AUTUMN FEEDING CYCLE OF THE BULL-DOG FISH, *GNATHONEMUS MACROLEPIDOTUS* (PISCES, MORMYRIDAE)

E. J. KRUGER
Lowveld Fisheries Research Station, Marble Hall, Transvaal

INTRODUCTION

It is often postulated that the time of day at which a fish is caught may influence the measured food volume and composition, but little is actually known about the dimensions of this 24-hourly rhythm (Darnell & Meierotto 1962, Keast & Welsh 1968). The rhythm may vary considerably due to habitat circumstances and generalizations must therefore be made with great caution. In order to evaluate the influence on the feeding cycle of the bull-dog fish, *Gnathonemus macrolepidotus*, a 24-hour study was undertaken in Loskop Dam, Transvaal, starting on 1 April 1970.

PROCEDURE

The surveys were performed in the Lombard's Bay section of Loskop Dam which offers protection against severe wave action whilst a pronounced littoral fringe vegetation is also present. Four gill nets, two each of meshes 80 and 120 mm (knot to knot) were used in the collections. It was considered unwise to use seine nets as netting would have been performed partly during the night and successive hauls would have disturbed the dam bottom appreciably. This could have interfered with the normal feeding of the fish under observation. A disadvantage in the use of gill nets lies in its more effective functioning during the dark period.

One net of each of the two mesh sizes was laid at right angles to the shoreline beginning at the fringe vegetation (viz. in the littoral zone) while the other two were fixed to submerged tree trunks within the limnetic zone. The nets were lifted at three-hour intervals to enable all the entangled fish to be removed. Notes were made of the relative positions of the fish in the nets. The stomach content of each fish was collected separately by severing the alimentary canal at either end of the stomach and inverting or stripping the latter, after which the contents were washed into a flask. Four per cent buffered formalin was used as preservative.

Prior to removal of the stomachs, estimates of fullness were made according to the numerical classification suggested by Swynnerton & Worthington (1940), viz. full (4), half full (2), quarter full (1) and empty (0).

RESULTS

The stomach of the bull-dog fish is well-defined and has a contractile muscle layer. Only the food items in the stomach were considered in the analyses. Although the gill nets were of only two different mesh sizes, selection occurred with regard to lengths and masses of fish caught. Specimens ranged in length from 170 to 250 mm with an average of 205 mm and in mass from 68,5 to 173,6 g with an average of 101,1 g.

Qualitatively, a wide range of food items occurred in the diet of *G. macrolepidotus* but fish remains were lacking entirely. This is not unexpected as the shape of the mouth rules out a piscivorous feeding habit. The frequency of occurrence of the various food items in the stomachs (Table 1) indicates that the larvae and pupae of the Chironomidae, Ceratopogonidae and Culicidae were mainly exploited as food. Larvae of the Tricoptera, Odonata and Ephemeroptera, as well as specimens of the Hydrachnellae (Acari), Mollusca and Copepoda only occurred sporadically. The larvae and pupae of *Chaoborus* (Culicidae) showed an interesting pattern of occurrence inasmuch as they were frequently present in the stomachs during the day but not at night (Figure 1). Larvae of the Trichoptera (*Ecnomus* and *Hydropsyche*) occurred in few stomach contents and then only during the dark period when most of the fish were to be found in the littoral zone.

