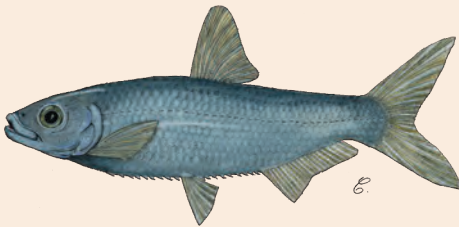


Diets and food webs



DIDIER
PAUGY

CHRISTIAN
LÉVÊQUE

All animals use food as their sole source of energy. The search for food is thus a key activity for fishes, which devote a significant portion to their time to this quest, and perhaps even the bulk of their activities.

A major problem for fish is deciding when and where to feed, for how long, identifying the most suitable prey (in terms of size and nutritional value), and finding and capturing such prey. That is the reason why some view feeding strategies as decision-making systems (Cézilly *et al.*, 1991). A fundamental axiom is that such strategies were shaped during natural selection, and that any decision tends to optimize variables such as the rate of energy assimilation, which is correlated with the concept of “fitness” (Pyke, 1984). Thus, given the different options available in their natural environment, animals do not choose their food at random. On the contrary, they carry out activities that provide the highest reproductive success (Pulliam, 1989). As a corollary, food research strategies are adaptations that allow fishes to address, as efficiently as possible, different environmental constraints such as competition, food scarcity, and unpredictable variations in resources.

Some results also suggest that fishes have the capacity to learn and use alternative behaviours that allow them to be more efficient in finding prey, and therefore live longer (Hart, 1986).

Diets and trophic groups

Characterizing a fish’s diet requires a qualitative and quantitative description of prey found in its stomach. The simplest assessment method is noting the presence or absence of a type of prey in stomachs. The data is then used to calculate the percentage of occurrence which is the ratio of the number of stomachs in which one type of prey is found with the total number of stomachs studied.

**COMPARATIVE ADVANTAGES OF THE METHODS
USED FOR THE ANALYSIS OF STOMACH CONTENTS**

Methods	Advantages	Failures
Occurrence	simple, easy, quick	rudimentary does not take into account the volume and the relative abundance of prey
Numerical	simple, quick	does not take into account the volume of each prey small-sized prey digested more quickly than large-sized prey difficulty of counting prey during digestion
Volumetric	determines the respective volume of each type of prey gives the most representative picture of the diet	difficult and long to implement difficulty to separate taxa after ingestion and/or at the beginning of digestion
Gravimetric	provides later knowledge of the caloric value of each type of prey	long to implement possible sources of error overestimates the contribution of large size prey
Subjective • dominances • points	allows quick integration of several parameters integrates numerical and volumetric methods	too subjective difficult comparison depending on the users and/or the “encoders”

(from Hynes, 1950 and Hyslop, 1980)

The numerical method consists of counting the number of individuals in a category of prey for the entire sample, then expressing it as a percentage of the total number of prey.

The volumetric or gravimetric methods consist of determining the relative importance in volume or weight of a category of prey in relation to the total volume (or total weight) of all prey.

Subjective methods consist of attributing points to each prey according to its presence or dominance in relation to all examined stomachs.

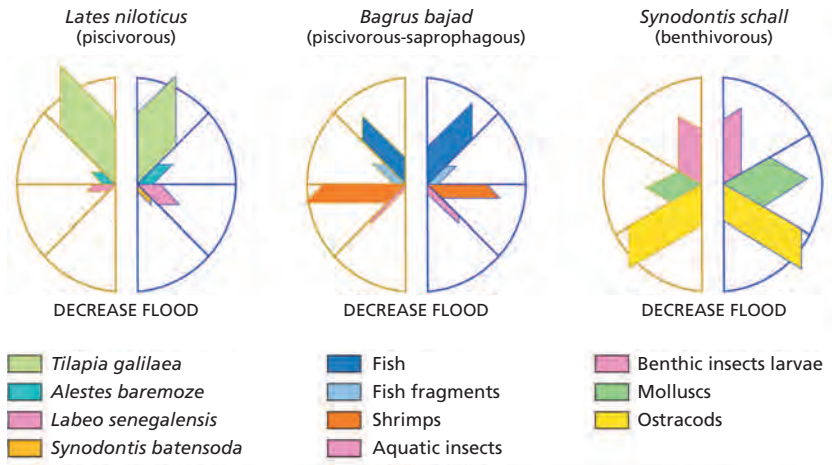
Lauzanne (1976) proposed the use of a Feeding Index (FI) that uses both the percentage of occurrence (%OC) and the volumetric method (%V):

$$FI = \frac{\% OC \times \% V}{100}$$

This index, which varies from 0 to 100, allows researchers to identify preferences and compare the relative importance of different prey in the diet. It is useful for comparing the diets of a single species according to size, seasons, or biotope, and lends itself well to a clear graphic representation (figure 12.1).

Following Lauzanne (1977, 1983), a few major trophic categories could be recognized in Lake Chad, and this classification can be extrapolated to most riverine tropical African fish communities.

FIGURE 12.1.
Diet composition of
Lates niloticus,
Bagrus bajad and
Synodontis schall
in Lake Chad (from
Lauzanne, 1976).



Dominant primary consumers

- phytoplanktivorous filter feeders consuming mainly planktonic algae, such as *Sarotherodon galilaeus*;
- grazers or macrophyte consumers such as *Brycinus macrolepidotus*;
- browsers eating the superficial layer of sediment usually composed of sedimented algae, or the periphyton growing on rocky substrates, e.g. *Labeo senegalensis*, *Citharinus citharus*, *Distichodus rostratus*;
- detritivores such as some tilapiines;

Dominant secondary consumers

- the zooplanktivores filtering zooplankton with their gill rakers: *Alestes baremoze*, *Synodontis batensoda*, *Synodontis membranaceus*;
- the benthivores, feeding mainly on benthic invertebrates: *Synodontis schall*, *S. clarias*, *Hyperopisus bebe*, *Heterotis niloticus*. A few species such as *Tetraodon lineatus* feed almost exclusively upon molluscs ;
- surface feeders, eating predominantly terrestrial invertebrates: *Brycinus macrolepidotus*;

Top consumers

- strictly piscivorous fish, feeding exclusively on living fish, such as *Lates niloticus* and all *Hydrocynus* species;
- less strictly piscivore species consuming both fish, shrimps and other invertebrates: *Schilbe mystus*, *Bagrus bajad*, and young *Hydrocynus*.

In practice, species feed on prey available in the ecosystem they inhabit, and diet can change from one site to another or according to the season . As a result, the above classification is only broadly valid (primary, secondary, top). Given this capacity of adaptation to available resources it is possible, for West Africa,

to retain just six broad trophic categories: limnivores, micro- and macrophytophages, zooplanktophages, invertivores, omnivores, and ichthyophages (Paugy, 1994).

The food habits of African fish have been the subject of much investigation, and the main findings are given below (table 12.1).

- Item almost exclusively consumed ● Item a major constituent of the diet ● Item occurring regularly in the diet but not dominant

TABLE 12.1

Selected data on the dominant food habits of adult fish from north tropical Africa. Bibliographic references: 1: Adebisi, 1981; 2: Arawano, 1982; 3: Daget, 1962a; 4: Ghazai *et al.*, 1991; 5: Harbott, 1982; 6: Hickley & Bailey, 1987; 7: Hopson, 1982; 8: Hopson *et al.*, 1982; 9: Hyslop, 1986; 10: Im, 1977; 11: King, 1989; 12: Lauzanne, 1975a; 13: Lauzanne, 1976; 14: Lauzanne, 1977; 15: Lek, 1979; 16: Lek & Lek, 1977; 17: Lek & Lek, 1978a; 18: Lock, 1982; 19: McLeod, 1982; 20: Merona, unpublished; 21: Mraja, 1982; 22: Nwadiaro & Okodie, 1987; 23: Ogari, 1982; 24: Pandare & Romand, 1989; 25: Paugy, 1994; 26: Paugy & Bénéch, 1989; 27: Robinson & Robinson, 1969; 28: Sagua, 1979; 29: Thiero Yatabary, 1983; 30: Tobor, 1972; 31: Vidy, 1976.

