria conditions for a period of 14 h overnight. The fish were not fed during this time in order to standardize hunger (Gardner 1981).

After acclimation 2 ml of live daphnids were introduced into each of the experimental tanks, resulting in a daphnid density of 18 per litre. The fish were allowed to feed for a period of 3 min after which they were simultaneously removed and killed by placing them on crushed ice. Dead fish were then fixed in 10 % formalin. Simultaneous removal of the fish was effected by a guaze net laid out on the bottom of the tank. At the end of the feeding period the net was simply lifted removing all the fish from the tank at the same time. Before analysing the gut contents the standard length and gape (vertical distance between upper and lower jaws at maximum expansion) of each fish in each replicate experiment was measured in mm. Stomachs were then removed and the number of cladocerans were counted and measured (top of the head to the base of the tail spine) to the nearest 0,1 mm, using a stereo microscope camera lucida. Prey size was plotted as a function of gape and the total number of prey items consumed were plotted against standard length.

Reactive distance experiment

Reactive distance is defined as the maximum distance at which a fish can locate prey (Vinyard & O'Brien 1976). The experiments to determine the effect of turbidity on the reactive distance of A. breviceps were carried out in glass aquaria (420 × 140 × 400 mm), containing 22 l of water. Four different turbidity levels (0, 8, 20, and 28 NTU) were created by mixing increasing amounts of silt from the Great Fish estuary with clear seawater. The sediments were kept in suspension by recirculating water pumps and the temperature was maintained at 20 ± 1°C.

The fish were acclimated to the experimental conditions for 14 h overnight (see Figure 2). During this time the fish were not fed. Two fish were then placed into each experimental tank. Reactive distances were obtained by observing the distance at which a fish first began pursuit of a prey item, measured against a 10 mm graphpaper grid stuck onto the back of the tank (Vinyard & O'Brien 1976). Direct orientation of the long axis of the predator toward the prey was regarded as the initiation of the pursuit sequence. Experiments were initiated by introducing ca. 25 cladocerans, of varying size, into the tank. Replicate observations per turbidity level were then carried out for a standard period of 5 min. Mean reactive distances were calculated and plotted as a function of turbidity. Experiments could not be carried out at turbidity levels higher than 28 NTU, as both prey items and the grid lines were obscured above this level.

Results

Field study results

A comparison of the physico-chemical characteristics of the lower reaches of the Kariega and Great Fish estuaries shows that they differ markedly in turbidity but are generally similar with respect to salinity, temperature and pH. Dissolved oxygen levels were slightly higher in the Kariega than in the Great Fish (Table 1). Based on these results we worked on the assumption that the differences in feeding strategy between the same species from the two estuaries could be attributed primarily to the different turbidity regimes. Obviously cogniscance has to be taken of the generally accepted theory that fish feed in proportion to the abundance and accessibility of prey (Whitfield & Blaber 1978; Blaber 1979; Cyrus & Blaber 1987a & b). However, considering the definition of turbidity it follows that turbidity per se would have the effect of making the prey less accessible to the predator, therefore indirectly reducing prey abundance.

The stomach content data, though collected on a seasonal basis, was lumped in order to get an overall picture of the diet of the fish. The number of stomachs examined, percent-
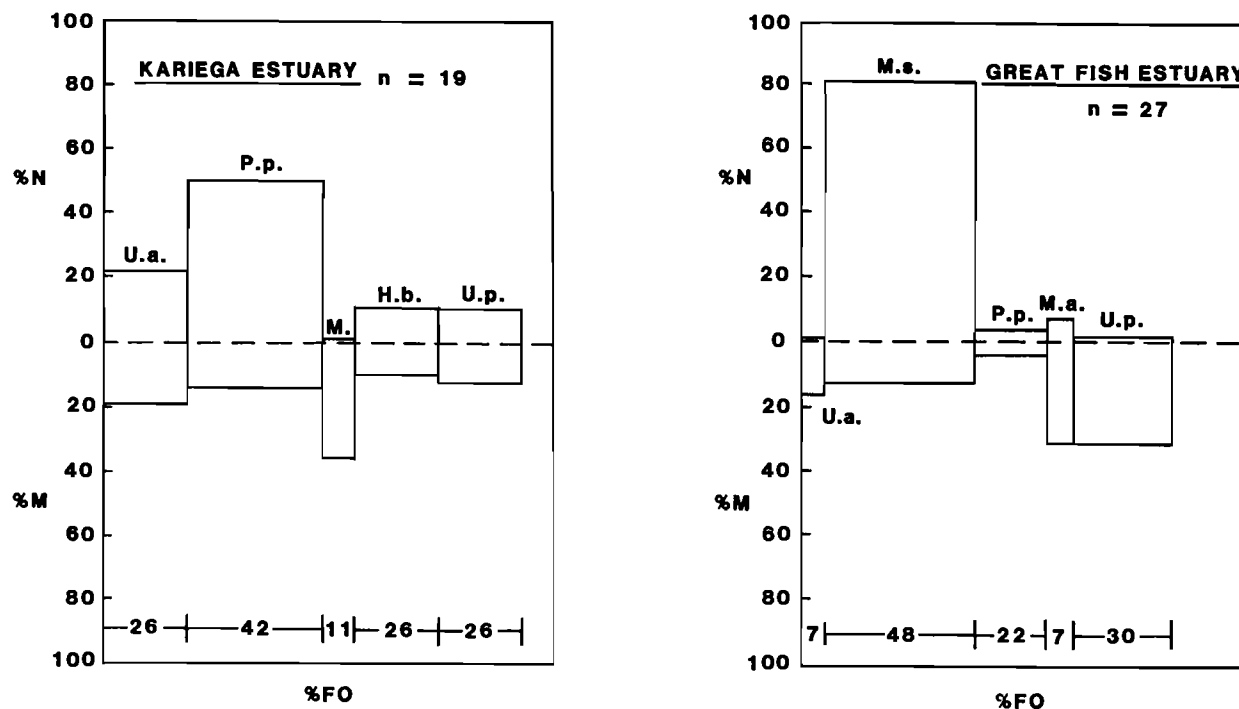
Figure 2 Major prey items of *Elops machnata* from the Kariega and Great Fish estuaries; G.a. = *Gilchristella aestuarius*, A.b. = *Atherina breviceps*, M = Mugilidae, M.a. = *Macropetasma africanum*, M.s. = *Mesopodopsis slabberi*, P.p. = *Palaemon pacificus*, U.a. = *Upogebia africana*, U.p. = unidentified pisces.

age of stomachs containing food, and feeding intensities of the fish examined is presented in Table 2. It is acknowledged that the sample numbers are low and thus the conclusions reached should be regarded as being of a tentative nature at this stage.

