15. Trophic relations of fishes in Lake Chad

Laurent Lauzanne

In a stable ecosystem, three main types of organisms can be distinguished: the producers, the consumers and the 'decomposers-transformers' (Dussart 1966).

The producers, which are autotrophic organisms, synthesize their own matter from mineral elements present in the environment. The energy used is usually solar (photosynthetic plants), but it can also be of chemical origin (chemosynthetic organisms, represented by some bacteria). The consumers use the organic matter produced by the autotrophic organisms to make their own biomass. All these consumers are connected by feeding relationships to form the predatory food chain.

The 'decomposers-transformers' degrade the organic matter of plants and dead animals to transform it into mineral salts. They are mostly heterotrophic bacteria and constitute the degradation food chain. The organic matter that is produced can then be used again by the autotrophs.

In fact the situation is more complex than this classical description of the food cycle (Elton 1927). In addition to the plant matter produced by photosynthesis, all the detritus from the predatory chain that is almost degraded and yet mineralized is available to the consumers. This detritus and the decomposer organisms, settle to the lake bottom and constitute the benthic organic cover. In the case of a deep lake, this organic cover is generally less important because mineralization will occur during settlement of the detritus. In shallow Lake Chad, the detritus settles rapidly and this organic cover is important. The detrivores consuming this cover, therefore, reintroduce organic matter into the food cycle which, without them, would have had to pass, as a whole through the group of the 'decomposers-transformers' to be reutilized by the ecosystem.

From these two original food sources of plant and detrital organic cover, we are therefore able to distinguish two food chains namely a grazing food chain and a detritus food chain (Fig. 1).

For each of these two chains, we will make the traditional distinction of trophic levels where the organisms from a level feed on organisms from the level immediately below it. We can distinguish fairly easily the first three levels where trophic relationships are relatively direct. The first level is composed of the

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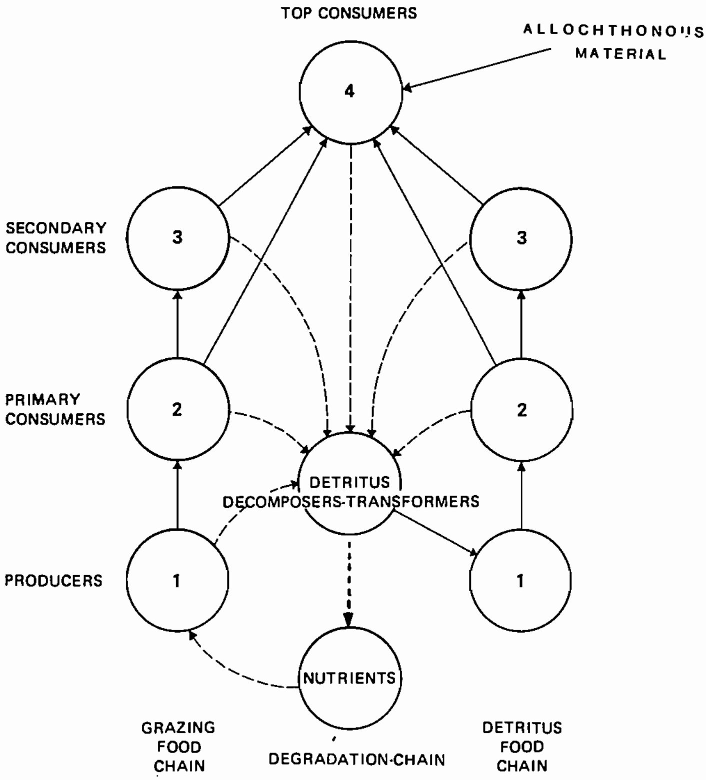

Fig. 1 Food cycle pattern in Lake Chad. Numbers correspond to trophic levels; arrows indicate the direction of energy transfers — continuous lines: by predation; dashed lines: by degradation (from Lauzanne 1976).

plants and detrital organic cover.* The second level includes the primary consumers which feed on plants and detritus. The third level is composed of the secondary consumers which feed mainly on the invertebrates of the zooplankton and benthos. A fourth level that is common to both chains gathers together the top consumers. These animals have complicated trophic relationships with the other three levels and even with organisms not belonging to the aquatic ecosystem (mainly terrestrial insects). In this case, we cannot refer to it as a food chain but rather as a food web (Cooper and Fuller 1945). In this report, we will deal with the study of trophic relationships through two approaches. First, a qualitative approach based mainly on the knowledge of the

* The first level ought to be strictly reserved for autotrophic organisms such as macrophytes, phytoplankton and some bacteria. The complex organic cover is however composed of a very high percentage of sedimented algae and fine plant debris, and thus placed in the first level.

diets of the fish and a quantitative approach describing the transfer of energy as organic matter moves from one trophic level to a higher one through predation.

15.1 Qualitative aspects

15.1.1 *The environment and available food*

The trophic relationships of the fishes in Lake Chad were studied mainly in its southeastern part which includes a zone of open water and an archipelago (Lauzanne 1976). The geographic, climatic and physico-chemical features of these two zones are described in detail at the beginning of this book and will not be repeated. Nevertheless, we should point out that the annual fluctuations in lake level follow the variations in the Shari flood after a time lag. Therefore, it is possible to distinguish a flood period in the lake from July to December and a period of low water from January to June. It will be shown later that this alternation of high and low water has an influence on the abundance of some prey.

In this ecosystem, nine major food types can be distinguished: phytoplankton, macrophytes, organic cover of the bottom, zooplankton, benthos, aquatic insects, shrimps, preyfishes and a food source from outside the aquatic ecosystem which is represented by terrestrial insects. These different types of food are described in varying detail in this volume. However, we will reconsider these different food classes by trying to define the features typical of the two main zones under study (archipelago and open water) and specifying the feeding preferences of each major group.

The phytoplankton

Generally, Cyanophyceae dominated the phytoplankton and always represented more than 90% of the total number of cells (Gras et al. 1967). The genera *Microcystis*, *Aphanocapsa* and *Anabaena* were the best represented. The seasonal variations in density were very low in the archipelago, while they were considerable in the open water. In the latter zone, phytoplankton density was very low from August to December due to a direct influence of the Shari flood.

The macrophytes

The open water did not contain macrophytes, while in the archipelago, each island was surrounded by a plant fringe several meters wide that was composed mainly of Cyperaceae and Graminaceae. Submerged aquatic plants, mainly *Potamogeton* and *Vallisneria* along with *Najas* and *Ceratophyllum* occurred in patches. The leaves of the aquatic plants and the seeds of various plants were utilized by several species of fish.

The organic bottom layer

This flaky-looking cover was composed of a detrital layer (fine plant debris, algae and planktonic crustacea which settled after death, faeces of the different organisms present in the overlying water and colloidal clay) and a live organic layer (bacteria, benthic diatoms, protozoa and Rotifera). it was very difficult to determine the importance of these different constituents, but the dominance of planktonic algae was shown through simple microscopical examination.

The zooplankton

In Lake Chad, the zooplankton was characterized by the predominance of crustacea such as the Copepoda and the Cladocera over the Rotifera, since the first grouping represented about 85% of the total number of individuals (Gras et al. 1967). The mean biomass in the archipelago was well above that of the open water and it was more stable over the year. The zooplankton in the open water, like the phytoplankton, underwent a sharp decrease from August to December, probably for the same reasons. The trophic structure of the zooplankton communities was similar in the different regions of Lake Chad (Gras et al. 1971) and most of the zooplankton was phytophagous since the predatory species represented only 6% of the total biomass.

The benthos

The benthic fauna in Lake Chad was composed mainly of molluscs, insect larvae and oligochaetes. Nematodes and Ostracoda were also present but they did not seem to make up a major part of the biomass (Dejoux et al. 1969). The true benthic species were of minor importance. The molluscs represented by seven main species and the Oligochaeta by three main species. The insect larvae were more diverse and were mainly chironomids.

The benthic molluscs were, either Gasteropoda that browsed on the organic cover of the bottom or Lamellibranchia that filtered the same cover. The Oligochaeta ingest the surface sediment from which they extract the organic matter (detritus, algae, bacteria). Generally, insects are detrivores, except the carnivorous Tanipodinae (Dejoux 1974). On the whole, it can be estimated that most of the benthic invertebrates were detrivores, and obtained their food from the organic layer on the bottom, the complexity of which has been emphasized.

The aquatic insects

The larvae of the chironomids, Ephemeroptera and Trichoptera were considered to be part of the benthos. Therefore, this section of the community consisted of the nymphs of Hemiptera, Chaoborus and Ephemeroptera adults of *Chaoborus* and imagos of chironomids and Trichoptera as well as Coleoptera.

The swimming insects which were only abundant in the submerged plants, were probably of little importance in high water.

Shrimps

During the period of 'Normal Chad', the shrimps (*Caridina africana* and *Macrobrachium niloticum* were very abundant in the archipelago and almost absent in the open water. The former was attached to the submerged plants while the latter was also found in offshore water. It appeared that the shrimps were much more abundant in low water than during the flood. *Caridina* feeds mainly on epiphytes and detritus (Fryer 1960) while *Macrobrachium* is clearly a detritus eater (Hopson 1972).