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
Primary consumers														
<i>Citharinus citharus</i>	Lake Chad	13		●										
<i>Citharinus latus</i>	Sudd	6		●										
<i>Citharinus latus</i>	Niger	3		●	●									
<i>Citharinus citharus</i>	Niger	3		●	●									
<i>Citharinus eburneensis</i>	Bandama	3		●	●									
<i>Citharidium ansorgii</i>	Niger	3		●	●									
<i>Citharinops distichoides</i>	Niger	3		●	●									
<i>Distichodus brevipinnis</i>	Lake Kainji	2	●		●									
<i>Distichodus engycephalus</i>	Lake Kainji	2	●		●									
<i>Distichodus engycephalus</i>	Senegal	25	●		●									
<i>Distichodus rostratus</i>	Lake Kainji	2	●		●									
<i>Distichodus rostratus</i>	Sudd	6	●		●									
<i>Distichodus rostratus</i>	Senegal	25	●		●									
<i>Labeo niloticus</i>	Sudd	6		●										
<i>Labeo parvus</i>	Bandama	20		●										
<i>Labeo parvus</i>	Senegal	25		●										
<i>Labeo senegalensis</i>	Lake Chad	13		●										
<i>Labeo senegalensis</i>	Senegal	25		●										
<i>Labeo roseopunctatus</i>	Senegal	25		●										
<i>Oreochromis niloticus</i>	Lake Turkana	5	●											
<i>Sarotherodon galilaeus</i>	Lake Chad	13	●											
<i>Sarotherodon galilaeus</i>	Sudd	6	●	●	●									
<i>Coptodon zillii</i>	Sudd	6	●		●									
Secondary consumers														
<i>Polypterus senegalus</i>	Sudd	6					●	●			●	●		
<i>Heterotis niloticus</i>	Lake Chad	13			●	●				●		●		
<i>Heterotis niloticus</i>	Sudd	6	●	●	●			●						
<i>Hyperopisus bebe</i>	Lake Chad	12			●				●	●				
<i>Brienomyrus brachyistius</i>	Mono	26						●						
<i>Brienomyrus brachyistius</i>	Cross	11						●						
<i>Brevimyrus niger</i>	Lake Chad	15				●		●			●			
<i>Brevimyrus niger</i>	Chari	15				●		●			●			
<i>Brevimyrus niger</i>	Nigeria	9				●		●						
<i>Hyperopisus bebe</i>	Senegal	25						●						
<i>Marcusenius mento</i>	Senegal	25						●						
<i>Marcusenius senegalensis</i>	Senegal	25						●						
<i>Mormyrops anguilloides</i>	Senegal	25						●						
<i>Mormyrus rune</i>	Senegal	25						●						
<i>Marcusenius brucei</i>	Mono	26						●						
<i>Marcusenius bruyerei</i>	Bandama	20						●						
<i>Marcusenius senegalensis</i>	Nigeria	9						●						
<i>Marcusenius furcidens</i>	Bandama	20						●						

TABLE 12.1 (CONT.)

● Item almost exclusively consumed ● Item a major constituent of the diet ● Item occurring regularly in the diet but not dominant

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
<i>Mormyrops anguilloides</i>	Mono	26						●		●				
<i>Mormyrus rume</i>	Mono	26						●						
<i>Petrocephalus bane</i>	Lake Chad	15				●		●						
<i>Petrocephalus bovei</i>	Mono	26						●						
<i>Petrocephalus bovei</i>	Bandama	20				●		●						
<i>Petrocephalus bovei</i>	Chari	15				●		●		●				
<i>Petrocephalus bovei</i>	Lake Chad	15				●		●		●				
<i>Petrocephalus bovei</i>	Nigeria	9				●		●						
<i>Petrocephalus bovei</i>	Senegal	25						●						
<i>Pollimyrus adspersus</i>	Nigeria	9				●		●						
<i>Pollimyrus isidori</i>	Lake Chad	15				●		●						
<i>Pollimyrus isidori</i>	Chari	15				●		●			●			
<i>Alestes baremoze</i>	Lake Chad	13				●		●						
<i>Alestes baremoze</i>	Lake Turkana	7				●	●	●						
<i>Alestes baremoze</i>	Senegal	25				●	●	●		●				
<i>Alestes dentex</i>	Lake Chad	13			●	●		●						
<i>Alestes dentex</i>	Sudd	6				●		●					●	
<i>Micralestes acutidens</i>	Chari	16				●		●						
<i>Micralestes acutidens</i>	Lake Chad	27				●		●						
<i>Brycinus leuciscus</i>	Niger	4					●	●			●			
<i>Brycinus longipinnis</i>	Mono	26					●	●						
<i>Brycinus macrolepidotus</i>	Mono	26					●	●			●			
<i>Brycinus macrolepidotus</i>	Lake Chad	13			●		●	●						
<i>Brycinus macrolepidotus</i>	Senegal	25			●		●	●		●	●			●
<i>Brycinus nurse</i>	Mono	26						●						
<i>Brycinus nurse</i>	Senegal	25				●	●	●		●				
<i>Brycinus imberi</i>	Mono	26					●	●			●			
<i>Micraleste acutidens</i>	Sudd	6				●		●						
<i>Nannocharax fasciatus</i>	Senegal	25						●						
<i>Barbus ablabes</i>	Mono	26						●						
<i>Barbus macrops</i>	Senegal	25				●	●	●						
<i>Barbus chlorotaenia</i>	Mono	26						●						
<i>Barbus callipterus</i>	Mono	26						●						
<i>Barbus bynni</i>	Lake Turkana	21						●	●	●				
<i>Barbus sacratus</i>	Senegal	25				●	●	●						
<i>Leptocypris niloticus</i>	Senegal	25						●						
<i>Raiamas senegalensis</i>	Senegal	25						●						
<i>Raiamas steindachneri</i>	Senegal	25						●						
<i>Chrysichthys auratus</i>	Mono	26						●	●					
<i>Chrysichthys auratus</i>	Nigeria	22			●			●						
<i>Chrysichthys auratus</i>	Senegal	25						●						
<i>Chrysichthys maurus</i>	Bandama	20						●	●					
<i>Auchenoglanis occidentalis</i>	Senegal	25						●						
<i>Clarotes laticeps</i>	Sudd	6						●	●		●	●		
<i>Schilbe mystus</i>	Bandama	20					●	●						
<i>Schilbe mystus</i>	Mono	26					●	●					●	
<i>Schilbe mandibularis</i>	Bandama	31				●		●						
<i>Amphilius atesuensis</i>	Bandama	20						●						
<i>Amphilius atesuensis</i>	Senegal	25						●						
<i>Clarias agboyiensis</i>	Mono	26						●						

Bibliographic references:

- 1: Adebisi, 1981;
- 2: Arawano, 1982;
- 3: Daget, 1962a;
- 4: Ghazai *et al.*, 1991;
- 5: Harbott, 1982;
- 6: Hickey & Bailey, 1987;
- 7: Hopson, 1982;
- 8: Hopson *et al.*, 1982;
- 9: Hyslop, 1986;
- 10: Im, 1977;
- 11: King, 1989;
- 12: Lauzanne, 1975a;
- 13: Lauzanne, 1976;
- 14: Lauzanne, 1977;
- 15: Lek, 1979;
- 16: Lek & Lek, 1977;
- 17: Lek & Lek, 1978a;
- 18: Lock, 1982;
- 19: McLeod, 1982;
- 20: Merona, unpublished;
- 21: Mraja, 1982;
- 22: Nwadiaro & Okodie, 1987;
- 23: Ogari, 1982;
- 24: Pandare & Romand, 1989;
- 25: Paugy, 1994;
- 26: Paugy & Bénech, 1989;
- 27: Robinson & Robinson, 1969;
- 28: Sagua, 1979;
- 29: Thiero Yatabary, 1983;
- 30: Tobor, 1972;
- 31: Vidy, 1976.

TABLE 12.1 (CONT.)