Table 2 Number of stomachs examined, per cent of stomachs containing food, and feeding intensity (weight of stomach contents as a per cent of body weight) for *Elops machnata, Pomadasys commersonnii* and *Atherina breviceps* (Gt F = Great Fish)

	E. machnata			P. commersonnii		A. breviceps	
	Kariega	Kowie	Gt F	Kariega	Gt F	Kariega	Gt F
Stomachs examined	33	29	33	21	57	33	39
% containing food	57,6	24,1	81,8	61,9	42,1	78,8	82,1
Feeding intensity	0,726	0,533	0,319	0,143	0,219	0,221	0,293
F.I. maximum	3,829	2,669	1,386	0,458	1,148	0,897	0,993

Diet of the pelagic piscivore, Elops machnata

In the Kariega estuary *E. machnata* ranged in size from 294 to 392 mm SL, those from the Kowie estuary from 284 to 398 mm SL, and in the Great Fish estuary from 285 to 434 mm SL. The parameters of the length / weight equations of the species from the three estuaries are shown in Table 3. There was no significant difference in the condition of the fish from the three estuaries ($p > 0,05$).

Table 4 shows the relative importance of different food items in the diet of *E. machnata* from all three estuaries. The data clearly indicate that in both the Kariega and the Kowie estuaries fish formed the major dietary component, comprising 24,6% by numbers, 67,3% by weight and 68,4% in terms of frequency of occurrence and 58,1%, 86,6% and 57,1% respectively in the Kowie estuary. On the other hand, crustaceans were the most important dietary items in the Great Fish estuary, comprising 96,9% by numbers, 64,9% by weight and 74,1% in terms of frequency of occurrence. The IRI value for crustaceans consumed in the Great Fish

Table 3 The parameters of the length/weight relationships ($W = aL^b$) for *Elops machnata, Pomadasys commersonnii* and *Atherina breviceps*

	E. machnata			P. commersonnii		A. breviceps	
	Kariega	Great Fish	Kowie	Kariega	Great Fish	Kariega	Great Fish
a	$4,89 \times 10^{-5}$	$2,57 \times 10^{-5}$	$1,03 \times 10^{-5}$	$4,35 \times 10^{-5}$	$1,21 \times 10^{-5}$	$7,58 \times 10^{-5}$	$7,13 \times 10^{-5}$
b	2,706	2,821	2,99	2,886	2,705	2,009	2,046
r^2	0,659	0,872	0,887	0,981	0,983	0,916	0,914
n	33	33	29	21	57	33	39
Size range (mm)	294–392	284–398	285–434	135–446	127–600	28,8–64,3	25,9–60,0

Table 4 Composite diet of *Elops machnata* from the Kariega, Kowie and Great Fish estuaries; n = number of stomachs containing food

Prey	Kariega (n = 19)				Kowie (n = 7)				Great Fish (n = 27)			
	%N	%W	%FO	IRI	%N	%W	%FO	IRI	%N	%W	%FO	IRI
Crustacea	75,4	32,7	47,4	5119	38,7	9,8	42,9	2080	96,9	64,9	74,1	11986
Unidentified												
Brachyura					3,2	1,7	14,3	70				
Hymenosoma orbiculare	2,3	0,1	10,5	26								
Anomura												
Upogebia africana	22,3	19,0	26,3	1088					0,7	16,6	7,4	128
Mysidacea					3,3	0,2	14,3	49				
Mesopodopsis slabberi									81,0	12,1	48,2	4482
Rhopalopthalamus terranatalis									3,1	1,7	14,8	71
Isopoda												
Eurydice longicornis	0,8	0,1	5,3	4					0,2	0,1	3,7	1
Macrura												
Palaemon pacificus	50,0	13,5	42,1	2674	32,3	8,0	28,6	1149	3,9	3,5	22,2	165
Macropetasma africanum									8,1	31,0	7,4	290
Mollusca					3,2	3,3	14,3	94				
Cephalopoda					3,2	3,3	14,3	94				
Pisces	24,6	67,3	68,4	6291	58,1	86,6	57,1	8265	3,1	35,1	44,4	1697
Unidentified	10,8	12,0	26,3	599	25,8	72,5	28,6	2808	1,5	31,3	29,6	972
Mugilidae	1,5	35,9	10,5	394	16,1	8,0	14,3	345	0,2	2,2	3,7	9
Gilchristella aestuarius					16,1	6,1	28,6	635	0,2	0,3	3,7	2
Atherina breviceps	10,8	10,3	26,3	555					1,3	1,3	7,4	19
Trachurus trachurus capensis	0,8	6,0	5,26	36								
Rhabdosargus holubi	0,8	3,2	5,26	21								
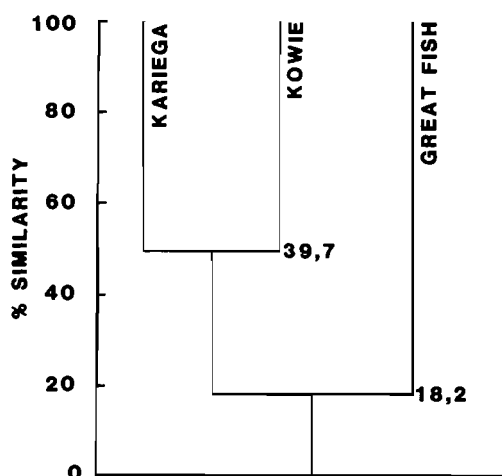
Figure 3 Similarity dendogram of the diet of *Elops machnata* from the Kariega, Kowie and Great Fish estuaries.

estuary was 11 986 as opposed to a value of 1697 for fish. This is in stark contrast to the IRI values for crustaceans and fish (5119 and 6291 respectively) in the Kariega and 8265 and 2080 for fish and crustaceans respectively in the Kowie estuary. These differences are also illustrated in Figure 2.

Similarities in the diet, according to IRI values, of *E. machnata* from the three estuaries are shown in Figure 3. It is evident that the diet is almost similar between fish from the Kariega and the Kowie estuaries, and least similar between fish from the Great Fish estuary and either of the other two. Feeding intensity was higher in fish from the

Kariega and the Kowie than in those from the Great Fish estuary. However a higher percentage of fish from the Great Fish estuary contained food in their stomachs (see Table 2).

Diet of the benthivore, Pomadasys commersonnii

Spotted grunter, *Pomadasys commersonnii* from the Kariega estuary ranged in size from 135 to 446 mm SL, whilst those from the Great Fish estuary ranged from 127 to 600 mm SL. The parameters of the length / weight relationships of the fish from the two estuaries are shown in Table 5. There was neither a significant difference in the condition of the fish from the two estuaries ($p > 0,05$), nor with season ($p > 0,05$).