TABLE 1

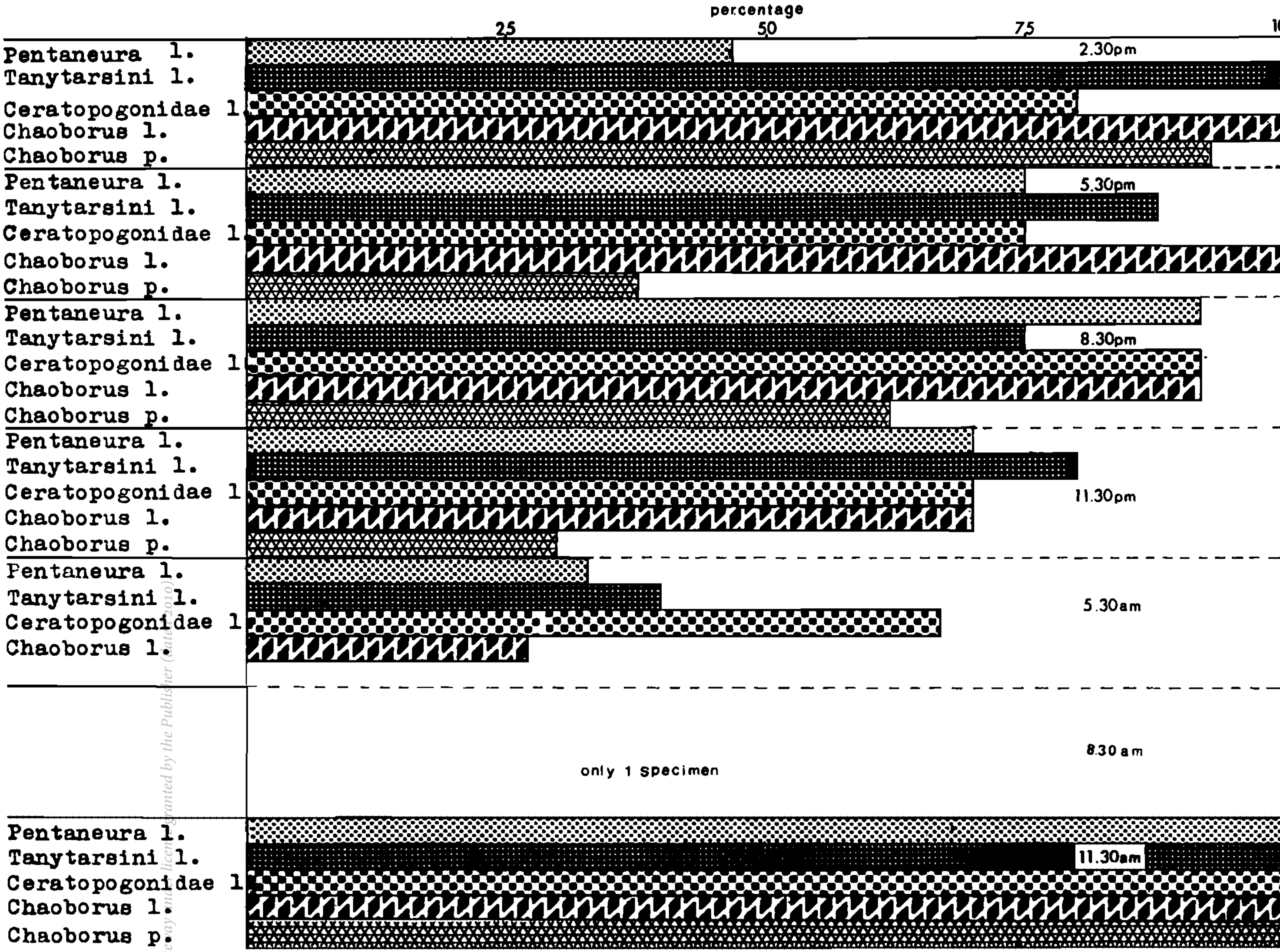
FREQUENCY OF OCCURRENCE OF THE VARIOUS FOOD ITEMS IN THE STOMACH CONTENTS OF *G. macrolepidotus* AT VARIOUS TIMES OF THE DAY-NIGHT FEEDING CYCLE

Time of survey	*2.30 p.m.*		*5.30 p.m.*		*8.30 p.m.*		*11.30 p.m.*		*5.30 a.m.*		*11.30 a.m.*	
Food items	*tot. occurrence*	*% occurrence*	*tot. occurrence*	*% occurrence*	*tot. occurrence*	*% occurrence*	*tot. occurrence*	*% occurrence*	*tot. occurrence*	*% occurrence*	*tot. occurrence*	*% occurrence*
Chironomidae l.												
Chironomus	8	53	2	25	4	33	2	20	5	33	2	100
Rheotanytarsus	3	20										
Pentaneura	7	47	6	75	11	92	7	70	5	33	2	100
Tanytarsini	15	100	7	88	9	75	8	80	6	40	2	100
Chironomidae p.	1	7			3	25	5	50	2	13		
Ceratopogonidae l.	12	80	6	75	11	92	7	70	10	67	2	100
Culicidae												
Chaoborus l.	15	100	8	100	11	92	7	70	4	27	2	100
Chaoborus p.	14	93	3	38	6	67	3	30			2	100
Ephemeroptera l.	1	7					2	20	4	27		
Mollusca												
B. (B) physopsis			1	13	2	17						
Trichoptera l.			1	13	3	25	2	20	2	13		
Odonata l.							1	10	1	7		
Copepoda									1	7		
Ostracoda	4	47	6	75	6	50	5	50	3	20	1	50
Acari	3	20					1	10				

l. = larvae; p. = pupae.
8.30 a.m.: no fish specimens.