Prey fishes

On reaching a certain stage of growth, all the species of fish could be eaten by larger fish. However, certain species were consumed more regularly than others, probably because they were more abundant. The following list mentions the species most often caught by predators. It includes young fish belonging to large and small species (the latter indicated with an asterisk).

Characidae	*Alestes baremoze*
	Alestes dentex
	*Alestes dageti**
	*Micralestes acutidens**
Schilbeidae	*Eutropius niloticus*
Mormyridae	*Pollimyrus isidori**
	Petrocephalus bane
Citharinidae	*Distichodus rostratus*
Cyprinidae	*Labeo* sp.
	Barbus sp.*
Cichlidae	*Tilapia* sp.
	*Haplochromis bloyeti**
Mochocidae	*Brachysynodontis batensoda*

Among the small species, *Barbus* and *Haplochromis* only occurred among submerged plants, and were not found in open water. The young of large species such as *Labeo*, *Distichodus*, *Alestes baremoze* were abundant during the flood. This can be explained by the fact that most species in the Chad basin reproduce at the beginning of the flood.

The terrestrial insects

For certain fishes, terrestrial insects were of major importance as a food source, especially in the open water. These insects which live and feed on the vegetation of the islands and reed islands were carried away by the winds to fall into the water and drown. The insects consumed were Coleoptera, Hemiptera and especially Orthoptera which were often relatively large. The fall-out of terrestrial insects was especially important during flooding of the lake.

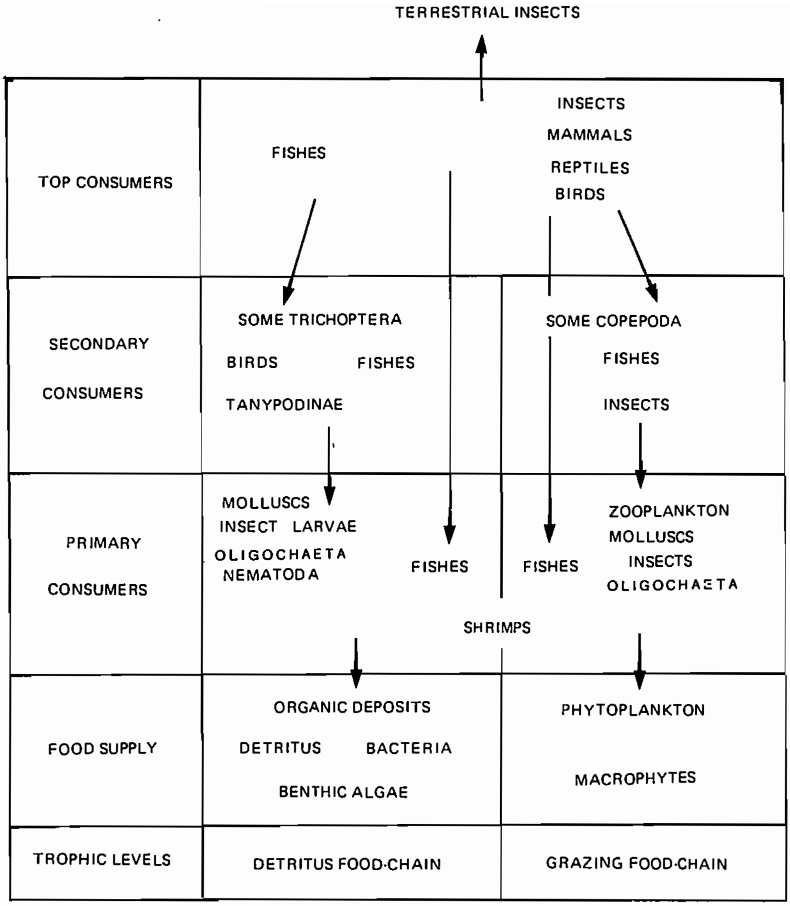

Fig. 2 Trophic relationships in Lake Chad; arrows indicate the direction of predation.

Based on the preceding observation on the feeding of the different groups of organisms, we have classified them according to their trophic levels (Fig. 2). Later, a discussion of their diets will show that the different species of fish were represented in all the consumer groups.

15.1.2 *Selection of species studied*

The choice of species was based on their importance in the population samples. In the archipelago, the results of catches by a large beach seine were used. This was relatively unselective since, theoretically, it took samples of all the species within a certain size range. In water where it was impossible to use this type of seine, we used as a base the catches from a set of 10 gill nets, in spite of doubts raised by their selectivity. We chose for study the species representing at least 1% of the total weight of the catches. They included 17 species in the archipelago and 17 in the open water (Table 1) of which 13 were common to the two biotopes. Thus, the total number of species was 21.

15.1.3 *The main types of diets – trophic levels*

The detailed results of the stomach content analyses of the species studied (Lauzanne 1976) were arranged according to ten food types. They include the nine types mentioned above, as well as fish debris such as large scales, vertebrae and spines. These results collect together the data without considering possible differences in diets related to the two hydrological seasons (flood and recession) and the two biotopes (archipelago and open water). For each species, the diets were determined by the percentage occurrence and the volumetric percentages

Table 1 Ponderal index of the main species in the Archipelago (Arch.) and the Open water (O.W.) expressed as a percentage of the biomass.

Species	Arch.	O.W.
Brachysynodontis batensoda (Mochocidae)	16.1	2.1
Sarotherodon galilaeus (Cichlidae)	12.5	–
Lates niloticus (Centropomidae)	11.5	12.4
Alestes baremoze (Characidae)	10.5	4.1
Alestes dentex (Characidae)	10.4	–
Hemisynodontis membranaceus (Mochocidae)	7.1	4.2
Hydrocynus forskalii (Characidae)	4.6	20.3
Hydrocynus brevis (Characidae)	3.4	4.3
Labeo senegalensis (Cyprinidae)	3.2	2.0
Schilbe uranoscopus (Schilbeidae)	2.7	14.1
Alestes macrolepidotus (Characidae)	1.8	–
Hyperopisus bebe (Mormyridae)	1.7	1.8
Eutropius niloticus (Schilbeidae)	1.7	10.8
Synodontis schall (Mochocidae)	1.6	3.3
Citharinus citharus (Citharinidae)	1.5	1.6
Heterotis niloticus (Osteoglossidae)	1.4	–
Bagrus bayad (Bagridae)	1.2	1.9
Distichodus rostratus (Citharinidae)	–	3.5
Labeo coubie (Cyprinidae)	–	2.9
Citharinus distichodoides (Citharinidae)	–	2.6
Synodontis clarias (Mochocidae)	–	1.8
Miscellaneous	7.1	6.3

(Hynes 1950) of each type of food and a food index, IA, which takes these two factors into account (Lauzanne 1975):

$$IA = \frac{\% \; OC \; X \; \% \; V}{100}$$

The results (Table 2) are illustrated by Fig. 3 where the species were grouped according to their food preferences and ranked among the major categories of consumers defined above.

15.1.3.1 *Dominant primary consumers.* This group of consumers included the phytoplanktophagous, the detritivorous and the macrophytophagous fishes. The phytoplanktophagous fishes were represented by a single species, *Sarotherodon galilaeus* and the detrivorous fishes by *Labeo senegalensis*, *Labeo coubie*, *Distichodus rostratus*, *Citharinus citharus* and *Citharinus distichodoides*. These five species fed on the organic bottom layer. In fact, the main difference between these two diets arose from differences in the feeding behaviour of the five species. *Sarotherodon galilaeus* is a filter-feeder which selects mainly algae and even certain types of algae (Lauzanne and Iltis 1975), while *Labeo*, *Citharinus* and *Distichodus* sample the whole bottom layer and even take a small amount of the underlying sediments. However, most of this cover was composed of sedimented algae, which led to the classification of these detrivorous fishes among the primary consumers. The dominant macrophyte-consuming fish was *Alestes macrolepidotus* (macrophytes forming 100% OC, 59% V) with a preference for the young leaves of *Potamogeton* and *Ceratophyllum*. However, insects, particularly terrestrial, were also important in the diet.

15.1.3.2 *Secondary consumers*

15.1.3.2.1 *Dominant zooplankton feeders.* This group was composed of the following four species: *Alestes baremoze*, *Hemisynodontis membranaceus*, *Brachysynodontis batensoda* and *Alestes dentex*. The first two species fed strictly on zooplankton, but the diets of the last two had secondary components. *Brachysynodontis* fed on insects, especially swimming larvae and nymphs. In addition to the zooplankton and the insects, *Alestes dentex* also consumed seeds (Graminaceae and Cyperaceae). The zooplankton taken by these four species was mainly crustacea (Copepoda and Cladocera), with Rotifera only of secondary importance.

15.1.3.2.2 *Dominant benthos feeders.* The four species representing this group were: *Synodontis clarias*, *Synodontis schall*, *Hyperopisus bebe* and *Heterotis niloticus*. These fishes fed mainly on benthic invertebrates present in the organic bottom cover (insect larvae, Ostracoda and molluscs). *Synodontis schall* was strictly benthophagous, while the other three species were less selective. *Synodontis clarias* fed almost entirely on benthos with the exception of a few terrestrial insects. *Hyperopisus bebe* also ingested seeds (*Hypomea*) and

Table 2 Percentages of occurrence and volume, food indices (IA = %C × %V/100) for the 21 species under study.