The relative importance of different food items in the diet of *P. commersonnii* throughout the year is presented in Table 5. The results show that crustaceans formed the major dietary component in both estuaries viz. IRI = 19 460 for the Kariega and 19 840 for the Great Fish estuary. In the Kariega the single most important prey item was the mud-prawn, comprising 72,7% in terms of numbers, 96,2% in terms of weight and 92,3% in terms of frequency of occurrence. In the Great Fish estuary mudprawn were of lesser importance, having values of 6,5%, 84,6% and 41,7% respectively for number, weight and frequency of occurrence. The other major prey items in the Great Fish were mysids and amphipods. These differences are graphically illustrated in Figure 4.

The percent similarity between the diets of *P. commersonnii* in the two estuaries was found to be 34,6% (Figure 5), which suggests that grunter are not as affected by turbi-

Table 5 Composite diet of *Pomadasys commersonnii* from the Kariega and Great Fish estuaries; *n* = number of stomachs containing food

| Prey	Kariega (*n* = 13) %N	%W	%FO	IRI	Great Fish (*n* = 24) %N	%W	%FO	IRI
Crustacea	95,4	99,1	100,0	19450	96,8	99,6	100,0	19840
Unidentified								
Brachyura					0,3	0,1	4,2	1
Hymenosoma orbiculare	1,5	1,4	7,7	23	7,7	9,5	8,3	143
Cleistostoma edwardsii					3,0	2,0	20,8	103
Anomura								
Upogebia africana	72,7	96,2	92,3	15594	6,5	84,6	41,7	3798
Mysidacea								
Mesopodopsis slabberi					49,1	2,4	37,5	1931
Rhopalopthalamus terranatalis					5,6	0,8	25,0	161
Isosoda								
Eurydice longicornis	1,5	0,1	7,7	12				
Amphipoda								
Grandidierella lignorum	18,2	0,1	7,7	140	26,6	0,3	33,3	897
Macrura								
Palaemon pacificus	1,5	1,4	7,7	23				
Mollusca	4,6	0,9	7,7	42	1,2	0,4	12,5	20
Pelycopoda					1,2	0,4	12,5	20
Solen spp.	3,0	0,9	7,7	30				
Gastropoda	1,5	0,1	7,7	12				
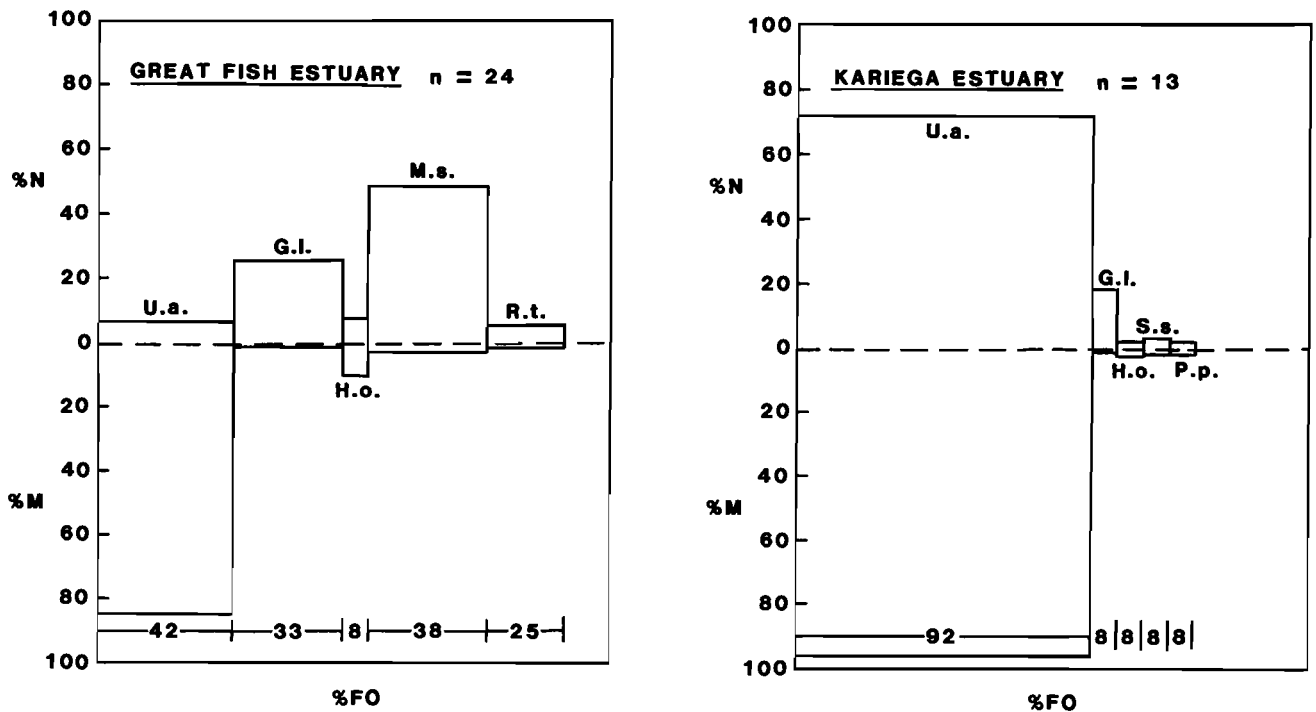
Figure 4 Major prey items of spotted grunter *Pomadasys commersonnii* from the Kariega and Great Fish estuaries; G.l. = *Grandidierella lignorum*, H.o. = *Hymenosoma orbiculare*, M.s. *Mesopodopsis slabberi*, P.p. = *Palaemon pacificus*, R.t. = *Rhopalopthalamus terranatalis*, S.s. = *Solen* spp., U.a. *Upogebia africana*.

dity (with respect to their feeding) as is *E. machnata.* Feeding intensity was found to be higher in the Great Fish than in the Kariega estuary, although a higher percentage of individuals from the Kariega estuary contained food in their stomachs (see Table 2).