FIGURE 1 (*Opposite*)

Frequency of occurrence of the dominant food items in the diet of *G. macrolepidotus* at different survey times during the day-night feeding cycle.


percentage
25
50
75
100
Pentaneura l.
Tanytarsini l.
Ceratopogonidae l
Chaoborus l.
Chaoborus p.
2.30pm
5.30pm
8.30pm
11.30pm
5.30am
8.30 am
only 1 specimen
11.30am

The relative numbers of the various food components clearly indicate the dominance of *Chaoborus* larvae, followed by the Tanytarsini larvae (Table 2, Figure 2). The former larvae comprised 50 per cent or more of the total number of food items during daytime but these numbers diminished markedly towards the 11.30 p.m. and 5.30 a.m. suveys. The pupae of *Chaoborus* showed the same overall pattern of presence in the stomach contents although their numbers were much less. This may merely be a reflection of their relative ratios in the available food.

During the survey only three specimens of the bull-dog fish were found with snail remains in their stomachs, though these three together consumed 52 small snails. This phenomenon may be attributed to individual preferences.

The mass composition of the various food items, as calculated from their average biomass values, once again points to the importance of chaoborid and chironomid larvae, which together comprised 80 per cent or more of the total mass of ingested food. The relatively larger food items like the larvae of the Trichoptera and Odonata were eaten in such small numbers that they had virtually no influence on the total food mass composition.

The actual average food masses per fish at the different time surveys are shown in Figure 3. It is evident that the food mass was highest after midday and lowest after midnight. To ensure that variation in fish size did not influence the results, the average food mass per unit fish mass was calculated. These figures correspond very well with the above. The graph showing the average estimates of fullness of the stomachs follows the same pattern closely. This shows that the stomachs were filled to capacity up to the 8.30 p.m. survey after which the food volume decreased, only to increase again after 8.30 a.m. The degree of fullness was mainly attributed to the intake of chaoborid larvae.

DISCUSSION

Little is known of the ecology of this shy inhabitant of the lowveld rivers and dams in the Transvaal. The bull-dog fish may attain a length of 250 mm, which is also the length limit obtained in this study. It is seldom caught by anglers (Le Roux & Steyn 1968).

The bull-dog fish was found to be quite suitable for food habit studies as the diet consists mainly, if not entirely, of food from animal origin. These food items are rarely broken up during the feeding action so that identification and quantitative evaluations are easily performed.

From the catch results in the littoral zone it seems as if the fish invade this zone only after sunset but abandon it again before daybreak. Most of the fish specimens caught in the limnetic zone were located in the lowest section of the gill-nets, thus suggesting a bottom-dwelling habit. Chaoborid larvae predominate in water over two metres deep, viz. outside the littoral zone, while chironomids occur on plants, stones and over the whole of the dam floor (Van Loggerenberg, personal communication). The dominance of both these food items in the stomach contents, whether in mass or numbers may be attributed to the fish movements whereby they were restricted to the bottom water layers during the day but moved to the shoreline at night.

Both the chironomids and chaoborids show cyclic rhythms in moulting from larvae to pupae. Macdonald (1956) noted a life cycle of two months for two chaoborid and one chironomid species in Lake Victoria. A lunar periodicity in transition was present. In the Transvaal

