The role of zooplankton in the feeding ecology of fish fry from some southern African estuaries

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The stomach contents of more than 1000 fish fry (< 30 mm S.L.), comprising 11 species, were examined from the Mhlanga and Swartvlei estuarine systems. Calanoid and cyclopoid copepods were the dominant food item of fry < 20 mm S.L., with the exception of *Diplodus sargus* and *Sarpa salpa* where harpacticoid copepods were the main invertebrate prey. Although the diet of fry < 20 mm S.L. varied according to the availability of different foods, zooplankton was the major prey category for this size class of fishes in estuaries with both low and high zooplankton biomasses. The advantages of feeding on zooplankton by estuarine fry and possible reasons for ontogenetic changes in diet are discussed.

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Die maaginhoude van meer as 1000 klein vissies (< 30 mm S.L.), wat 11 spesies insluit, is in die Mhlanga- en Swartvlei-getyriviersisteme ondersoek. Calanoiëde en cyclopoiëde Copepoda was die dominante voedselitem van vissies < 20 mm S.L., met die uitsondering van *Diplodus sargus* en *Sarpa salpa* waar harpacticoiëde Copepoda die belangrikste ongewerwelde prooi was. Alhoewel die dieet van vissies < 20 mm S.L. volgens die beskikbaarheid van verskillende voedselsoorte gewissel het, was soöplankton die hoof prooikategorie van hierdie vislengtegroep in getyriviere met lae en hoë soöplanktonbiomassas. Die voordele van soöplanktonvoeding deur getyriviervissies en moontlike redes vir ontogenetiese veranderings in die dieet word bespreek.

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Although the diet of juvenile and adult fish in South African estuaries has received considerable attention (e.g. Blaber 1976; Whitfield & Blaber 1978; Coetzee 1982; Marais 1984), knowledge of the food and feeding ecology of postlarval stages is lacking. This situation does not appear to apply to many overseas estuarine systems where the diet of fry has been intensively studied (e.g. Darnell 1961; Kjelson, Peters, Thayer & Johnson 1975; Peters & Kjelson 1975; Kjelson & Johnson 1976). Information on the feeding of estuarine fish fry is necessary when investigating the trophic structure and habitat choice of individual species, as well as understanding the overall resource utilization by fishes within an estuary.

This paper reports on the postlarval diet of 11 fish species from two estuarine systems and emphasizes the role of zooplankton in supporting the millions of fish fry which enter southern African estuaries each year. An attempt has also been made to examine the position of fry in the estuarine community and to postulate reasons for the ontogenetic changes in diet of estuarine fishes.

Materials and Methods

Sampling

Fish fry (< 30 mm standard length) were collected from the Mhlanga estuary during 1978 using a seine-net (3 m × 1 m × 1,5 mm bar mesh), from Swartvlei during 1980 using a lift net (2 m × 2 m × 2,0 mm bar mesh) and from the Swartvlei estuary during 1983 using a seine-net (10 m × 2 m × 5,0 mm bar mesh). All captured fish were preserved in 10% formaldehyde for analysis in the laboratory.

A description of the Mhlanga estuary (29°42′S/31°06′E) is given in Whitfield (1980) and the Swartvlei system (34°0′S/22°46′E) by Whitfield (1984).

Analyses

In the laboratory fish were identified, measured (mm standard length) and stomachs removed under a binocular microscope. The stomach contents were analysed using four methods:

(i) Percentage frequency of occurrence; the number of stomachs in which each prey item occurred was recorded and expressed as a percentage of the total number of stomachs examined.

(ii) Percentage numerical occurrence; the number of individuals of each food type in all stomachs was expressed as a percentage of the total number of food items recorded.

(iii) Percentage points; the percentage fullness of a stomach was assessed, food items were sorted into taxonomic groups and points were then allocated to each group according to the proportion they represented in relation to the other groups present and the fullness of the stomach.

(iv) Percentage dry mass; plant material from fish stomachs was weighed after oven drying at 55°C. Each invertebrate taxon in a stomach was counted and the dry mass obtained by multiplication using zooplankton data from Blaber (1979). Gravimetric values for the various food items were summed and the results expressed as a percentage of the total food weight.

The method of diet analysis used in each estuary depended mainly on the type of food consumed, e.g. numerical occurrence could not be used for species feeding on filamentous algae. The diet of fish fry from the Mhlanga estuary was analysed using methods (i) and (iii), those from Swartvlei using methods (i) and (ii), and from the Swartvlei estuary using methods (i) and (iv).

