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Dedicated to Professor Dr. H. Engel

The food and feeding habits of the Tiger-fish, *Hydrocyon vittatus* (Cast., 1861) in Lake Kariba *)

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ABSTRACT

H. vittatus is the main and most efficient predator in lake Kariba and is also present in very large numbers.

The impact of predation falls mainly on small and young fish of the families Characidae and Cichlidae of which the latter are very important economically.

Due to the particular (unstable) environmental conditions prevailing in Kariba, the young of many commercially important species, in particular *Tilapia* (the young of *Labeo* spp. stay up the rivers) are excessively exposed to predation during a critical period of their lives.

INTRODUCTION

The Tiger-fish is one of the most important and conspicuous species in the man-made lake of Kariba. Ecologically, its importance lies in the fact that it is the major fish-eating predator and virtually the only one whose impact is such that it profoundly affects the dynamics of the fish population. Economically, it is important as a food-fish and its fame as a sporting-fish, attracting anglers from all over the world, need not be emphasized.

It may seem surprising that the ecology of such a common and widespread species is still poorly known, especially as regards its breeding habits. Somewhat more is known about its feeding however, and Jackson (1961c) published a comprehensive study of its predatory impact, mainly in the Bangwelo and Middle Zambesi areas.

The research carried out over 1964-65 at the Lake Kariba Fisheries Research Institute to a large extent corroborates and reinforces Jackson's conclusions, but also shows some interesting and significant differences. Some of the reults obtained are inconclusive, others only tentative as it was not possible to collect and analyse sufficient data over the period spent at Kariba

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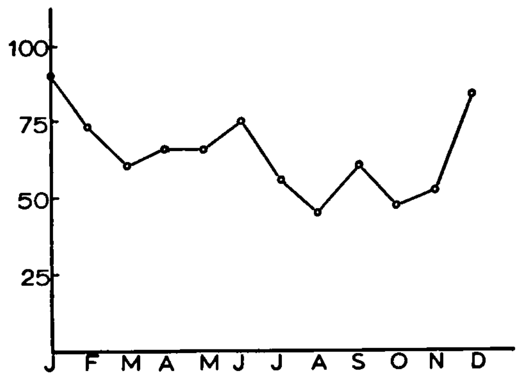

FIG. 1. Variation in percentage of *H. vittatus* with empty stomachs during the year (lake Kariba, 1964-65).

and produce entirely conclusive evidence. However, the degree to which the results match previous findings (see table VI) and the trends which appear certainly establish their significance.

MATERIALS AND METHODS

The majority of samples examined came from gill-net catches, but most juveniles of less than 15.0 cm (total length) were caught by seining, rotenone poisoning, electrical fishing or hand-netting. A total of 353 fish were studied for stomach contents as well as for other purposes. The stomachs of most larger fish were examined in the field, right after capture, but generally juvenile specimens were preserved and studied later in the laboratory.

No volumetric measurements or weights were taken of stomachs and/or prey but the numbers and total length of the prey were recorded whenever possible. Data were recorded on special Ecology sheets and on Fish Stat. Form 6 (most gill-net catches).

FOOD AND FEEDING HABITS

1. Field and aquarium observations

Young fry are found up rivers during the summer, in pools and quiet stretches, especially those less than 2 cm T.L., where they feed on both phyto- and zooplancton as well as on small bottom invertebrates to some extent. Slightly older fry also occur in small, loose shoals in the lake in sheltered bays and near rivermouths. These still feed mainly on planctonic organisms.

The change-over in diet from plancton plus other invertebrates to an almost exclusively ichthyophageous one occurs when the young Tiger-fish are between 4 and 5 cm T.L. This is a very clear-cut change with no intermediate stage of, for instance, insect-eating. Juveniles over 5 cm length usually occur in small groups of a dozen or so roaming freely everywhere along the littoral shallows or over shallow water off-shore, where submerged trees are present.

