ADVANCES IN THE ECOLOGY OF LAKE KARIBA

Edited by Jacques MOREAU

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Cover Top: Typical ringnets as utilized in Kapenta fisheries on Lake Kariba
Bottom: Lake Kariba: The littoral area and draw-down zone
Back cover: Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

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THE FEEDING ECOLOGY OF TWO NILE CROCODILE POPULATIONS IN THE ZAMBEZI VALLEY

Ian Games and Jacques Moreau

INTRODUCTION

The objective of this study was to assess the impact of crocodiles (*Crocodylus niloticus*) on the fish populations of Lake Kariba as compared to the one of fisheries. The lake supports a successful crocodile management scheme based on egg collection for rearing and release of three-year- old animals, which is operated by the Department of National Parks and Wildlife Management. The fishery has expanded since independence in 1980 (Murphree *et al.* 1989) and there is pressure to open up areas that were previously closed to fishing. Conflicts exist between fishermen and crocodiles (Chimbuya and Hutton 1988) with many of the problems centering around competition for the resource (i.e. fish and space for fishing or for nesting activity). This study is the first to estimate fish consumption by crocodiles in a natural ecosystem and it is hoped that it might be representative of other places in Africa. Previous studies were combinations of data from several localities (Cott 1961) or from populations of a cool water reservoir: Ngezi reservoir, Zimbabwe (Hutton 1984) or of a lake surrounded by desertic zones: Lake Turkana, Kenya (Graham 1968).

STUDY AREAS

The Zambezi River rises in the highlands of Angola and Zambia and flows for more than 2500 km through six countries before reaching the Indian Ocean. Two large artificial lakes have been created on the river at Kariba and Cahora Bassa (Figure 1, introduction of this volume).

Lake Kariba is one of the most intensively studied lakes in Africa and a large body of information on all aspects of its limnology and ecology exists (e.g. Balon and Coche 1974, Bowmaker 1973, Marshall 1984, J.M. Hutton Pvt. Ltd. 1991). The lake supports both inshore and pelagic fisheries which differ in the areas they exploit and in their capital input and yields. The kapenta fishery began in 1973 and now produces approximately 23,000 tonnes, almost 10 times as much as the more primitive and under-capitalized inshore fishery (Sanyanga and Muchabaiwa 1994). A succession of drought years since 1980 has depressed the mean operating level of the lake to 480 m. a .s. l. (area 5,000 km^2) where it remained throughout the study period (see Figure 3, introduction this volume).

Lake Cahora Bassa has a shoreline of approximately 1200 km and a surface area of 2665 km^2 when at the planned operating level of 326 m. a. s. l. (Bernacsek and Lopes 1984). Since 1981 the mean operating level has dropped to 315 m. a.s.l. and this has led to a fluctuating lake/river interface at the head of the lake close to the Zimbabwean border in the Zumbo basin. Most samples were collected in this basin.

In Lake Kariba, the main study site was the Ume estuary which is protected on one side by the Matusadona National Park (Figure 8.1) and is relatively undisturbed by egg collection activities. The crocodile is protected in Zimbabwe and all samples were taken from live animals which were subsequently released. A commercial cropping programme on Lake Cahora Bassa in Mozambique allowed the collection of data and samples from a shot sample in the lake (in Zumbo basin, 300 km downstream from Lake Kariba) for comparison purposes (Games *et al.* 1989).

This study was carried out simultaneously in the two sites in order to ensure the accuracy of results obtained on the Lake Kariba population. However, the principal aim of the investigation in Cahora Bassa was to obtain a sample of large crocodiles as they were proving difficult to catch in Lake Kariba.

POPULATION SIZE AND STRUCTURE

The size and age structure of the crocodile populations in both lakes were estimated using methods suggested and summarised in Bayliss (1988) and Graham (1988). These are detailed briefly below.

The size structure of the two populations in three broad categories was assessed from cropping and was compared with data from the literature (Table 8.1). Consequently the following mean figures can be regarded as acceptable for Lake Kariba: 46% juveniles, 34% sub-adults and 20% adults (e.g. animals able to reproduce).

Table 8.1 Percentage of the three major size class divisions in various populations of Nile crocodiles

Area	*Juveniles* < 1.4 m	*Sub-adults* 1.4 to 2.6 m	*Adults* > 2.6 m TL	*Methods*	
Turkana	50	31	19	Shot sample	A
Uganda	54	25	21	Aerial Survey	B
	41	38	21	idem	B
Ngezi	44	33	23	Mark recapture	C
Cahora	48	34	18	Shot sample	D
Kariba	46	54 (*)		Several methods	D

(*) Sub-adults and adults are mixed (in fact 34% sub-adults and 20% adults).