Results and Discussion

The stomach contents of 1141 fish fry, comprising 11 species, were examined. Analyses of the diet of the fry are shown in Tables 1, 2 and 3.

Gerres rappi (evenfin pursemouth)

The fry of this species consumed mainly copepods in the Mhlanga estuary (Table 1) which is similar to the feeding of *G. rappi* fry in the Kosi system (Figure 1) where copepods were the dominant food item (Cyrus & Blaber 1983a). *G. rappi* larger than 40 mm switch to a zoobenthic diet with bivalves, crabs and chironomid larvae comprising 89% of their diet in the Kosi system (Cyrus & Blaber 1983b).

Rhabdosargus holubi (Cape stumpnose)

Copepods were the dominant component in the diet of *R. holubi* fry (Tables 1, 2 and 3) with the exception of the 20 – 29 mm size group in the Swartvlei estuary where diatoms and filamentous algae predominated (Table 3). *R. holubi* larger than 30 mm feed mainly on benthic invertebrates, filamentous algae and aquatic macrophytes (Blaber 1974; Whitfield 1984).

Terapon jarbua (thornfish)

The fry of *T. jarbua* consumed a wide range of food items

Table 1 Diet of marine/estuarine fish fry (< 30 mm S.L.) from the Mhlanga estuary

	Gerres rappi		*Rhabdosargus holubi*		*Terapon jarbua*		*Liza macrolepis*				*Valamugil cunnesius*				*Myxus capensis*			
	(11 – 28 mm) n = 14		(22 – 28 mm) n = 10		(11 – 29 mm) n = 70		(15 – 19 mm) n = 6		(21 – 29 mm) n = 11		(11 – 19 mm) n = 10		(22 – 29 mm) n = 27		(13 – 15 mm) n = 9		(20 – 29 mm) n = 9	
Food item	% F	% P	% F	% P	% F	% P	% F	% P	% F	% P	% F	% P	% F	% P	% F	% P	% F	% P
Amphipoda	–	–	10	3,6	34	18,2	–	–	–	–	–	–	–	–	–	–	44	25,4
Bivalvia	–	–	–	–	3	0,2	–	–	–	–	–	–	–	–	–	–	–	–
Brachyura: Zoeae	–	–	–	–	5	0,1	–	–	–	–	–	–	–	–	–	–	–	–
Cladocera	7	3,4	–	–	17	8,2	33	46,2	–	–	20	22,2	4	6,5	–	–	22	4,4
Copepoda	86	74,5	90	55,0	44	17,2	66	53,8	27	7,7	80	59,2	26	11,7	78	58,9	56	18,4
Crustacea: Larvae	21	8,3	20	5,0	14	9,0	–	–	–	–	20	9,3	33	11,1	67	35,6	22	3,5
Cumacea	–	–	50	33,6	3	1,3	–	–	9	2,6	–	–	–	–	11	5,5	22	13,2
Insecta: Chironomidae	–	–	–	–	6	3,5	–	–	9	5,1	–	–	22	6,5	–	–	–	–
Other	–	–	–	–	18	7,7	–	–	–	–	10	9,3	–	–	–	–	33	32,5
Isopoda	–	–	–	–	13	4,4	–	–	–	–	–	–	–	–	–	–	–	–
Oligochaeta	7	2,1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Osteichthyes	–	–	–	–	10	14,5	–	–	–	–	–	–	–	–	–	–	–	–
Ostracoda	7	3,4	10	2,8	4	0,9	–	–	9	1,7	–	–	7	1,0	–	–	15	2,6
Polychaeta	7	4,8	–	–	26	13,0	–	–	–	–	–	–	4	1,9	–	–	–	–
Scales	–	–	–	–	11	1,8	–	–	–	–	–	–	–	–	–	–	–	–
Tanaidacea	7	3,4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Unicellular algae	–	–	–	–	–	–	–	–	82	37,6	–	–	81	17,3	–	–	–	–
Filamentous algae	–	–	–	–	–	–	–	–	9	5,1	–	–	4	0,3	–	–	–	–
Macrophyte material	–	–	–	–	–	–	–	–	–	–	–	–	7	1,3	–	–	–	–
Flagellates	–	–	–	–	–	–	–	–	9	0,9	–	–	26	5,5	–	–	–	–
Particulate matter	–	–	–	–	–	–	–	–	82	39,3	–	–	81	36,8	–	–	–	–

Length range (S.L.) given in parentheses; % F = percentage frequency of occurrence; % P = percentage points; n = number of stomachs containing food.