TABLE 2

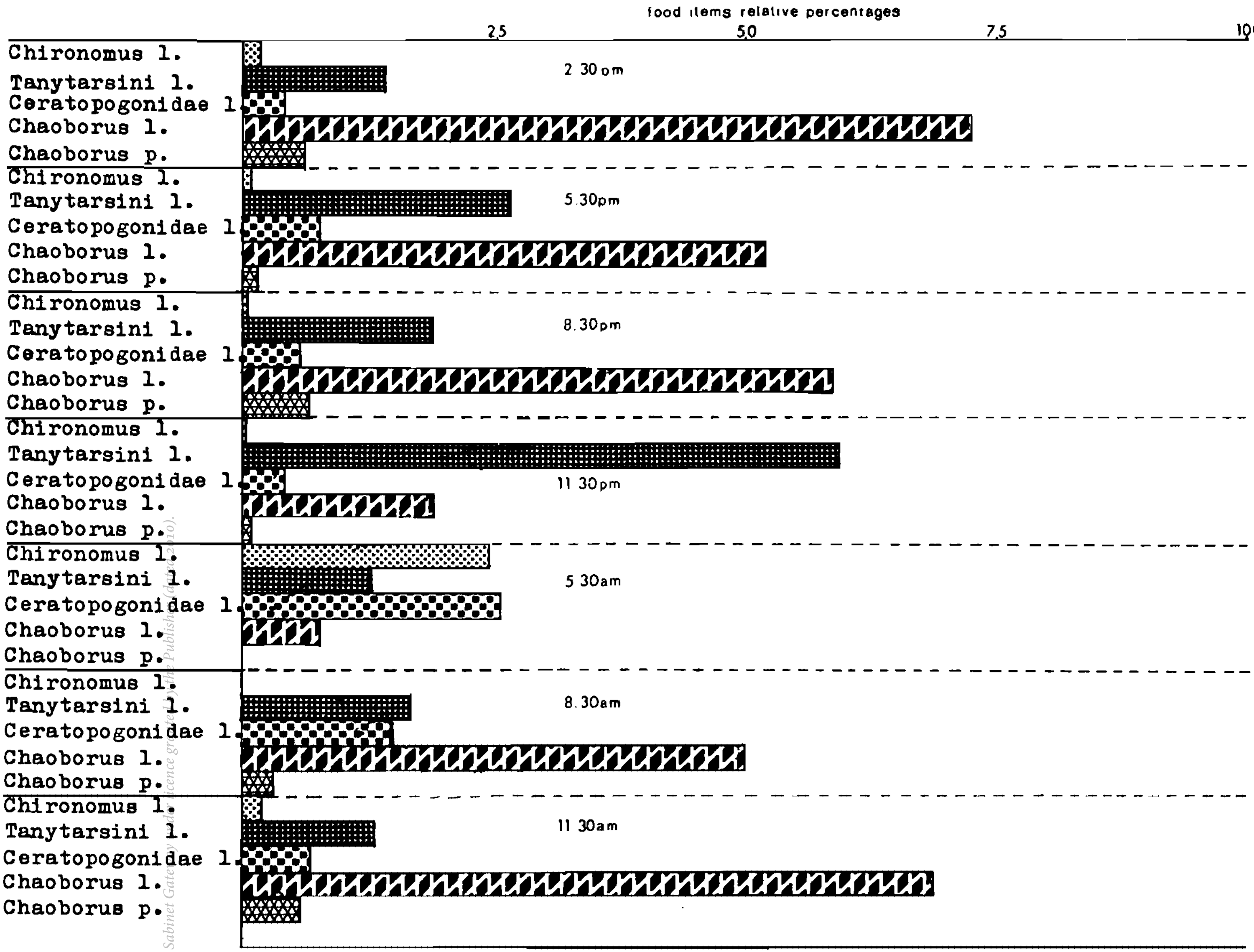
RELATIVE PERCENTAGES OF THE VARIOUS FOOD ITEMS IN THE STOMACH CONTENTS OF *G. macrolepidotus* AT DIFFERENT TIMES OF THE DAY-NIGHT FEEDING CYCLE