Diet of the pelagic planktivore, Atherina breviceps

The size of *A. breviceps* from the Kariega estuary ranged from 28,8 to 64,3 mm SL, whereas fish from the Great Fish estuary ranged from 25,9 to 60,0 mm SL. The parameters of the length / weight relationships of the fish from the two

Table 6 Composite diet of *Atherina breviceps* from the Kariega and Great Fish estuaries; *n* = number of stomachs containing food

Prey	Kariega (n = 26)				Great Fish (n = 32)			
	%N	%W	%FO	IRI	%N	%W	%FO	IRI
Rotifera	5,3	2,4	11,5	88				
Crustacea								
Unidentified	12,6	17,6	34,6	1045	0,8	4,1	15,2	74
Ostracoda	0,2	0,4	3,9	2	5,5	8,2	45,5	623
Cumacea	0,2	1,1	3,9	5				
Copepoda								
Pseudodiaptomus hessei	11,9	7,7	30,8	602	84,5	50,3	69,7	9395
Isopoda								
Unidentified	3,7	5,5	23,1	211	1,1	9,3	21,2	221
Exosphaeroma hylecoetes	1,6	8,9	7,7	80	0,7	2,4	15,2	46
Amphipoda	5,7	18,3	38,5	924	0,3	2,5	9,1	26
Mysidacea								
Mesopodopsis slabberi	2,3	4,0	7,7	48	4,2	14,7	42,4	803
Decapoda								
Hymenosoma larvae	0,7	0,7	3,9	5				
Zoea larvae	51,5	31,5	26,9	2233	2,8	7,6	33,3	346
Insecta	4,4	2,2	15,4	22	0,1	0,9	6,1	6
Chironomidae	4,4	2,2	15,4	22	0,1	0,9	6,1	6
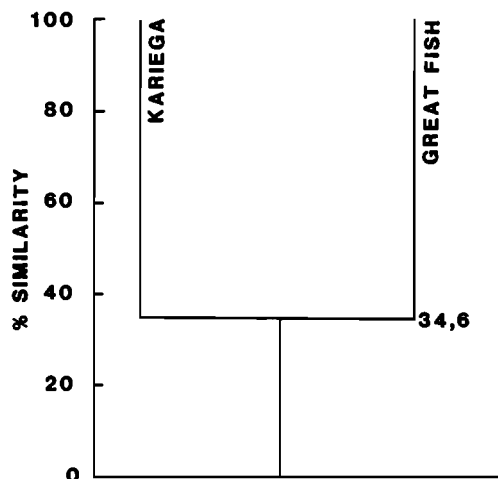
Figure 5 Similarity dendogram of the diet of *Pomadasys commersonnii* from the Kariega and Great Fish estuaries.

estuaries are shown in Table 3 and there was no significant difference in condition (*b* exponent) between the fish from the two systems at *p* > 0,05.

The relative importance of different food items of *A. breviceps*, throughout the year, is presented in Table 6. In the Kariega, decapod zoea were the major dietary component, comprising 51,5% by number, 31,5% by weight and 26,9% by frequency of occurrence, while in the Great Fish estuary the calanoid copepod *Pseudodiaptomus hessei* was the major dietary item, accounting for 84,5%, 50,3% and 69,7% by number, weight and frequency of occurrence respectively. These differences are shown in Figure 6.

The percent similarity between the diets of *A. breviceps* in the two systems was found to be 16,2% (Figure 7). This value is comparable to that of *E. machnata* in the two sys-

tems, the significance of which is discussed later. Feeding intensity was slightly higher in the Great Fish, as was the percentage of fish containing food in their stomachs (see Table 2).

Experimental results

Size selection and feeding rate

The duplicate set of results of the experiments carried out at 0 and 120 NTU showed that daphnids of a similar size range were consumed by *A. breviceps* (Figure 8), indicating that turbidity does not appear to influence prey size selection. There was also no indication that larger fish selected larger prey items. The positive slope of the regression analyses of numbers of daphnids consumed as a function of standard length (Figure 9) indicates that there was a trend for larger fish to consume more prey during the given feeding period. However, only the regression line in Figure 9a showed a statistically significant correlation (*p* < 0,05). The reduced slopes of the regression lines for the turbid water in comparison to the slopes in the 0 NTU water would suggest, however, that fish of comparable size consumed less prey in the turbid water during the allocated feeding period, indicating that feeding rate is reduced by turbidity.

Reactive distance experiment

Figure 10 shows that the trend of mean reactive distance with increasing turbidity for *A. breviceps*, decreases from a mean value of 81 mm at 0 NTU to 37 mm at 28 NTU. Plotting a regression line of mean reactive distance against turbidity predicts that reactive distance would be zero at 40 NTU, on condition that the relationship between reactive distance and turbidity is linear. Obviously this is not the case, since the fish still manage to feed at turbidities of 120 NTU, suggesting a change in feeding strategy.
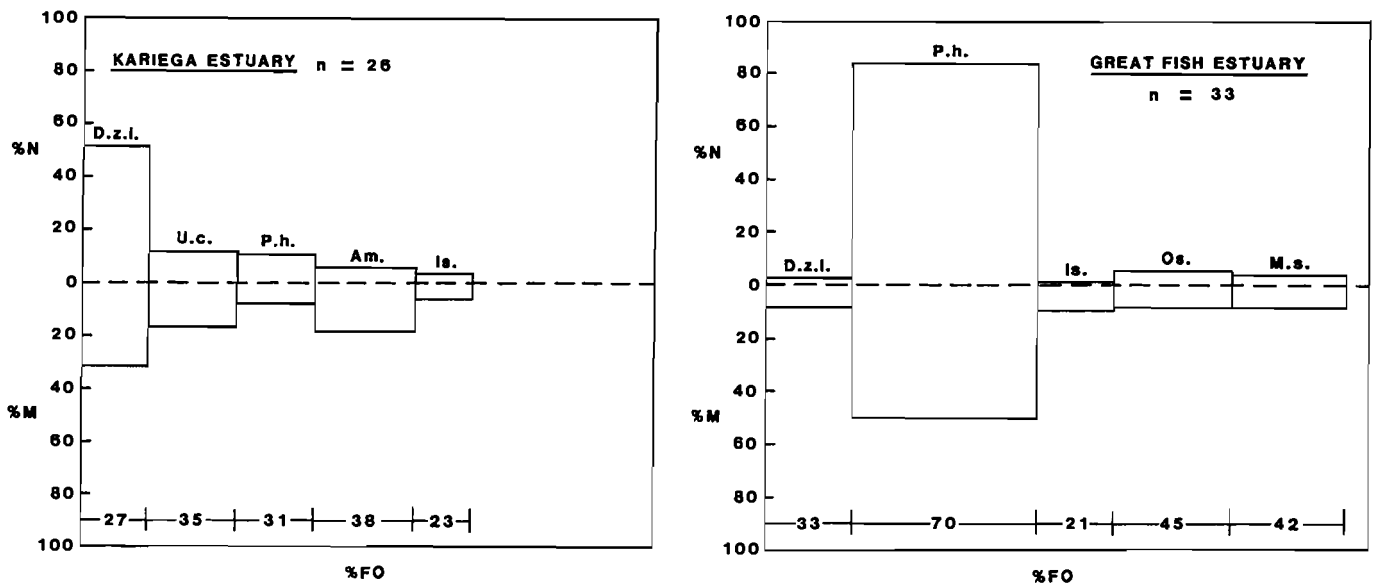
Figure 6 Major prey items of *Atherina breviceps* from the Kariega and Great Fish estuaries; Am. = Amphipoda, D.z.l. = decapod zoea larvae, Is. = Isosoda, M.s. = *Mesopodopsis slabberi*, Os. = Ostracods, P.h. = *Pseudodiaptomus hessei*, U.c. = unidentified crustaceans.
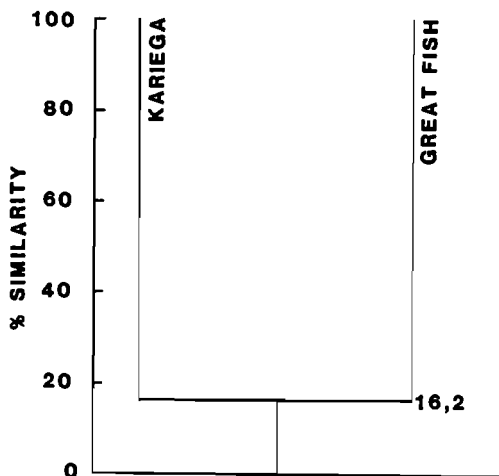