Table 2 Diet of marine/estuarine fish fry (< 30 mm S.L.) from Swartvlei

	Lithognathus lithognathus (17 – 29 mm) n = 16		*Monodactylus falciformis* (19 – 29 mm) n = 19		*Rhabdosargus holubi* (20 – 29 mm) n = 13	
Food item	% F	% N	% F	% N	% F	% N
Amphipoda	94	34,0	79	11,3	31	10,6
Brachyura: Zoeae	–	–	5	1,1	8	9,2
Copepoda	81	65,1	95	76,4	92	69,5
Chironomidae	–	–	21	8,5	15	7,8
Isopoda	–	–	5	0,5	–	–
Ostracoda	–	–	16	2,2	8	2,8
Polychaeta	19	0,9	–	–	–	–

Length range given in parentheses; % F = percentage frequency of occurrence; % N = percentage numerical occurrence; n = number of stomachs containing food.

Table 3 Diet of marine/estuarine fish fry (< 30 mm S.L.) from the Swartvlei estuary

	Monodactylus falciformis		*Sarpa salpa*		*Rhabdosargus holubi*				*Diplodus sargus*				*Liza richardsoni*			
	(10–29 mm) n = 126		(19–29 mm) n = 335		(10–19 mm) n = 105		(20–29 mm) n = 58		(11–19 mm) n = 110		(20–29 mm) n = 98		(11–19 mm) n = 78		(20–29 mm) n = 17	
Food item	% F	% M	% F	% M	% F	% M	% F	% M	% F	% M	% F	% M	% F	% M	% F	% M
Amphipoda	–	–	–	–	0,9	0,6	–	–	0,9	0,6	3,1	0,6	–	–	–	–
Bivalvia: Spat	–	–	–	–	–	–	–	–	8,2	0,2	4,1	0,1	6,4	0,4	–	–
Brachyura: Zoeae	–	–	–	–	–	–	–	–	2,7	0,6	–	–	7,7	6,0	–	–
Copepoda	99,2	87,6	43,3	0,3	99,0	64,6	91,4	1,4	99,1	15,7	87,8	3,5	88,5	46,9	29,4	30,3
Gastropoda: Larvae	–	–	0,3	+	–	–	–	–	–	–	–	–	2,6	0,1	5,9	9,1
Insecta: Chironomidae	22,2	5,7	17,9	0,7	36,2	24,1	5,2	0,4	38,2	9,7	57,1	5,9	5,1	6,9	–	–
Other	–	–	–	–	–	–	–	–	–	–	–	–	7,7	3,5	5,9	60,6
Isopoda	0,8	0,4	–	–	1,9	3,4	–	–	–	–	–	–	–	–	–	–
Macrura: Larvae	–	–	0,6	+	–	–	–	–	1,8	0,2	2,0	+	29,5	36,2	–	–
Ostracoda	64,3	6,3	0,6	+	18,1	1,7	5,2	+	60,9	6,2	39,8	1,0	–	–	–	–
Diatoms	25,4	n.d.	–	–	7,6	5,6	74,1	57,1	0,9	1,2	6,1	20,0	34,6	n.d.	94,1	n.d.
Filamentous algae	–	–	97,3	99,0	–	–	62,1	41,1	42,7	65,6	71,4	68,9	–	–	–	–
Particulate matter	–	–	–	–	–	–	–	–	–	–	–	–	1,3	n.d.	76,5	n.d.

Length range (S.L.) given in parentheses; % F = percentage frequency of occurrence; % M = percentage dry mass; n = number of stomachs containing food; n.d. = food contribution not determined; + = trace.