A: Graham 1968 B: Parker and Watson 1969 in Games 1990

C: Hutton and Woolhouse 1989 D: Games 1990

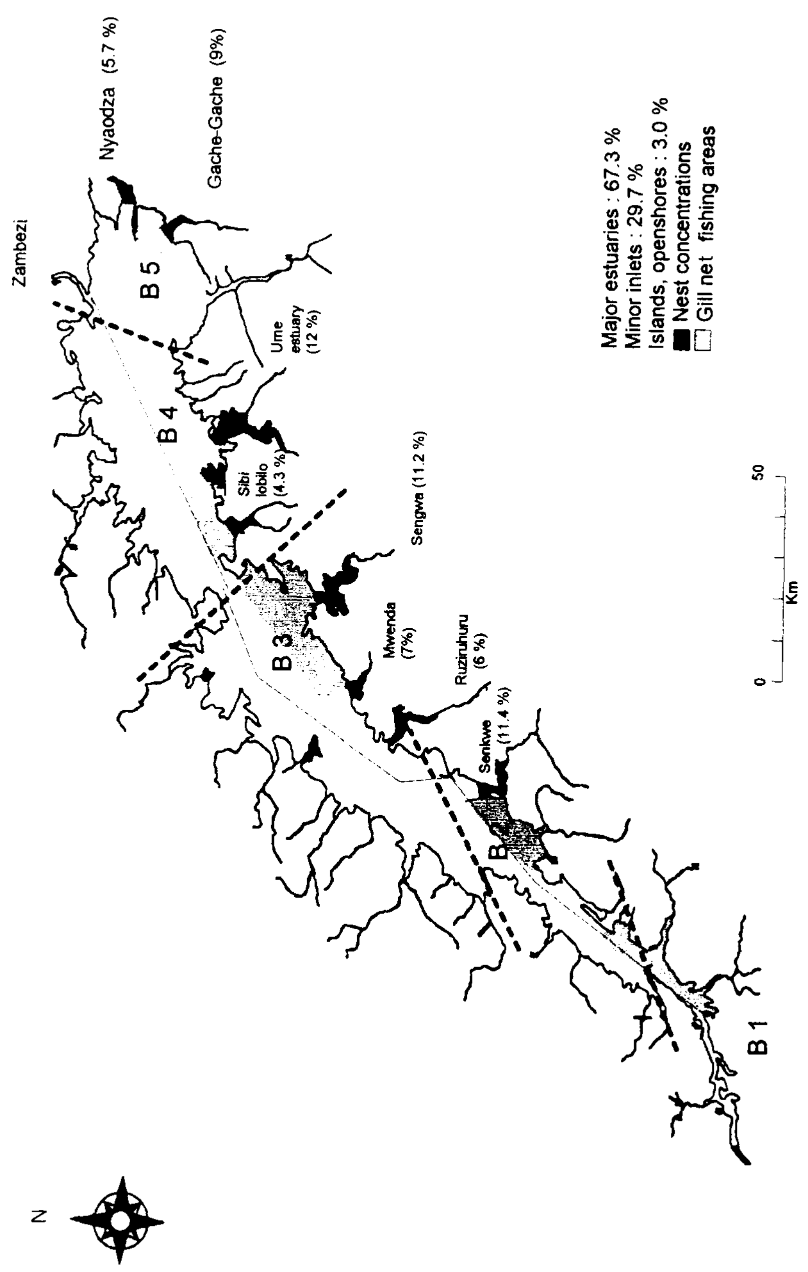

Figure 8.1 Crocodile concentration as indicated by nest concentrations on Lake Kariba (Data from Department of National Parks and Wildlife Management)

The size of the Kariba population was estimated from catch and recapture data, from aerial surveys operated only in the Ume estuary and from nest counts all over the Zimbabwean side of the lake. Incidentally, it was observed that the majority of nests (67.3%) are concentrated in the eight major river estuaries. The minor rivers and flooded inlets account for a further 29.7% of the nests and only 3% are to be found on islands, rocky shores or exposed shores. Nearly 16% of the nests were found on the Matusadona National Park shoreline (Figure 8.1).

The size of the Cahora Bassa population was estimated by aerial survey, spotlight counts, cropping and nest counts and it has been shown that these various methods gave similar results (Games 1990).

Consequently, as population estimates from nests counts agreed with other methods used in Cahora Bassa, it was decided to put confidence in the population estimates from nest counts for Lake Kariba. By this method, the mean population estimate for the Zimbabwean side of Lake Kariba was 6,500 crocodiles of all sizes with approximately 3,350 of these being larger than 1.2 m total length (i.e. sub-adults and adults). The maximum estimate using correction factors from Hutton and Woolhouse (1989) which intend to avoïd possible under-evaluation by the above mentioned methods was approximately 11,500 animals with nearly 6,000 of these being sub-adults and adults.