Habitually, these young Tiger-fish occur in association with the abundant shoals of *Micralestes acutidens* (Peters, 1852) and *Alestes lateralis* Boulenger, 1901 (small Characins), on which they prey. Surprisingly, though they regularly attack these fish from behind, biting at their tails, damaging them and finally eating them, the small Characins appear to tolerate young *Hydrocyon* without any signs of panic provided they are not larger than roughly twice the size of the largest individuals among them. In an aquarium experiment (see fig. 2), a 17 cm *Hydrocyon* was kept for a few months with several

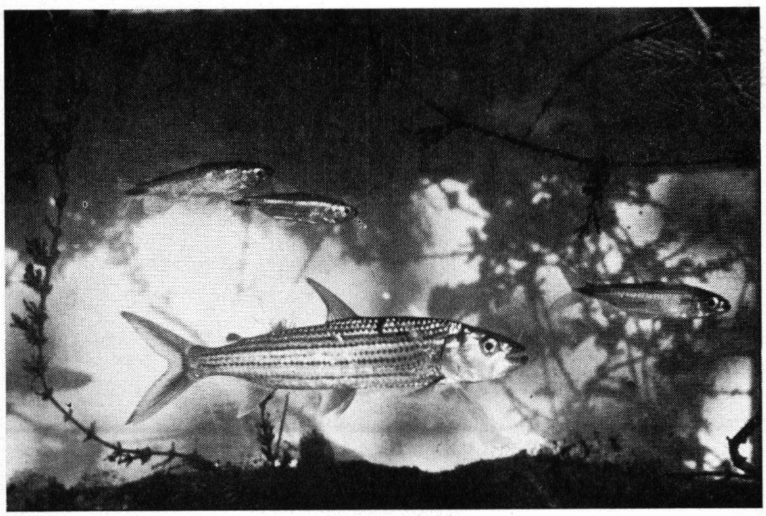

FIG. 2. *Hydrocyon vittatus* with *Alestes lateralis* in aquarium (from lake Kariba, 1965).

Alestes lateralis of 6 to 8 cm T.L. (measurements taken at end of experiment), one of which was attacked (tail damage) and eventually eaten. The Tiger-fish was fed on *Aplocheilichthys*, *Haplochromis* and *Tilapia* fry. Contrary to the *Alestes*, these fish were clearly aware of the predator's menace and extremely scared, dashing away in panic to seek shelter among weeds and/or stones.

As they grow larger, the bands of young Tiger-fish gradually seek deeper and more open waters, so that it is rare to see juveniles of more than about 15 cm associating with Characin shoals. Although Tiger-fish of all sizes may be observed in the littoral waters, especially from September to May, the larger fish tend to go much deeper and (usually big) specimens have been obtained or observed at depths of over 35 m in the lake and over 50 m in the stilling pool below the Dam wall (aqualung observations). In the colder winter season (May to September) most Kariba fish move to deeper waters and the *Hydrocyon* follow suit.

When in the littoral zone, diving and other observations showed how these very efficient predators hunt, i.e. often in small bands loosely strung out, apparently endeavouring to make the small fish hiding on the bottom break cover, then dashing at their prey to seize it. On several occasions when benthic fish were poisoned with rotenone and swam groggily to the surface, they were attacked by Tiger-fish, even large specimens being cut up by their razor-sharp teeth and eaten. *Synodontis zambesensis* Peters, 1852, in particular, were bitten through just behind their sharp spines, only the body being eaten.

In general however, the prey is swallowed whole, head-first, and fish in the stomachs rarely exceed 40% of the predator's length. However, in Kariba, larger fish bearing mutilations (e.g. tail bitten off) due probably to Tiger-fish — other predators capable of doing this e.g. crocodiles and otters are rare — are not infrequent, and on several occasions fish found in stomachs, especially of *Hydrocyon* smaller than 30 cm, exceeded 40% of predator length (up to 64% once).