● Item almost exclusively consumed ● Item a major constituent of the diet ● Item occurring regularly in the diet but not dominant

Species	Basins	References	Phytoplankton	Superf. Organic layer	Vegetation	Zooplankton	Terrestrial insects	Aquatic insects	Molluscs	Other benthic invert.	Vegetal detritus	Shrimps	Fish	Fish detritus / scales
<i>Heterobranchius isopterus</i>	Mono	26					●	●					●	
<i>Heterobranchius isopterus</i>	Senegal	25			●		●	●		●			●	
<i>Synodontis batensoda</i>	Lake Chad	13				●		●						
<i>Synodontis membranaceus</i>	Lake Chad	13				●								
<i>Synodontis clarias</i>	Lake Chad	12					●	●	●	●				
<i>Synodontis frontosus</i>	Sudd	6	●											
<i>Synodontis schall</i>	Lake Chad	13					●			●				
<i>Synodontis schall</i>	Lake Turkana	18				●		●	●	●		●	●	
<i>Synodontis schall</i>	Niger	29				●		●	●	●				
<i>Synodontis schall</i>	Bandama	20					●	●	●					
<i>Synodontis frontosus</i>	Lake Chad	10									●			●
<i>Synodontis frontosus</i>	Lake Chad	30						●	●		●			
<i>Synodontis frontosus</i>	Chari	10									●			●
<i>Synodontis obesus</i>	Mono	26						●			●			
<i>Synodontis ocellifer</i>	Senegal	25						●						
<i>Synodontis schall</i>	Senegal	25						●						
<i>Nothobranchius</i>	Sudd	6				●								
<i>Aphyosemion geryi</i>	Guinea	24					●	●						
<i>Chromidotilapia guntheri</i>	Bandama	20				●		●	●					
<i>Chromidotilapia guntheri</i>	Senegal	25				●				●				
<i>Nematogobius maindroni</i>	Senegal	25						●						
<i>Ctenopoma petherici</i>	Sudd	6			●			●						
<i>Mastacembelus nigromarginatus</i>	Bandama	20						●						
<i>Tetraodon lineatus</i>	Lake Chad	14							●					
Top consumers														
<i>Mormyrops anguilloides</i>	Ogun	1										●	●	
<i>Gymnarchus niloticus</i>	Lake Chad	30											●	●
<i>Hepsetus odoe</i>	Ogun	1						●					●	●
<i>Hydrocynus brevis</i>	Lake Chad	13											●	●
<i>Hydrocynus forskalii</i>	Lake Chad	13						●				●	●	
<i>Hydrocynus forskalii</i>	Lake Turkana	8											●	●
<i>Hydrocynus forskalii</i>	Senegal	25											●	●
<i>Ichthyoborus besse</i>	Lake Chad	17						●				●	●	●
<i>Bagrus bajad</i>	Lake Chad	13						●				●	●	
<i>Bagrus bajad</i>	Lake Turkana	18						●				●	●	
<i>Bagrus docmak</i>	Lake Turkana	18						●	●			●	●	
<i>Schilbe niloticus</i>	Lake Chad	13						●	●	●		●	●	
<i>Schilbe niloticus</i>	Mono	26						●	●		●		●	●
<i>Schilbe uranoscopus</i>	Lake Chad	13						●	●	●		●	●	
<i>Schilbe uranoscopus</i>	Lake Turkana	18						●	●	●		●	●	
<i>Schilbe mystus</i>	Senegal	25						●	●	●		●	●	
<i>Malapterurus electricus</i>	Lake Kainji	28											●	●
<i>Parachanna obscura</i>	Sudd	6			●			●					●	●
<i>Parachanna obscura</i>	Senegal	25											●	●
<i>Lates niloticus</i>	Lake Chad	13										●	●	
<i>Lates niloticus</i>	Senegal	25											●	●
<i>Lates longispinis</i>	Lake Turkana	19										●	●	
<i>Haplochromis macconneli</i>	Lake Turkana	23										●	●	
<i>Hemichromis fasciatus</i>	Ogun	1						●					●	
<i>Hemichromis fasciatus</i>	Senegal	25						●					●	

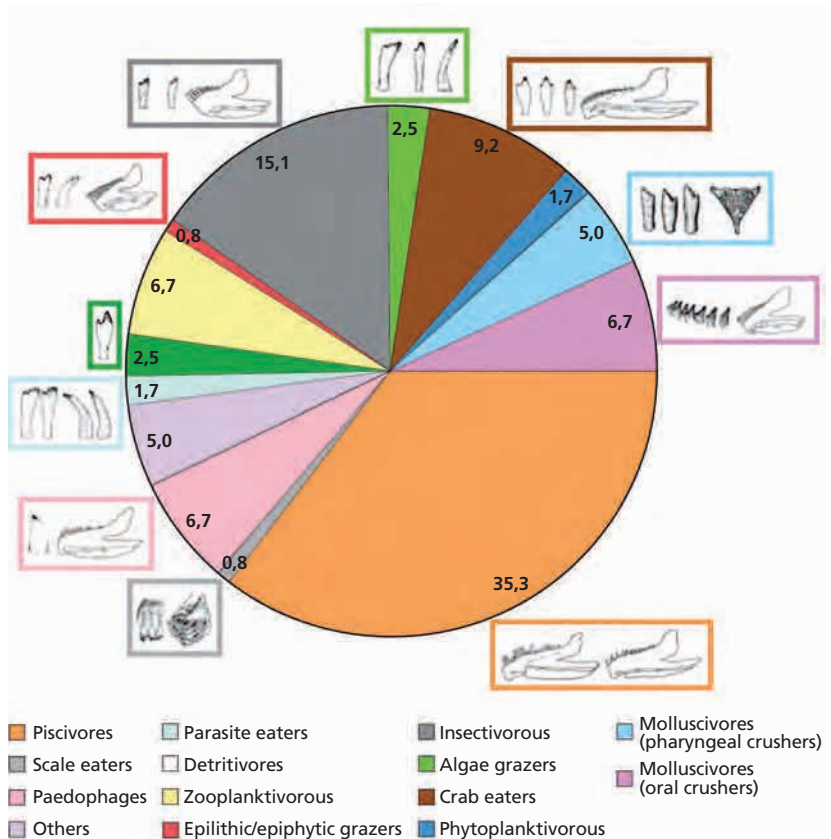
Bibliographic references:

- 1: Adebisi, 1981;
- 2: Arawano, 1982;
- 3: Daget, 1962a;
- 4: Ghazai *et al.*, 1991;
- 5: Harbott, 1982;
- 6: Hickley & Bailey, 1987;
- 7: Hopson, 1982;
- 8: Hopson *et al.*, 1982;
- 9: Hyslop, 1986;
- 10: Im, 1977;
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- 12: Lauzanne, 1975a;
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- 17: Lek & Lek, 1978a;
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- 21: Mraja, 1982;
- 22: Nwadiaro & Okodie, 1987;
- 23: Ogari, 1982;
- 24: Pandare & Romand, 1989;
- 25: Paugy, 1994;
- 26: Paugy & Bénéch, 1989;
- 27: Robinson & Robinson, 1969;
- 28: Sagua, 1979;
- 29: Thiero Yatabary, 1983;
- 30: Tobor, 1972;
- 31: Vidy, 1976.

In the East African great lakes, fishes have developed particular trophic specializations as part of adaptive radiations. It seems that all available resources are used by Cichlidae, and even used exclusively by them. This leads us to distinguish numerous trophic categories (Witte & van Oijen, 1990; Yamaoka, 1991) (figure 12.2):

- detritivores, bottom feeders eating a mixture of planktonic and benthic components;
- phytoplanktivores;
- epilithic (rocks) and epiphytic (plants) algal grazers;
- phytophagous, eating plants;
- molluscivores, consuming shells and gastropods; including oral crushers and pharyngeal crushers;
- zooplanktivorous;
- insectivorous;
- prawn and crab eaters;
- piscivorous;
- paedophages eating eggs and embryos from other species;
- scale eaters consuming mainly scales from other species;
- external parasite eaters...

FIGURE 12.2.
Trophic specializations among haplochromines in Lake Victoria. Relative number of species and relationship between diet and teeth (data from Witte & van Oijen, 1990).



Morphological adaptations to feeding behaviour

If species ended up occupying equivalent ecological niches in different types of ecosystems, they would theoretically have displayed similar adaptive responses to identical selective pressures. For diet, scientists thus advanced the hypothesis that there could be a correlation between the general morphology of species and their diet. For African fish, studies on morphology-diet relationships are scarce, with most only providing descriptions of the general diet of the taxa being analysed. Nonetheless, a few studies show that there is indeed a significant relationship between diet and species morphology (Winemiller *et al.*, 1995 ; Hugueny & Pouilly, 1999). More specifically, some morphological characteristics appear to be associated with the type of diet.

These include, for instance:

- mouth size and body size in piscivorous fish;
- gut length correlated with the behaviour of detritivores ;
- orientation or position of the mouth explaining both benthic and detritivore diets.

Similar results were obtained from observations of the same family (Winemiller *et al.*, 1995) or in a community composed of different taxons belonging to different families (Hugueny & Pouilly, 1999). They thus seem to refute the common idea that ecomorphological studies only provide valid results when they are limited to comparisons between families (Douglas & Matthews, 1992).

Later in the chapter, we shall provide examples of close correlations between diet and different morphological characteristics.