However, in recent years, attempts have been made to collect crocodile eggs from areas outside the National Parks and this will affect recruitment into the population. Also Zimbabwe's release programme of farmed animals is underway and this will also affect the size and age structure of the population and the total number of animals in the lake.

INDIVIDUAL GROWTH AND AGEING

Skeletochronology (Ferguson 1984, Hutton 1986, Games 1991) was used here in order to assess growth of crocodiles in both study sites. In addition, tagged and recaptured animals provided a measure of the growth rate of crocodiles in the wild in Lake Kariba. For Lake Cahora Bassa, additional material was obtained from Craig *et al.* (1989). The results for Lake Kariba are summarized in Table 8.2 and Figure 8.2.

As in other animals, data were fitted to the von Bertalanffy growth function (VBGF) for length which is expressed as follows (von Bertalanffy 1938):

$$Lt = Loo\,(1 - \exp(-K(t-to))\ \text{for length and}$$

$$Wt = Woo\,(1 - \exp(-K(t-to))^{b}\ \text{for weight}$$

where Loo and Woo are asymptotic sizes, or the mean size the animals would reach if they were to grow indefinitely according to the model, K is a growth constant and to is the "age" the animal would have at length or weight 0 if they had always grown according to the equation, while Lt and Wt are the predicted sizes at age t. The VBGF for weight is obtained using the length–weight relationship:

$$W(t) = a * L_t(t)^{b}$$; for *Crocodylus niloticus* in Lake Kariba

mm

$a = \exp(-16.25)$ $b = 3.47$ (Games 1990).

It appears that crocodiles in Zambezi River grow faster and mature some 15 years earlier than in Lake Ngezi (Figure 8.3). Juveniles grew slowly for the first

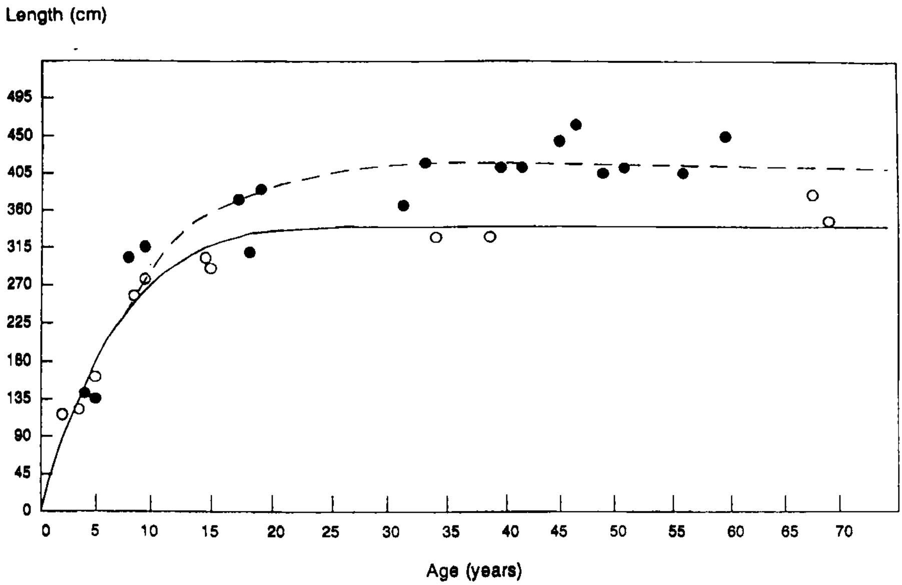

Figure 8.2 Length-at-age data for crocodiles in Lake Kariba fitted to the von Bertalanffy growth function:
(•) Males: L_∞ = 415 cm K = 0.111 yr^{-1} to = –0.066 yr
(o) Females: L_∞ = 356 cm K = 0.114 yr^{-1} to = –0.012 yr

Table 8.2 Length-at-age data for crocodiles from Lake Kariba as obtained from skeletochronology (Number N is 1 except otherwise specified)

Males			*Females*		
Age(years)	*TL(cm)*	*N*	*Age(years)*	*TL(cm)*	*N*
4	139	4	3	110	
5	134	2	4	118	3
8	294		5	145	5
10	305		6	188	4
18	279	2	7	209	2
21	357		9	248	
23	372		10	250	
31	330		14	268	
33	382		15	258	
40	380		34	293	2
42	386		39	294	
45	416		70	343	
47	445		72	312	
49	386				
51	390				
56	378				
61	416				

two years and then the growth rate increased until about 1 m TL after which it declined again. Females matured at between 15 and 20 years of age. The growth of the Cahora Bassa animals was similar to the one recorded in Lake Kariba which suggests that these growth curves are probably representative of growth in wild Nile crocodiles.