Figure 7 Similarity dendogram of the diet of *Atherina breviceps* in the Kariega and Great Fish estuaries.

Discussion

Gut content analysis

Caillet (1976) points out that the different methods of gut content analysis reflect different aspects of the feeding habits of the fish. Numerical importance and frequency of occurrence principally reflect the process of behavioural selection of prey by fish. These methods do not, however, provide information about the energy content of the prey item, and may also overestimate the importance of small prey items (Hyslop 1980). On the other hand, the gravimetric method provides an indication of the nutritional importance of a prey item, but may also overestimate the importance of large prey items (Hyslop 1980). Pinkas *et al.* (1971) attempted to overcome these disadvantages by combining the three methods to give an index of relative importance (IRI) for each prey item. While Windell (1971) and King & Clark (1984) support the IRI rationale for combining the results of various methods, Hyslop (1980) on the other hand

is of the opinion that IRI values may compound sources of error in the methods. Although this might very well occur, we were of the opinion that IRI values provide a realistic method of evaluating prey importance of the same species from different estuaries.

The predator, *E. machnata* was found to prey upon both fish and crustaceans in all three of the estuaries from which samples were obtained. However, the relative importance of the two prey groups was markedly different. In the Kariega and the Kowie estuaries fish was found to be the major dietary component, whereas in the highly turbid Great Fish estuary the mysid, *M. slabberi* was the dominant prey item. Mysids are known to form dense swarms (Wittman 1977; Wooldridge & Bailey 1982) and it is suggested that *E. machnata* either takes large mouthfuls or swims through the swarms sieving out its prey. The latter suggestion is quite probable considering the large mouth and the well developed gill rakers of the fish (Smith & Heemstra 1986). *M. slabberi* also occurs in the Kariega, although their abundance there is lower than in the Great Fish estuary (Allanson & Read 1987). However, *M. slabberi* were not found in the stomachs of *E. machnata* from the Kariega estuary.

Moreover, although the penaeid shrimp *Palaemon pacificus* is more abundant in the Great Fish estuary than in the Kariega (G. Read, Zoology Department, Rhodes University, unpublished data), IRI values for this prey item are higher from the Kariega (IRI = 2674), than from the Great Fish (IRI = 165). This suggests prey selection, rather than random ingestion and hence can be interpreted as an indication of a change in feeding strategy.

It would appear therefore that increasing turbidity levels cause a change in feeding strategy from fast moving prey organisms with a high escape probability (e.g. fish and penaeid prawns) to slow-moving organisms with a low escape probability (e.g. mysids). This suggestion is supported by the work of Marais (1984) who studied the diet of *E. machnata* in four other eastern Cape estuaries, viz. the
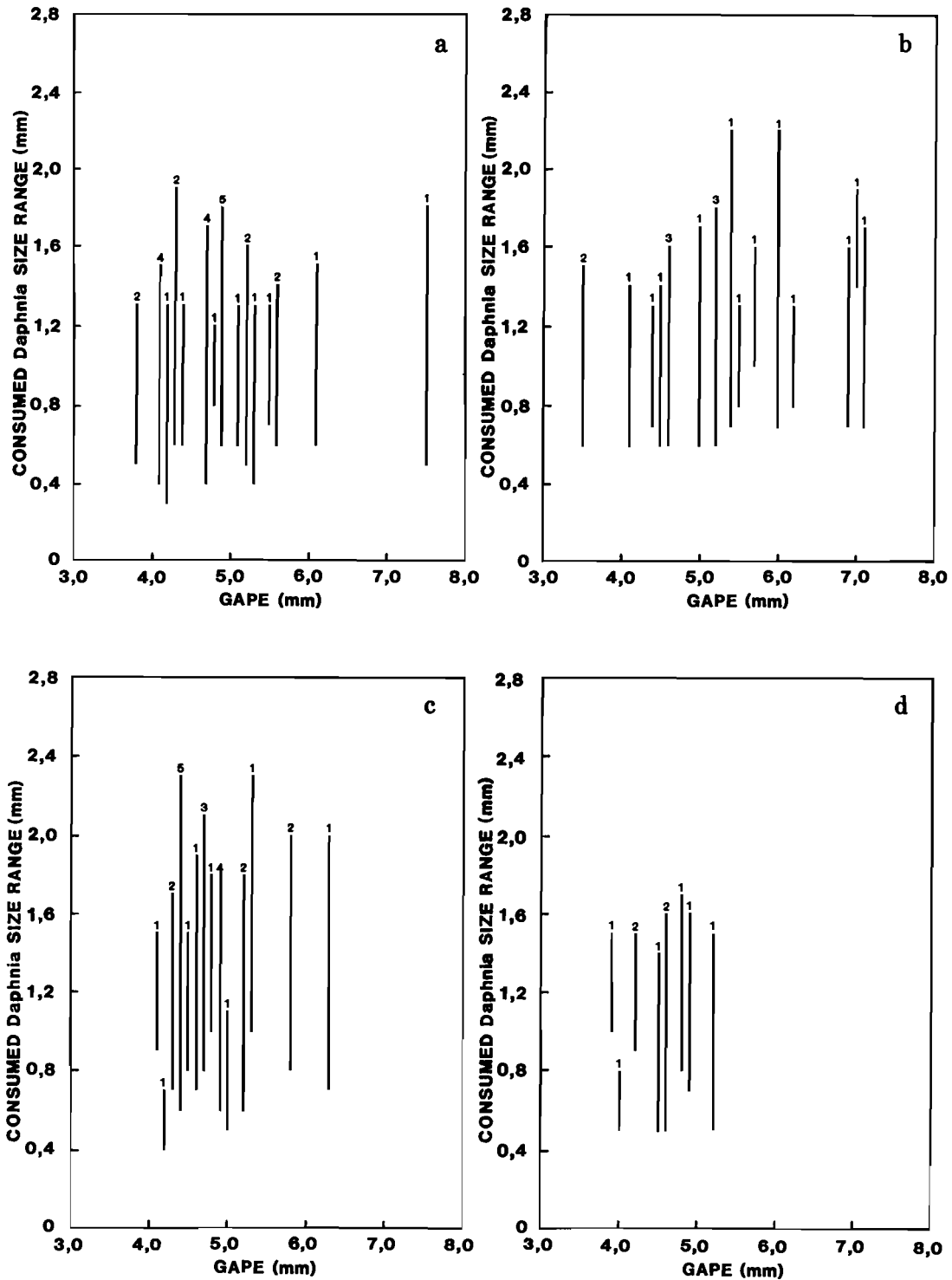
Figure 8 Size range of consumed daphnids as a function of fish gape for experimental trials a and c at 0 NTU and b and d at 120 NTU. Vertical bars indicate size range; numbers above bars indicate number of fish with the same gape size.