Species	Entire fishes			Fish detritus			Shrimps			Aquatic insects		
	%OC	%V	IA	%OC	%V	IA	%OC	%V	IA	%OC	%V	IA
Sarotherodon galilaeus												
Labeo senegalensis												
Labeo coubie												
Citharinus citharus												
Citharinus distichodoides												
Distichodus rostratus												
Alestes macrolepidotus										83.8	11.4	9.5
Alestes baremoze												
Hemisynodontis membranaceus												
Alestes dentex										27.8	18.7	5.2
Brachysynodontis batensoda										30	4.3	1.3
Synodontis schall												
Synodontis clarias												
Hyperopisus bebe												
Heterotis niloticus							18.9	10.7	2.0			
Lates niloticus	100	100	100									
Hydrocynus brevis	100	100	100									
Hydrocynus forskalii	86.1	74.5	64.1				24.0	25.3	6.1	0.2	0.1	
Bagrus bayad	57.0	68.3	38.9	34.0	9.4	3.2	44.0	7.1	3.1	29.0	1.4	0.4
Eutropius niloticus	36.0	30.0	10.8	31.8	16.0	5.1	2.5	0.8	0.1	13.8	1.2	0.2
Schilbe uranoscopus	52.5	67.0	35.2	18.2	13.5	2.4	24.2	9.6	2.3	17.2	0.6	0.1

Table 2 (continued).

Species	Terrestrial insects			Benthos			Zooplankton			Phytoplankton		
	%OC	%V	IA	%OC	%V	IA	%OC	%V	IA	%OC	%V	IA
Sarotherodon galilaeus										100	100	100
Labeo senegalensis												
Labeo coubie												
Citharinus citharus												
Citharinus distichodoides												
Distichodus rostratus												
Alestes macrolepidotus	78.4	30.0	23.5									
Alestes baremoze							100	100	100			
Hemisynodontis membranaceus							100	100	100			
Alestes dentex							94.4	68.0	64.2			
Brachysynodontis batensoda							100	95.7	95.7			
Synodontis schall	20.0	2.9	0.6	100	97.1	97.1						
Synodontis clarias	27.0	1.4	0.4	100	98.6	98.6						
Hyperopisus bebe				97.7	96.2	94.0						
Heterotis niloticus				100	61.1	61.1	32.4	11.8	3.8			
Lates niloticus												
Hydrocynus brevis												
Hydrocynus forskalii												
Bagrus bayad	16.0	7.1	1.1	20.0	6.7	1.3						
Eutropius niloticus	67.1	50.3	33.7	17.3	1.7	0.3						
Schilbe uranoscopus	20.2	6.9	1.11	38.4	2.4	0.9						

Table 2 (continued).

Species	Organic deposits			Macrophytes			Number of stomachs studied	Limits of standard lengths (mm)
	%OC	%V	IA	%OC	%V	IA		
Sarotherodon galilaeus							*	155–275
Labeo senegalensis	100	100	100				81	200–460
Labeo coubie	100	100	100				22	180–450
Citharinus citharus	100	100	100				55	160–500
Citharinus distichodoides	100	100	100				16	350–550
Distichodus rostratus	100	100	100				38	180–400
Alestes macrolepidotus				100	58.7	58.7	37	125–210
Alestes baremoze							*	150–265
Hemisynodontis membranaceus							118	250–340
Alestes dentex				18.9	13.3	2.5	90	145–265
Brachysynodontis batensoda							110	100–160
Synodontis schall							135	145–260
Synodontis clarias							37	180–240
Hyperopisus bebe				9.4	3.8	0.4	128	200–440
Heterotis niloticus				81.1	16.3	13.2	37	350–435
Lates niloticus							73	390–1310
Hydrocynus brevis							86	270–610
Hydrocynus forskalii							251	150–380
Bagrus bayad							100	160–435
Eutropius niloticus							283	110–235
Schilbe uranoscopus							99	180–235

* Some hundreds.

TERRESTRIAL INSECTS

TROPHIC LEVELS	DETRITUS FOOD-CHAIN	GRAZING FOOD-CHAIN
4 TOP CONSUMERS	*LATES NILOTICUS* *HYDROCYNUS BREVIS* *HYDROCYNUS FORSKALII*	*BAGRUS BAYAD* *SCHILBE URANOSCOPUS* *EUTROPIUS NILOTICUS*
3 SECONDARY CONSUMERS	*SYNODONTIS SCHALL* *SYNODONTIS CLARIAS* *HYPEROPISUS BEBE* *HETEROTIS NILOTICUS*	*BRACHYSYNODONTIS BATENSODA* *HEMISYNODONTIS MEMBRANACEUS* *ALESTES DENTEX* *ALESTES BAREMOZE*
2 PRIMARY CONSUMERS	*CITHARINUS CITHARUS* *DISTICHODUS ROSTRATUS* *CITHARINUS DISTICHODOIDES* *LABEO COUBIE* *LABEO SENEGALENSIS*	*SAROTHERODON GALILAEUS* *ALESTES MACROLEPIDOTUS*
1 FOOD SUPPLY	ORGANIC DEPOSITS	PHYTOPLANKTON EPIPHYTES MACROPHYTES

Fig. 3 The different kinds of consumers in Lake Chad.

Heterotis niloticus consumed shrimps and zooplankton in addition to benthos and seeds.

The main insect larvae consumed were Chironomids (Chironominae and Tanipodinae), Ephemeroptera (*Povilla adusta*) and Trichoptera (*Dipseudopsis* and *Ecnomus*).

Predation upon molluscs was mostly on undersized individuals. They were small species (young and adult *Gyraulus, Bulinus, Anisus, Segmentorbis, Gabbia, Pisidium, Eupera*), but also young immature individuals of larger species (*Bellamya, Cleopatra, Biomphalaria, Melania, Corbicula*).

15.1.3.3 *Top consumers*. This carnivorous group was composed of six species of which two were piscivorous only, while four of them had diets with more or less varied secondary components.

15.1.3.3.1 *Strictly piscivorous group*. *Lates niloticus* and *Hydrocynus brevis* are predators which feed only on living fishes. *Lates niloticus* can grow very large (maximum length observed: 132 cm for a weight of 78 kg), and has a stocky poorly streamlined shape.

Hydrocynus brevis does not grow so large (maximum length observed: 80 cm for a weight of 10 kg), but unlike *L. niloticus*, it is extremely streamlined and swims very fast. It is a tireless pursuer which does not give its prey many chances. Its jaws have formidable teeth enabling it to cut its prey into two parts with a single bite. It will even attack large fishes to take a bite from them as shown by Lewis (1974) in Lake Kainji.

15.1.3.3.2 *Less strictly piscivorous group*. The common characteristic of the four species in this group was that all of them consumed shrimps and aquatic insects in addition to fish. *Schilbe uranoscopus*, *Eutropius niloticus* and *Bagrus bayad* consumed not only whole fishes which were probably caught when alive but also a considerable amount of fish debris composed mainly of very large scales, large vertebrae and several bones such as spines and pectoral fins of *Synodontis*. It initially seemed as if this debris came from whole prey which were degraded by digestive juices, but it became obvious after investigation that the size of the predator was not great enough for ingestion of prey corresponding to the size of debris found. In these three species, the terrestrial insects played a significant role and were even very important for *Eutropius niloticus*. These three species with saprophagous tendencies were clearly different from *Hydrocynus forskalii* which fed mainly on live prey such as fish but also on large quantities of shrimps.

15.1.4 *Comparison of trophic relationships in the archipelago and in the open water*

As already observed, the trophic relationships of fish in trophic levels 2 and 3, that is the primary and secondary consumers, were rather direct. When, most of the food consumed by a given level comes from the next lower level it is part of a food chain. The trophic relationships of top consumers are much more complex as the food comes from all the trophic levels and even from food sources outside the aquatic ecosystem (terrestrial insects). Moreover, nutritional relationships can exist between the different constituents of this level, forming a food web. Lauzanne (1976) quoted figures which showed the trophic relationships of fishes in the archipelago and the open water where the inputs from each trophic level were indicated (as volumetric percentages) in the diet of each species.

15.1.4.1 *Primary and secondary consumers.* It was observed that trophic relationships were direct in the open water with the exception, however, of the inclusion of a small number of terrestrial insects in the diet of the secondary consumers of the detrital chain. In the archipelago (Fig. 4), the trophic relationships were less direct. For instance only 59% of the food of *Alestes macrolepidotus* (dominant primary consumer) consisted of macrophyte leaves. Some dominant secondary consumers obtained a certain amount of food from level 1 (macrophyte seeds).

15.1.4.2 *Top consumers.* The food web of the top consumers in the archipelago (Fig. 6) was complex and requires further explanation.

1. The secondary benthos feeders were not part of the food of the top consumers.

2. Of the primary consumers, *Sarotherodon* (phytoplankton feeder) and shrimps (detritus feeders) were important in the diet of *Lates niloticus* (75% *Sarotherodon galilaeus*) and *Hydrocynus forskalii* (56% shrimps). Fishes that ate detritus occurred in the diets of *L. niloticus*, *H. forskalii* and *H. brevis*.

