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The food of *Bagrus docmac* (Forsk.) (Pisces: Siluriformes) and its relationship with *Haplochromis* Hilgendorf (Pisces: Cichlidae), in Lake Victoria, East Africa

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The diet of the siluriform fish *Bagrus docmac* (Forsk.) is described in relation to various localities in Lake Victoria, East Africa. Invertebrates which are the principal food of young fish, but generally of little significance in adults, are particularly poorly represented in fishes from Tanzanian waters and most important in those from the Kavirondo Gulf where the ontogenetic changes in diet differ from those found elsewhere in the Lake. *B. docmac* starts feeding piscivorously at about 10 cm standard length with the transition from a principally invertebrate to a primarily piscivorous diet occurring at 15 cm S.L. In adult *B. docmac* fish are found in over 95% of individuals with food. *Haplochromis* is the all important food type, and *Tilapia*, the most valuable commercial fish in the lake, is not preyed upon at all. Bathymetric changes with respect to the invertebrate food are noted, and it is shown that piscivorous feeding occurs mainly by day and invertebrate feeding by night. Quantitative estimates of consumption of *Haplochromis* by *B. docmac* are computed from the results of a series of 24 h fishing surveys and found to exceed published data from elsewhere. The formula for the computation of a daily ration is given as Log R=2·973 Log L−3·36089 and it is calculated that the mean annual consumption of *Haplochromis* by *B. docmac* is approximately 75% of the mean standing stock of the prey fish, as compared with a commercial catch of about 5% of the mean standing stock.

I. INTRODUCTION

The predominant interest in the biology of the siluriform fish *Bagrus docmac* (Forsk.) in Lake Victoria has centred round the inter-relationships existing between it and its major prey, the cichlid genus *Haplochromis* Hilgendorf. Graham (1929) during the first fisheries survey of the lake established that *B. docmac* was widely distributed and fed mainly piscivorously on *Haplochromis*. Corbet (1961) in a comprehensive survey of the food of all non-cichlid fishes from the northern part of the lake detailed the diet of *B. docmac* in relation to substrate and pointed out that it is the major predator indigenous to Lake Victoria, depending almost entirely on *Haplochromis* when above 15 cm total length. Elder (1960, 1962) reported preliminary investigations into the *B. docmac* breeding cycle and the relationships existing between its food intake and growth in aquaria. Chilvers (1969) estimated its growth rate from length frequency data and (1971) established trawl cod-end mesh selectivity for the species. Bergstrand & Cordone (1970) reporting on the results of a bottom trawling survey of Lake Victoria, demonstrated that *B. docmac* was the commonest and most widespread siluriform present, being well represented at all depths from 10–60 m and established

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that it comprised approximately 7% of the total fish biomass. It is the most important non-cichlid caught commercially, accounting in 1968 for 14% of the total fish landing (114 000 metric tons) taken by the traditional gill net, seine net and long line fishery. There are indications (see Tanzania 1964–1968, Uganda 1967–1968) that catches of this valuable species are declining. At the time that Corbet (1961) carried out his investigations he concluded that *B. docmac* served as the major link between man and the relatively unexploited large stocks of *Haplochromis* extant in Lake Victoria. Gee & Gilbert (1967) and Bergstrand & Cordone (1970) showed that *Haplochromis* dominated the lake fish community, comprising over 80% of the estimated fish biomass. It is not unexpected that since Corbet carried out his investigations, the genus *Haplochromis*, of which more than 120 species are known, has been subject to an increased fishing effort by traditional methods which, in 1968, produced a catch of 26 600 metric tons, 24% of the total landings. Further commercial exploitation of the genus is envisaged with the introduction of more efficient modern methods of capture (trawling) and processing (canning and the manufacture of fish meal) and it is proposed to increase the catch of *Haplochromis* by about 15 000 metric tons per annum. In addition to the increased commercial exploitation of the genus, *Haplochromis* is now subject to further predation pressure through the introduction to Lake Victoria within the past decade of *Lates niloticus* (Linné), a well known predator of African waters (Gee, 1964). As yet the stocks of this species are relatively small and localized but while it may be less specific in its feeding habits (Hamblyn, 1966) than *B. docmac*, a preliminary analysis of its food in Lakes Victoria and Kyoga (Gee, 1969*a*) indicated that at present it also feeds principally on *Haplochromis*. In view of these recent changes and with the initiation of a Food and Agricultural Organization project on Lake Victoria with the concomitant operation of a much larger and better equipped research vessel than has hitherto been available, a programme of research was instituted in January 1969 to reappraise the inter-relationships existing between *B. docmac* and *Haplochromis*. This is important from the point of view of both the continued production of the *B. docmac* fishery and as a guide to the possible level of exploitation of the *Haplochromis* stocks which may be allowed.

II. MATERIALS AND METHODS

This study is based on material collected from a bottom trawling survey of Lake Victoria carried out during the first six months of 1969 and between December 1969 and early February 1970. In all, 7137 *B. docmac* were examined from the localities shown in Fig. 1 and briefly described below.

1. *Kavirondo Gulf.* This virtually landlocked gulf was fished by day and over a 24 h period in June 1969 but much of the water along the north, east and south shores was too shallow (less than 4 m) for effective trawling. The bottom type at the eastern end of the gulf (east of Homa Point) where the water was from 4–10 m deep was generally soft mud, often flocculent, with large quantities of rotting papyrus roots and vegetable detritus derived from the large number of papyrus islands found floating in that part of the gulf. West of Homa Point the depth was generally 10–25 m (except in Homa Bay itself) and the bottom was firm mud with little or no vegetable detritus.

2. *Kenya coast north of Kavirondo Gulf.* This exposed area extends southwards from Berkeley Bay to Rusinga Island. It is perhaps the most heavily fished part of the lake and the presence of large numbers of gill nets hampered trawling operations. Berkeley Bay in the north is generally shallow (4–8 m) with a soft mud bottom containing much vegetable detritus. The depth range south of this was generally 16–26 m and the bottom was of mud, although some sand and rock was encountered round Mageta Island.

Berkeley Bay was sampled by day in January and the rest of the area in January and June 1969.

3. *Kenya coast south of Kavirondo Gulf.* This generally exposed area was sampled by day in June 1969 and extends along the coast from Rusinga Island southwards to Karungu Bay and up to nine miles west into the open water of Lake Victoria. The depth ranged from 10–66 m (mostly 25–55 m) and the bottom type was firm mud except in the sheltered Karungu and Kisingiri Bays, where the mud was soft with vegetable detritus.

4. *Musoma.* Sheltered Mara Bay off Musoma and exposed bays to the south were fished by day during December 1969. The substrate was mud of variable consistency, depending on the exact location, and the depth varied from 16–30 m.

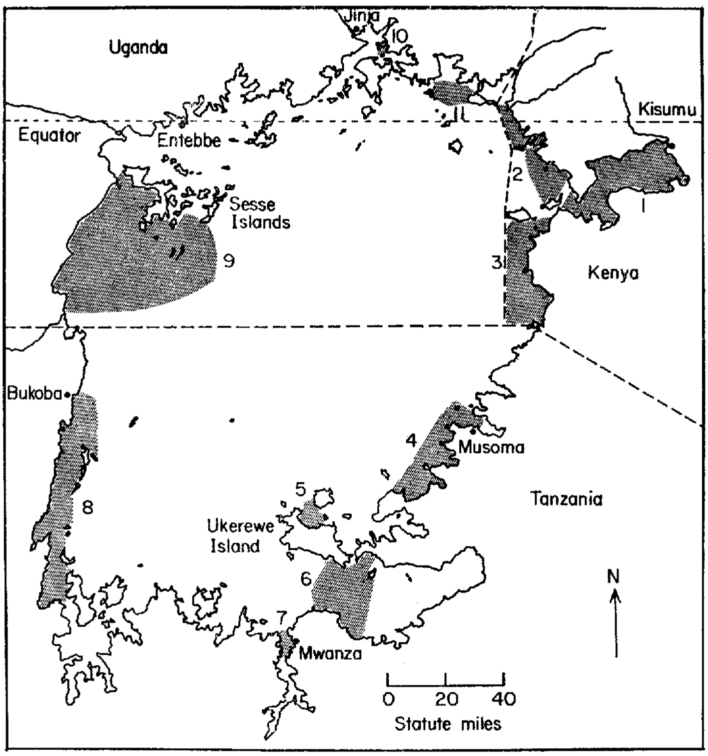

FIG. 1. A map of Lake Victoria showing the areas fished for *Bagrus docmac*. Localities numbered as in the text.

5. *Grant Bay.* This relatively sheltered area on the north shore of Ukerewe Island was fished over 24 h in December 1969 at a depth of 24–28 m. The substrate was firm mud.

6. *Speke Gulf. B. docmac* samples were taken by day and over 24 h from a moderately protected area at the western end of the gulf between Nafuba and Kunene Islands during late March and early April 1969. The depth range was principally 20–45 m, although parts of some hauls were only 8 m and the bottom type was generally of firm mud with no vegetable detritus.