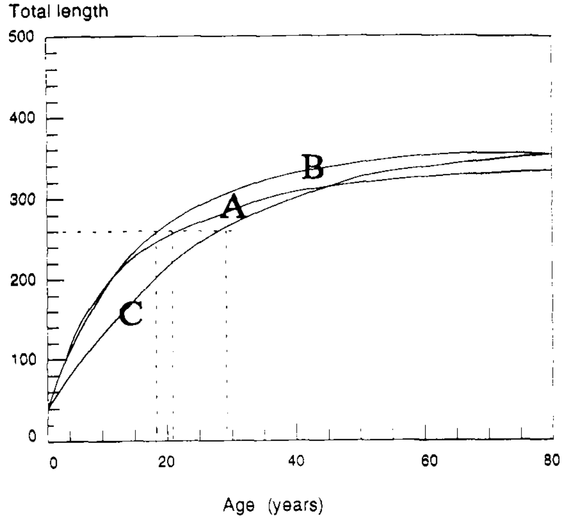

Figure 8.3 Comparison of female Nile crocodile growth curves
A: Lake Kariba B: Lake Cahora Bassa C: Ngezi dam

FEEDING HABITS

Most of the food samples from crocodiles in Lake Kariba were taken from animals captured at night using various methods (Games 1990). A small sample of sub-adults was shot as part of a control exercise. Stomach contents were removed from live animals within 12 hours of capture using a modification of the stomach pumping method outlined by Taylor *et al.* (1978). All stomachs from the Cahora Bassa study were excised from freshly killed animals. The weight and volume of the various food items were measured for further evaluation of their relative importance in the diet (see Games 1990 for details).

The percentage of empty stomachs was quite high: about 65% for juveniles, 60% for sub-adults and 85% for adults.

In order to assess the changes in feeding habits with size, the overlapping target size method of analysis for stomach contents (Webb *et al.* 1991) was used here. Briefly, in this method, the 15 smallest crocodiles constituted the first size category. The next size category encompassed the next five larger crocodiles and excluded the five smallest animals and so on. This gave a continuous measurement of possible trends in changes of feeding habits according to the size. The results given here concern Lake Kariba only.

This study showed some dietary changes within the juvenile size classes (animals less than 140 cm TL) as quoted on Figure 8.4. The juveniles appear to feed on terrestrial insects, small mammals and frogs until they are about 60 cm TL when their intake increases significantly (see below). This increase is associated with a shift from terrestrial to aquatic invertebrates in their diet. Increased amounts of food in the stomachs were associated with high water levels. This seems to come from a higher availability of food because of food production of flooded area. However, high water period occurs during the cool season; thus, a low food consumption and related low growth and metabolism associated with low water temperature would have been expected.