Head and mouth morphologies

It has been suggested that one key innovation, the pharyngeal mechanism, was one of the major reasons for the extraordinary explosive speciation undergone by the cichlid fish in the African Great Lakes (Liem, 1973). The sharpest morphological specialization concerns adaptations to the head to collect different types of prey. Adaptive changes in the jaws are particularly striking, for example in the huge difference between the elongated mandibles of the piscivorous *Rhamphochromis*, and the squat, almost square-cornered jaws of the scraper *Labeotropheus* (Fryer, 1991) (figure 12.3).

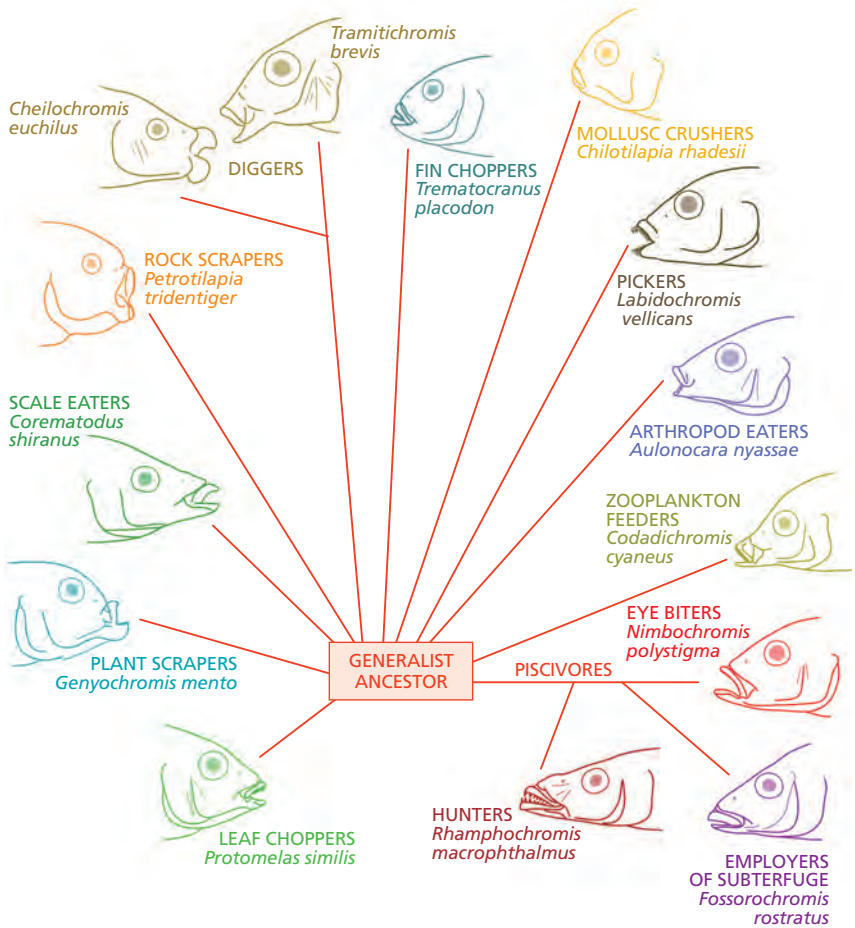
In many species of cyprinids, there are feeding adaptations in the shape of the mouth. In the so-called *Varicorhinus* mouth form, the horny (or keratinized) lips are adapted for scraping algae and aufwuchs from submerged rocks or other hard substrates. The complex ventral mouths of *Labeo*, with homodont pharyngeal teeth which are set close together to form a single grinding surface, are specialized to feed on epibenthic algae.

Length of the gut

There is a correlation between the diet and the length of the gut relative to body length (Kapoor *et al.*, 1975). Carnivorous fish usually have a large stomach

FIGURE 12.3.

Example of adaptive radiation (morphological adaptation of the shape of the mouth) for a few cichlids of Lake Malawi (redrawn from Fryer & Iles, 1972).



and a short gut (ratio less than 1). That is the case for *Lates* and *Hydrocynus*, but also for many invertebrate feeders. Conversely, in sediment browser fish such as *Labeo*, the stomach is often absent or small, and the gut is usually more than ten times longer than the body length (table 12.11). Generally speaking, omnivorous fish, zooplankton feeders or invertebrate feeders have fairly short intestines, less than three times the length of the body. Furthermore, it seems that there is no significant relationship between these types of diet and the length of the gut (Paugy, 1994).

Electric organs

Peculiar adaptations have been developed among electric fish. The catfish *Malapterurus electricus* is a sluggish swimmer, but it feeds almost exclusively on fish. A powerful volley of high frequency electric organ discharges emitted close to fish can paralyse its prey (see box "Electric organ of *Malapterurus electricus*"). This explains why *M. electricus* is a more effective predator of fish in general (Sagua, 1979).

TABLE 12.II.

Relative length of the gut and dominant diet in various African fish species (from Paugy, 1994).

LG: length of the gut; SL: standard length.

Species	Diet	LG/SL	Species	Diet	LG/SLs
Notopteridae			<i>Garra dembensis</i>	micro/macrophyt.	4.50
<i>Papyrocranus afer</i>	omnivore	0.18	<i>Labeo horie</i>	limnivore	16.75
Mormyridae			<i>Labeo lineatus</i>	limnivore	16.10
<i>Brienomyrus brachyistius</i>	invertivore	0.45	<i>Labeo niloticus</i>	limnivore	16.90
<i>Hyperopisus bebe</i>	invertivore	0.67	<i>Labeo parvus</i>	limnivore	10.00
<i>Marcusenius mento</i>	invertivore	0.55	<i>Labeo roseopunctatus</i>	limnivore	13.39
<i>Marcusenius senegalensis</i>	invertivore	0.74	<i>Labeo senegalensis</i>	limnivore	13.36
<i>Mormyrops anguilloides</i>	invertivore	0.46	<i>Labeo variegatus</i>	limnivore	17.00
<i>Mormyrus rume</i>	invertivore	0.78	<i>Leptocypris modestus</i>	invertivore	0.93
<i>Petrocephalus bovei</i>	invertivore	0.68	<i>Leptocypris niloticus</i>	invertivore	0.52
Alestidae			<i>Opsaridium chrystyi</i>	invertivore	0.73
<i>Alestes baremoze</i>	omnivore	0.89	<i>Raiamas moorei</i>	invertivore	0.73
<i>Brycinus macrolepidotus</i>	omnivore	1.16	<i>Raiamas steindachneri</i>	invertivore	0.32
<i>Brycinus nurse</i>	omnivore	1.31	Claroteidae		
<i>Hydrocynus forskalii</i>	piscivore	0.85	<i>Auchenoglanis occidentalis</i>	invertivore	0.88
<i>Hydrocynus vittatus</i>	piscivore	1.06	<i>Chrysidichthys auratus</i>	invertivore	1.98
Distichodontidae			Schilbeidae		
<i>Distichodus engecephalus</i>	micro/macrophyt.	4.71	<i>Schilbe mystus</i>	omnivore	0.86
<i>Distichodus niloticus</i>	micro/macrophyt.	2.77	Amphiliidae		
<i>Distichodus rostratus</i>	micro/macrophyt.	2.79	<i>Amphilius atesusensis</i>	invertivore	0.51
<i>Hemistichodus mesmaekersi</i>	invertivore	0.42	Clariidae		
<i>Hemistichodus vaillanti</i>	invertivore	0.37	<i>Clarias anguillaris</i>	omnivore	0.86
<i>Ichthyborus besse</i>	piscivore	1.10	<i>Heterobranchius isopterus</i>	omnivore	1.32
<i>Nannocharax fasciatus</i>	invertivore	0.43	Mochokidae		
<i>Nannocharax lineomaculatus</i>	invertivore	0.37	<i>Synodontis ocellifer</i>	invertivore	2.18
<i>Nannocharax occidentalis</i>	invertivore	0.34	<i>Synodontis schall</i>	invertivore	1.96
<i>Nannocharax ansorgii</i>	invertivore	0.52	Channidae		
<i>Paradistichodus dimidiatus</i>	micro/macrophyt.	1.83	<i>Parachanna obscura</i>	piscivore	0.55
<i>Xenocharax spilurus</i>	omnivore	1.83	Latidae		
Citharinidae			<i>Lates niloticus</i>	piscivore	0.52
<i>Citharidium ansorgii</i>	micro/macrophyt.	5.67	Cichlidae		
<i>Citharinops distichoides</i>	micro/macrophyt.	4.48	<i>Chromidotilapia guntheri</i>	omnivore	3.01
<i>Citharinus citharus</i>	micro/macrophyt.	6.13	<i>Haplochromis adolphifrederici</i>	invertivore	1.68
<i>Citharinus congicus</i>	micro/macrophyt.	4.40	<i>Haplochromis astatodon</i>	micro/macrophyt.	2.84
<i>Citharinus eburneensis</i>	micro/macrophyt.	7.00	<i>Haplochromis gracilor</i>	omnivore	1.56
<i>Citharinus gibbosus</i>	micro/macrophyt.	5.29	<i>Haplochromis graueri</i>	invertivore	1.92
<i>Citharinus latus</i>	micro/macrophyt.	6.78	<i>Haplochromis kamiranzovu</i>	micro/macrophyt.	3.05
<i>Citharinus macrolepis</i>	micro/macrophyt.	4.46	<i>Haplochromis nigroides</i>	omnivore	1.88
Cyprinidae			<i>Haplochromis olivaceus</i>	micro/macrophyt.	3.32
<i>Raiamas senegalensis</i>	invertivore	0.38	<i>Haplochromis paucidens</i>	invertivore	1.42
<i>Acapoeta tanganicae</i>	micro/macrophyt.	5.00	<i>Haplochromis scheffersi</i>	omnivore	1.72
<i>Barbus anoplus</i>	omnivore	0.80	<i>Hemichromis fasciatus</i>	piscivore	0.78
<i>Barbus macrops</i>	omnivore	0.82	<i>Oreochromis mossambicus</i>	micro/macrophyt.	6.80
<i>Barbus sacratus</i>	omnivore	1.63	<i>Sarotherodon galilaeus</i>	micro/macrophyt.	6.54
<i>Chelaethiops elongatus</i>	zooplanktivore	0.75	<i>Coptodon zillii</i>	micro/macrophyt.	5.03
<i>Chelaethiops minutus</i>	zooplanktivore	0.70	Gobiidae		
<i>Coptostomobarbus wittei</i>	zooplanktivore	0.80	<i>Nematogobius maindroni</i>	invertivore	0.37
<i>Garra congoensis</i>	micro/macrophyt.	4.50			