7. *Mwanza Gulf.* A sheltered area at the north end of the gulf, opposite Mwanza town was sampled in March 1969, all trawling here being carried out at night. The depth range was 4–16 m and the bottom type varied from soft mud, sometimes with considerable quantities of vegetable matter, on the shallower west side of the gulf to firm mud in the centre and east sides.

8. *Bukoba.* This exposed to sheltered area extends northwards from Emin Pasha Gulf along the Ruwondo, Igusi and Bumbireh Channels to Bukoba, and eastwards from the coast for up to 13 km. The depth is approximately 10–43 m and the bottom type is soft flocculent mud in the Ruwondo Channel (10–23 m) and in part of the Igusi Channel (20–28 m) changing to firm mud in the Bumbireh Channel grading to clay off Bukoba (21–43 m). The whole area was sampled by day in May 1969 with an additional haul made off Bukoba in January 1970.

9. *Sesse Islands.* A small number of samples were taken by day in the Williams Bay area, immediately west of Buninga Island in May 1969. During January and February 1970, Kagegi Gulf, north of the Kagera River and the deep water east of the Sesse Islands was extensively fished by day and during 24 h over the depth range 5–52 m. The substrate varied from gravel close inshore to firm mud in the deepest area.

10. *Ekunu Bay.* A small, sheltered, shallow bay just north of Buvuma Island. Here the depth range is 4–10 m and the bottom is very soft, flocculent mud with large quantities of vegetable detritus and occasional quantities of man made refuse. The bay was principally sampled for *B. docmac* in May 1969 over 24 h but occasional specimens caught here throughout the six month period January to June 1969 were also examined.

11. *Dagusi Island.* This moderately exposed region extends across the mouth of Macdonald Bay between Dagusi and Sigulu Island. The depth range is approximately 10–25 m and the bottom of firm mud with some rock. It was sampled over 24 h in January 1969 and by day in June 1969.

Data on catch rates and general distribution of *B. docmac* will be given elsewhere but briefly it may be stated that catch rates varied considerably between and within localities and demonstrated an approximately 2 : 1 ratio between day and night hauls. Total catches or subsamples (1 : 3 or 1 : 5), using tables of random numbers (Fisher & Yates, 1949) were examined at sea as soon as possible after capture. All fish in the sample were measured, sexed and weighed when lake conditions allowed. Standard length, from the tip of the snout to the junction of upper and lower series of hypural bones (Chilvers, 1970) was used throughout unless otherwise stated. Fish up to 20 cm standard length were measured to the nearest 0·1 cm below and thereafter to the nearest 0·5 cm below. The well defined cardiac limb of the stomach was slit open and the stomach contents expressed into a shallow, white container; the mucosa was scraped clean and any additional material so collected added to the container in which the contents were washed and sorted by eye. In view of the adverse conditions under which the material was examined, on deck and with limited time available, usually only the occurrence of a given food item was noted although the numbers of recognizable fish and of the larger immature insect stages were also recorded. Prey length measurements (again standard length) were taken only on fish prey which were in an early stage of digestion. The raw data were later tabulated under both major group headings, e.g. Crustacea, Insecta, Pisces and also under more specific taxa, e.g. *Caridina*, Chironomidae, *Haplochromis*, arranged in 10 cm predator length classes for each haul, summed for each locality and the number of occurrences of each item expressed as a percentage of the number of fish containing food. Attention should be drawn to the unknown degree of force feeding which was suspected to have occurred in certain trawl hauls of up to 2 h duration. This phenomenon is more serious with respect to the quantitative and not the qualitative aspects of the diet and is discussed in more detail elsewhere. The principal prey item likely to be affected is fish but the results obtained here are in reasonable agreement with those of Corbet (1961) who used gill nets as his method of capture and whose results therefore would be adversely affected by such factors as partial regurgitation and continued digestion after capture but before examination. No attempt was made to differentiate between those items taken directly by the predator and those which may have been derived indirectly from the prey. This would principally affect insect food types found in larger *B. docmac* (over 20 cm) and as the occurrence of insects was extremely low compared with other food types in these larger predators the effects of including such possible items of prey diet were obviously negligible.

III. THE FOOD OF *BAGRUS DOCMAC*

A. TYPES OF FOOD IN RELATION TO LOCALITY

The most recent work on the food of *B. docmac* is that of Corbet (1961) who examined 1389 specimens from the north of Lake Victoria. Prior to this, Graham (1929) examined 266 *B. docmac* from Lake Victoria and Worthington (1929) examined a number of specimens from Lakes Kyoga and Albert. In all cases they concluded that the adult fish are principally piscivorous but that invertebrates, particularly insects and/or *Caridina*, contribute to the diet to a certain extent. Corbet (1961) analyzed the food of *B. docmac* in relation to the habitats in which they were caught (i.e. over a hard, mixed or soft bottom) and found little correlation between the two except that insects were taken more frequently over a hard bottom and of these Anisoptera nymphs were the most important. *Caridina* and *Potamon*, were of some importance but showed no consistent relationship with habitat. In the present study *B. docmac* from each locality sampled have been treated separately. The bottom types of all localities, except the shallow inshore area of Kagegi Gulf would be included, under 'soft', in Corbet's classification, but in fact these varied from clay to very soft flocculent mud. As shown earlier, there is also considerable variation in depth and degree of exposure between localities and there are indications that these factors also affect the relative importance (based on occurrence) of the invertebrate elements in the diet. The summarized data from each locality are shown in Table I arranged in geographical sequence working clockwise round the lake from the north-east shore. The only exception is that the Kavirondo Gulf data are tabulated first since they differ somewhat from the other data, notably in the much higher occurrence of *Caridina* and Gastropoda. The overall importance of any item is expressed as a total percentage occurrence in all feeding fish and as the mean of the locality percentage occurrences, thus avoiding undue bias in favour of those localities from which large samples were examined by giving equal weight to each locality. Neither method gives a true indication of the relative importance of each item since the localities vary in area and the numbers of specimens examined were dependent not upon the area of the locality but upon the trawling effort and the density of the *B. docmac* found, for which no adjustments have been made. However, it may be seen that the two totals give good agreement. The arrangement of Table I groups the localities by country. *B. docmac* from Tanzanian waters had very few invertebrate species represented in their diet and in the Mwanza area the invertebrate quantitative contribution is exceptionally poor. *B. docmac* from the most northerly locality, Ekunu Bay, exhibited similar low numbers of invertebrates in stomach contents. Both of these localities were shallow, well protected bays and few *B. docmac* below 20 cm were taken from either location. This could indicate that the degree of protection may be a factor limiting the distribution of smaller *B. docmac* and may be the over-riding factor governing the importance of invertebrates in the diet of larger fish. The converse of this may also apply as the highest percentage occurrences of fish as an item of diet were found in these localities. Table I shows that the highest incidence of invertebrates was in *B. docmac* from Kavirondo Gulf where the occurrence of the prawn *Caridina nilotica* (60·0%) exceeded that of all the other invertebrate forms combined (32·5%). Graham (1929) was of the opinion that *Caridina* was probably of importance in the food of *B. docmac*, particularly those found in deep water. As the majority of his samples apparently came from Kavirondo Gulf his observations are in agreement with the present results and it may be seen from Fig. 2 that the prawn was an important element in the diet of all sizes of *B. docmac* from this locality. Around Dagusi, *Caridina* was also the predominant invertebrate taken but elsewhere it was of only minor importance, although in Speke Gulf its incidence was lower than that of any other invertebrate item. These three localities in which *Caridina* is the dominant invertebrate food type are all similar in that they are large inshore gulfs or bodies of water with a moderate degree of shelter, the bottom is of firm mud and the depth of water intermediate, 12–25 m. The variations in the incidence of *Caridina* in the food of *B. docmac* would appear therefore to be a reflection of their distribution with depth and bottom type but it may be concluded that when they are available they are actively taken and form an important supplement to the fish diet, even of larger *B. docmac*.

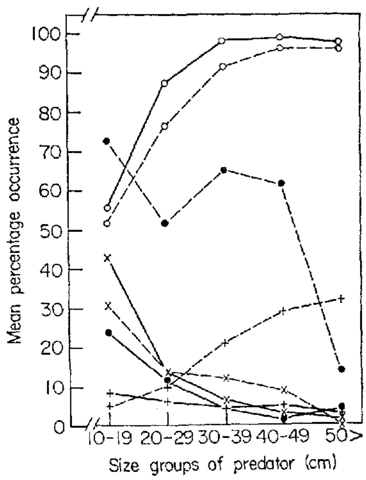

FIG. 2. The ontogenetic changes in the major dietary items of *B. docmac* from the Kavirondo Gulf (– – – – –) and elsewhere (———) in Lake Victoria. ●, Crustacea; ×, Insecta; +, Mollusca; ○, Pisces.