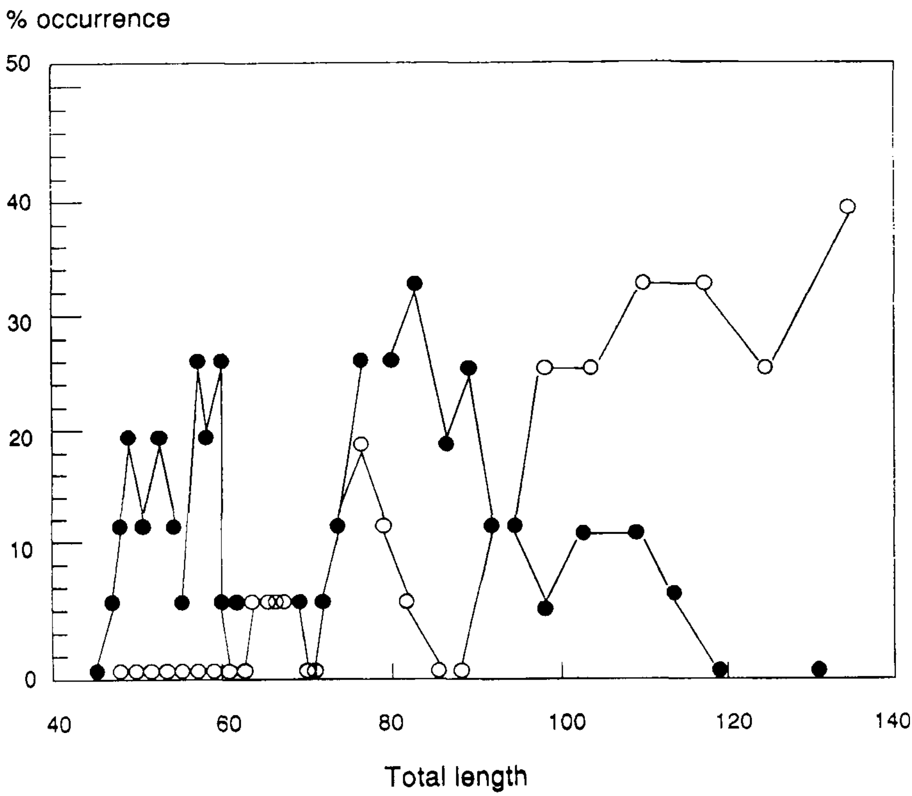

Figure 8.4 Percentage occurence of fish (o) and mammals (•) in the stomachs of juvenile crocodiles from Lake Kariba in relation to the mean total length. Each point represents 15 animals using the overlapping group method of analysis (see text for this concept)

The importance of fish in the diet of crocodiles increases while they are between 140 cm TL and 260 cm TL. When estimated by weight, fish accounts for 98% of the diet. This figure declines to around 33% in adult crocodiles which mostly feed on mammals (Figure 8.5).

These results are supported by the data pertaining to Cahora Bassa (Games 1990) and this helps to put confidence in the small sub-adult sample from Lake

Kariba. It should be reminded that samples were collected only during a single time of the year in Cahora Bassa because of political problems there. This study shows that sub-adult and adult crocodiles can eat fish belonging to various families as already observed by Cott (1961). It should be noted that this was the first study of feeding in large Nile crocodiles that did not require wholesale slaughter which should be avoïded even when operated "in the name of science" as urged by Gans and Pooley (1976).

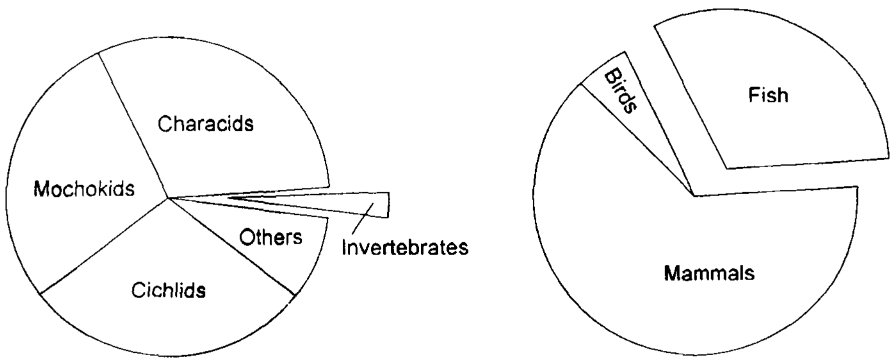

Figure 8.5 Percentage intake (weight) of major prey types by sub-adults (left) and adults (right) crocodiles from Lake Kariba

DIGESTION

Rates of digestion were investigated in different size classes of crocodiles using the methodology described by Games (1990). Briefly, the rate of disappearance of food from the gut was evaluated by pumping the stomach content at regular intervals after a forced feeding with various foods, the initial dry weight of which was known. The digestion pattern of fish was investigated in juveniles, sub-adults and adults and it was shown that fish were digested to 10%–20% of their original volume after 2 days in the stomach (Figure 8.6). This information was necessary in order to assign an "age" to prey items found in wild crocodile stomachs and it was used in order to estimate feeding frequencies.

FOOD CONSUMPTION

Generally, food consumption of aquatic animals can be estimated from data on diet, daily intake, feeding frequency, digestion rates and growth whenever they are obtained through laboratory experiments or field observations. For fish, see for instance, Backiel (1971), Thorpe (1977), Pauly (1987), Palomares and Pauly (1989). For crocodiles it should be more particularly referred to Whitfield and Blaber (1979) and to Webb *et al.* (1991).