ELECTRIC ORGAN OF *MALAPTERURUS ELECTRICUS*

(SOURCE FRESSARD, 1958)

The African *Malapterurus*, like nearly 250 species of marine and freshwater fish, can emit an electric discharge in a close conducting space. The shock produced by the electric discharge is significant because it can reach 450 volts. This value ranks this species among those presenting the highest electrical discharges. Only the electric eel (*Electrophorus electricus*), in the Amazon River emits stronger discharges (550 volts). Specific observations have shown that *Malapterurus* has a constant and coordinated use of its discharge in its feeding behaviour. Thus, a *Malapterurus* emitting no discharge released 110 in two hours when it was

in the presence of prey. Small fish become inert when subjected to the discharges, and are suffocated when their breathing stops. After, the predator often touches its prey with the anterior portion of its organ. At the same time, it curves its body to the same side to form a loop discharge with maximum efficiency. Then, after having rejected and caught its prey several times, it swallows the prey, continuing meanwhile to emit some discharges. Finally, when the animal is sated, no stimulus, even provoked, seems able to cause a reaction, and no more electric discharge is emitted.

Species	Common names	Habitat	Discharge power (V)
<i>Raja undulata</i>	painted ray	marine	4
<i>Torpedo marmorata</i>	electric ray	marine	45
<i>Torpedo californica</i>	electric ray	marine	50
<i>Uranoscopus scaber</i>		marine	0.2-0.4
<i>Astroscopus spp.</i>		estuarine	5-50
<i>Apteronotus albifrons</i>		freshwater	0.0003-0.001
<i>Electrophorus electricus</i>	electric eel	freshwater	115 (200 mm)
<i>Electrophorus electricus</i>	electric eel	freshwater	500 (1000 mm)
<i>Gymnarchus electricus</i>	aba	freshwater	3-7
<i>Malapterurus electricus</i>	electric catfish	freshwater	30 (50 mm)
<i>Malapterurus electricus</i>	electric catfish	freshwater	350 (500 mm)
Mormyres	elephant fish	freshwater	0.1
<i>Mormyrus kannume</i>	elephant fish	freshwater	2

Body form and feeding types

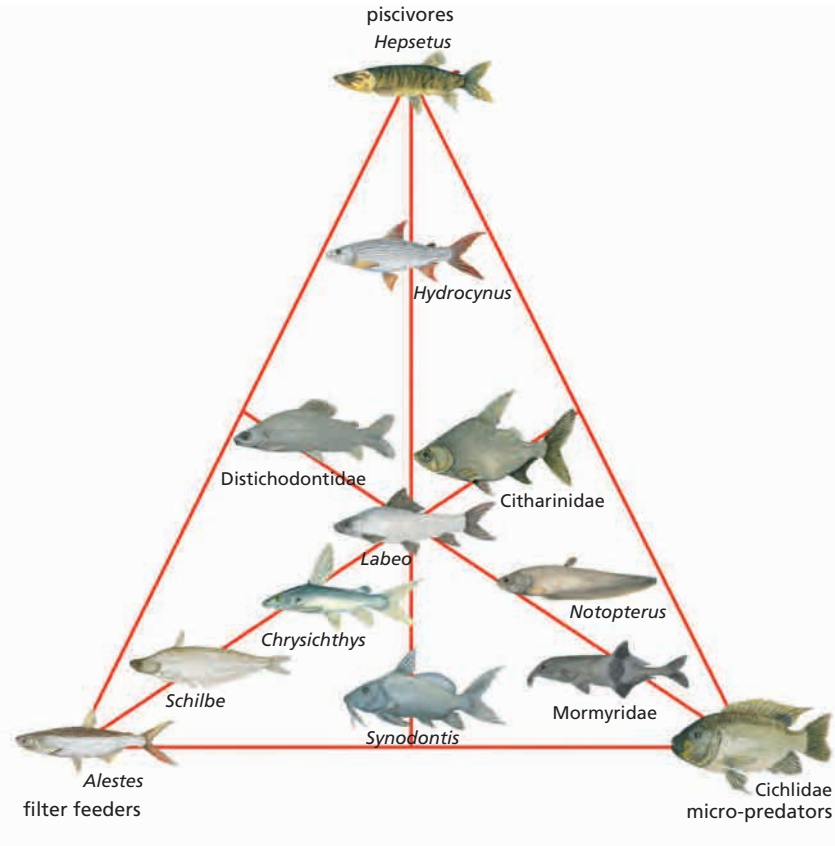
Behavioural strategies for foraging are constrained by morphology, including mouth shape and position as well as body form.

Webb (1984), while looking for correlations between locomotor morphology and the feeding niche, distinguished three basic functional locomotory mechanisms which may be linked to foraging (figure 12.4):

- to exploit food widely distributed in space and time, fish have to move at speeds that sample the greatest volume for the least expenditure of energy. This applies both to macrophage and filter-feeders that have, generally, a streamlined anterior body and a very forked caudal fin. The typical example for African fish is *Alestes baremoze* that filters zooplankton in the lacustrine environment (Lauzanne, 1970) and is an excellent swimmer able to perform long-distance migrations.
- to exploit very vagile food, fish have to catch their prey very quickly before they can escape and reach shelter. Therefore, they must be able to accelerate

FIGURE 12.4.

Ternary diagram “function-morphology” representing the different types of fish swimming. Angles of the triangle are three major modes of foraging; the species closer to the centre are more generalist (adapted from Webb, 1984).



rapidly. In Africa, the typical example is *Hepsetus odoe* (African pike), which has a flexible body and very secluded dorsal fin to accelerate very briefly but with unbelievable speed;

- to exploit prey sometimes hidden in holes or lying on bottom, fish have to swim in very restricted spaces. The median and paired fins allow better manoeuvrability. Many cichlids fit these characteristics as well as mormyrids, notopterids, etc.

It is not possible to combine all the optimum features for the different types of swimming in one fish: the optimum design for manoeuvring excludes the elements that favour high performance in accelerating or in cruising. The three basic design are therefore mutually exclusive. Locomotor specialists represent only a small proportion of fish species and the majority of fish are locomotor generalists.

However, locomotor adaptations for food capture are of diminished importance among locomotor generalists, and other adaptations (e.g. suction or protrusible jaws) which are vital to food selection and the extension of diet breadth, are more common in foraging.