Swartkops, Sundays, Krom[me] and Gamtoos estuaries. In the slightly turbid Sundays estuary with a mean secchi disc reading of 580 mm ($\approx$ 17,7 NTU Cyrus 1984) the IRI value for mysids was 5471, and that for penaeid prawns was 39. The IRI values for prey of *E. machnata* in the Swartkops estuary (mean secchi disc readings = 1150 mm $\approx$ 1,4 NTU) were 3094 and 248 for mysids and penaeid prawns respectively. By combining the data obtained by Marais (1984) and those obtained in this study, a comparison of the relative IRI values for fish and crustaceans in the diet of *E. mach-*

nata from two turbid (Great Fish and Sundays) and four clear estuaries (Kariega, Kowie, Swartkops and Krom) can be made (Figure 11). Crustaceans represent a greater portion of the diet in turbid estuaries, while fish are the major dietary items in clear estuaries.

The relatively high per cent similarity between diets of *E. machnata* in the Kariega and the Kowie estuaries in comparison with the low per cent similarity between either of the above two estuaries and the Great Fish estuary (Figure 3), also lends support to the hypothesis that turbidity causes
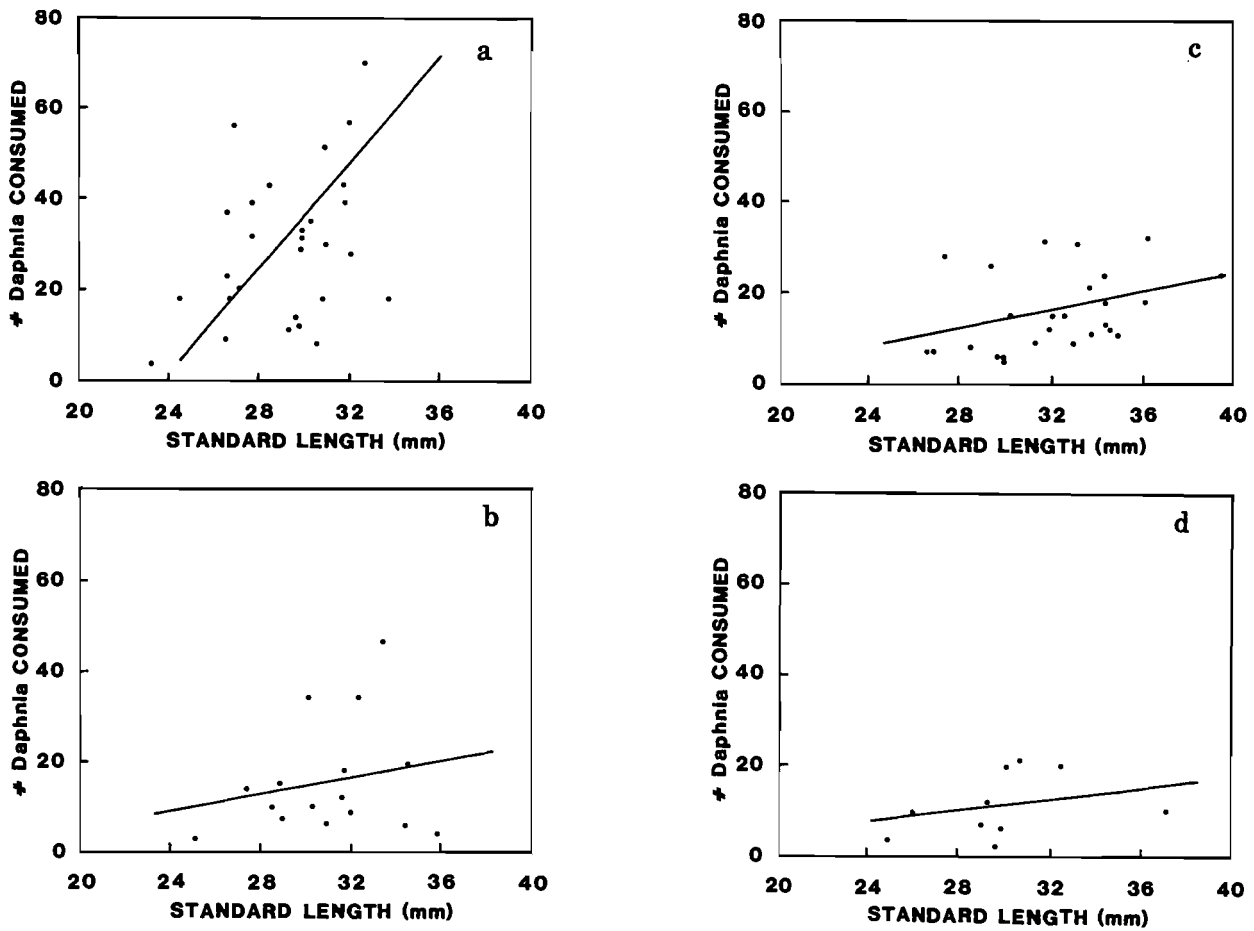
Figure 9 Regression lines of number of daphnids consumed as a function of fish standard length for experimental trials a and c at 0 NTU and b and d at 120 NTU. (a) $r^2 = 0,454$; $p < 0,05$; (b) $r^2 = 0,125$; $p > 0,05$; (c) $r^2 = 0,135$; $p > 0,05$; (d) $r^2 = 0,108$; $p > 0,05$.
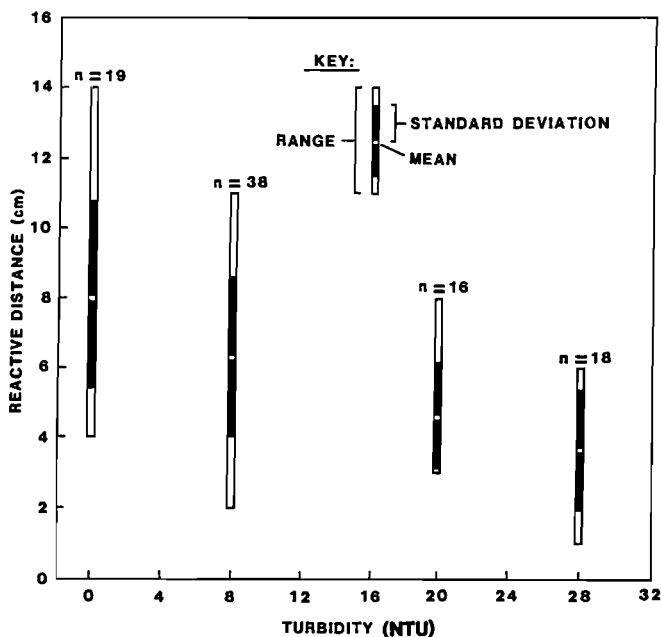