These observations differ somewhat from Jackson's (l.c.) findings, but it may be that over the period covered prey was relatively scarce and the Tiger-fish less choosy, this being a time when the predator population seems to have reached its peak and the numbers of the other species were still declining strongly after the initial population explosion following the formation of the lake.

Sometimes, *Hydrocyon* were observed eating flying termites fallen into the water and once subadults were feeding on emerging mayflies in the pool below the Dam.

2. Food (see tables I and II)

The prey of *Hydrocyon* from about 5 cm upwards is almost exclusively fish; the young eat mainly zooplancton (copepods, Cladocera, rotifers) as well as some phytoplancton (*Volvox*) and various more or less benthic invertebrates

TABLE I

Frequency occurrence of prey classes in stomach contents of H. vittatus ranging 1.1 to 70.3 cm T.L.

FOOD CLASSES	Fish only	Insects only	Zoo-plancton only	Other only	Other + zoo-plancton	Zoo-plancton + phyto-plancton	Insects + other	Fish + Insects	Fish + other	Empty	Total	Percent-age total
Frequency occurrence	96	13	8	4	5	4	3	2	1	217	353	-
Percentage occurrence	27.2	3.7	2.3	1.1	1.4	1.1	0.9	0.6	0.3	61.5	100.1	-
Frequency occurrence fish	96	-	-	-	-	-	-	2	1	-	99	67.3
Frequency occurrence insects	-	13	-	-	-	-	3	2	-	-	18	12.2
Frequency occurrence zooplancton	-	-	8	-	5	4	-	-	-	-	17	(11.6)
Frequency occurrence other	-	-	-	4	5	-	3	-	1	-	13	8.8

TABLE II

Frequency occurrence of prey classes in stomach contents of H. vittatus arranged by length classes.

Total lengths (cm)	Plancton	Fish	Insects	Other	Plancton + other	Insects + other	Other combinations	Empty	Total	Percentage of total empty
1.0– 4.9	9	1	-	-	3	-	1	7	21	33.3
5.0– 9.9	3	8	1	1	1	-	1	11	26	42.3
10.0–14.9	-	7	1	-	-	1	-	10	19	52.6
15.0–19.9	-	9	1	-	-	-	-	12	22	54.5
20.0–24.9	-	19	1	1	-	1	1	46	69	66.7
25.0–29.9	-	22	3	-	-	1	-	63	89	70.8
30.0–34.9	-	12	2	1	-	-	1	32	48	66.7
35.0–39.9	-	6	2	1	-	-	-	16	25	64.0
40.0–44.9	-	7	1	-	-	-	-	8	16	50.0
45.0–49.9	-	1	-	-	-	-	-	2	3	66.7
50.0–54.9	-	2	-	-	-	-	-	5	7	71.4
55.0–59.9	-	-	1	-	-	-	-	3	4	75.0
60.0–64.9	-	1	-	-	-	-	-	1	2	50.0
65.0–69.9	-	-	-	-	-	-	-	1	1	(100.0)
70.0–74.9	-	1	-	-	-	-	-	-	-	(0)
Totals	12	96	13	4	4	3	4	217	353	-
Percentage total	3.4	27.2	3.7	1.1	1.1	0.9	1.1	61.5	100.0	–

(ostracods, harpacticoid copepods, insect nymphs, oligochaetes, etc.). Jackson (1961a) noticed a sharp increase in the numbers of insects eaten by *Hydrocyon* in the Middle Zambesi at low water, during the dry season, prior to flooding by the Dam. This is very definitely no longer the case, and hardly any seasonal changes in diet appeared over the period studied. There was only a slight increase in occurrence of food other than fish during the spring and early summer in adults.

The percentage of food other than fish is nevertheless quite high in Lake Kariba, viz., 32.6% but this figure includes juveniles which have a different diet. If these are disregarded, the percentage is 23.8 and fish will total 76.2% of the food. These figures are much higher than in Bangwelo where Jackson (table VI) found that fish comprised about 95% of the diet, but they agree closely with Dekimpe's (1964) findings for lake Moero.