In Lake Kariba, daily intake of juvenile crocodiles was estimated by identifying fresh prey consumed (i.e. during the last 24 hours) and extrapolating its original mass using target size/mass regressions provided by Games (1990). It was found that, on average, juveniles (less than 140 cm TL) consume 2.34 g of

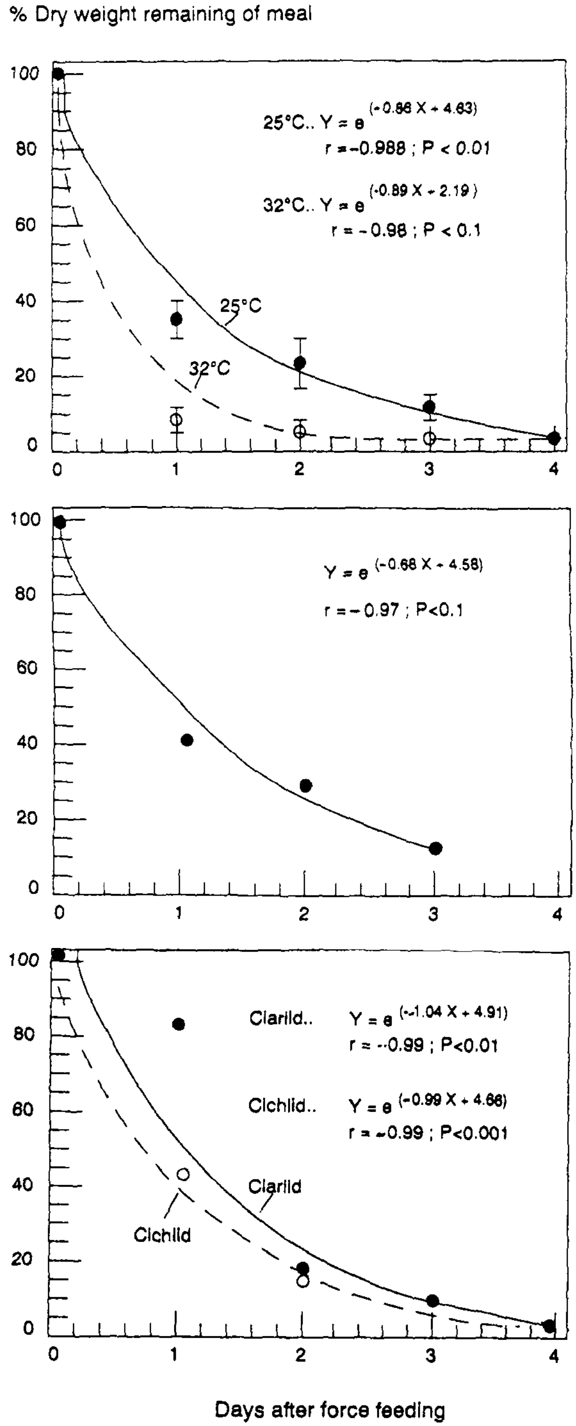

Figure 8.6 Digestion of food by crocodiles from Lake Kariba
Top: Juveniles Middle: Sub-adults Bottom: Adults

food a day or 854 g per year, about 50% of which is a mass of vertebrates, including 10% of fish. This daily amount of food eaten by wild juvenile crocodiles is 0.34% (< 60 cm TL average weight: 325 g.) and 0.26% (60–130 cm TL average weight: 1700 g.) of their body weight (Games 1990). Wild juvenile crocodiles ate small amounts of food when compared to captive ones which were fed *ad libitum* but the data of Games (1990) suggest that they were more efficient at converting it.

Feeding frequency in sub-adult and adult crocodiles was determined and intake estimated by using a model developed for predatory fish (Diana 1979, Medved *et al.* 1988). This model required measurement of both the quantity of food found in the stomachs and the gastric digestion rate. The feeding frequency was also estimated using a model developed by Games (1990). The feeding interval was found to be about 4 days in Lake Kariba and 8 days in Lake Cahora Bassa. These figures are in the range of similar observations by other authors (see Table 8.3)

Table 8.3 Feeding interval (days) for various crocodile populations in Africa

Population	*Size class (m TL)*	*Feeding interval (days)*	*Source*
Central Africa	2–3 m.	5.1	Cott (1961)
	3–4 m.	3.6	
	4–5 m.	4.0	
Lake Turkana	All sizes	3.2	Graham (1968)
Okavango	1.25–1.5 m.	2.6	Blomberg (1976)
Delta	1.5–2.25 m.	3.8	
	> 2.25 m.	3.6	
Okavango	1.5–2.4 m.	4.7	Taylor (1973)
Delta	> 2.4 m.	2.9	
Cahora Bassa	1.4–2.6 m.	7.8	Games (1990)
	> 2.6 m.	9.9	
Lake Kariba	1.4–2.6 m.	3.8	Games (1990)
	> 2.6 m.	4.5	

Using the feeding frequencies, the daily food consumption, the demographical structure and the abundance of crocodiles, an annual estimate of fish consumption from Lake Kariba can be computed and proposed (mean = 140.14 tonnes; upper estimate 225.39 tonnes, Table 8.4).