Figure 10 Reactive distance as a function of turbidity for *Atherina breviceps*; n = number of observations at each turbidity level.
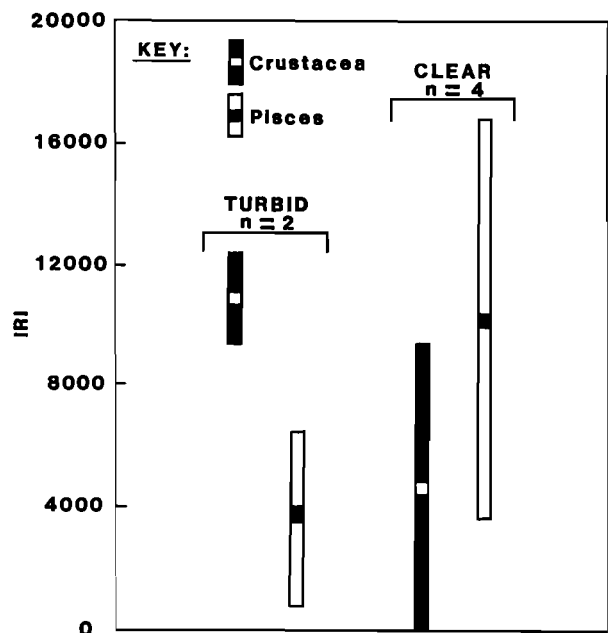

Figure 11 Mean IRI values ($\pm$ standard deviation) for crustaceans and fish in the diet of *Elops machnata* from two turbid and four clear estuaries. (Data from Marais 1984 and this study).

a change in feeding strategy. The change is from active (probably visual) selection of prey items with a high escape probability to a possible non-visual, non-selective capture of

prey items with a low escape probability.

While this study and others in the eastern Cape (Marais 1984) provide convincing evidence that turbidity indeed

causes a change in the feeding strategy of *E. machnata* there is also evidence, which at first glance would appear to be to the contrary. Whitfield & Blaber (1978) studied the feeding biology of piscivorous fishes in Lake St Lucia, a large, predominantly turbid estuarine / lake system along the coast of Natal, and found fish to be the most important prey of this species, followed by crustaceans. One of their general conclusions was that piscivorous fish in Lake St Lucia appear to feed in proportion to prey abundance and accessibility. During the winter months they found *E. machnata* to feed mainly on fish but during the summer months they switch principally to penaeid shrimps, when these are more abundant (Joubert & Davis 1968), although fish prey abundance also increases. Based on Whitfield & Blaber's (*op cit.*) study, Cyrus (1984) suggested that *E. machnata* showed a preference for turbid water (> 50 NTU) and suggested that the species may be adapted for hunting in turbid waters. This is contrary to the hypothesis presented here. Nevertheless, in support of Cyrus (1984) it can obviously also be argued that *E. machnata* is indeed well adapted for hunting in turbid waters by virtue of its exceptionally large mouth and well developed gill rakers. Examination of a later study by Cyrus (1988), however, shows that turbidity levels in the St Lucia system are significantly higher in summer than in winter. This in turn lends support to the hypothesis that changes in turbidity indeed result in changes in feeding strategy. Our hypothesis also fully supports the conclusion that fish feed in proportion to prey accessibility (Whitfield & Blaber *op cit.*), as turbidity, by definition, to a large extent determines the optical accessibility of prey.

The benthivorous spotted grunter, *P. commersonnii* in both estuaries was found to feed primarily on mudprawn, *U. africana*. Mudprawns were also found to be the single most important dietary item of this species in the Swartkops estuary (van der Westhuizen & Marais 1977), in the Swartkops, Sundays and Gamtoos estuaries (Marais 1984), whereas in the Mhlanga estuary in Natal sandprawn, *Callianassa kraussi* were the most important dietary item (Whitfield 1980). It was of interest to note, however, that grunter feed almost exclusively on mudprawns (73% by number) in the Kariega estuary, whereas in the Great Fish estuary this component is reduced to 6,5%; its place being taken by planktonic mysids (50%) and amphipods (25%). The grunter in the Great Fish estuary also have a much broader prey spectrum than in the Kariega (see Table 5). It is tempting to speculate that the broader dietary spectrum is as a consequence of the higher turbidity, for the following reason. Under conditions of high turbidity, visibility is reduced, resulting in a more non-selective feeding strategy. However, in the absence of more quantitative information on prey abundance this conclusion should be regarded with caution. The only prey abundance data available to us were for the amphipod, *G. lignorum* (Allanson & Read 1987). A comparison of the occurrence of the amphipod in the diet of grunter in the two estuaries supports the above, though tentative, conclusion.

The relatively high per cent similarity (34,6%) between diets of *P. commersonnii* from the two estuaries suggests that turbidity does not play as important a role in affecting feeding strategy as it does for a visual pelagic predator such as *E. machnata*. This is most likely due to the feeding habit

of grunter which force their prey from burrows by a jet of water 'blown' down the burrows (van der Elst 1981). In other words the fish does not have to visually orientate on the prey item except at close quarters. Thus turbidity should not have a drastic effect on the feeding strategy except possibly becoming more non-selective.