Along the eastern and western shores (North and South Kenya, Musoma, Bukoba, Sesse Islands and in Grant Bay) immature insects show the highest occurrence amongst the invertebrate dietary elements, characterized mainly by *Chaoborus* or the chironomids, the former predominating only in the exposed eastern localities, South Kenya and Musoma, and the latter elsewhere. This differs from Corbet's (1961) finding that anisopteran nymphs were the most important invertebrate food but the discrepancy may be due to the different bottom types over which the respective samples were taken. The small size and low numbers of *Chaoborus* or chironomids usually encountered in the *B. docmac* stomachs, indicate that except in the very small fish these items can comprise only a minute fraction of the total food volume. Mollusca were of significance in the diet only in the shallower areas of Musoma, Grant Bay, Sesse Islands and the Kavirondo Gulf. The gastropod *Melanoides tuberculata* was the commonest form which could be identified but an ancylid, *Ferrissia* sp. was also frequently found, occasionally as many as ten being present in one stomach. Lamellibranchs, mainly *Sphaerium* sp., were rare as stomach contents except in fishes from the Kavirondo Gulf and Musoma but even here their percentage occurrences were much lower than for gastropods. Additional food items found in the present survey and not mentioned by Corbet (1961) are the annelids and the fish louse *Argulus* sp. The absence of these forms from Corbet's data could be due to the fact that his material was taken mainly from gill nets which allow continued digestion to occur after capture but before examination, and annelids, lacking a hard exoskeleton are rapidly digested. They never occurred in more than 2% of the fish examined from any locality and were found only in those exposed localities possessing some sheltered marginal swamp. The presence of *Argulus* sp. in the trawl-caught fish is possibly an artefact produced by the close proximity of parasitized fish in the cod-end, since many of the specimens found in the stomach were alive. Neither item was of great importance in the diet of *B. docmac* as shown by the total percentages.

The results given in Table I confirm past observations inasmuch as they show that in all localities sampled, fish always form the major part of the food both in the number of occurrences (usually 78–99%) and in the relative volumes of food consumed (based on observation). Of the identifiable fish found in the stomachs, cichlids of the genus *Haplochromis* (which includes associated monotypic genera) were found most frequently, in 63·1% of all fish containing food (60·3% mean occurrence). There was a large number of *Haplochromis* species represented in the stomach contents but most appeared to belong to the 'generalized bottom feeding' and 'insectivorous' trophic groups of Greenwood (1964). The other cichlid genus, *Tilapia*, which forms the basis of the commercial fisheries on Lake Victoria, was almost absent from the stomach of *B. docmac*. Out of 5202 fish containing food, *Tilapia* were recorded from the stomachs of only three individuals, two caught in the western Kavirondo Gulf and one in Kagegi Gulf. This absence of *Tilapia* cannot be explained on grounds of total unavailability. In some areas from which large samples of *B. docmac* were examined (notably Kavirondo Gulf, Mwanza Gulf and the south end of the Bukoba region) trawl catches indicated the presence of considerable numbers of *Tilapia* of an acceptable prey size (i.e. within the prey size range) at least for the larger predators. Unidentified fish, usually fish remains in an advanced stage of digestion, occurred overall in 30·3% of the *B. docmac* with food. In view of the fact that cichlids were identified in 67% of the stomachs and non-cichlids in only 7·5% of all stomachs, it is reasonable to assume that the majority of the unidentified remains were in fact cichlid, and so *Haplochromis*. Thus the figures for the percentage occurrence of *Haplochromis* should in fact be much higher than those shown in Table I (i.e. probably in the region of 90% occurrence). The *Cyprinidae* are the only non-cichlid fish inhabitating Lake Victoria which appear to be of any importance in the diet of *B. docmac*. The two genera represented are *Barbus* (referrable to *B. radiatus* and *B. paludinosus*) which were most common from Grant Bay but absent from North Kenya, Musoma and Ekunu Bay, and *Engraulicypris argenteus*, present in stomachs from all localities except Musoma and Grant Bay (almost contiguous areas both sampled in December 1969). *Engraulicypris argenteus* features most frequently in the shallow, sheltered localities such as Ekunu Bay and in the exposed, open lake localities like the Kenya coast. Little is known of the biology of this species but it is thought to be a pelagic shoaling fish which probably breeds in shallow water and then gradually moves out into deeper water. It is not certain whether their presence in the stomach of *B. docmac* indicates that the predator has been feeding in mid-water or whether *E. argenteus* is only taken when it is found near the bottom. The low figures for percentage occurrence and the small numbers encountered (very rarely more than one or two specimens found in one stomach) would indicate that they were only taken occasionally and these facts are not indicative of mid-water shoals. The other non-cichlids were very rare as stomach contents and except for *Clarias mossambicus* and one of the six *Bagrus docmac* prey specimens, were all small. Although the predators which contained these fish were actually caught over a mud bottom it was usually in the vicinity of a rocky coastline, tending to endorse Corbet's (1961) thesis that the young of non-cichlids in the lake tend to adopt the same habitats as in the rivers. Only seven *C. mossambicus* were encountered in the stomachs examined and three of these came from very large *B. docmac* (80–90 cm) and were themselves relatively large (the two *Clarias* measured were 38 cm from a 82 cm *B. docmac* and 44 cm from an 88 cm *B. docmac*). The small clariids found belonged to the genus *Xenoclarias*, a small bottom living form which, unlike *Clarias*, practices only aquatic respiration. This genus occurred as stomach contents in the western end of the Kavirondo Gulf, where they were relatively common, and also in the Dagusi area and off the Sesse Islands. The group ' unidentified and other material ' consisted principally of detritus, occasional plant fragments and ' cichlid eggs '. These are regarded as accidental stomach contents and as such have not been considered further.

B. TYPES OF FOOD IN RELATION TO DEPTH

Bergstrand & Cordone (1970) reported that the yields of *B. docmac* were fairly uniform at depths from 10–59 m with an apparent concentration in 10–29 m. The majority of the samples examined in the course of the present work came from this latter range. However in January 1970 at the Sesse Islands, sufficient specimens were caught over the whole depth range to make correlations between depth and food types possible. It was found that with increasing depth the proportion of small *B. docmac* in the catches increased considerably and to avoid undue bias through such size segregation only data from *B. docmac* above 20 cm length are presented in Table II. The mean lengths of the samples from each depth zone decrease with increase in depth. Fishing over the same transect for 24 h was carried out in the 30–39 m depth range and these data are tabulated for day and night samples to show diel variations in diet. All other samples were caught by day with the exception of material from one set made in the 5–9 m zone just after sunset. The main points to be noted from Table II are the decrease in the proportion of fish containing food with increasing depth from the 10–19 m zone; the high incidence of insects in the 5–9 m zone, particularly of the anisopteran nymphs, which may be related to the shallowness of the water or to the hard nature of the bottom; the decrease in the importance of insects and molluscs to the 20–29 m zone followed by an increase to the 40–49 m zone; the absence of invertebrates in the deepest water despite the fact that *B. docmac* from this depth zone had the smallest mean size. Considering the day and night samples from the 30–39 m zone, it is apparent that invertebrates are more commonly taken at night, whilst fish are preyed on by day, although the proportion of *B. docmac* containing food remains constant. There is a striking reduction in the incidence of *Haplochromis* between the day and night samples with a reverse trend for the unidentified (well digested) fish which would be expected if *B. docmac* feeds piscivorously mainly by day. The increasing importance of *Bagrus* as an item of food at depths beyond 30–39 m should be noted and may be related to the higher proportion of small individuals found with increase in depth. The much lower percentage occurrence of fish as an item of diet in the 40–49 m depth zone is also of interest since Bergstrand & Cordone (1970, Table E7) recorded a slight low in the catch/hour of *B. docmac* at this depth in their grouped lakewide data and there may well be a correlation between these two facts.