Refering to the longevity of crocodiles (about 80 years) and to the growth curves (Figure 8.2), it can be estimated that a female will spend 6% of her life as a juvenile, 19% as a sub-adult and 75% as an adult while a male will spend 6% as juvenile, 11% as a sub-adult and 83% as an adult. This means that a female will consume more fish than a male as fish are the most important food item for sub-adult crocodiles in Lake Kariba. In fact, it appears that a female crocodile eats 1841 kg of fish in an 80–year life span while a male consumes 1671 kg (Games 1990).

This is the first time that such an information is made available for a single natural population in a subtropical environment. Graham (1968) attempted a food consumption estimate for a population living in Lake Turkana, Kenya, but admitted that this may not be representative of other populations in Africa because the lake is surrounded by a desert. He also assumed a rate of feeding extrapolated from scanty data on captive animals.

Table 8.4 Fish consumption from Lake Kariba by crocodiles (from Games 1990)

Size	*% Fish in diet*	*Mean population*	*Maximum population*	*Mean fish consumption*	*Maximum fish consumption*
Juveniles	10	3095	5464	0.17	0.29
Sub-adults	98	2053	3870	110.39	207.08
Adults	33	1290	2094	29.58	48.02
Total		6448	11428	140.14	225.39

Juveniles: <140 cm TL: avg. length 76.5 cm avg. weight: 890 g
Sub-adults: 140–260 cm TL: avg. length 210 cm avg. weight: 29.5 kg
Adults: > 260 cm TL: avg. length 340 cm avg.weight: 157.4 kg
Average length and weight computed from Games (1990)

DISCUSSION

The food consumption per unit biomass

Pauly (1987) and Palomares and Pauly (1989) introduced the concept of relative consumption Q of food per unit biomass B. The computation of this parameter takes into account the age-structure of the population and the fact that juveniles eat more food relative to their individual weight than adults. In order to assess the accuracy of the present evaluation of food consumption by crocodiles on the Zimbabwean side of Lake Kariba, Q/B was evaluated through two different methods:

- A first estimate of Q/B can be directly obtained by refering to Table 8.4 (maximum population estimate and maximum consumption).The biomass of juveniles, sub-adults and adults are 4.9; 114.2 and 329.6 tonnes respectively. Their yearly total food consumptions are 2.9; 211.3 and 144.1 tonnes respectively. For the whole crocodile population, Q/B is 361.2/448.7 = 0.80.
- The method of Pauly (1987) is based on the demographical status of the population and on the knowledge of the growth efficiency for various sizes of individuals which is used to compute a parameter called Beta (see Pauly 1987 and Palomares and Pauly 1989 for details).

The necessary data (Table 8.5) lead to a value of Q/B = 0.78 as computed with the MAXIMS Software (Jarre *et al.* 1990). Additional informations are:

- Gross efficiency = 0.31%
- Daily intake = 0.21% of the total biomass
- Daily intake at the asymptotic size = 0.135% of individual weight.

These figures are in agreement which is observed on crocodiles in Lake Kariba (see Tables 5.3, 8.3 and 8.4 in Games 1990) which help to put confidence in both the method of Pauly (1987) to estimate Q/B and the data from Games (1990).

Table 8.5 Input required for Q/B estimate using the method of Pauly (1987)

Loo = 371.6 cm (a)	Woo = 214.23 kg. (b)	K= 0.114 year^{-1}	to = –0.002 year
Z = 0.25 (c)	Wr = 100 g	Wmax = 203 kg (d)	Beta: 0.20 (e)

(a) Data for males and females in Table 8.2 were merged and fitted to the VBGF using the method of Gaschütz *et al.* (1980).
(b) L/W relationship for crocodile in Lake Kariba; see text.
(c) computed from length converted catch curve from data of Figure A.5.2 (Games 1990) using the method of Pauly (1980).
(d) range of size (here weight) to be considered here.
(e) An index related to gross efficiency: value suggested by Palomares (1991) for large predatory fishes.

The possibility of competition with fisheries

On the Zimbabwean side of Lake Kariba, the boundaries of the fishing areas are separated from those of crocodiles (Figure 8.1). There are some exceptions to this but it would appear that most of the crocodiles are concentrated in the river estuaries which are outside the artisanal fishing zones. Initially, the exclusion of the estuaries was not for the protection of the crocodiles but rather to protect the fish and allow them to breed in these areas (B. Marshall pers., comm.).