The planktivore, *A. breviceps* in the two estuaries shows some interesting differences with respect to their feeding biology. In the Kariega estuary the fish show a fairly broad prey spectrum with no single species showing a much higher level of importance than any of the others. In the Great Fish estuary, on the other hand, the copepod, *P. hessei* was the dominant prey item. This could obviously be a reflection of the higher abundance of the copepod in the Great Fish estuary, but is nevertheless also an indication that the animals' feeding strategy has changed.

It is possible that the high frequency of occurrence of ostracods in the diet of *A. breviceps* in the Great Fish estuary is linked to turbidity, since ostracods in general can be regarded as zooplankton with a low escape probability. Overall, the low per cent similarity between the diets of *A. breviceps* in the two estuaries (16,2%) suggests that turbidity plays an important role in determining feeding strategy, as is expected for a planktivore.

Laboratory experiments

Several authors have suggested that high turbidity levels may alter prey size selectivity patterns in predators (Eggers 1976; Vinyard & O'Brien 1976). The results of our experiments to test this hypothesis, however, show that turbidity does not appear to affect the size range of prey consumed by *A. breviceps*. Similarly, Gardner (1981) working with bluegill sunfish, *Lepomis macrochirus* also found that turbidity had no effect on size selectivity patterns.

Furthermore, our experimental results show that there was a trend for fish in turbid water to consume less zooplankters than fish of a comparable size in clear water. These results therefore lend support to the hypothesis that turbidity reduces feeding rate (Gardner 1981). Because daphnids are relatively slow-moving zooplankters and less likely to escape predation (Drenner, Strickler & O'Brien 1978), feeding rates on prey with a higher escape probability, such as copepods or mysids (which occur in the diet of *A. breviceps* from the Great Fish estuary) may be further reduced by turbidity. The reduction of feeding rate in turbid water must theoretically therefore reduce feeding efficiency. However, if the fish compensate for this by increasing their forage time, they decrease the time available for other activities and also increase the probability of falling prey to larger predators (Gerritsen & Strickler 1977).

The reactive distance of *A. breviceps* was substantially reduced by increased turbidity levels. Vinyard & O'Brien (1976) found the same for bluegill sunfish. A reduction in reactive distance would theoretically limit the volume of water a fish can search in a given period of time and is thus probably the major factor causing reduced feeding rates of visual predators in turbid waters. The relationship between reactive distance and prey escape can be summarized as follows. Once a prey item has moved out of an attacking predator's reactive distance, it has escaped and the predator

must begin to search again. Thus, when reactive distance is
reduced, as under conditions of high turbidity, the escape
probability of prey is increased (Vinyard & O'Brien 1976).
It follows therefore that hunting under these conditions may
become energetically unprofitable, which might be the
trigger mechanism leading to a more cost effective feeding
strategy, such as filter feeding, on condition that prey
density is adequate. The field and laboratory results of this
study support this hypothesis.

General conclusions

The results of our experiments at various turbidity levels
suggest that visual predators in a turbid estuary have a
reduced feeding rate, which is caused by a reduction in
reactive distance. If the reduced feeding rate results in
reduced energy acquisition, this in turn could be reflected
either by a poor condition factor of the fish from turbid
estuaries relative to those in clear estuaries or by reduced
fish abundance in turbid estuaries. However, the results
obtained in this study show that there was no significant
difference between condition factor of fish from the two
estuaries. Moreover, there was no indication that fish were
more abundant in the clear estuary. In fact, *P. commersonnii*
appears to be more abundant in the turbid estuary, and in a
quantitative assessment Bok (1983) found a greater abun-
dance of mullet and other species, including *P. commerson-
nii*, in the Great Fish estuary than in the less turbid Kowie
and Swartkops estuaries. The conclusion that can be drawn
from this is that changes in turbidity result in changes in
feeding strategies. This is most notable for the visual preda-
tors as shown by the lower percentage similarities between
the diets of *E. machnata* and *A. breviceps* than that for *P.
commersonnii* in the two estuaries.

To what extent the difference in diet similarities are due
to differences in prey abundance or to turbidity levels in the
two estuaries is, however, not known at this stage. Never-
theless it would appear from a careful analysis of the litera-
ture that changes in turbidity cause changes in prey abun-

dance and composition. The predator thus either has to leave
an estuary when turbidity levels rise or it has to have the
ability to change tactics in order to obtain the necessary
energy for growth and reproduction. Future studies on the
effect of turbidity on feeding strategies should thus include
temporal and spatial assessments of prey abundance, where-
upon greater clarity of the interrelationship between turbidi-
ty and alternative feeding strategies can be obtained and
possibly quantified using a measure such as Shorigin's
index of selectivity.

The final conclusions that can be drawn from this study
are; (i) that visual predators are more affected by turbidity in
terms of feeding than are macrobenthic feeders, (ii) that
turbidity decreases the reactive distance of visual predators
and hence reduces feeding efficiency, and (iii) the reduction
in feeding efficiency is not reflected by a lowered condition
factor nor decreased abundance of fish in turbid estuaries
but rather by a change in feeding strategy. These conclu-
sions are presented in the form of a compartmental model in
Figure 12.

Acknowledgements

The project was funded by grants from the Hans Merensky
Foundation, the Foundation for Research Development and
the Rhodes University Research Committee. Andy Scholtz
is thanked for his enthusiastic help and technical assistance
in the field and the laboratory. The two anonymous referees
provided very constructive criticism for which they are
thanked.

Figure 12 Compartmentalized model showing causes (adapted from Bruton 1985) and effects of turbidity on feeding strategies of fish in estuaries.

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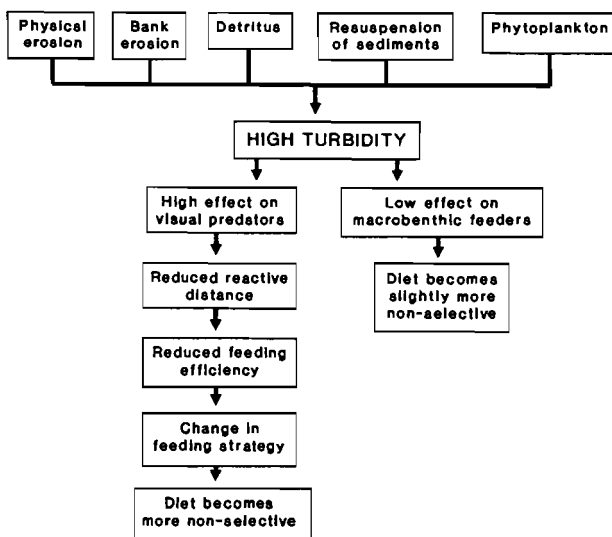
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