Prey selection

The best prey for a predator is theoretically one that, in a given context, provides it with the greatest amount of energy for the least cost of capture.

Zooplanktivorous fish have two different feeding modes (Lazzaro, 1987):

- particle feeders attack and ingest individual prey that have been visually selected;
- filter feeders do not detect prey individually but retain plankton in their gill rakers. They thus engage in passive selection of prey, and efficient filtration depends to a large extent on gill structure and the size of the particles.

Field workers have used “electivity indices” (E) such as that devised by Ivlev, expressed as

$$E = \frac{(r_i - p_i)}{(r_i + p_i)}$$

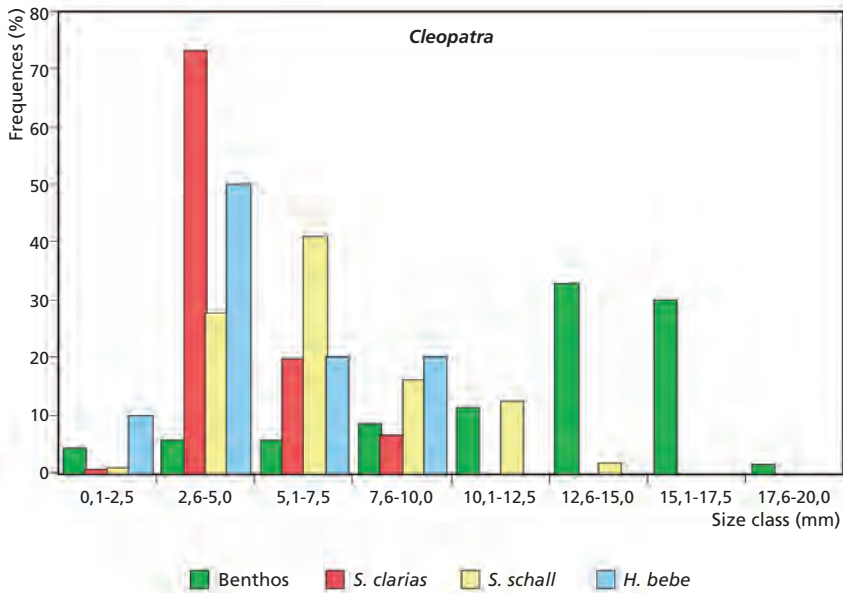
where r_i is the proportion of food item i in the diet, and p_i the proportion of item i in the environment. This index is useful when investigating whether a prey species is or is not being eaten in proportion to its abundance in the habitat, but does not distinguish mechanisms behind any selection revealed.

In filter feeders like *Synodontis batensoda* in Lake Chad, the smallest captured prey measured 80 μm , but the proportion of rotifers and nauplii retained by the gill rakers increases progressively with size, up to 260 μm . The selection of the largest planktonic crustaceans depends essentially on their ability to avoid predators. In this respect, the large cladoceran *Moina micrura*, with poor mobility, is easily captured whereas the more vagile diaptomids are hardly ever caught (Gras *et al.*, 1981). Meanwhile, large *Alestes baremoze* adults do not retain small nauplii or rotifers in their gill rakers, but only particles larger than 400 μm . Above 880 μm all planktonic elements are retained (Lauzanne, 1970). These two zooplanktivorous fish species thus have different behaviours and do not consume the same type of prey in the physical system where they live in sympatry.

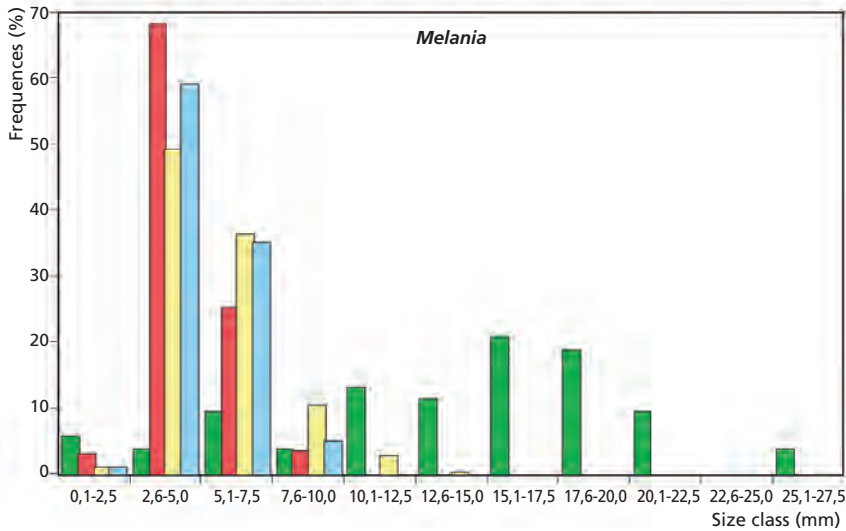
In Lake Victoria, it has also been shown that the decrease in the proportion of shrimp *Caridina nilotica* in the stomach contents of *Lates niloticus* is partly a result of larger spaces between gills as the fish grows larger (Hughes, 1992). Beyond 70 cm LT, the spaces are too large to retain the shrimp.

Benthic fishes can also exert selective pressure on prey species. Three benthivore species of Lake Chad, *Synodontis clarias*, *S. schall*, and *Hyperopisus bebe*, essentially consume small molluscs, as shown in the comparison of size distribution of molluscs in the benthos and in the stomach contents of predator fishes (figure 12.5) (Lauzanne, 1975a).

Still in Lake Chad, up to 50 mm LS *Tetraodon lineatus* consumes mainly microcrustaceans and insect larvae, then, up to 125 mm LS, larger lunged molluscs living in vegetated areas (*Gabbia* sp., *Anisus* sp., *Bulinus* spp). Beyond 200 mm LS, *T. lineatus* only consumes benthic molluscs with thicker shells (*Bellamya unicolor*, *Melania tuberculata*, *Corbicula africana*) (Lauzanne, 1977)

**FIGURE 12.5.**

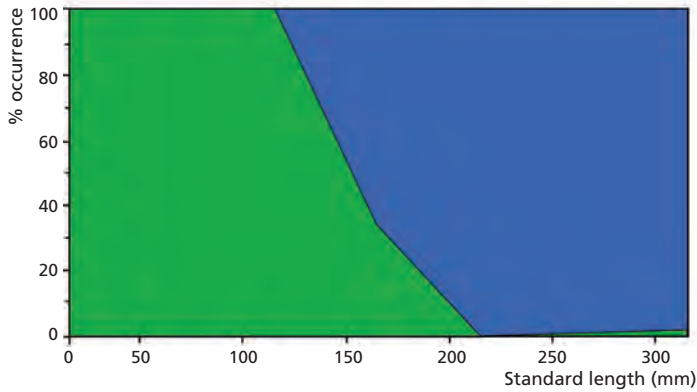
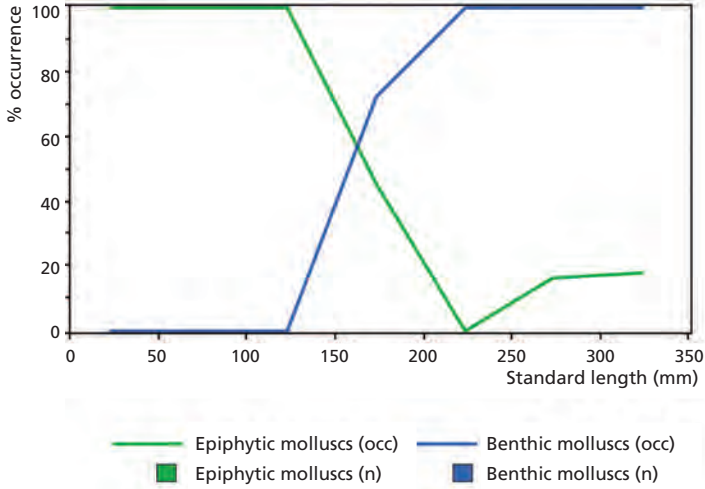
Comparison of size distribution of two species of benthic molluscs (*Cleopatra bulimoides* and *Melania tuberculata*) in the Lake Chad benthos and in the stomach contents of three malacophagous fish species (*Synodontis clarias*, *S. schall* and *Hyperopisus bebe*) (from Lauzanne, 1975a).



(figure 12.6). Similar behaviour has been observed in the lagoon fish *Trachinotus teraia* (Trébaol, 1991). Up to 125 mm LS, it feeds on Clupeidae larvae and juvenile shrimp, while larger individuals consume mainly *Corbula trigona* bivalves in Ébrié lagoon (Côte d'Ivoire).