The families of prey fish identified in the stomach contents (table IV a and b) compare closely with Jackson's (l.c.) observations for the Bangwelo Tiger-fish, especially when the differences in faunal composition and ecological conditions are taken into consideration.

Quantitative data

Because digestion is so rapid (Matthes, 1964), lasting only a few hours, many Tiger-fish have empty stomachs. This is especially true of fish sampled

TABLE III

Comparison of frequency of empty stomachs in gill-net samples and in samples obtained by other methods

	Number caught in gill-nets			Number caught by other methods			Percentage empty	
Length-class (cm)	Food present	Empty	Total	Food present	Empty	Total	Gill-net catches	Other catches
1.0 - 4.9	—	—	—	14	7	21	—	33.3
5.0 - 9.9	—	—	—	15	11	26	—	42.3
10.0 - 14.9	1	3	4	8	7	15	75.0	46.7
15.0 - 19.9	8	11	19	2	1	3	72.7	33.3
20.0 - 24.9	22	43	65	1	3	4	66.2	75.0
25.0 - 29.9	23	63	86	3	—	3	73.3	
30.0 - 34.9	14	32	46	2	—	2	69.6	
35.0 - 39.9	9	15	24	—	1	1	62.5	
40.0 - 44.9	8	7	15	—	1	1	46.7	66.7
45.0 - 49.9	1	1	2	—	1	1	50.0	(length-
50.0 - 54.9	2	1	3	—	4	4	33.3	classes
55.0 - 59.9	1	2	3	—	1	1	66.7	25.0 - 74.9)
60.0 - 64.9	1	—	1	—	1	1	—	
65.0 - 69.9	—	1	1	—	—	—	—	
70.0 - 74.9	—	—	—	1	—	1	—	
Total	90	179	269	46	38	84	—	—
Percentage empty	—	66.5	—	—	45.2	—		

TABLE IV a

Frequency occurrence of various fish prey in stomach contents of *H. vittatus* from Lake Kariba

prey family	number of occurrences	percentage occurrence
Characidae	9	23.7
Micralestes acutidens	7	18.4
Alestes (*A. lateralis*)	2	5.3
(Total Characidae)	(18)	(47.4)
Cichlidae	3	7.3
Haplochromis (mainly *H. darlingi*)	4	10.5
Tilapia spp.	3	7.9
T. melanopleura	2	5.3
T. mossambica	1	2.6
(Total Cichlidae)	(13)	(34.2)
Cyprinodontidae		
(*Aplocheilichthys johnstoni*)	3	7.9
Cyprinidae (*Barbus*)	2	5.3
Mormyridae	1	2.6
Mochokidae (*Synodontis*)	1	2.6
Total	38	100.0

TABLE IV b

Frequency occurrence of various fish prey in stomach contents of H. vittatus from Bangwelo (from Jackson, 1961 c).

prey family/species	percentage occurrence
Characidae	31.7
Cichlidae	41.7
Cyprinidae	19.0
Synodontis	3.7
Mormyridae	2.7
Other	1.2
Total	100.0

from gill- nets where they may have been caught long before being examined. Hence most are empty (table III), i.e. 66.5% as against 45.2% on average for fish caught by other methods. Thus about 20% of empty stomachs in gill-net samples are directly imputable to the method itself. Eversion of stomachs in the gill-nets is another factor which could be important but field observations indicate only a low incidence of everted stomachs (only considerable in deep-set gill-nets). However this does not preclude the fish vomiting its prey during its struggles to escape. In most cases where food is present in stomachs from gill-net samples it is in an advanced state of digestion and fresh material is rarely encountered.