3. The secondary consumers of the algal chain represented an important part of the diets. Zooplankton feeders were consumed by all the predators but were particularly important especially in the diets of *H. brevis* and *S. uranoscopus*. Fish eating periphytic zooplankton which were small species found among submerged plants (*Barbus*, *Haplochromis*) formed the diet only of the smaller predators (*E. niloticus*, *S. uranoscopus* and *H. forskalii*).

4. The input of aquatic insects, benthic invertebrates and fish debris could be of some significance for *Eutropius* and *Bagrus*.

5. The food supply from outside the aquatic ecosystem was composed of terrestrial insects and was only of major importance in the diet of *Eutropius*.

6. The nutritional relationships between the top consumers were fairly limited; *Eutropius* was only consumed by *H. brevis* (19%) and *Bagrus* (15%).

The food web of the top consumers in the open water was much simpler than that in the archipelago (Fig. 7).

1. As in the archipelago, predators did not feed on the secondary benthos feeders

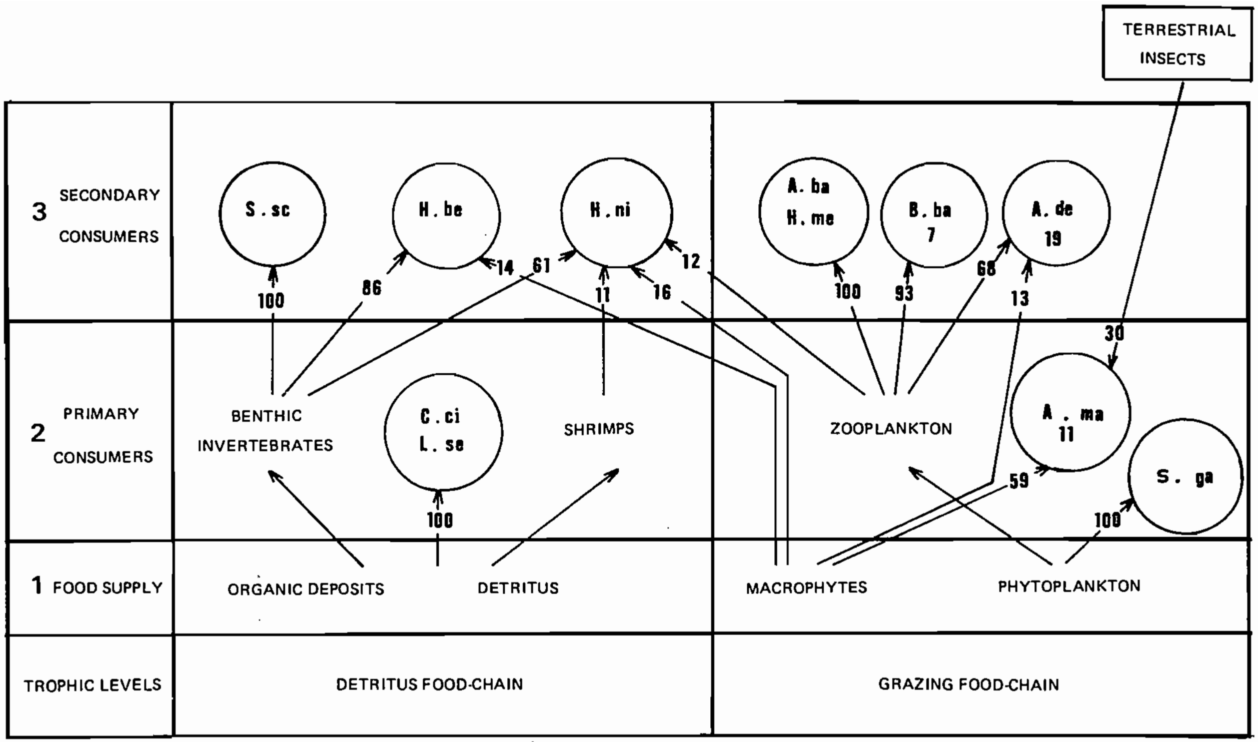

Fig. 4 Food webs of primary and secondary consumers in the Lake Chad archipelago. Arrows indicate the direction of transfers and the numbers correspond to the volumetric percentages of the input to the diets. Numbers in circles correspond to prey whose trophic position is unknown; S. sc = *Synodontis schall*; H. be *Hyperopisus bebe*; H. ni = *Heterotis niloticus*; A. ba = *Alestes baremoze*; H. me = *Hemisynodontis membranaceus*; B. ba = *Brachysynodontis batensoda*; A. de = *Alestes dentex*; A. ma = *Alestes macrolepidotus*; S. ga = *Sarotherodon galilaeus*; C. ci = *Citharinus citharus*; C. di = *Citharinus distichodoides*; L. se = *Labeo senegalensis*; L. co = *Labeo coubie*; D. ro = *Distichodus rostratus*; S. cl = *Synodontis clarias*.

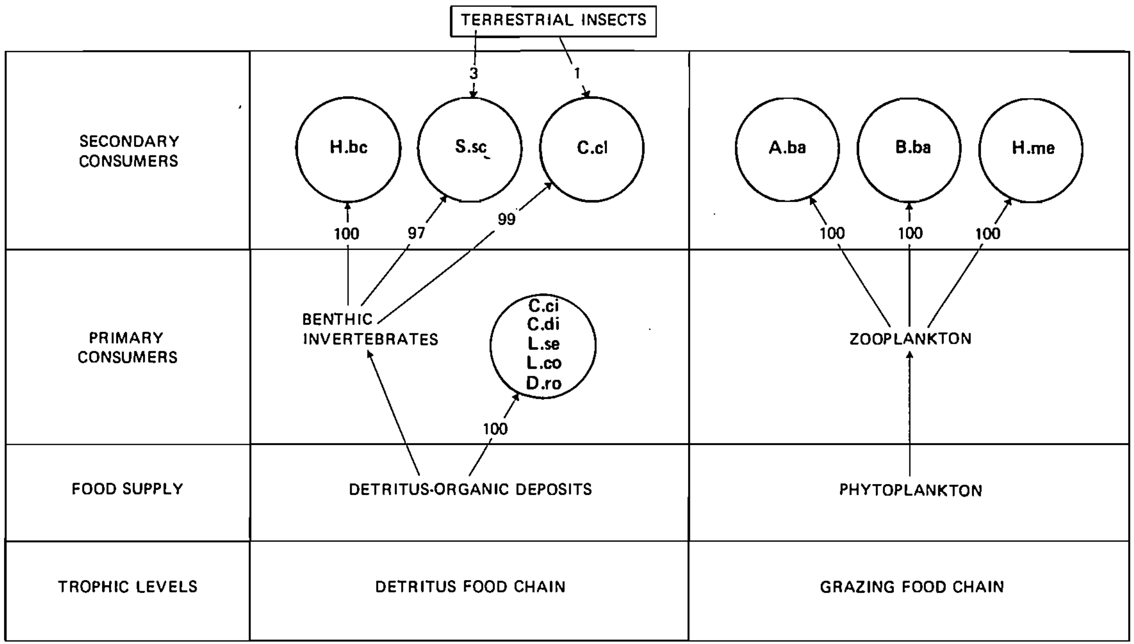

Fig. 5 Food webs of primary and secondary consumers in Lake Chad open water (see Fig. 4).