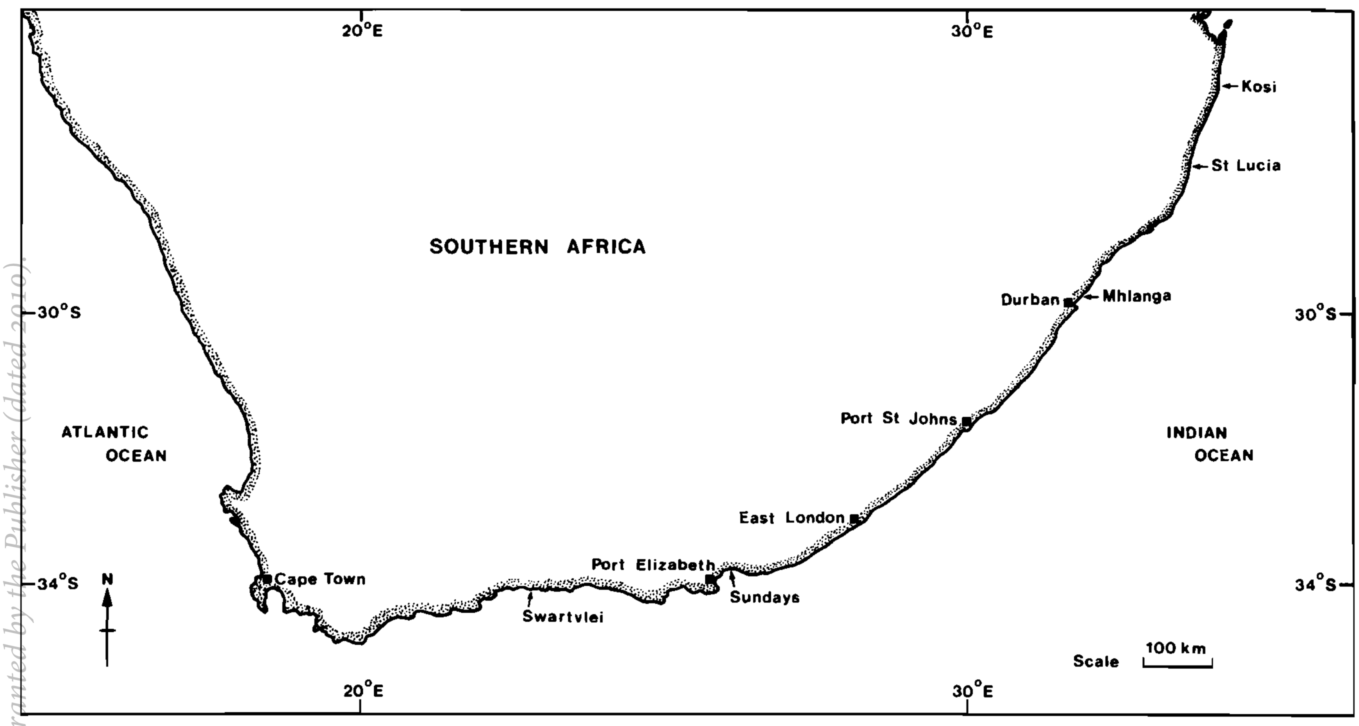

Figure 1 Map of southern Africa showing the localities of estuarine systems mentioned in the text.

(Table 1) with copepods and amphipods the two most important groups. Juvenile and adult *T. jarbua* have been recorded preying on aquatic and terrestrial invertebrates, small fishes and fish scales removed from living fishes (Whitfield & Blaber 1978).

Lithognathus lithognathus (white steenbras)

Copepods and amphipods were the dominant food of *L. lithognathus* fry from Swartvlei (Table 2) and the Sundays estuary (Wooldridge & Bailey 1982). Juvenile and adult *L. lithognathus* feed on zoobenthos (Mehl 1973).

Monodactylus falciformis (Cape moony)

The fry of this species feed mainly on copepods in both the Swartvlei and Sundays estuaries (Tables 2 & 3; Wooldridge & Bailey 1982). Juvenile *M. falciformis* larger than 50 mm consume epiphytic fauna and flora, insects and small fishes (Whitfield 1984).

Sarpa salpa (strepie)

Filamentous algae dominated the diet of *S. salpa* fry from the Swartvlei estuary but harpacticoid copepods living amongst the algal filaments occurred in 43% of the stomach contents examined (Table 3). Unfortunately almost all the specimens examined were larger than 20 mm, by which stage the transition to a herbivorous diet has already occurred (Christensen 1978).

Diplodus sargus (blacktail)

The diet of *D. sargus* fry comprised a mixture of plant and animal material, with increasing amounts of filamentous algae and diatoms being recorded with an increase in fish size (Table 3). Harpacticoid copepods were the dominant invertebrate food item. Christensen (1978) found that in the eastern Cape marine environment harpacticoid copepods, polychaetes and amphipods were important food items for *D. sargus* of less than 30 mm. According to Day, Blaber & Wallace (1981) *D. sargus* of 20 – 50 mm feed on zooplankton but then change their diet to *Zostera*, filamentous algae and epifauna.