Table I. The percentage occurrence of food items in *B.*

Food item	Kenya: Kavirondo Gulf	Kenya: North Kenya	Kenya: South Kenya	Ta[...]: Musoma	Ta[...]: Grant Bay
	1406	198	292	150	423
	88·0	77·3	67·8	62·0	64·5
				Occurrence of	
Annelida	0·4	0·7	—	1·1	—
Oligochaeta	0·4	0·7	—	—	—
Hirudinea	—	—	—	1·1	—
Crustacea	61·4	3·9	5·6	2·2	11·4
Ostracoda	—	—	—	—	—
Branchiura *Argulus*	2·2	0·6	1·0	—	2·6
Decapoda *Caridina*	60·0	3·3	4·6	2·2	9·2
Potamon	—	—	—	—	—
Insecta	12·4	20·3	24·2	29·0	24·5
Terrestrial	0·4	0·7	0·5	—	—
Hemiptera	—	—	—	—	—
Odonata Anisoptera	2·7	1·3	8·1	—	—
Ephemeroptera *Povilla*	1·4	—	2·5	—	—
Caeniidae	—	—	0·5	—	—
Trichoptera	0·2	—	—	—	—
Diptera	0·9	0·7	—	—	—
Culicidae *Chaoborus*	+	9·8	11·6	21·5	7·0
Chironomidae	7·9	13·7	5·6	8·6	20·9
Mollusca	19·7	0·7	3·0	9·7	8·4
Gastropoda	16·3	0·7	3·0	6·5	7·3
Lamellibranchia	6·5	0·7	—	4·3	1·1
Pisces	87·1	87·6	88·4	86·0	83·2
Cichlidae *Haplochromis*	74·3	41·2	59·0	69·9	68·5
Tilapia	0·2	—	—	—	—
Unidentified	0·5	14·4	1·0	2·2	—
Cyprinidae *Barbus*	0·7	—	0·5	—	8·4
Engraulicypris	3·9	12·4	7·1	—	—
Unidentified	—	—	—	—	—
Siluriformes *Clarias*	0·2	—	—	—	0·7
Xenoclarias	1·9	—	—	—	—
Bagrus	+	—	—	—	—
Schilbe	0·3	0·7	—	—	—
Synodontis	+	—	—	2·2	0·4
Unidentified	—	—	—	—	1·5
Opisthomi *Mastacembelus*	+	—	0·5	—	—
Unidentified fish remains	32·9	28·1	33·3	31·2	17·2
Unidentified and other material	0·7	3·3	1·5	3·2	2·2

The symbol + represents less than 0·1 % occurrence.

docmac from various localities in Lake Victoria

anzania			Uganda			Total	
Speke Gulf	Mwanza Gulf	Bukoba	Sesse Islands	Ekunu Bay	Dagusi	Occ.	Mean
Number in sample							
846	250	634	2100	169	669	7137	
% with food							
58·2	77·2	70·2	70·6	68·0	77·6	72·9	71·0
food items in fish containing food (%)							
—	—	0·7	2·0	—	0·2	0·8	0·5
—	—	0·7	1·9	—	0·2	0·7	0·4
—	—	—	+	—	—	+	0·1
6·5	—	5·8	15·6	—	31·6	24·3	13·1
—	—	—	2·3	—	—	0·7	0·2
—	—	1·6	3·0	—	0·8	1·8	1·1
6·5	—	4·3	10·5	—	30·8	21·9	11·9
—	—	—	0·2	—	—	+	+
4·0	0·5	13·2	21·1	1·7	13·3	15·2	14·9
0·4	—	1·6	0·1	—	—	0·3	0·3
—	—	—	0·3	—	—	+	+
—	—	—	1·3	—	0·6	1·4	1·3
—	—	0·7	1·8	—	—	1·0	0·6
—	—	—	—	—	—	+	+
—	—	—	2·2	—	0·2	0·7	0·2
—	—	—	—	—	—	0·2	0·1
3·2	0·5	4·5	1·8	—	5·8	3·3	6·0
0·4	—	11·0	17·7	1·7	9·5	10·6	8·8
2·0	4·7	2·9	7·8	1·7	3·7	8·7	5·8
2·0	4·2	2·5	7·4	1·7	2·9	7·5	5·2
—	0·5	0·4	0·9	—	0·8	2·1	1·4
92·0	99·0	90·8	81·0	96·5	78·5	85·7	88·2
50·4	65·3	61·3	68·8	68·7	36·2	63·1	60·3
—	—	—	+	—	—	+	+
4·9	23·8	7·9	2·0	1·7	6·0	3·8	5·9
1·0	2·6	0·9	1·1	—	0·4	1·3	1·4
1·6	6·2	3·8	1·4	17·4	1·7	3·2	5·0
—	—	—	0·3	—	—	+	+
—	1·0	—	—	—	—	0·1	0·2
—	—	—	0·1	—	0·4	0·6	0·2
—	—	—	0·3	—	0·2	0·1	+
—	0·5	—	—	—	—	0·1	0·1
—	—	—	+	—	—	0·1	0·2
—	—	—	—	—	—	+	0·1
—	1·0	—	0·3	—	—	0·2	0·2
41·6	37·3	28·8	20·0	43·5	45·1	30·3	32·6
0·6	2·6	4·0	2·7	—	4·1	2·1	2·3

Table II. The percentage occurrence of food items in *B. docmac* above Sesse Islands in January

				]
	5–9	10–19	20–29	
				Da
	Day/Night	Day	Day	
				N
Food item	96	152	171	
				Mean]
	36·91	40·64	37·26	
	66·7	82·9	75·4	
			Occurrence of food	
Annelida	—	—	—	
Oligochaeta	—	—	—	
Crustacea	4·7	4·0	7·0	
Ostracoda	—	—	—	
Branchiura *Argulus*	3·1	3·2	7·0	
Decapoda *Caridina*	—	0·8	—	
Potamon	1·6	—	—	
Insecta	21·9	4·0	3·1	
Terrestrial	1·6	—	—	
Odonata Anisoptera	15·6	1·6	—	
Ephemeroptera *Povilla*	—	—	—	
Trichoptera	—	—	—	
Culicidae *Chaoborus*	1·6	—	—	
Chironomidae	6·3	2·4	3·1	
Mollusca	15·6	13·5	3·9	
Gastropoda	12·5	11·9	3·9	
Lamellibranchia	4·7	4·8	—	
Pisces	90·6	97·6	96·1	
Cichlidae *Haplochromis*	73·4	84·9	73·6	
Tilapia	1·6	—	—	
Unidentified	—	0·8	1·6	
Cyprinidae *Barbus*	—	0·8	—	
Engraulicypris	3·1	0·8	—	
Unidentified	—	—	—	
Siluriformes *Xenoclarias*	—	—	0·8	
Bagrus	—	—	—	
Opisthomi *Mastacembelus*	—	1·6	0·8	
Unidentified fish remains	37·5	31·7	32·6	
Unidentified and other material	25·0	1·6	0·8	

20 cm length from different depth zones around the
1970

epth zone (m)			
30–39		40–49	> 50
y or night sample			
Day	Night	Day	Day
umber in sample			
269	129	48	31
ength of sample (cm)			
33·95	34·78	32·40	30·80
% with food			
74·3	74·4	56·3	35·5
items in fish containing food (%)			
0·5	4·2	—	—
0·5	4·1	—	—
2·5	8·3	40·7	—
0·5	—	—	—
1·5	5·2	7·4	—
—	3·1	33·3	—
0·5	—	—	—
4·5	8·3	7·4	—
—	—	—	—
—	—	—	—
—	2·1	—	—
—	1·0	7·4	—
—	—	—	—
4·5	6·2	—	—
6·0	8·3	11·1	—
6·0	8·3	3·7	—
—	—	7·4	—
98·5	95·8	77·8	100·0
95·5	88·5	51·9	81·8
—	—	—	—
1·0	—	—	—
—	—	3·7	—
—	—	—	—
0·5	—	—	—
—	—	—	—
0·5	—	3·7	9·1
—	—	3·7	—
16·5	24·0	33·3	9·1
0·5	—	3·7	—

C. ONTOGENETIC CHANGES IN FOOD TYPES

The occurrence of the food items was analyzed in relation to five arbitrarily selected size groups (see Figs 2 and 3) of *B. docmac* for each locality sampled. As the general trends for all taxa were similar from each locality with the exception of Kavirondo Gulf, the *mean* percentage occurrence of the major groups from the Kavirondo Gulf and from the other localities *in which they occurred* has been plotted separately in Fig. 2.

There is little similarity between the trends for Crustacea and Mollusca from the two areas. In Kavirondo Gulf the Crustacea (all *Caridina*, Table I) are of primary importance in the smallest group and maintain a high percentage occurrence fluctuating around 60% in *B. docmac* of all sizes up to 50 cm, beyond which they decline

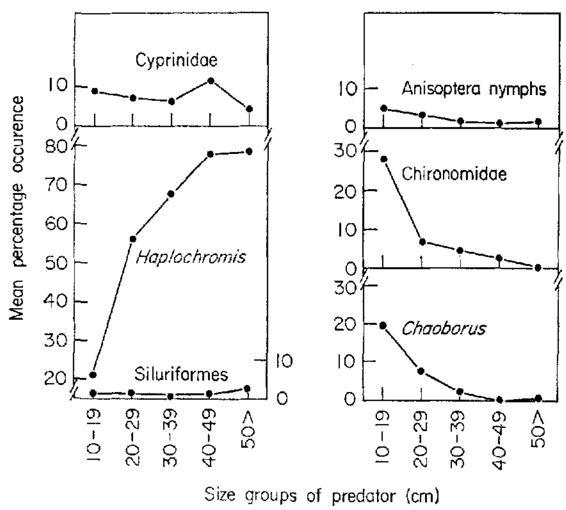

FIG. 3. The mean percentage occurrence of individual items in relation to predator size.

steeply to below the level for Mollusca. The Mollusca exhibit a reverse trend from the other invertebrate groups, increasing in importance with increase in predator size. The figure demonstrates that in Kavirondo Gulf the invertebrate elements of the diet are more important, particularly for the larger *B. docmac*, than they are from elsewhere in the lake. This is corroborated by the somewhat lesser importance of fish as an item of diet in Kavirondo Gulf compared with the other areas although the trends for fish as a dietary item are similar in all areas. In the lake, fish are of primary importance in all size groups shown and reach nearly 100% mean occurrence in individuals >30 cm long. The Crustacea and Insecta exhibit progressively declining importance with increase in predator size similar to that observed by Corbet (1961) whilst the Mollusca form a steady low level item of diet irrespective of size of *B. docmac*. The dominant invertebrate element for all sizes of lake fish is provided by the Insecta which are further analyzed together with the fish component in Fig. 3 to demonstrate that within the Insecta, the chironomids are the predominant group for all except the very largest fish, in which Anisoptera nymphs dominate. It should be noted that *Chaoborus* are taken by fish only below 40 cm.