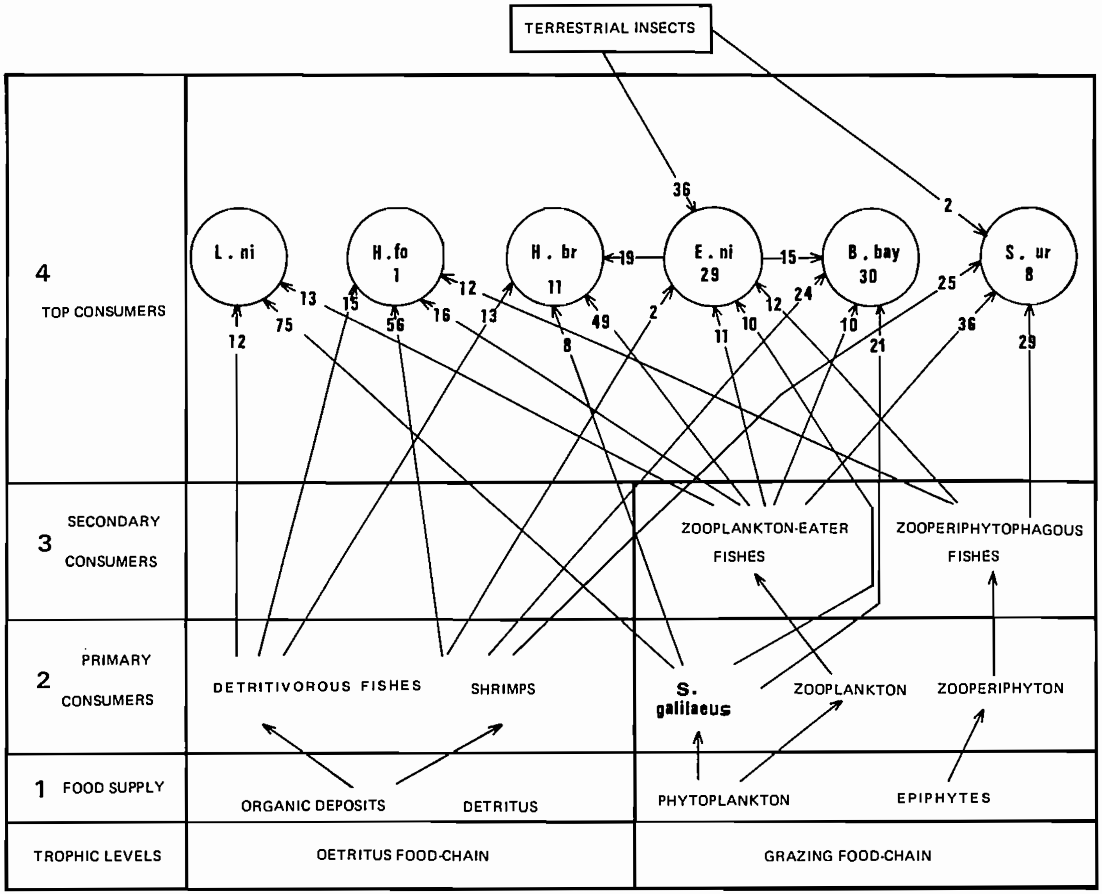

Fig. 6 Food webs of top consumers in the Lake Chad archipelago; L. n = *Lates niloticus*; H. fo = *Hydrocynus forskalii*; H. br = *Hydrocynus brevis*; E. ni = *Eutropius niloticus*; B. bay = *Bagrus bayad*; S. ur = *Schilbe uranoscopus*.

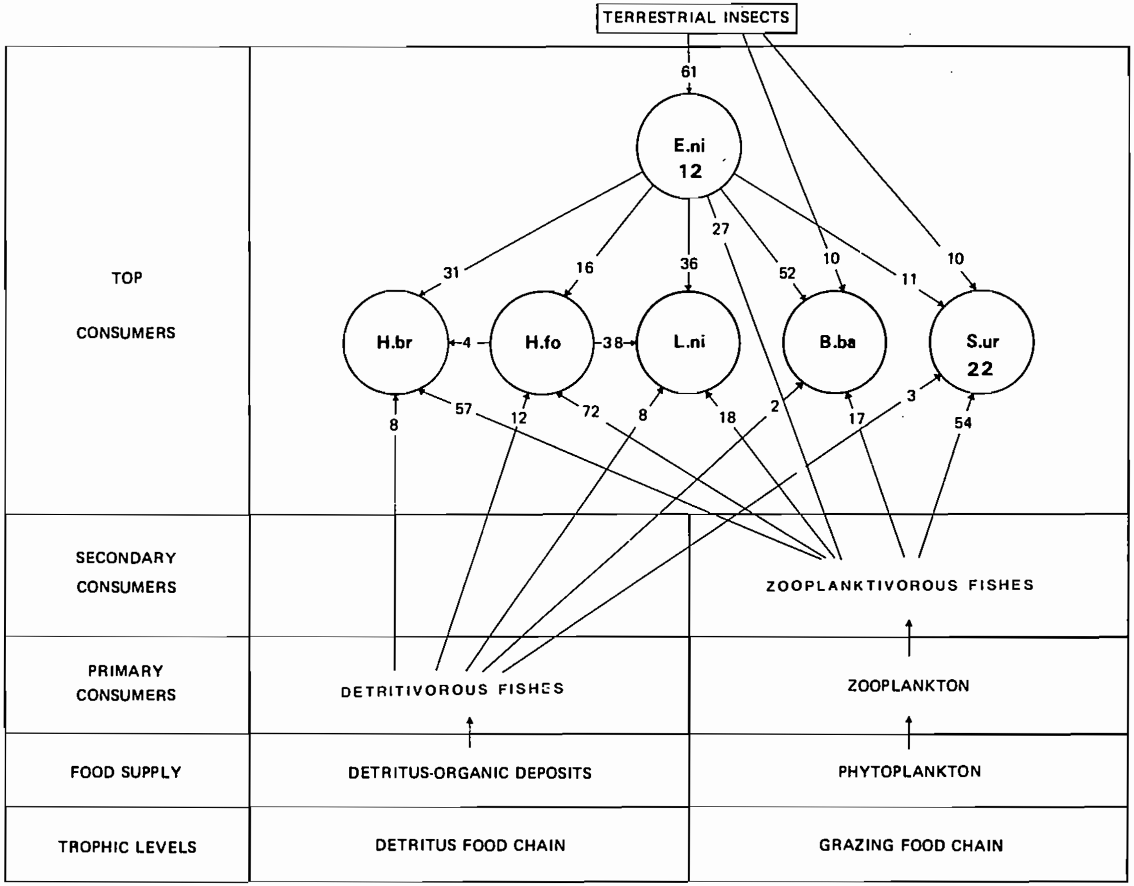

Fig. 7 Food webs of top consumers in Lake Chad open water (see Fig. 6).

2. The primary consumers were represented only by detritivores which constituted a small part of the diets.

3. The secondary consumers of the grazing food chain were important in the diets of all the predators.

4. The supplies of aquatic insects, benthos and fish debris were less important than in the archipelago.

5. The terrestrial insects played a secondary role in the feeding of *Bagrus* and *Schilbe* but were important for *Eutropius* (61%).

6. The food relationships between the predators were characterized by the role of *Hydrocynus forskalii* in the diet of *Lates* (38%), and especially by the considerable importance of *Eutropius* in the diets of the five species. In short, it can be estimated that the trophic relationships were much more diversified in the archipelago than in the open water. This was because of the absence of certain types of food (macrophytes, shrimps and periphytic zooplankton) in the open water.

15.1.5 *Comparison of the importance of the various consumer groups between the archipelago and the open water*

In the previous section, it was shown that within the four major group of consumers, the diets could differ considerably according to the biotope.

They were more varied in the archipelago where the types of food were more diversified. It was also observed that certain groups of organisms could become very important quantitatively in the diets, depending on the zone under study (the molluscs and terrestrial insects in the open water and shrimps in the archipelago). Nevertheless, these four groups were present in the two zones and it is interesting to compare their relative importance. From Fig. 8 (Lauzanne 1976) the following can be concluded:

1. The primary consumers, whether they were detrivorous or phytophagous, were of moderate importance in the archipelago (19%) as well as in the open water (13%).

2. The secondary consumers were present in small numbers in the open water (benthos, feeders, 7%; zooplankton feeders, 10%), while they dominated in the archipelago (benthos feeders, 5% and particularly zooplankton feeders: 44%).

3. The top consumers which were well represented in the archipelago (25%) played a major role in the open water (64%).

These two zones in the southeast of Lake Chad differed greatly in the abundance of the various consumer groups. In the archipelago, the zooplankton feeders dominated, while the open water was characterized by the abundance of the top consumers, due to the particular trophic relationships in each zone. On the one hand these consumers fed on zooplanktophagous fishes such as the two small species *Pollimyrus* and *Micralestes* which probably had

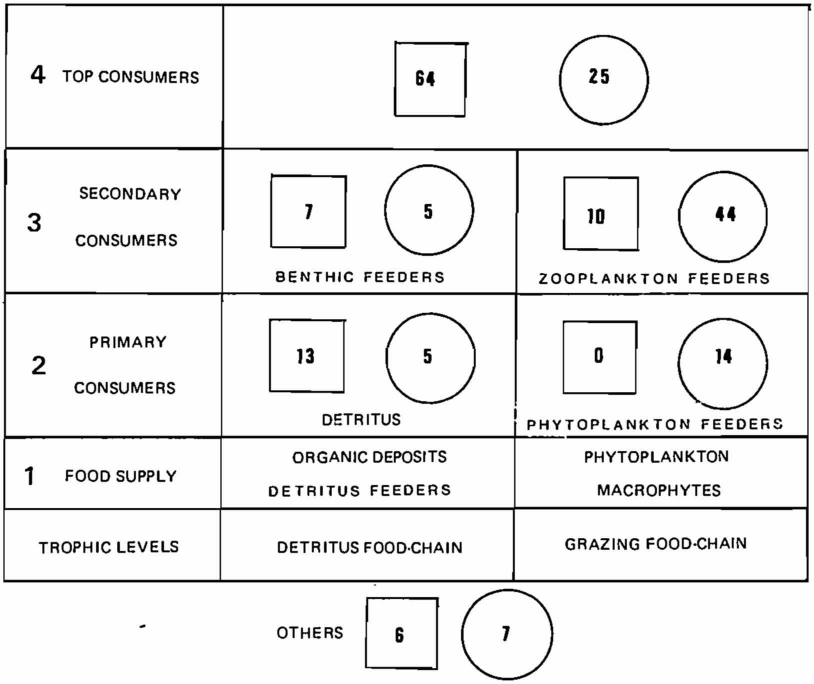

Fig. 8 Comparison of the importance of various consumer groups in the archipelago (circles) and the open water (squares). Numbers expressed as percentage of the biomass.

high production. On the other hand, they fed on the terrestrial insects which constituted the major food of *Eutropius niloticus* which was itself consumed in large quantities by all the other predators.