Hardly any of the specimens examined had entirely full stomachs, the exceptions being usually plancton-eating fry. Therefore, it has not been possible to produce any quantitative data on this. The numbers of prey (fish) found rarely exceeds 1 to 3 per stomach, the maximum observed being 9 (*Tilapia* fry).

From both tables II and III it appears that juveniles up to about 10 cm T.L. seem to be able to find food more frequently than larger fish, the percentage of empty stomachs being significantly lower. The gradual decrease

TABLE V

Variation in percentage of empty stomachs in samples arranged by months (1964 - 1965)

Month	Number specimens with food in stomach	Number specimens empty	Total	Percentage empty
J	1	9	10	90.0
F	4	11	15	73.3
M	38	58	96	60.4
A	6	12	18	66.7
M	5	10	15	66.7
J	8	24	32	75.0
J	7	9	16	56.3
A	7	6	13	46.2
S	9	15	24	62.5
O	13	12	25	48.0
N	36	40	76	52.6
D	2	11	13	84.6
Total	136	217	353	61.5

of empty stomachs in the gill-net catches by length-class appears inexplicable other than by suggesting a higher metabolic rate and possibly a scarcity of prey during a critical period of their lifecycle (e.g. change in habitat) for the younger fish. The percentage of empty stomachs in the different length-classes rises till the fish attain a length of about 30 cm after which it decreases again till they reach about 45 cm. Data on larger fish are insufficient however, to decide whether the subsequent increase is significant. It may well be that between 30 and 45 cm the Tiger-fish is at its peak efficiency physiologically and at optimum size in relation to its most abundantly available prey. Kariba Tiger-fish over 60 cm long become fat and sluggish and their fins remain small in relation to body size, all factors which combine to make it harder for them to catch prey.

The monthly variations in percentages of empty stomachs (table V and fig. 1) expressing the changes in feeding activity over the year show a clear correlation with the summer breeding migrations upriver (Dec. to Febr. mainly) when the running fish don't feed; a subsequent increase of feeding towards the end of the summer after spawning (March); a decrease in feeding activity during autumn and early winter (May-June) and a high degree of activity during late winter and spring (July-Nov.) when the fish also often have a considerable amount of fat in the body cavity.

Discussion

As can be seen from tables IV and VI, the types of fish preyed upon by *H. vittatus* are mainly Cichlidae and Characidae, either of which will dominate in the diet according to availability. Thus, in Kariba during 1964-65 Characins were more commonly eaten and diving observations showed these to be very abundant, often appearing in large shoals, even in the open lake. The Cichlids on the other hand, except for abundant *Tilapia* fry and small *Haplochromis* in the shallows and in weedy bays during the summer and autumn, where the Tiger-fish can't easily get at them, were much less in evidence. Possibly the heaviest predation occurs on small Cichlids during the winter and spring seasons when the summer-born young grow larger and move into deeper water, seeking cover among the drowned trees. This cover provides less protection than aquatic plants in the shallows and these also die off in the winter when the *Salvinia* mats develop and clog up the bays, sheltered areas, etc. cutting off the sunlight. This tends to drive the littoral fish (mainly Cichlids) into deeper water where they are more susceptible to predation. It was extremely noticeable that e.g. *Tilapia mossambica* (Peters, 1852) in the 12 to 26 cm range were very rare (both in catches and during diving observations) and it is certain that the above combination of factors has to do with the decline of and the poor recruitment to the *Tilapia* population.

Among the other food eaten by *Hydrocyon* in African lakes and rivers, shrimps and insects, as well as plancton in the fry, are dominant. The percentage of food other than fish eaten appears to vary considerably in dif-

TABLE VI. Summary of data on food of *H. vittatus* in previous publications.