The general trend for *Haplochromis* as prey shown in Fig. 3 differs somewhat from that for fish in Fig. 2 insofar as the slope to the asymptote at a predator size of 40–49 cm is much steeper. This is due to the higher incidence of unidentified cichlid fry in the smaller *B. docmac*, the majority of which were probably *Haplochromis*, as were the unidentified fish remains (see p. 489). Corbet (1961) in his analysis of food types and predator size showed a gradual decrease in the percentage occurrence of non-cichlids with increase in size of predator. In Fig. 3, the two main non-cichlid prey groups, the Cyprinidae and the Siluriformes, are plotted separately. The former show a general decrease in occurrence with size, except for a pronounced peak in the penultimate size group whereas the Siluriformes exhibit steady low level occurrence rising slightly in the largest group. Considering the general size differences between the prey species in these two groups (maximum length of *Engraulicypris* being 8 cm, Greenwood, 1966), these are expected variations and it is surprising that the Cyprinidae are so readily taken by the fish in the 40–49 cm group.

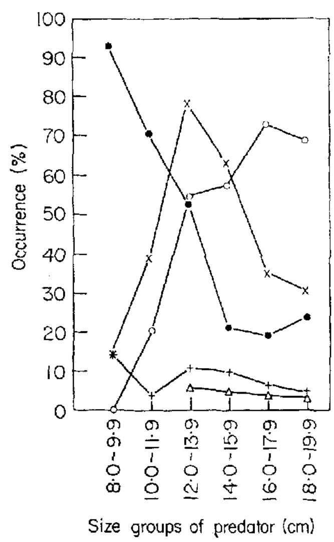

FIG. 4. Ontogenetic changes in dietary items amongst the smallest *B. docmac* examined. ●, Crustacea; ×, Insecta; +, Mollusca; △, Annelida; ○, Pisces.

Figure 2 shows that even in the smallest size group of *B. docmac* (10–19 cm), fish are already the dominant food element in the lake predators. Further analysis of the smallest size group revealed that the transition from a principally insectivorous to a piscivorous diet occurs at a length of about 15 cm as shown in Fig. 4 (which includes data from 14 feeding *B. docmac* below 10 cm length and not included in Figs 2 and 3). None of these small *B. docmac* contained fish whereas four out of 60 individuals measuring between 10·0 and 10·9 cm, contained *Haplochromis*. It would appear therefore, that in the lake *B. docmac* starts to feed piscivorously when they reach a length of 10 cm which is in fair agreement with Corbet's (1961, addendum) findings following examination of a sample of very small fish from Entebbe. In Kavirondo Gulf the smallest *B. docmac* found to contain fish, unidentifiable cichlids, measured 12·0 cm. Figure 4 also shows a further transition from a diet consisting largely of Crustacea, *Caridina* and Ostracoda, to a insectivorous diet, mainly chironomid larvae, at approximately 12 cm.

IV. PREDATOR/PREY RELATIONSHIPS

A. SIZE RELATIONSHIPS

Complete maceration of fish prey before ingestion is found (in Lake Victoria) only in the cichlid predators of the genus *Haplochromis* which possess well developed pharyngeal teeth to facilitate this process (see Greenwood, 1962). Some non-cichlid species, which include fish in their diet, such as *Alestes jacksoni* and *Schilbe mystus*, appear to partly macerate the prey with the jaw teeth but the principal African non-cichlid predators, notably *Hydrocynus vittatus* (Cast.) (Jackson, 1961), *Lates niloticus* (Linné) (Hamblyn, 1966) and *Bagrus docmac* all swallow their prey whole regardless of the differences in dental morphology between these species. In these

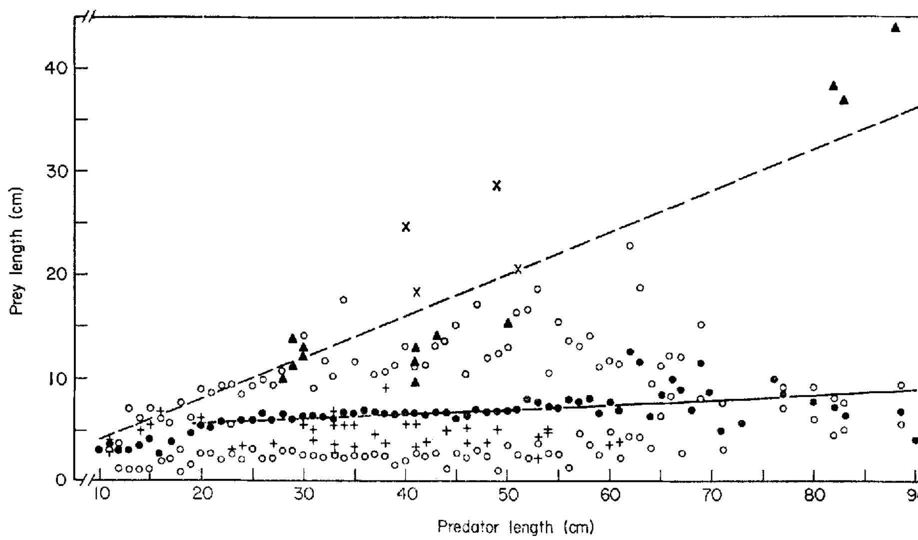

FIG. 5. Graph of the relationships between predator and prey lengths. 40% of predator length (- - - - -) and the regression of mean *Haplochromis* on *B. docmac* length (———) ($Y=4{\cdot}87+0{\cdot}043X$) are also shown. ●, *Haplochromis*—mean length; ○, *Haplochromis*—maximum or minimum length; +, Cyprinidae; ▲, Siluriformes; ×, *Mastacembalus*.

predators the gape, the volume of the buccal cavity and of a fully distended stomach will all help to determine the size, in terms of volume, of the prey which can be ingested. The size of prey is usually expressed in terms of length and, as the volume/length relationship varies between different prey species, the maximum length of prey which can be swallowed whole by a predator will vary accordingly. It will also, of course, be controlled by the maximum length attained by the prey species.

The actual lengths of those measurable individuals of prey species, other than *Haplochromis*, are shown plotted against predator length in Fig. 5. For *Haplochromis*, only the maximum, mean and minimum lengths present in each 1 cm length category of *B. docmac* are plotted in view of the large number (3192) of specimens measured. *Haplochromis*, in general, have a relatively high volume/length relationship and over 99% of the specimens measured were found to be below 40% of the predator length. The 40% limit is shown in Fig. 5 as a broken line and it is apparent that the smaller predators (below 23 cm) more commonly take relatively longer *Haplochromis* than the larger *B. docmac*. These larger predators are still capable of ingesting prey of a length greater than 40% of their own length, as shown by the distribution of the points for the siluriform and *Mastacembelus* prey. The latter are eel-like in form and in consequence may be coiled within the stomach. In the larger *B. docmac* prey specimens were not always wholly contained in the predator's stomach, their caudal peduncles often projecting forwards into the branchial region or the buccal cavity. Such occurrences were rare in smaller *B. docmac*. It may be deduced that the maximum volume to which the stomach can be distended is relatively greater in small *B. docmac*. This may be due to greater elasticity of the stomach wall and/or the relatively larger coelomic space available for stomach expansion as a result of the absence of mature gonads and large quantities of fat. The maximum absolute size of *Haplochromis* eaten shows a fairly linear increase up to 22·7 cm with increase in predator size up to 62 cm but beyond this point it apparently decreases with increasing predator length. This may be correlated with the more sluggish behaviour pattern of larger fish, as observed in aquaria, and it is of interest that the largest *B. docmac* feed on a size range of *Haplochromis* less than that of 20 cm specimens. Figure 5 demonstrates that the minimum absolute size of *Haplochromis* hardly changes over the predator size range 20–70 cm. The mean size of the *Haplochromis* prey approximately doubles between 10 and 20 cm predator length but thereafter increases only slightly in accordance with the least squares regression $Y=4{\cdot}87+0{\cdot}043X$ where Y and X are the prey and predator lengths respectively. Below 20 cm the regression may well be curvilinear but over the linear portion between 20 and 60 cm predator length (the major bulk of the specimens examined) the mean length of the *Haplochromis* prey only changes from a calculated 5·3–7·5 cm. This is well below the modal values established by Gee (1969*b*) for the total length retention curves of 5·1 cm mesh codends from two areas in Lake Victoria, but approximating to the mean length calculated for 3·81 cm codends in Kavirondo Gulf (Cordone & Kudhongania, 1970). To define the relationship of *Haplochromis* prey to predator length more precisely, the data from *B. docmac* over 20 cm from each locality were subject to bivariate analysis, grouping *Haplochromis* lengths by 0·5 cm and *B. docmac* by 5·0 cm classes. The results of these analyses are set out in Table III arranged in ascending order of the first set of regression coefficients.