The ecological production of the littoral zone of Lake Kariba can be estimated by multiplying the standing crop by the production/biomass ratio which is species specific (Balon and Coche 1974, Mahon and Balon 1977, Marshall and Langeman 1988, Hustler and Marshall 1990). This production is about 44,000 tonnes yr^{-1} (Table 9.12 in Hustler this volume). The predation by crocodiles (maximum 225 tonnes yr^{-1}) is removing only 0.5% of this amount. The actual catch by gill net fishermen on the littoral zone was about 2000 tonnes in 1985–1990 on the Zimbabwean side of Lake Kariba (Sanyanga and Muchabaima 1994) and crocodiles are only eating the equivalent of 10–15% of what is removed by artisanal fisheries. So, we can infer that the potential impact of predation by crocodiles on fish populations is negligible when compared to the one of fisheries.

CONCLUSION

This work shows that there is no major competition between crocodiles and fishermen for the fish resources of Lake Kariba. The crocodile industry is valuable and provides income at both the local and national level and also generates foreign currency (an estimated US $ 3 million in 1990). Further investigations are needed in order to assess the suitability of a new zonation of the shoreline to exclude fishermen from crocodile areas. It might also be advisable to remove crocodiles from heavily fished areas, preferably by trapping as it is possible that these animals will eventually be caught in nets and drowned. Their removal could also be seen as an attempt to balance issues affecting the artisanal fishery as the major source of conflict between fishermen and crocodiles is the destruction of nets (Nauen 1995); these are expensive to replace and time consuming to repair. This exercise has already started with the removal of large crocodiles from sensitive areas in 1992.

Although there may be several sources of error in the estimate of intake of fish by crocodiles from Lake Kariba (e.g. numbers, feeding interval, mean prey size), this study clearly shows the small relative impact of fish predation by crocodiles when compared to fishing. Information of this nature will be extremely important when management decisions are made, especially as one can only expect the conflict (real or imagined) between crocodiles and fishermen to increase for various reasons (pressure to have new gill net fishing grounds, damages on gill nets by crocodiles). In this aspect, Lake Kariba may be representative of other African lakes which sustain artisanal fisheries.

SUMMARY

The primary objective of this paper was to assess the impact of crocodiles on the fish populations of Lake Kariba as compared to the one of fisheries.

First, the age structure and size of the population was estimated in a protected area of Lake Kariba (the Ume estuary). A second study site was located in Cahora Bassa, Mozambique, 300 km downstream from Lake Kariba for comparison purposes. As a result, the mean population estimate for the Zimbabwean side of Lake Kariba was 6,500 crocodiles of all sizes with approximately 3,500 of these being larger than 1.4 m TL (i.e. sub-adults and adults). The size structure of the Zambezi population in three broad categories was assessed to be 46% juveniles, 34% sub-adults and 20% adults. Using skeletochronology, length at age data were obtained and it was estimated that a female crocodile in Lake Kariba will spend 6% of her life as a juvenile, 19% as a sub-adult and 75% as an adult. As males grow quicker they will spend 6% as juveniles, 11% as sub-adults and 83% as adults (longevity assumed to be 80 years).

A feeding study showed that the importance of fish in the diet increases while crocodiles are between 1.4 m and 2.6 m TL. When estimated by weight fish accounts for 98% of the diet. This figure declines to around 33% in adult crocodiles. Fish were digested to 10% of their original volume after 2 days in the stomach.

Feeding frequency in sub-adult and adult crocodiles and gastric digestion rate were determined and intake estimated by using a model developed during this study. Using the feeding frequencies an annual estimate of fish consumption from Lake Kariba was proposed (mean = 140.14 tonnes; upper estimate 225.39 tonnes).

If the estimate of total offtake (225 tonnes) is accepted then crocodiles (working with the upper estimate of the population size) are only eating the equivalent of 10–15% of what is removed by the artisanal fishery. Consequently, there is no major competition between crocodiles and fishermen for the fish resources of Lake Kariba. The crocodile industry is valuable and provides income at both the local and national level and also generates foreign currency (an estimated US $ 3 million in 1990). In order to avoid possible conflicts between artisan fishermen and crocodiles industry, it is suggested that crocodiles be removed from heavily fished areas as already operated on a pilote scale.

ADVANCES IN THE ECOLOGY OF LAKE KARIBA

This book assembles contributions of several authors engaged in the SAREC/UZ Project on the Ecology of Lake Kariba. Various problems, regarded as particularly important, are dealt with, for instance:

- The evolution of the lake in time;
- The function of the pelagic ecosystem with focus on *Limnothrissa miodon* and the reason of variations of yields;
- The relations between the primary production and the fish production in the littoral area;
- The possible impact the large water level fluctuations on the nutrient flow and production on the grass land and in the littoral region;
- The utilisation of the mussel resource;
- The competition between fishermen, fish-eating birds and crocodiles.

This is an essential reading for students, academics and environment managers interested in tropical aquatic ecology in Zimbabwe and in the rest of the world.

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