Source	Fish		Other		Number empty	Total number	Percentage empty	Percentage fish	Percentage other	Size-range of prey	Remarks
	Nature	Number	Nature	Number							
Fisheries Research Bulletin 1963-64	—	62 101 40	prawns, weeds, sand, mud	2 22 6	491 738 867	555 861 913	88.5 85.7 95.0	96.9 82.1 87.0	3.1 17.9 13.0	—	period October to May (1961-64), summer spawning Lufubu river, lake Tanganika.
Coke (1966)	*Tilapia* fry *Haplochromis* *Micralestes*	16 4 1	insects	11	31	63	49.5	65.6	34.4	—	23-11-66, lake Kariba, prior to spawning.
Crass (1964)	*Barbus*, *Labeo*, gobies	—	insects & other	—	—	—	—	—	—	to over 1/3 predator's length	Natal rivers.
Dekimpe (1964)	*Alestes*, *Synodontis*	—	Caridine shrimps	—	—	—	75	73	27	—	lake Moero.
Gosse (1963)	fry	—	Entomostraca insect larvae	—	—	—	—	—	—	—	juveniles Central Congo basin.
Jackson (1961)	—	972 —	*Caridina nilotica* vegetable matter insects Copepods, ostracods, other, zooplancton & insects (caddis larvae)	40 7 5	—	—	—	95.0	5.0	up to 40% predator length, usually less than 1/3	Bangwelo area Juveniles; changeover in diet at 5—6 cm, complete at 8—9 cm.
Jubb (1961)	Fish, including *Hydrocyon*	—	termites, grasshoppers (during rainy season)	—	—	—	—	—	—	—	Zambesi, Kariba, Limpopo, etc.
Matthes (1964)	Clupeids, characins, cichlids, citharinids, siluroids	—	prawns, vegetable matter (dead), sand Ephemeroptera & Odonata nymphs, shrimps	—	—	—	—	—	—	—	Central Congo basin (lake Tumba) Juveniles digestion very rapid.
Poll (1953)	*Callochromis* *Cardiopharynx*	4 1	—	—	—	—	—	—	—	—	1 spec., 48 cm T.L. lake Tanganika.
Ricardo (1939)	*Tilapia* *Alestes* *Barbus*? *Schilbe*?	4 2 1 1	—	—	39	47	83	—	—	—	lake Rukwa (September-November).
Worthington & Ricardo (1937)	*Xenotilapia* *Cyathopharynx* *Limnothrissa*	—	—	—	—	—	—	—	—	—	lake Tanganika.

ferent areas und under different conditions, as well as seasonally to a greater or lesser extent (tables I and II). It may be as low as practically nil and as high as 34.4%.

The percentage of fish with empty stomachs generally appears to average 60 to 70% and shoots up to over 80% when the fish are running upriver to breed (tables V, VI and fig. 1).

It appears thus that in general, despite the rather low number of specimens available, the results of this study tally with what little has been published previously about *H. vittatus* elsewhere. Tiger-fish in Kariba apparently have fewer empty stomachs than elsewhere and it may be that the ecological conditions — still pretty unstable — favour the annual development of large numbers of young fish which at a later stage fall an easy prey to the Tiger-fish when cover (and possibly food) becomes seasonally scarce. Jackson's (1961 c) paper is quite explicit on these relations between cover and numbers of small species, spawning migrations, etc. in the presence of *Hydrocyon.*

Recommendations

It is recommended that:

1. Fishing effort be intensified on *H. vittatus*, especially with the use of 2 to 3 inch (stretch) mesh, surface-set gill-nets, which are the most efficient and catch mainly the abundant 20 to 30 cm size range.

2. Abrupt lowering of lake level due to spilling at Kariba Dam be avoided, especially during the summer, as this destroys breeding grounds, fry and water plants. A rate of drop in waterlevel not exceeding 8 inches per week is recommended.

3. Any economical means of ridding the bays, inlets, estuaries, etc. of *Salvinia auriculata* (Kariba weed), especially during winter and spring be applied as soon as possible.

4. Further study to be made of the biology of Tiger-fish in the lake, especially in relation to further ecological changes, and of its commercial value which may be made more attractive by various processes (e.g. smoking, kippering).

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