It may be seen that there is a certain amount of variability between the regressions and that the degree of correlation is never very great. The calculation of the correlation coefficients may not be valid procedure since neither variable has a unimodal normal distribution. The data from the two well protected areas Mwanza and Ekunu Bay, exhibit almost complete disassociation, but their regression coefficients of prey on predator length do not differ significantly from zero. It may be assumed therefore, that all sizes of *B. docmac* from these two localities prey indiscriminately over a restricted size range of *Haplochromis* available. Attention has already (p. 487) been drawn to the similarity of the general diet from these two localities with its paucity of invertebrate elements and this may well lead to greater predation pressure against the *Haplochromis* populations with a consequent reduction in size selection. Samples from the other localities, with the exception of Musoma, all show significant correlation. The sample size from Musoma was too small but neglecting these and the Mwanza and Ekunu Bay data, a test of the correlation coefficients from the other localities gave $P=0{\cdot}75$ for 6 degrees of freedom and a mean correlation coefficient of 0·229. A better equation for the linear relationship between *Haplochromis* prey (Y) and predator length above 20 cm (X) is therefore given by $Y=4{\cdot}32+0{\cdot}046X$. *B. docmac* appears to feed more actively on fish by day and further analyses of the 24 h series were carried out to establish whether any conclusions could be reached

TABLE III. The regression of prey length (Y) and predator length greater than 20 cm (X) by bivariate analysis for ten localities in Lake Victoria

Locality	n	Regression of Y on X	r	Regression of X on Y	$\bar{X}$	$\bar{Y}$
Mwanza	178	$Y=6{\cdot}33-0{\cdot}003X$	$-0{\cdot}023$	$X=44{\cdot}91-0{\cdot}203Y$	43·65	6·20
Ekunu Bay	92	$Y=6{\cdot}96-0{\cdot}001X$	$-0{\cdot}006$	$X=42{\cdot}49-0{\cdot}037Y$	42·23	6·91
Musoma	53	$Y=6{\cdot}01+0{\cdot}022X$	0·105	$X=36{\cdot}53+0{\cdot}512Y$	40·05	6·87
Speke Gulf	265	$Y=6{\cdot}23+0{\cdot}028X$	0·147	$X=37{\cdot}15+0{\cdot}780Y$	42·95	7·43
Kavirondo Gulf	985	$Y=3{\cdot}35+0{\cdot}035X$	0·184	$X=33{\cdot}56+0{\cdot}967Y$	38·10	4·69
Grant Bay	232	$Y=4{\cdot}73+0{\cdot}038X$	0·177	$X=40{\cdot}15+0{\cdot}820Y$	45·45	6·46
Kenya Coast	151	$Y=4{\cdot}64+0{\cdot}045X$	0·357	$X=25{\cdot}81+2{\cdot}818Y$	44·55	6·65
Dagusi	96	$Y=3{\cdot}72+0{\cdot}047X$	0·240	$X=35{\cdot}93+1{\cdot}229Y$	42·97	5·73
Sesse Islands	835	$Y=4{\cdot}53+0{\cdot}050X$	0·243	$X=33{\cdot}59+1{\cdot}172Y$	41·34	6·61
Bukoba	214	$Y=5{\cdot}68+0{\cdot}054X$	0·315	$X=29{\cdot}07+1{\cdot}837Y$	43·86	8·05

concerning this diurnal variation in feeding pattern. The only consistent result which emerged was that the mean *Haplochromis* prey size was smaller by night and in consequence the intercepts of the regression equations were, in certain localities, lowered considerably. This observation would suggest that the larger prey forms are not available at night, i.e. there is a migration of the larger *Haplochromis* species (and possibly small *B. docmac*) away from the *B. docmac* feeding grounds either towards the surface waters or into the shallower inshore waters of the lake. Coulter (1962, Table 2B1, pp. 14–16) demonstrated by analysis of day and night beach seine catches that large night-time inshore migrations do occur in Lake Tanganyika. Some of the principal species involved are of the family Cichlidae but a similar tendency is noted on a small scale among the Bagridae (*Chrysichthys* sp. and *Phyllonemus* sp.). The species composition of *Haplochromis* populations found in water deeper than about 15 m is imperfectly known. It would appear however, that, as in shallow water, there are a large number of small species of adult sizes about 6–9 cm S.L., some of which are described by Greenwood & Gee (1969). These probably form the bulk of the prey fish taken by *B. docmac* but also included would be immature forms of bigger species such as *H. empodisma*. Below 6 cm most of the *Haplochromis* taken are likely to be immature forms.

B. NUMBERS OF *HAPLOCHROMIS* TAKEN PER UNIT TIME

In order to arrive at any estimate of the total weight of *Haplochromis* taken by *B. docmac* over a unit period of time, it is necessary to formulate a method of computing the actual numbers of prey taken during unit time, in addition to calculating the predator/prey length relationship. To establish this, trawling on the same transects over a 24 h period was carried out in certain localities. All fish prey taken by *B. docmac* were assigned to easily recognizable, crude digestion stages based on the presence or absence of certain features, and the numbers present in each stage recorded for every stomach examined. With experience it was found that well digested fragments could be readily identified at least to family from such characteristics as muscle colour, myotome shape and skeletal material. All cichlid fragments were classed as *Haplochromis* in view of the negligible numbers of recognizable *Tilapia* found throughout the lake survey. Since the immediate interest is in the actual intake of *Haplochromis* over 24 h, only the freshly taken, relatively undigested, positively identified specimens are considered here. Their mean numbers per 10 cm predator length class above 20 cm were calculated for each haul from the appropriately sampled localities, using all *B. docmac* examined, irrespective of whether or not they contained food. These mean numbers were then plotted against mid-haul time as in Fig. 6 for each locality. Fig. 6, showing the results from a 24 h trawl series in Kigegi Gulf, is an example and demonstrates that within each predator length class a varying number of modes may be found. Aquarium experiments, to be reported elsewhere, established that the mean gastric digestion time for *Haplochromis* in *B. docmac* approximated to 22 h and that the digestion stage used above would be recognizable for between 2–4 h after ingestion. It was assumed, and verified from the experimental work, that feeding would occur twice during a 24 h period, with piscivorous feeding occurring mainly by day, as shown above (p. 490). It was also assumed that the number of fish taken during one feeding period would be distributed normally about a mean feeding time. Fig. 6 may be interpreted as representing either one or two normally distributed feeding curves in each length class with some overlap occurring between the two normal distributions in the 20–29 cm and 40–49 cm length classes to produce a further apparent mode at 18.00 h. The major feed in each of the three smaller classes occurred during the morning at 11.00 h with a subsidiary fish feed, rather protracted in the smallest 20–29 cm class, at 23.00 h. Table II showed that the major invertebrate feed, which is likely to be more important in the smallest class, occurred at night. In the largest class however, only one feeding distribution curve is apparent, with the mode occurring at approximately 13.00 h, but the data are scanty, particularly at night. Very similar patterns in the corresponding classes were found for the Kavirondo Gulf and Grant Bay data but in the Speke Gulf two well pronounced modes were apparent for the largest length class as in the other smaller

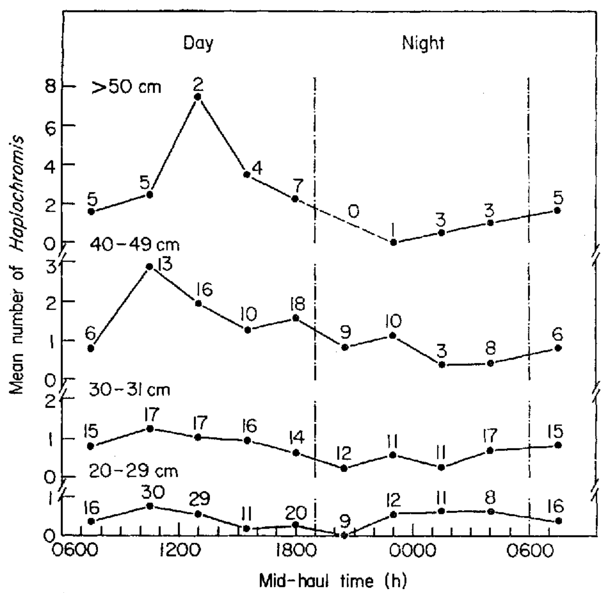

FIG. 6. The mean numbers of freshly ingested *Haplochromis* in 10 cm predator length classes at mid-haul times during a 24 h fishing exercise in Kigegi Gulf. The figure at each point on the graph indicates the number of *B. docmac* examined.

classes. If this interpretation is correct then the mean total number of *Haplochromis* taken over 24 h will approximate to the sum of the mean numbers at modal times for each length class in each locality. These numbers are set out in Table IV together with the sum of the numbers of *B. docmac* examined at each mode.