Time of survey	*2.30 p.m.*			*5.30 p.m.*			*8.30 p.m.*			*11.30 p.m.*		
Food item	*total no.*	*% of total food*	*no./fish*	*total no.*	*% of total food*	*no./fish*	*total no.*	*% of total food*	*no./fish*	*total no.*	*% of total food*	*no./fish*
Chironomidae l.												
Chironomus	73	1,7	4,9	14	0,8	1,8	8	0,6	0,7	2	0,3	0,2
Rheotanytarsus	16	0,4	1,1									
Pentaneura	24	0,5	1,6	98	5,7	12,3	67	5,2	5,6	66	11,7	6,6
Tanytarsini	608	13,9	40,5	454	26,5	56,8	245	18,8	20,4	368	59,5	36,8
Chironomidae p.	1		0,1	1	0,1	0,1	3	0,2	0,3	6	1,0	0,6
Ceratopogonidae l.	171	3,9	11,4	128	7,5	16,0	71	5,5	5,9	24	3,9	2,4
Culicidae												
Chaoborus l.	3174	72,4	211,1	897	52,3	112,1	759	58,4	63,3	119	19,3	11,9
Chaoborus p.	263	6,0	17,5	29	1,7	3,6	87	6,7	7,3	5	0,8	0,5
Ephemeroptera l.	4	0,1	0,3							3	0,5	0,3
Trichoptera l.				1	0,1	0,1	4	0,3	0,3	3	0,5	0,3
Odonata l.										1	0,2	0,1
Copepoda												
Ostracoda	57	1,3	3,8	85	5,0	10,6	11	0,8	0,9	20	3,2	2,0
Mollusca Bulinus (B)				7	0,4	0,9	45	3,5	3,8			
Acari Hydrachnellae	3	0,1	0,2							1	0,2	0,1

TABLE 2—continued

Time of survey	*5.30 a.m.*			*8.30 a.m.*			*11.30 a.m.*		
Food items	*total no.*	*% of total food*	*no./fish*	*total no.*	*% of total food*	*no./fish*	*total no.*	*% of total food*	*no./fish*
Chironomidae l.									
Chironomus	29	24,6	1,9				6	1,8	3,0
Rheotanytarsus									
Pentaneura	9	7,6	0,6	3	8,3	3,0	12	3,6	6,0
Tanytarsini	15	12,7	1,0	6	16,7	6,0	43	13,0	12,5
Chironomidae p.	5	4,2	0,3						
Ceratopogonidae l.	30	25,4	2,0	5	13,9	5,0	22	6,7	11,0
Culicidae									
Chaoborus l.	9	7,6	0,6	18	50,0	18,0	228	69,1	114,0
Chaoborus p.				1	2,8	1,0	18	5,5	9,0
Ephemeroptera l.	7	5,9	0,5						
Trichoptera l.	4	3,4	0,3						
Odonata l.	1	0,8	0,1						
Copepoda	2	1,7	0,1						
Ostracoda	7	5,9	0,5	3	8,3	3,0	1	0,3	0,5
Mollusca Bulinus (B)									
Acari Hydrachnellae									

l. = larvae; p. = pupae.


food items relative percentages
25
50
75
100
2 30 pm
5.30pm
8.30pm
11 30pm
5 30am
8.30am
11 30am
Chironomus l.
Tanytarsini l.
Ceratopogonidae l.
Chaoborus l.
Chaoborus p.

lowveld, Frank (1965) found *Procladius brevipetiolatus* (Chironomidae) to follow a monthly lunar periodicity in life stages. When studying the stomach contents of fish over a period of time this factor has to be borne in mind as the fauna composition may change according to the phase of the moon. The difference in relative numbers of chaoborid larvae and pupae in the stomach contents of the bull-dog fish may merely be a reflection of their changing ratio on the dam bottom due to the above-mentioned phenomenon.

Chaoborus larvae show day-night vertical migrations since they spend the daylight hours in the mud but venture into the plankton at night to feed on it (Woodmansee and Grantham 1961). Diurnal bottom feeders like the bull-dog fish would therefore find *Chaoborus* more abundant in the day than at night, as was revealed by the stomach analyses.

The visual estimation of stomach fullness seems justified in this species as material other than food, such as large quantities of mucus, was not present to affect the results as was the case with other species (Kruger 1971).

The number of mormyrid species steadily declines southwards from central Africa so that only two, *Gnathonemus macrolepidotus* and *Petrocephalus catostoma* are present in Loskop Dam. Petr (1968) showed that all the mormyrids of Black Volta Lake, Ghana, are insectivorous, but *Mormyrops deliciosus* revealing a slight piscivorous tendency. *Chaoborus* larvae were eaten in the riverine section of the lake by five per cent of the *Mormyrus rume* and *M. macrocephalus* specimens whereas chironomid larvae were utilized more freely. The Loskop Dam daytime usage of chaoborid larvae by *G. macrolepidotus* was much higher. This may be due to the daytime shore-avoidance noted in the latter instance.