15.1.6 *Variations in diets and changes of trophic levels*

In Lake Chad, where food was abundant and varied, the adult fishes fed permanently on the same trophic level. However, their diets could undergo small variations depending upon the biotopes and the seasons. As already described, the diets of fishes in the open water were thus less diverse than those in the archipelago, mainly because there was a shortage of the food supply such as the shrimps and macrophytes in the first biotope while these were abundant in the second one. The influence of the hydrological seasons in Lake Chad upon the diets (Lauzanne 1976), was especially pronounced in the top consumers. So, during the flood, the predators consumed a greater number of young fishes of the large species than during the fall (Fig. 9b). This phenomenon was due to the

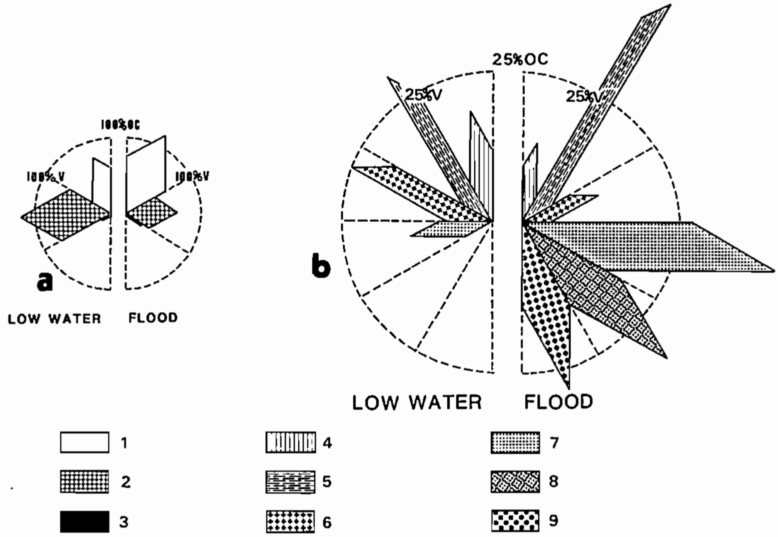

Fig. 9 Diet of *Hydrocynus forskalii* in the Lake Chad archipelago; (a) diet composition; (b) fishes; 1 = fish; 2 = shrimps; 3 = *Micronecta*; 4 = *Barbus callipterus*; 5 = *Micralestes acutidens*; 6 = *Haplochromis bloyeti*; 7 = *Alestes dentex* and *A. baremoze*; 8 = *Labeo* sp.; 9 = *Distichodus* sp. Each sector corresponds to a type of food. The percentage occurrence is put on the upper radius of the sector and the volumetric percentage on the lower one. The area of the parallelogram is proportional to the food index.

spawning of most species at the beginning of the flood and the abundance of young fish during the period of high water level. The terrestrial insects were also consumed in greater quantities during the flood which corresponded partly with the rainy season, and with the growth of herbaceous vegetation which was not the case during lake contraction. This phenomenon was well illustrated by *Eutropius niloticus* (Fig. 10). In the archipelago, the consumption of shrimps was greater during low water when these crustacea occurred in high densities, as shown by *Hydrocynus forskalii* in Fig. 9a.

It was found that the diets of the fishes changed profoundly during their life cycles. Most of the young fishes were initially zooplankton feeders before becoming adult. All the top consumers (level 4) underwent a secondary consumer period (level 3) as young fish. For instance, the young of *Hydrocynus forskalii* (Fig. 11a) were zooplanktophagous (level 3) and then had a temporary insectivorous period before consuming fishes (level 4). Some fishes changed their chain without changing their trophic level, as in the case of *Tetraodon fahaka*. (Fig. 11b). Adult fish fed on molluscs (level 3 – detritus food chain) but the young consumed zooplankton (level 3 – grazing food chain). The example of *Alestes baremoze* (Lauzanne 1973) provides a good summary of changes in diet during the life cycle. *Alestes baremoze* is a migratory fish which reaches

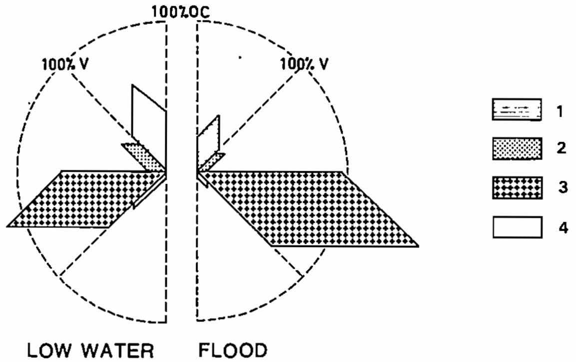

Fig. 10 Diet of *Eutropius niloticus* in open water. 1 = whole fish; 2 = fish debris; 3 = terrestrial insects; 4 = benthic invertebrates.

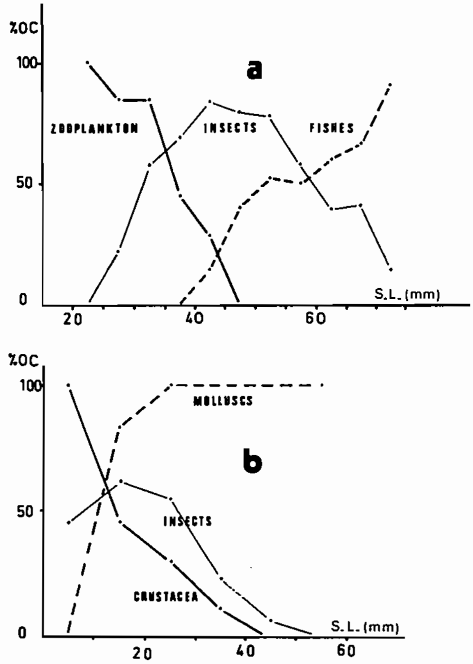

Fig. 11 Variation in diet of young *Hydrocynus forskalii* (a) and young *Tetraodon fahaka* (b).

adulthood in Lake Chad where it feeds strictly on zooplankton. During the dry season (low water), the brood fish moved up the Shari and the Logone Rivers where they found poor nutritional conditions and consumed rare Chironomids, terrestrial insects and crustacea. After spawning, the adults followed the rising waters and entered the flood zones where they found an abundance of food composed mainly of leaves and seeds. The yearlings also entered the flooded plain where their food was composed of epiphytic organisms such as Copepoda, Cladocera, Ostracoda and Chironomidae. During their catadromous migration towards the lake, when there was a lowering of water, they continued to feed upon crustacea and insects. So, the young fishes reached the lake where they were able to grow rapidly by feeding on the zooplankton. Thus, this species changed its trophic level from the third level (zooplankton feeder) to the second level (feeding on leaves and seeds), over its migratory cycle.

Changes of trophic levels also occurred as a result of profound modifications of the biotopes. So, after the considerable drought of 1972–1973, the archipelago was divided by the lowering of water in the lake. There was a sharp decrease in the zooplankton and benthos due to drying up. In a study of diets of Mochocidae in 1974, Im (1977) observed that all the diets were then based upon fine plant detritus. During the period of 'Normal Chad', these fishes were either zooplankton or benthos feeders and therefore, ecological disturbances forced them from the third to the second trophic level.

15.2 Quantitative aspects

15.2.1 *General*

When organic matter is transferred from one trophic level to a higher level, it is accompanied by a loss of energy which depends mostly upon the precise energy efficiency of the consumer. Following the works of Ivlev (1939–1961) and Winberg (1956), Warren and Davis (1967) suggested an equation which considered the energy balance in fishes:

$$C = F + U + \Delta B + R$$

in which C is the amount of energy contained in the food consumed, F is the energy value of the excrements, U is the energy lost through urine and through the skin and gills, ΔB is the amount of energy corresponding to the increase in weight and R is the energy necessary for metabolism. The food efficiency can be characterized by several coefficients. The most commonly used one is the first order energy coefficient of growth (K1)

$$K1 : \frac{\Delta B}{C}$$

This ratio which is calculated from the wet weight is called the conversion rate and the inverse ratio which is often used is called the food coefficient or trophic coefficient. This coefficient, K1, characterizes a gross efficiency, as, the amount of energy consumed is not used only to achieve growth. So, a second order energy coefficient of growth was proposed:

$$K\,2 = \frac{\Delta B}{C - (F + U)}$$

Some authors also use an assimilation index: AS:

$$AS = \frac{\Delta B + R}{C}$$

This coefficient accounts for the energy that is really used for growths and metabolism. These last two indices whose calculation is difficult were not considered because they must be studied in detail in the laboratory. From the field methods used, the conversion rate of food could be calculated from caloric equivalents (Lauzanne 1978) for three species, each characterizing a trophic level of consumers. The second trophic level was characterized by *Sarotherodon galilaeus*, a phytoplankton eater (Lauzanne 1978). The third level was characterized by the zooplanktivorous *Alestes baremoze* and the fourth level by the piscivorous *Lates niloticus* (Hamblyn 1966, Lauzanne 1977).