Liza richardsoni (southern mullet)

Copepoda were the dominant food of *L. richardsoni* fry < 20 mm but diatoms and particulate organic matter were important to individuals > 20 mm (Table 3). Juvenile and adult *L. richardsoni* feed mainly on particulate organic matter and unicellular algae derived from benthic substrata (Masson & Marais 1975; Whitfield 1982).

Liza macrolepis (largescale mullet)

Copepods and cladocerans were the only food items recorded in the diet of *L. macrolepis* < 20 mm but were unimportant in specimens > 20 mm (Table 1). Blaber & Whitfield (1977) also determined that *L. macrolepis* switch to a microbenthic diet at approximately 20 mm. Juvenile and adult *L. macrolepis* feed on diatoms, particulate organic matter, filamentous algae and foraminiferans (Blaber 1977).

Valamugil cunnesius (longarm mullet)

The diet of *V. cunnesius* < 20 mm was dominated by copepods and cladocerans followed by a switch to particulate organic matter and unicellular algae from benthic substrata between 20 – 30 mm (Table 1). Juvenile and adult *V. cunnesius* consume mainly particulate organic matter and diatoms (Blaber 1976; Whitfield 1980).

Myxus capensis (freshwater mullet)

All individuals < 30 mm were recorded feeding on animal material with copepods dominating in the < 20 mm size class (Table 1). According to Blaber & Whitfield (1977) the final change to feeding on microbenthos occurs when *M. capensis* are longer than 30 mm and this would account for the absence of particulate organic matter and diatoms in the diet of fry from the Mhlanga estuary (Table 1). Particulate organic matter, diatoms, filamentous algae and terrestrial plant debris are the main food items of juvenile and adult *M. capensis* (Blaber 1977; Whitfield 1980).

Trophic relationships

Table 4 summarizes the available information on the feeding of fish fry < 20 mm. Although the diet of these fry varies between and within species, depending on the availability of different foods, zooplankton appear to be the major prey for this size class of fishes. The data listed in Table 4 is derived from studies in estuaries with relatively low and high zooplankton biomasses (e.g. low in Mhlanga and Swartvlei, high in St Lucia and Sundays). The former group of estuaries have zooplanton stocks of < 10 mg m^{-3} (Whitfield 1980; Coetzee 1981) whereas in the latter group zooplankton biomasses exceed 1000 mg m^{-3} (Blaber 1979; Wooldridge & Bailey 1982). Calanoid and cyclopoid copepods were the dominant food item of fry in most estuaries despite variations in zooplankton composition. Calanoid copepods undergo both vertical and horizontal migrations in South African estuaries (Grindley 1972; Wooldridge & Erasmus 1980) and this is likely to have a major impact on the feeding behaviour of estuarine fish fry (Robertson & Howard 1978). Blaber & Whitfield (1977) have shown that mullet fry in southern African estuaries feed

Table 4 Summary of important food items for fish fry < 20 mm S.L. in South African estuaries