The stomachs of mormyrids in Lake Victoria were seldom empty and in most cases merely reflected the faunal composition on the dam bottom (Corbet 1961). Okedi (1971) found that the larvae of *Povilla* and the Chironomidae were the primary food items. In the inflowing Sio River though, the Coleoptera and Annelida were of major importance in addition to the chironomid larvae. Ostracods, water mites and plant fruits were taken less frequently. This wide spectrum of food items agrees with the findings in Loskop Dam regarding *G. macrolepidotus*, except for plant material which was lacking entirely. Corbet (1961) found that *Mormyrus kanume* was the only larger mormyrid species utilizing chaoborid larvae to any appreciable extent while *Marcusenius grahami* revealed similar tendencies among the smaller species (Okedi 1971). Stomach contents analyses of *Gnathonemus victoriae* corresponded well with that of the closely related *G. macrolepidotus* in Loskop Dam.

The affinity of some bull-dog fish specimens for snails may be of ecological significance: the intermediate hosts of the human bilharzia parasites, the snails *Bulinus* (*Physopsis*) and *Biomphalaria pheifferi* both occur in Loskop Dam, though in small numbers. It may well be that this fish species plays an important but inconspicuous rôle in the biological control of these vectors. This manner of control is also advocated for Lake Kariba by Hira (1969). Munro (1967) found the bull-dog fish to be an intensive carnivore in Lake McIlwaine (Rhodesia). The chief source of food was chironomid larvae although chaoborid larvae were abundantly available, while the

FIGURE 2 (*Opposite*)

Relative numbers (as percentage) of the dominant food items in the diet of *G. macrolepidotus* at different survey times during the day-night feeding cycle.