The impact of selective predation on the dynamics of planktonic or benthic natural populations may thus be significant (see chapter *Role of fish in ecosystems functioning* and chapter *Species introductions*).

FIGURE 12.6.
Ontogenic change
in diet of
Tetraodon lineatus
in Lake Chad (from
Lauzanne, 1977).



Ontogenic shifts in feeding behaviour

Most fish species vary greatly in body size during their lifetimes and often undergo drastic changes in ecology as they grow. Their dietary requirements and their feeding behaviour also undergo changes which are usually related to the ability of growing animals to handle particular food types. Several studies on African fish have highlighted these ontogenetic changes. We have already discussed the case of *Tetraodon lineatus*. Examples also exist in piscivorous species. Thus, in the Chari River, juveniles of *Hydrocynus forskalii* are strictly zooplanktivorous up to 30 mm in length. Between 30 and 45 mm, they consume both zooplankton and insects. Over 50 mm, they become frankly piscivorous. In the Southeast archipelago of Lake Chad, the pattern is the same, but the transition from one diet to another occurs in larger sizes (figure 12.7).

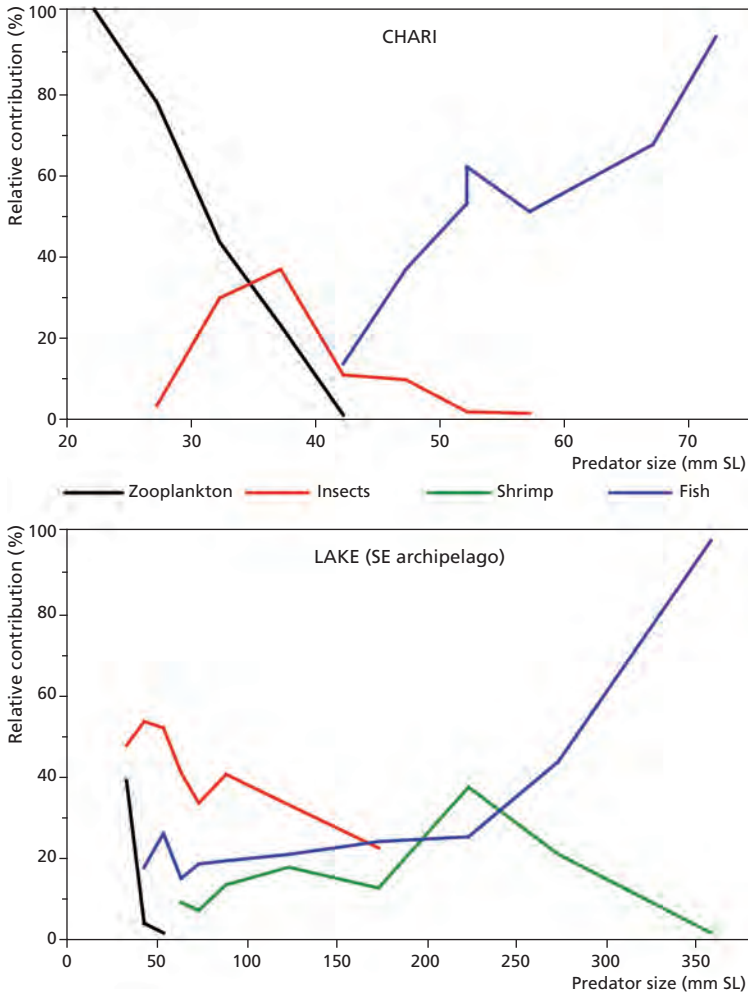


FIGURE 12.7. *Hydrocynus forskalii*: change in the proportion of food items depending on size in the Chari and Lake Chad (Southeast archipelago) (from Lauzanne, 1975b).

Diet also changes with individual growth in cichlids. A peculiar behavioural and morphological development has been reported for *Docimodus evelynae*, a cichlid species from Lake Malawi, in which small juveniles (less than 50 mm SL) are facultative cleaners, removing fungi from other cichlids. From 50 to 70–80 mm SL, they are no longer cleaners, and feed upon plankton, insects and aufwuchs. Above 80 mm SL, their dentition changes (the juvenile tricuspid teeth are replaced by adult unicuspid teeth) and adult *D. evelynae* alter their diet to feed upon scales, fins and skin of their fish prey. Field data has also provided evidence that as *D. evelynae* grow, they move into deeper water. As a result of the depth restricted distributions observed for many species in Lake Malawi, the cichlids cleaned by juvenile *D. evelynae* in shallow water are not the same as those preyed upon by adults in deeper water (Ribbink, 1990).

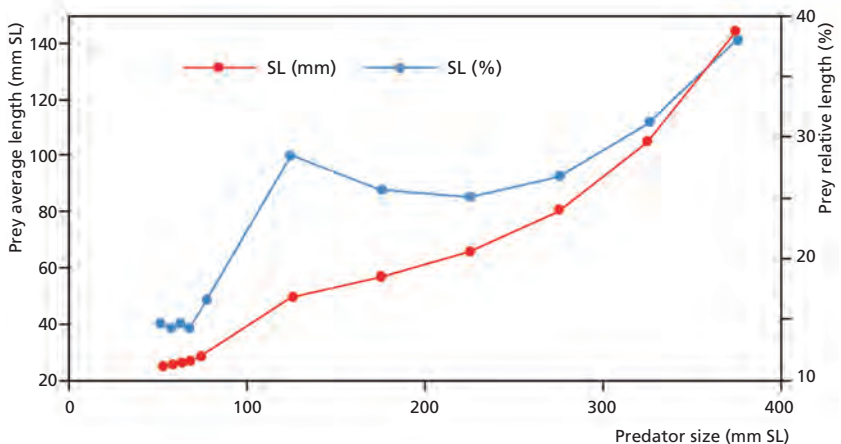
Relationship between predator size and prey size

For many fishes, there is a prey size that minimizes cost of capture by providing the greatest amount of energy to the predator. This type of relationship has been especially studied in piscivorous fishes, which are the most eclectic from this point of view. Generally it can be observed that the relative prey size (size of the prey in relation to the predator) is greater in small and large predators. The relationship thus follows a U-shaped curve.

The relationship between the length of *Lates niloticus* and the size of prey was studied by Hopson (1972). *Lates* at all lengths are able to eat fish up to approximately one-third of their own length. The largest prey in relative size were eaten by the smallest *Lates*, 30 to 40 mm TL. Relative prey size fell steeply from 38% in the smallest *Lates* to 6% in the 30-36 cm TL group. Between 300 and 800 mm TL there was a slight increase in the relative size of prey from 6 to 10%. A marked change was noted in *Lates* over 850 mm TL with prawns and small characins virtually disappearing from the diet. The result is a steep rise in both relative size and average size.

In Lake Chad, the mean relative prey size of *Hydrocynus forskalii* is about 10% for small fish (50-75 mm SL) eating mainly invertebrates, but varies between 20 and 33% for fish from 100 to 400 mm SL (Lauzanne, 1975b) (figure 12.8). A relationship between predator size and prey size has also been recorded for *Ichthyoborus besse*, a less common predator than those cited previously. The mean relative size of prey varies from 20 to 30% for individual fish less than 100 mm SL and from 30 to 40% for *I. besse* above 100 mm SL. The highest relative prey length observed was 50% that of the predator (Lek & Lek, 1978b).

FIGURE 12.8.
Hydrocynus forskalii:
relationship
between the length
of the predator and
the size of the prey
in Lake Chad (from
Lauzanne, 1975b).



Variability in diet of adults

Different field studies have suggested that many fish may vary their diet according to the seasons or environments. It seems that fish broaden their diet to include less preferred prey as the availability of the preferred prey declines. In other words, when food is scarce, they are less demanding about its quality.

For example, *Synodontis batensoda*, a detritivorous fish in the river systems of the Chari (Blache *et al.*, 1964), the Nile (Sandon & El Tayib, 1953) and the Niger (Daget, 1954), was exclusively a filter feeder in Lake Chad before the drought period (Lauzanne, 1972; Tobor, 1972). When the food offered is composed of zooplankton and floating organisms, *S. batensoda* swim on their backs in order to filter the food at the water surface. If the food offered is composed of benthic detritus and mud, the fish swims in a ventral position and filters sediment. In 1974, during the drying phase of Lake Chad, when the zooplankton became less abundant, lake populations of *S. batensoda* exhibited both these feeding behaviours (Im, 1977).