15.2.2 *Conversion rate and first order growth energy coefficient* (K1)

We will point out again that the food conversion rate is the ratio of the increase in weight of the fish during a given period of time to the weight of the food ingested during the same period. To evaluate the first parameter, it is necessary to know the growth curve of the fish under study. The second parameter (weight of food ingested) was obtained from a knowledge of the daily food intake which depends upon the weight of the fish and the water temperature. We will not dwell on the method used to estimate daily food intake (Lauzanne 1969, 1978), but only mention that is is based on a knowledge of the daily feeding periodicity and the rate of gastric evacuation. Conversion rates are listed in Table 3 for the three species under consideration. The piscivorous *Lates niloticus* had the highest rate and the poorest was for the phytoplankton eater *Sarotherodon galilaeus*, while the zooplankton eater, *Alestes baremoze*, had an intermediate value. This conversion rate (or its inverse, the food coefficient) which was calculated from the wet weights is interesting for the fish culturist since it provides information about the amount of food required to produce a certain amount of fish tissue. However, it could be misleading in connection with the energy efficiency of the predator. As a matter of fact prey and predators are far from being composed of equal proportions of water, mineral salts and organic matter, the only components used to obtain an energy value. The relationships between the various prey and predator constituents as well as the caloric equivalents of the organic matter were calculated (Lauzanne 1978). These relationships permitted the calculation of the conversion rate from

Table 3 Conversion rate (%) for the three species under study.

	S. galilaeus	*L. niloticus*	*A. baremoze*
Wet weight	3.1	22.4	8.8
Dry weight	5.5	24.9	34.7
Organic matter	11.5	26.4	39.2
Calories (K1)	18.9	27.3	44.8

dry matter to organic matter and finally to express it in terms of energy (Table 3). From this it was apparent that *Alestes* (zooplankton feeder) had the best energy efficiency, above that of *Lates* (piscivorous), while the K1 for *Sarotherodon* remained by far the lowest.

The differences between the various conversion rates for *Lates niloticus* were not very great. This phenomenon was due to the similar water and mineral salt contents of predator and prey so that the caloric equivalents of the organic matter were not very different for *Lates* and the fishes on which it fed. For contrary reasons, *Sarotherodon* and *Alestes* had conversion rates which were very different according to the calculation method.

Generally, results in the literature are not directly comparable with ours. Most of them are results of laboratory experiments where the conditions differ greatly from those existing in the natural environment. Nevertheless, these various results (Table 4) which must be prudently considered, suggest at least three important points:

1. For the same type of food, it is observed that K1 is always higher in warm-water fishes than in fishes living in temperate waters.

2. For the same thermic preference of fishes (warm waters, temperate waters), it seems that the lowest efficiency is obtained in phytoplankton eaters and particularly plant feeders. In this last class, *Ctenopharyngodon* is a particularly good example since this species uses only 2% of the energy consumed for its growth and moreover, it assimilates only 13% of the energy ingested, while 81% of the latter is lost in the form of waste products (Fisher 1970). Although it is very long, the digestive system of the phytophagous fishes does not seem to be as well adapted to the assimilation of plant matter, especially cellulose as that of some insects and mammals.

3. For carnivorous fishes the highest efficiency is obtained in fishes that eat crustacea such as zooplankton, *Gammarus* and shrimps and benthic invertebrates, while the lowest efficiency is obtained in the ichthyophagous fishes. This last remark is contrary to the general opinion that efficiencies increase as we go up the trophic chain. In fact, it seems that two groups must be considered, the herbivores with low efficiency and the carnivores with higher efficiency. The energy efficiency of the detritivorous fishes on which we have no information, ought logically to be intermediate, since their food is composed of more or less

Table 4 Values of K1 for the different fish species. The warm-water species are underlined.

Species	Food	T°C	K1 (%)	Authors
<u>*Tilapia mossambica*</u>	phytoplankton	25	22.2	Mironova (1974–75)
<u>*Sarotherodon galilaeus*</u>	phytoplankton	26	18.9	present study
Ctenopharyngodon idella	macrophytes	23	1.9	Fisher (1970)
<u>*Alestes baremoze*</u>	zooplankton	26	44.8	present study
Perca fluviatilis	*Gammarus*	14	20.4	Solomon, Brafied (1972)
Salmo trutta[a]	*Gammarus*	?	25.1	Surber (1935)
Salmo trutta	*Gammarus*	?	33.1	Pentelow (1939)
Salmo trutta	*Gammarus*	?	42.5	Schaeperclaus (1933)
<u>*Ophiocephalus striatus*</u>	*Metapeneus*	28	26.0–51.1	Pandian (1967)
Pseudopleuronectes americanus	*Nereis*	10	23.5–20.6	Chesney, Estevez (1976)
		20	23.9–19.7	
Limanda yokohamae	?	?	15.8–21.8	Hatanaka et al. (1956)
Stizostedion vitreum vitreum	amphipodes	20	14.3	Kelso (1972)
	crayfish	16	12.7	
	fish	12	13.9	
Esox lucius	fish	?	14.9	Backiel (1971)
Stizostedion luciopera	fish	?	15.1	
Silurus glanis	fish	?	13.9	
<u>*Lates niloticus*</u>	fish	26	27.3	present study

[a] The results for *Salmo trutta* were given as fresh weight. They were converted to obtain K1 by taking 845 cal/g for *Gammarus* (Mann 1965) and 1400 cal/g for *S. strutta* which is a mean value given for Salmonidae (Cummins and Wuycheck 1971).

degraded plants and animals. Within these groups, the value of K1 can vary greatly (Table 4). It does not seem that these differences can be explained only through variations in energy values of the various foods. Their protein, lipid and glucose contents are likely to be important along with the varying ability of fishes to assimilate these constituents.

15.2.3 *Energy transfer along food chains*

In the first part of this chapter, we described the qualitative relationships between the different trophic levels. These results provided an example of the energy transfer in the food pyramid. We will consider two hypothetical cases. In the first one, *Lates niloticus* feeds only on *Sarotherodon galilaeus* and in the second one on *Alestes baremoze*. In the first case, the food chain is composed of three links (3 trophic levels) and of four links in the second one (Fig. 12). The amount of energy accumulated by the zooplankton (considered here only as phytophagous) was estimated by using the results of Petipa et al. (1973) where

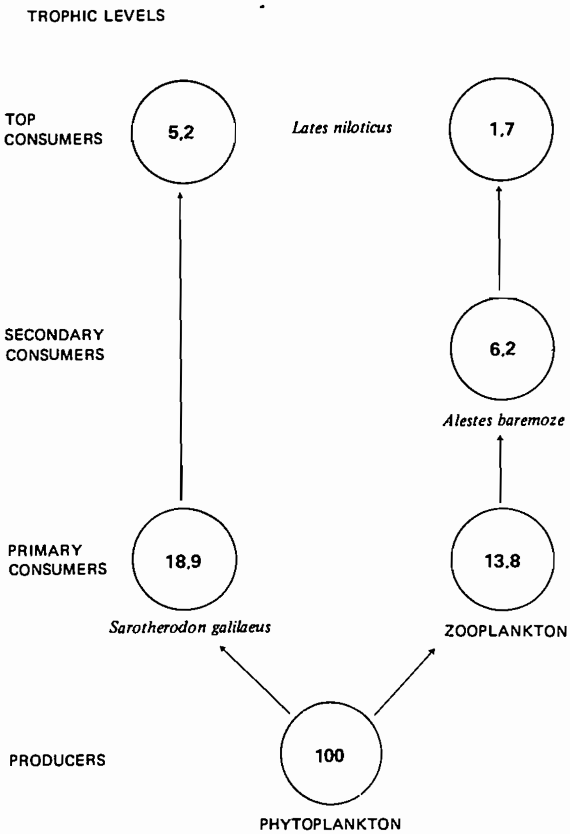

Fig. 12 Energy accumulated by *Lates niloticus* (in calories) according to the food chain used, starting from 100 calories for phytoplankton (from Lauzanne 1977).

K1 is equal to 13.8%. We observe that of 100 calories supplied by the algae (level 1), *Lates niloticus* accumulates 1.7 of them with the chain composed of two intermediate links (zooplankton and *Alestes baremoze*) and 5.2 of them, that is three times more, with a chain composed of a single intermediate link (*Sarotherodon galilaeus*). This example shows that the longer the food chain, the greater the loss in energy. The most efficient hypothetical cycle would be one where the algal production is consumed by a phytoplanktivore such as *S. galilaeus*, and the waste products partly transformed by a detritivore.

15.3 Conclusions

During the period of 'Normal Chad', the main species of the archipelago and the open water in the southeastern part of the lake could be classified into major consumer groups according to the trophic levels. The first level was composed of the original food sources such as algae and detritus and the second one of primary consumers such as phytoplankton feeders, macrophyte feeders and detritivores. The third level consisted of the benthos and zooplankton feeders and the fourth one of the top consumers especially piscivores.