With the exception of Kavirondo Gulf data, agreement is fair. In view of the differing predator/prey length relationships established and the varying importance of the invertebrate elements in the diet from the different localities, the variations are not unexpected.

C. THE MEAN DAILY RATION OF *HAPLOCHROMIS* EATEN

It is possible to make some estimate of the mean daily ration of *Haplochromis* consumed by converting to weight the *Haplochromis* mean lengths ingested by any length of predator, derived from the regression formulae in Table III. The length/weight relationship of the actual material was not determined on board ship where weighings of such small individuals could lead to grave error. Rather, seined samples of *Haplochromis* from Napoleon Gulf at Jinja were examined under laboratory conditions together with some trawled and gill netted larger specimens. All data were lumped together and the regression equation,

$$\log W = 3{\cdot}180 \log L - 1{\cdot}69723$$

calculated for the size range 2·5–10·5 cm, where W and L are *Haplochromis* weights and lengths in g and cm respectively. This formula was used to convert all estimated lengths to weight. The mean daily ration may be obtained in one of two ways for any length or weight class of *B. docmac*. The first is to calculate the average product of the computed mean weights and the mean numbers for each locality. The second method is to calculate the product of the generalized predator/prey length regression (p. 494) converted to weight and the weighted mean numbers shown in Table IV.

TABLE IV. The calculated mean numbers (no.) of *Haplochromis* taken over 24 h by 10 cm length classes of *B. docmac*; the number (obs.) of *B. docmac* examined and the weighted mean numbers (excluding Ekunu Bay data)

Length class (cm)	Kavirondo Gulf		Grant Bay		Speke Gulf		Sesse Islands		Ekunu Bay		Weighted mean
	obs.	no.	obs.	no.	obs.	no.	obs.	no.	obs.	no.	no.
20–29	10	1·80	20	1·25	37	0·48	41	1·41	5	1·33	1·09
30–39	62	5·70	20	2·20	22	1·21	28	1·81	20	2·19	3·60
40–49	22	11·03	8	5·33	13	1·70	23	4·02	3	4·66	6·06
>50	—	—	15	5·66	13	7·10	2	7·50	5	6·66	6·40

Ekunu Bay data are omitted in calculating these weighted mean numbers as they were from the calculation of the generalized predator/prey length regression in view of their significantly different regression coefficients. The Ekunu Bay regression coefficient did not differ significantly from zero and will be considered as such in the calculation of the daily rations, the steps of which are set out in Table V.

The two estimates of the mean daily ration for each mid-class length of *B. docmac* above 20 cm are shown in the last two lines of Table V where it may be seen that for any given length they differ quite considerably. In logarithmic form the grand mean daily rations are linear in relation to predator length as shown in Fig. 7 where the least squares regression is given by

$$\log \text{daily ration} = 2{\cdot}973 \log \text{length} - 3{\cdot}36089$$

and $\chi^2 = 0{\cdot}233$ with $P = 0{\cdot}97$. The estimated rations from the generalized data do not give such a good fit in logarithmic, semi-logarithmic or arithmetic form and therefore the above regression equation is considered to yield the best estimate of the mean daily ration of *Haplochromis* taken by any length of *B. docmac*. The data presented above are supported by observations on the maximum ration taken by *B. docmac* in aquaria when given unlimited *Haplochromis* prey. These observations are shown plotted in Fig. 7 as open circles and demonstrate that the rations computed as above are of the right order although somewhat higher than for aquarium held *B. docmac*. This difference is perhaps not unexpected in view of the limited water volume available

TABLE V. Steps followed in arriving at the mean daily ration of *Haplochromis* ingested by the mid-class lengths of *B. docmac* above 20 cm from Lake Victoria

A. Mean length of *Haplochromis* prey from the regressions shown in Table III and from the average regression shown on p. 494.

	Mid-class length (cm)			
	25	35	45	55
Kavirondo Gulf	4·23	4·78	5·13	5·48
Grant Bay	5·68	6·06	6·44	6·82
Speke Gulf	6·30	7·21	7·49	7·77
Sesse Islands	5·78	6·28	6·78	7·28
Ekunu Bay	6·96	6·96	6·96	6·96
Average regression	5·41	5·83	6·25	6·67

B. Weight of *Haplochromis* ($\log W = 3{\cdot}18 \log L - 1{\cdot}69723$)

Kavirondo Gulf	1·96	2·91	3·64	4·39
Grant Bay	5·03	6·18	7·50	9·00
Speke Gulf	6·99	10·72	12·12	13·63
Sesse Islands	5·32	6·92	8·83	11·08
Ekunu Bay	9·60	9·60	9·60	9·60
From average regression	4·31	5·47	6·82	8·39

C. Number of *Haplochromis* taken per day (Table IV)

Kavirondo Gulf	1·80	5·70	11·03	—
Grant Bay	1·25	2·20	5·33	5·66
Speke Gulf	0·48	1·21	1·70	7·10
Sesse Islands	1·41	1·81	4·02	7·50
Ekunu Bay	1·33	2·19	4·66	6·66
Weighted mean	1·09	3·60	6·06	6·41

D. Daily ration of *Haplochromis* (B × C)

Kavirondo Gulf	3·53	16·59	39·79	—
Grant Bay	6·29	13·60	39·98	50·94
Speke Gulf	3·36	12·97	20·60	105·91
Sesse Islands	7·50	12·53	35·50	83·10
Ekunu Bay	12·76	21·02	44·73	63·94
Grand Mean	6·57	15·66	35·66	75·97
Average × weighted mean	4·70	19·70	41·33	53·78

in aquaria with the subsequent lower expenditure of energy involved in the capture of prey specimens by the predator.

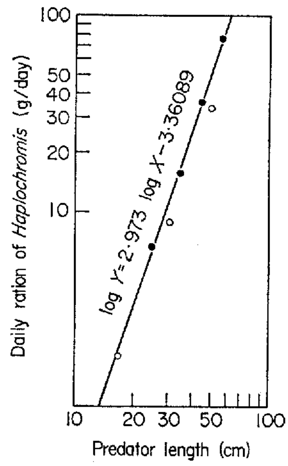

FIG. 7. The regression of mean daily rations of *Haplochromis* taken by the mid-class length of *B. docmac*, computed from field data (●) and, for comparison, the maximum daily rations taken by aquarium held *B. docmac* (○).

D. THE ESTIMATED ANNUAL CONSUMPTION OF *HAPLOCHROMIS* IN LAKE VICTORIA

Cordone (unpublished) estimated the mean standing stocks of *B. docmac* and *Haplochromis* as 6·7 and 82·6 kg/ha respectively. Bergstrand & Cordone (1970) demonstrated that the *B. docmac* population was restricted to water depths of less than 70 m. Recalculating the mean standing stocks for only the area inhabited by the predator yields mean standing stocks of 8·2 and 99·6 kg/ha. To convert the *B. docmac* gravimetric to numerical standing stock and to estimate somewhat crudely the total consumption of *Haplochromis*, the actual numbers of *B. docmac* caught in each 10 cm length class greater than 20 cm from the localities sampled over 24 h were expressed as a proportion of their sum, and the mean length of these fish was computed. From the mean length the mean weight was estimated and the numerical standing stock calculated by dividing the sample mean weight into the gravimetric standing stock less 10%, which was assumed to be the proportion due to *B. docmac* of less than 20 cm. The number of predators in each length class was then calculated from their proportional representation and the daily and annual consumption computed as in Table VI from the mean daily ration derived from the previous equation.

The annual consumption calculated in this manner, 75·18 kg/ha, represents the approximate percentage of the *Haplochromis* mean standing stock consumed by the predator, since this approximates to 100 kg/ha. Consumption would appear to be very high but is possibly in accord with Dunn's finding (pers. comm.) that from Lake George, Uganda, the commercial catch of a much larger cichlid, *Tilapia nilotica* (L.) is approximately five times its standing stock. Considering that few *Haplochromis* species, so far as can be ascertained from length frequency data, have a life span exceeding three years and that throughout the year a proportion of *Haplochromis* are always spawning, then the actual production of this genus may well be as much as ten times the mean standing stocks. The dynamics of the *Haplochromis* species complex in Lake Victoria are little known and although it is tempting to try to estimate their mortality brought about by the predation of *B. docmac*, such an exercise would have little substance in fact. What may be estimated is the annual tonnage of *Haplochromis* consumed by *B. docmac* over the lake. The area over which *B. docmac* is found amounts to approximately $6{\cdot}0 \times 10^6$ ha and given the mean annual consumption as 75·18 kg/ha, then the total annual consumption is 450 000 metric tons, approximately 17 times the commercial *Haplochromis* catch of 26 600 metric tons made in 1968.