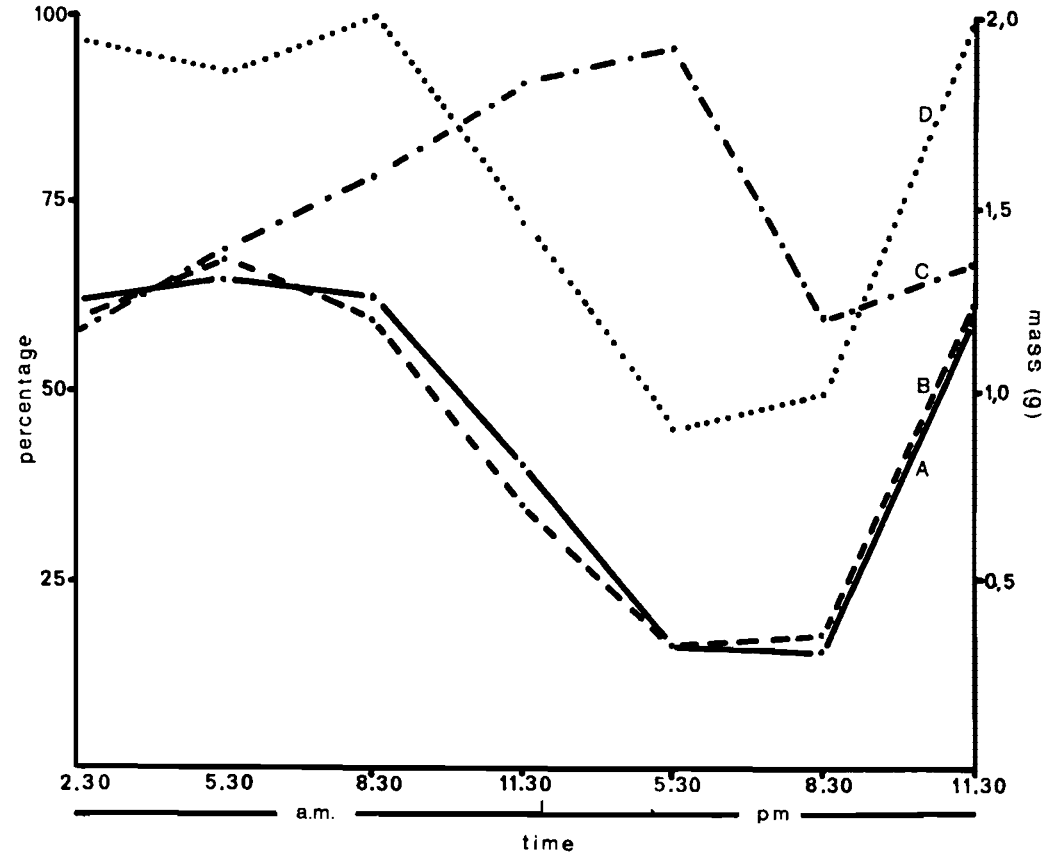


FIGURE 3

Graphs showing, A: average stomach mass, B: average stomach mass per unit fish mass (× 10⁻³), C: percentage of partially digested food, and D: average stomach fullness, of *G. macrolepidotus* at different survey times during the day-night feeding cycle.

latter was the chief food source in Loskop Dam during the present study irrespective of the chironomids. Keast & Welsh (1968) studied the day-night feeding habits of the banded killifish, *Fundulus diaphanus* in Lake Opinicon and found maximum activity in the afternoon. This differs somewhat from the bull-dog fish which seems to feed right through the day light period. The black bullhead, *Ictalurus melas*, showed two peak feeding times, a primary peak before daybreak and a secondary one after sunset (Darnell & Meierotto 1962). Here the stomach food composition was uniform throughout the 24-hour period which stands in contrast to the findings of Keast & Welsh (1968) and also to the bull-dog fish in the present study.

The daily meal of a fish is described as the quantity of food consumed over a 24-hour period. In practice this means the calculation of the amount of food added to that already present in the stomach within 24 hours. In measuring this the following points have to be considered:

1. *Digestion rate:* The food in the stomach is emptied into the intestine at a fairly constant rate, depending very much on the water temperature. No digestion rates for the bull-dog fish were calculated so use was made of applicable literature. Seaburg & Moyle (1964) and Windell (1967) give digestion rates for carnivorous species at 20°C (Table 3).

TABLE 3

DIGESTION RATES OF CARNIVOROUS FISH SPECIES

Species	*Temperature (°C)*	*50% reduction (hours)*	*Authors*
Lepomis macrochirus	22	7	Seaburg & Moyle (1964)
Lepomis macrochirus	22	6	Seaburg & Moyle (1964)
Lepomis macrochirus	18–22	6	Windell (1967)
Lepomis macrochirus (only Insecta and Crustacea)	33	4	Seaburg & Moyle (1964)
Lepomis gibbosus	22	5	Seaburg & Moyle (1964)
Pomoxis nigro-maculatus	22	6	Seaburg & Moyle (1964)

It is clear that the rate of digestion of 50% of the stomach volume or mass may vary somewhat. An average criterion of 6 hours for 50% reduction in stomach mass is taken. A 1:1 volume–mass relationship is assumed.

2. *Feeding time:* It is necessary to know whether feeding is nocturnal, diurnal or continuous. The bull-dog fish showed a primarily diurnal feeding habit with much reduced feeding at night. Three 6-hour digestion periods within 24 hours are therefore taken. Thus,

$$D = \frac{\bar{m}}{2} \times 3$$

where D = daily meal
m = average food mass
3 = number of 6-hour digestion periods

The term daily ration is the daily meal expressed as a percentage of the fish mass and is used as such by Ricker (1946), Seaburg & Moyle (1964) and Keast & Welsh (1968). This ratio is widely used in fisheries management. In the case of the bull-dog fish within the size limit of this study the daily ration is 0,7%. This value is low compared to rations of between 1 and 4% obtained by the above-mentioned authors.

It must be borne in mind that this study was undertaken in the autumn so that this ratio may not represent the maximum usage. Under intensive cultivation the carp, *Cyprinus carpio*, can utilize up to 6% of its own body-mass of food per day. In laboratory tests at 22°C *Tilapia mossambica* showed a maximum daily ration of 1,8% (Morgan 1969). Another factor contributing to the low recorded rations may be interspecific competition for food. In this respect the minnows may play a major role. These small non-economic fish species occur in vast numbers in Loskop Dam (Göldner 1969) and stand in direct competition for food with all the other carnivorous species.

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