The diets could undergo variations according to the biotopes, the hydrological seasons, the age of the fish or changes in the environment. These modifications could be modest if the fish remained in the same trophic level. They could also be very pronounced and then, the fish changed its trophic level. The importance of the different groups of consumers which was evaluated in the southeast of the lake was considerably different in the archipelago and the open water. The archipelago was characterized mainly by the abundance of the planktivores, especially zooplanktivores which represented 44% of the fish biomass. The open water was largely characterized by the top consumers which represented 64% of the fish biomass. The dominance of the planktivores in the archipelago resulted doubtless from the high planktonic biomass which was stable throughout the year. In the open water, the top consumers consisted of six species of which five were mainly piscivores and one, *Eutropius niloticus*, consumed mainly terrestrial insects. This last species was eaten in great quantities by the other five which also ate many small zooplanktivores such as *Micralestes* and *Pollimyrus*. Therefore, it seemed that this high biomass depended indirectly on terrestrial insects and the abundance of the small zooplanktivores which probably had a high production.

The food supply seemed to be rather well utilized. However, the phytoplanktivores such as *Sarotherodon* which were important in the archipelago were absent from the open water almost certainly for reasons of reproduction. Submerged macrophytes of the archipelago would certainly support denser population of grazers. The zooplankton was particularly well used by species of commercial importance (*Alestes* and *Synodontis*), but also by many young fishes belonging to the large species and by small prey species (*Micralestes*, *Pollimyrus*). The benthophages which did not represent a significant biomass consumed mainly insect larvae, especially Chironomidae, and Ostracoda and molluscs. Worms (Oligochaeta and Nematodes) which had, however, a high biomass seemed to be ignored by most of the benthic feeders. The first order energy coefficient of growth (K1) which was determined for three species, each representing a trophic level, was lowest for the phytophagous fishes and highest for the zooplanktivores, while the piscivores had intermediate efficiencies. Similarly, we showed that the energy lost when organic matter moved to an upper level was considerable. These two remarks led to the conclusion that the total energy efficiency of the fish community in the archipelago which was composed mainly of zooplantivorous fish must be well above that of the community in the open water which was composed mainly of top carnivores.

References

Backiel, T., 1971. Production and food consumption of predatory fish in the Vistula river. J. Fish. Biol. 3: 369–405.

Chesney, E. J. and Estevez, J. I., 1976. Energetics of winter flounder (*Pseudopleuronectes americanus*) fed the polychaete, *Nereis virens*, under experimental conditions. Trans. am. Fish. Soc. 105 (5): 592–595.

Cooper, G. P. and Fuller, J. L., 1945. A biological survey of Moosehead lake and Haymock lake, Maine. Maine Dept. Inland Fish. Game, Fish. Surv. Rept. 6: 1–160.

Cummins, K. W. and Wuycheck, J. C., 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Ver. Limnol. 18, 158 pp.

Dejoux, C., 1974. Synécologie des Chironomides du lac Tchad (Diptères Nematocères) Trav. Doc. ORSTOM, No. 56, 161 pp.

Dejoux, C., Lauzanne, L. and Lévêque, C., 1969. Evolution qualitative et quantitative de la faune benthique dans la partie est du lac Tchad. Cah. ORSTOM. Sér. Hydrobiol. 3: 3–58.

Dussart, B., 1966. Limnologie. Gauthier-Villars, Paris, 677 pp.

Elton, C., 1927. Animal Ecology. MacMillan Co., New York, 107 pp.

Fischer, Z., 1970. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.) Part I. Pol. Arch. Hydrobiol. 17, 4: 421–434.

Fryer, G., 1960. The feeding mechanism of some Atyid prawns of the genus *Caridina* Trans. Soc. Edinb. 64: 217–244.

Gras, R. Iltis, A. and Lévêque-Duwat, S., 1967. Le plancton du Bas Chari et de la partie est du lac Tchad. Cah. ORSTOM. Sér. Hydrobiol. 1: 25–96.

Gras, R., Iltis, A. and Saint-Jean, L., 1971. Biologie des crustacès du lac Tchad. II. Régime alimentaire des Entomostracés planctoniques. Cah. ORSTOM. Sér. Hydrobiol. 5: 285–286.

Hamblyn, E. L., 1966. The food and feeding habits of Nile perch *Lates niloticus (*(Linné) (Pisces: Centropomidae). Rev. Zool. Bot. Afr. 74: 1–28.

Hatanaka, M., Kosaka, M. and Sato, Y., 1956. Growth and food consumption in plaice. Part I. *Limanda yokohamae* (Günther). Tohoku J. Agric. Res. 7: 151–162.

Hopson, A. Y., 1972. A study of the Nile perch in Lake Chad. Overseas Res. Pupl. London, 19, 93 pp.

Hynes, H. B. N., 1950. The food of freshwater stickbacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. J. anim. Ecol. 19: 36–58.

Im, B. H., 1977. Etude de l'alimentation de quelques espèces de *Synodontis* (Poissons, Mochocidae) du Tchad. Thèse de spécialité, Toulouse, 150 pp.

Ivlev, V. S., 1939. The energy balance of the growing larva of *Silurus glanis*. Dolk. Akad. Nauk. S.S.S.R. new ser. 25: 87–89.

Ivlev, V. S., 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn., 302 pp.

Kelso, J. R. M., 1972. Conversion, maintenance and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet and temperature J. Fish. Bd. Can. 29: 1181–92.

Lauzanne, L., 1969. Etude quantitative de nutrition des *Alestes baremoze* (Pisc. Charac.). Cah. ORSTOM Sér. Hydrobiol. 3: 15–27.

Lauzanne, L., 1970. La sélection des proies chez *Alestes baremoze* (Pisc., Charac.). Cah. ORSTOM Sér. Hydrobiol. 3: 15–27.

Lauzanne, L., 1972. Régimes alimentaires des principales espèces de poissons de l'archipel oriental du lac Tchad. Verh. int. Ver. Limnol. 18: 636–646.

Lauzanne, L., 1973. Etude qualitative de la nutrition des *Alestes baremoze* (Pisces, Characidae). Cah. ORSTOM Sér. Hydrobiol. 7: 3–15.

Lauzanne, L., 1975a. La sélection des proies chez trois poissons malacophages du lac Tchad. Cah. ORSTOM Sér. Hydrobiol., 9: 3–7.

Lauzanne, L., 1975b. Régimes alimentaires d'*Hydrocyon forskalii* (Pisces, Characidae) dans le lac Tchad et ses tributaires. Cah. ORSTOM Sér. Hydrobiol. 9: 105–121.

Lauzanne, L., 1976. Régimes alimentaires et relations trophiques des poissons du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 10: 267–310.

Lauzanne, L., 1977. Aspects qualitatifs et quantitatifs de l'alimentation des poissons du Tchad. Thèse d'Etat, Paris, 284 pp.

Lauzanne, L., 1978a. Croissance de *Sarotherodon galilaeus* (Pisces, Cichlidae) dans le lac Tchad. Cybium S.3, 3: 5–14.

Lauzanne, L., 1978b. Equivalents caloriques de quelques poissons et de leur nourriture. Cah. ORSTOM. Sér. Hydrobiol. 12: 89–92.

Lauzanne, L., 1978c. Etude quantitative de l'alimentation de *Sarotherodon galilaeus*. Cah. ORSTOM Sér. Hydrobiol. 12: 71–81.

Lauzanne, L. and Iltis, A., 1975. La sélection de la nourriture chez *Tilapia galilaea* (Pisces, Cichlidae) du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 9: 193–199.

Mann, K. H., 1965. Energy transformation by a population of fish in the river Thames. J. anim. Ecol. 34: 253–275.

Mironova, N. V., 1974. The energy balance of *Tilapia mossambica*. J. Ichtyol. 14: 431–438.

Pandian, T. J., 1967. Food intake, absorption and conversion in the fish *Ophiocephalus striatus*. Helgoländer Wiss. Meeresunters 15: 637–647.

Pentelow, F. T. K., 1939. The relation between growth and food consumption in the brown trout (*Salmo trutta*). J. exp. Biol. 16: 446–473.

Petipa, T. S., Pavlova, E. V. and Mironov, G. N., 1973. The food web structure, utilization and transport of energy by trophic levels in the planktonic communities, 142–167 In J. H. Steele, (ed.), Marine Food Chains, Oliver and Boyd, Edinburgh. Reprint by Otto Koeltz Antiquariat, Keenigstein, 552 pp.

Schaeperclaus, W., 1933. Text book of pond culture. Translated by E. Hund, U.S. Fish and Wildlife Service fish leaflet 311, 260 pp.

Solomon, D. Y. and Brafield, A. E., 1972. The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis L.*) J. anim. Ecol. 41: 699–718.

Surber, E. W., 1935. 65th annual meeting. Trans. am. Fish. Soc.

Warren, C. E. and Davis, G. E., 1967. Laboratory studies on the feeding, bioenergetics and growth of fish, 175–214, In S. D. Gerking, (ed.), The Biological Basis of Freshwater Fish Production. Blackwell Scientific Publications. Oxford, 495 pp.

Winberg, G. G.–956. Rate of metabolism and food requirements of fishes. Traduit du russe par: J. Fish. Bd. Can. trans. ser. 194 (1960), 253 pp.

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Ecology and Productivity of a Shallow Tropical Ecosystem

Edited by

J.-P. CARMOUZE, J.-R. DURAND and C. LÉVÊQUE

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