TABLE VI. Showing the steps followed in computing the consumption of *Haplochromis* by *B. docmac* in Lake Victoria

Mid-class length (cm)	Proportion in each class	No. in each class/ha	Daily ration (g)	Daily consumption (g/ha)	Annual consumption (kg/ha)
25	0·332	3·39	6·24	21·15	7·72
35	0·431	4·40	16·97	74·67	27·25
45	0·175	1·79	35·82	64·12	23·40
55 } 57·2	0·050 } 0·062				
65	0·010	0·63	73·09	46·05	16·81
75	0·002				
Sum	1·000	10·21	—	205·99	75·18

Mean length=34·81 cm.
Mean weight=0·725 kg.
Mean gravimetric standing stock in water depth less than 70 m=8·2 kg/ha.
Mean gravimetric standing stock less 10%=7·4 kg/ha.

$$\text{Mean numerical standing stock} = \frac{7{\cdot}4}{0{\cdot}725} = 10{\cdot}21 \text{ fish/ha.}$$

V. DISCUSSION

In general, the description of the diet of *B. docmac* from the various localities around the lake supports the observations of Corbet (1961) although there are distinct differences between the invertebrate components in the diet of fishes from different parts of the lake. This is undoubtedly related to the annual cycle of stratification and phytoplankton growth described by Talling (1966). The paucity of the invertebrates in the diet of fish from the southern part of the lake possibly points to a much greater influence of the south-east trade winds on the dispersion of phytoplankton, the pelagic stages of benthic juvenile insects, and possibly their aerial adult stages, than has hitherto been supposed, since the *B. docmac* specimens may be regarded as a sampling device with a variable bias governed by the availability or otherwise of specific food items.

In the past, the importance of *Bagrus* as a piscivorous predator in African fresh waters has not been fully appreciated and has been overshadowed by such genera as *Lates* and *Hydrocynus*. The present study re-emphasizes the fact that *B. docmac* is a major predatory species and there are many similarities between it and *Lates niloticus*. Both are large predators although *Bagrus* does not reach the same maximum size as *L. niloticus*, rarely growing to more than about 25 kg in weight. Poll & Damas (1939) did report a specimen from Lake Edward with an estimated weight of 75 kg. Both genera feed predominantly on invertebrates when young but by the time the average adult size is reached both species are almost 100% piscivorous. Size selection of prey is a common characteristic but although they are capable of consuming prey of a length slightly greater than 40% of the body length of the predator, the prey size taken reaches an asymptote long before maximum predator size is attained. In many of these predators fish prey selection by species is minimal, i.e. the types of food taken are determined more by locality or seasonal differences in availability than by active selection of any particular species. This has been shown by Gee (1969*a*) to be the case for *Lates niloticus* in three different lakes in East Africa and by Jackson *et al.* (1963) for *Bagrus meridionalis* in Lake Malawi, to mention but two examples. In Lake Victoria, *Haplochromis* probably occur in over 90% of the *B. docmac* examined which may not be surprising in view of the fact that they form between 60 and 90% by weight of trawl catches made in Lake Victoria. This may indicate a low level of prey selectively especially when considered along with the fact that certain of the non-cichlid species increase in occurrence as stomach contents of *B. docmac* in those areas of the lake where they form a higher proportion of the fish population, as for example *Xenoclarias* at the mouth of the Kavirondo Gulf and small *B. docmac* (as prey) in the deep waters of the Sesse Islands (see Table II). However, the fact that *Tilapia* sp. only occurred in 0·07% of *B. docmac* which contained fish is something of an anomaly. Although *Tilapia* are rarely found in water over 20 m deep, Lowe (1956), there were a number of places where, on a non-selective basis, pure chance capture by *Bagrus* should have given a much higher occurrence than this. In Mwanza Gulf, Bukoba and Kigegi Gulf considerable quantities of *Tilapia* of a size well within the 40% limit were caught at the same time as *B. docmac* and yet none were found to have ingested *Tilapia*. This could indicate that species selection is being exercised by *B. docmac* or it may be that the shape of *Tilapia* (a higher depth to length ratio than most prey), their behaviour pattern, warning systems or some other factors, make them inaccessible to *B. docmac* even though they occur in the same lake area. *Tilapia* sp. feature much more prominently in the diet of *L. niloticus* in Lake Victoria. Gee (1969*a*) found that out of 75 *L. niloticus* which contained food 12 had eaten *Tilapia* (at an average rate of two per fish). *Lates niloticus*, with a highly mobile and extensible premaxilla which produces a relatively wider gape to the jaws, is much more suited for preying on deep bodied fishes than is *B. docmac*, which has a slightly dorso-ventrally flattened head, a fused premaxilla and non-functional maxilla, resulting in a much more restricted jaw gape. Similarly, the less manoeuvrable, near anguilliforme swimming motion of *B. docmac* may be a disadvantage compared to the typical perciforme swimming action of *L. niloticus* if the prey species has a highly developed sensory system and can take rapid avoiding action.

Published quantitative data concerning the inter-relationships of predators and their prey species in African lakes are limited and therefore present little opportunity for comparisons. Munro (1967) estimated the daily fish ration of two size groups (20–30 cm and 30–40 cm) of *Hydrocynus vittatus* as 5·2 and 3·9 ml/kg respectively. It was noted that these rations were about 25% less than the maintenance ration established experimentally by Elder (1962) for Lake Victoria *B. docmac* of equivalent sizes. This is surprising as *H. vittatus* is regarded as an active ‘chasing’ predator while *B. docmac* is regarded as a more inactive ‘lurking’ predator Lowe (1959), Jackson (1961). Assuming that the fish prey have a density of 1, then Munro's values account for only approximately 21 and 13% respectively of mean daily rations computed as above for equivalent sizes of *B. docmac*. Certain of Elder's data (1962, Table I, p. 22) support the mean daily rations computed here. Two fish fed at 'rates probably exceeding any attained normally under natural conditions', received daily rations of 13·5 g and 8·1 g for calculated lengths of 32 cm and 29 cm respectively. These rations are in good agreement with those of 13·1 and 9·7 calculated from the regression of the computed mean daily ration (Fig. 7) and Elder gives no evidence to support his contention that these fish were receiving excessive quantities of food. The experimental aquarium data plotted in Fig. 7 and that of Elder (1962) both support the regression of the mean daily rations computed from field observations and indicate that the fears expressed earlier, concerning suspected force feeding in the trawl, may have been without foundation. Force feeding was suspected to have occurred because small *Haplochromis* were often to be found completely filling the buccal cavity of large *B. docmac* and, on occasions alive within the stomachs. Hamblyn (1966) performed some experimental feeding of *Lates niloticus*. As stated above this species resembles *B. docmac* in many respects and it is of interest that the calculated mean daily rations of three solitary *L. niloticus*, when adjusted for the length measurements used, fall close to the regression curve for the *B. docmac* ration. It might appear that similar types of predators have similar food consumption levels. Balon (1970) likened the biology of Lake Kariba *Hydrocynus vittatus* to that of the European pike, *Esox lucius* and later (Balon, 1972) utilized the annual food ration of 3 kg/kg of body weight computed by Johnson (1966) for pike, in assessing the inter-relations of *H. vittatus* and *Alestes lateralis*. This annual food ration although exceeding that found by Munro (1967) bears little resemblance to the value calculated for the mean size of *B. docmac* as approximately $27 \div 0{\cdot}725 = 37$ kg/kg of body weight. The great disparity between the pike and the *B. docmac* annual ration may be a function of ambient bottom water temperatures. At similar depths of 60 m the bottom temperature of Lake Windermere varies between 5° and 6° C while that of Lake Victoria fluctuates between 23·6° and 24·8° C (see Talling, 1965). Lake Kariba bottom temperatures fluctuate between approximately 21° and 29° C (Harding, pers. comm.) and it might be expected therefore that the *H. vittatus* ration would more closely resemble that of *B. docmac* than the pike.

The ratio of the *B. docmac* and *Haplochromis* biomass from the area of Lake Victoria less than 70 m deep is 1 : 12·1 which is of similar order of magnitude to the ratio of 1 : 15·4 for *Bagrus* and *Haplochromis* in the much richer Lake George, established from fish kill data supplied by Dunn (pers. comm.). The estimate of an annual consumption by *B. docmac* of approximately 75% of the mean standing stock may not be too high, especially when, from data in Balon (1972), it can be calculated that *H. vittatus* consumes 80% of the mean standing stock of *A. lateralis* (189 metric tons) in Lake Kariba, and this according to Matthes (1968) represents about 5% of the diet of *H. vittatus*.

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