Family	Species	Food	Reference
Gerreidae	*Gerres acinaces*	Copepoda$^+$, Polychaeta, Amphipoda$^+$, Cumacea$^+$	Cyrus & Blaber (1983)
	Gerres filamentosus	Copepoda$^+$, Polychaeta	Cyrus & Blaber (1983)
	Gerres rappi	Copepoda$^+$, Polychaeta, Amphipoda$^+$	Cyrus & Blaber (1983)
		Copepoda$^+$, Crustacean larvae$^+$	This study
Monodactylidae	*Monodactylus falciformis*	Copepoda$^+$, Chironomid larvae, Ostracoda$^+$	This study
		Copepoda$^+$	Wooldridge & Bailey (1982)
Mugilidae	*Liza alata*	Copepoda$^+$, Insect larvae	Blaber (pers. comm.)
	Liza dumerili	Ostracoda$^+$, Insect larvae, Foraminifera, Diatoms	Blaber (pers. comm.)
	Liza macrolepis	Copepoda$^+$, Insect larvae, Fish eggs$^+$, Diatoms	Blaber (pers. comm.)
		Copepoda$^+$, Cladocera$^+$	This study
	Liza richardsoni	Copepoda$^+$, Macruran larvae$^+$	This study
	Mugil cephalus	Copepoda$^+$, Fish eggs$^+$, Ostracoda$^+$, Diatoms	Blaber (pers. comm.)
	Myxus capensis	Copepoda$^+$, Crustacean larvae$^+$, Cumacea	This study
		Copepoda$^+$, Insect larvae	Blaber (pers. comm.)
	Valamugil buchanani	Copepoda$^+$, Ostracoda$^+$, Amphipoda$^+$, Diatoms	Blaber (pers. comm.)
	Valamugil cunnesius	Copepoda$^+$, Cladocera$^+$, Crustacean larvae$^+$	This study
	Valamugil seheli	Copepoda$^+$, Brachyuran zoeae$^+$	Blaber (pers. comm.)
Pomadasyidae	*Pomadasys commersonni*	Copepoda$^+$, Mysidacea$^+$	Wooldridge & Bailey (1982)
Soleidae	*Heteromycteris capensis*	Copepoda$^+$, Ostracoda$^+$, Mysidacea$^+$	Wooldridge & Bailey (1982)
	Solea bleekeri	Copepoda$^+$, Ostracoda$^+$, Mysidacea$^+$	Wooldridge & Bailey (1982)
Sparidae	*Diplodus sargus*	Copepoda^1, Chironomid larvae, Filamentous algae	This study
	Lithognathus lithognathus	Copepoda$^+$, Amphipoda$^+$, Polychaeta	This study
		Copepoda$^+$, Amphipoda$^+$, Ostracoda$^+$	Wooldridge & Bailey (1982)
	Rhabdosargus holubi	Copepoda$^+$, Cumacea$^+$, Chironomid larvae	This study
		Copepoda$^+$, Mysidacea$^+$, Amphipoda$^+$	Wooldridge & Bailey (1982)
	Sarpa salpa	Copepoda^1, Filamentous algae	This study
Teraponidae	*Terapon jarbua*	Copepoda$^+$, Amphipoda$^+$, Fish larvae$^+$, Polychaeta	This study

$^+$ Represents groups which are often part of the zooplankton; ^{1} exclusively Harpacticoida which are mostly benthic and not planktonic.

initially on zooplankton, then vertically migrating zooplankton and meiobenthos, and finally microbenthos. The role of vertically migrating zooplankton in initiating dietary switches by estuarine fish fry may be significant.

The importance of zooplankton as a nutritional resource for larval and postlarval fishes in rivers (Crecco & Blake 1983), freshwater lakes (Lemly & Dimmick 1982), brackish lakes (Darnell 1961), estuaries (Kjelson *et al.* 1975), bays (Houde & Lovdal 1984) and oceans (May 1974) is widely recognized. However, aspects such as the uniformity in fry diet of a wide range of fish species in different habitats and the early onset of changes in foraging patterns have received little attention. Clearly larval and postlarval fishes are restricted by mouth dimensions to the size of invertebrate prey that can be consumed. Larval fishes feed mainly on microzooplankton (Houde & Lovdal 1984) whereas postlarval fishes utilize both microzooplankton and macrozooplankton (Hodson, Hackman & Bennet 1981).

Zooplankton often have a higher energy content than benthic invertebrate groups and this can be explained by the ability of planktonic invertebrates to store large amounts of lipids (Norrbin & Bamstedt 1984). Since lipids are an important energy reserve for fishes, the value of preying on zooplankton during the early growth stages is apparent. Blaber (1975) determined that differences in fat content of juvenile *Rhabdosargus holubi* in two east Cape estuaries were related to the lipid content of the food. Why then do estuarine fish fry, which are still capable of preying in zooplankton, switch to an alternative food source with a lower energy value? A possible explanation may be found in the low zooplankton stocks of most South African estuaries (Blaber, Cyrus & Whitfield 1981) relative to zoobenthos and detritus based food resources (McLachlan & Grindley 1974; Whitfield 1980; Blaber, Kure, Jackson & Cyrus 1983). According to Vernberg & Vernberg (1972) zooplankton are the dominant primary consumers in oceanic waters but in estuaries benthic herbivores and detritivores represent the critical link between primary producers and consumers. Although this pattern is reflected in most South African estuaries (Whitfield 1983) a large proportion of energy transfer in the St Lucia and Sundays estuarine systems is via the zooplankton food chain (Blaber 1979; Wooldridge & Bailey 1982). According to Grindley (1981) zooplankton in southern African estuaries is very variable with east coast estuaries tending to have a higher biomass ($1 - 1200$ mg m^{-3}) than south coast estuaries ($1 - 112$ mg m^{-3}). Laboratory and field investigations into the growth and survival of fish fry under different zooplankton densities would contribute towards our understanding of the role of zooplankton in supporting the millions of fry which enter South African estuaries each year.

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