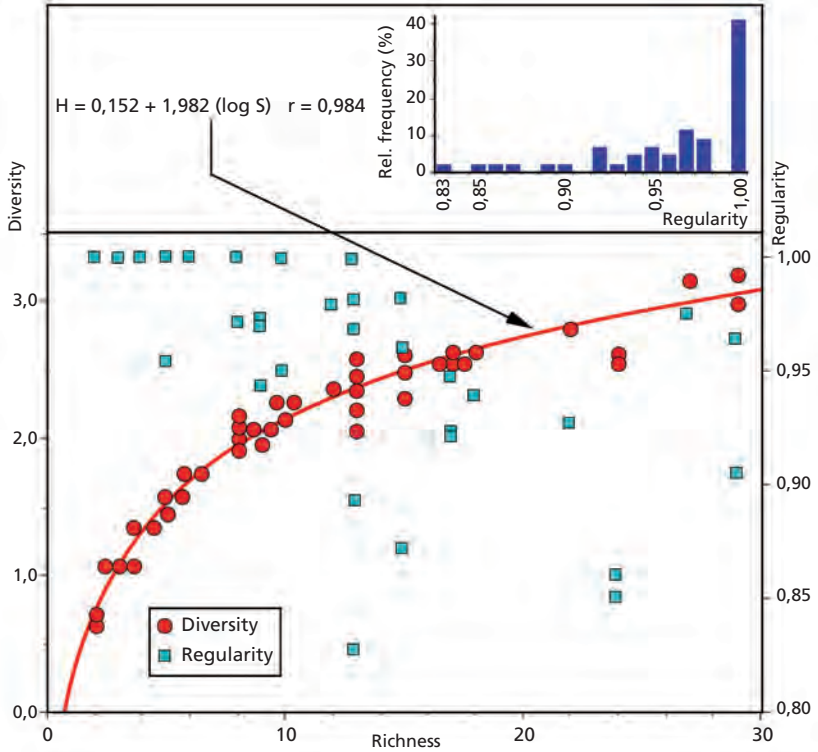
Alestes baremoze is strictly zooplanktivore in Lake Chad (Lauzanne, 1976) and Lake Turkana (Hopson, 1982). In rivers, where zooplankton is scarce, it becomes partly phytophagous in the Chari River as well as in the Niger River but with a significant component of emerging insects (Daget, 1952). In Côte d'Ivoire, aquatic insects and terrestrial invertebrates constitute the bulk of the diet of *A. baremoze* in rivers (Paugy, 1978), whereas in the Kossou man-made lake, this species is zooplanktivore (Kouassi, 1978).

More broadly, many species adapt their diets according to the restrictions of the physical system. For samples taken from different ponds of a temporary watercourse in Mali, it was shown that for the majority of species, diet similarities are greater within a sample than between same species from different samples (Paugy, 1994). This indicates that to survive in sometimes extreme conditions, species adapt – within certain limits – their diets to the available dominant resources. We can thus show that when faced with poor food diversity which is also related to poorer quality, species use the most abundant resources, and when prey becomes more numerous, fishes feed on a larger number of prey taxa. In other words, food diversity which depends on the richness of ingested prey is apparently dependent on the prey available in the environment (figure 12.9).

There is a large body of literature on the degree of trophic specialization of endemic Cichlidae in the East African lakes. It appears that the majority of species can consume a much wider range of food than their morphological specialization would initially suggest.

In fact, many of the Malawi Cichlidae can use one resource or another, based on availability, and are quite opportunistic (Ribbink, 1990). Species that usually graze on the biological surface layer of rocks can shift to a planktonic diet and even consume eggs or larvae of another species. Contrary to a number of common beliefs, the trophic specialization of these Cichlidae does not limit their dietary range, but could give them a competitive advantage in using

FIGURE 12.9. Fish of the Baoulé River (Upper Senegal River in Mali): relationship between the diversity (Shannon index) or the regularity of feeding (ratio between diversity of items and the maximal theoretical diversity for a same number of taxa; also called equitability) and the richness of ingested preys (from Paugy, 1994).



certain types of food, particularly during food shortages, given that they are able to switch to a more general or opportunistic diet at any time (Witte, 1984).

Other groups have also developed this capacity to share resources by “adapting” their morphology. An example is the *Barbus* (Cyprinidae) species flock in Lake Tana where each of the 14 species studied has developed a specific food strategy that avoids interspecies competition. The morphological study carried out on these 14 species also led to the creation of a predictive food model (FFM: *Food-Fish Model*) whose results are consistent with the biological reality observed in the stomach contents of different *Barbus* (Sibbing & Nagelkerke, 2001).

Feeding activity patterns

Change in fish activity during a 24-hour period is a well-known phenomenon. It is generally linked to feeding habits. There are species that are mainly active during the day, or at night or during periods of rapidly changing light intensity (dawn and dusk) (table 12.III).

Major foraging activities include movements between resting sites and foraging areas as well as movements to follow, if necessary, daily activity patterns of prey. For example, vertical migrations of Lake Victoria haplochromines are

TABLE 12.III.

Feeding activity of African fish species (from Lévêque, 1997a).

Species	Basins	Sources	Diel feeding activity
Diurnal diet			
<i>Alestes baremoze</i>	Lake Chad	Lauzanne, 1977	diurnal feeder; peak stomach fullness in the afternoon
<i>Alestes baremoze</i>	Lake Turkana	Hopson, 1982	chiefly diurnal feeder
<i>Brycinus leuciscus</i>	Niger River	Ghazai <i>et al.</i> , 1991	chiefly diurnal feeder, but less during the full moon
<i>Hydrocynus forskalii</i>	Lake Turkana	Hopson <i>et al.</i> , 1982	diurnal feeder; peak fullness in the afternoon
<i>Labeo parvus</i>	Bandama	Mérona, unpub. data	diurnal feeder; stop feeding at night
<i>Lates longispinis</i>	Lake Turkana	McLeod, 1982	non-feeding between sunset and midnight; peak fullness in the afternoon
<i>Oreochromis niloticus</i>	Lake Turkana	Harbott, 1982	diurnal feeder; marked diel feeding pattern
<i>Oreochromis niloticus</i>	Lake George	Moriarty, 1973	diurnal feeder; marked diel feeding pattern
<i>Sarotherodon galilaeus</i>	Lake Chad	Lauzanne, 1977	diurnal feeder
<i>Trachinotus teraia</i>	Ébrié Lagoon	Trébaol, 1991	diurnal feeder
Nocturnal diet			
<i>Bagrus bajad</i>	Lake Turkana	Lock, 1982	peak stomach fullness at night but feeding occurs also during the day
<i>Synodontis batensoda</i>	Lake Chad	Lauzanne, 1977	nocturnal feeder
<i>Hydrocynus brevis</i>	Lake Kivu	Losseau-Hoebeke, 1992	feeds on haplochromines at night and usually hides between rocks during the day
<i>Malapterurus electricus</i>	Niger River	Belbenoit <i>et al.</i> , 1979	nocturnal feeder; peak hunting and feeding period of 5-6 h immediately following sunset
<i>Schilbe uranoscopus</i>	Lake Turkana	Lock, 1982	peak stomach fullness at night; most active at sunset and during the early part of night
<i>Syndontis schall</i>	Lake Turkana	Lock, 1982	peak stomach fullness in the dawn and morning; little feeding in the afternoon
Diurnal and nocturnal diet			
<i>Aphyosemion geryi</i>	Guinea	Pandaré & Romand, 1989	feeds both day and night, but a peak of feeding between 10-19 h

assumed to follow the migration of the prey *Chaoborus* larvae which stay in the muddy bottom during the day and migrate to the water surface during the night to feed on the zooplankton (Witte, 1984).

Similarly, in Lake Kariba, field observations and echo-sounding surveys demonstrated that the clupeid *Limnothrissa miodon*, which feeds principally on *Bosmina longirostris*, shows a pattern of diurnal vertical migration similar to that of its prey (Begg, 1976).

In species that detect prey visually, lunar phases may have an influence on circadian dietary rhythms. For example, in *Brycinus leuciscus* which usually feeds during the day, feeding activity tends to be limited during the full moon, even

though feeding has no nocturnal importance. In fact, it appears that diurnal feeding decreases owing to gregariousness that occurs in preparation for the migratory phase that follows the full moon (Ghazai *et al.*, 1991).

Food webs

Food webs are diagrams depicting which species in a community interact in feeding. "Food webs are thus caricatures of nature" (Pimm, 1982) but they give a picture of the processes at work in ecosystems. According to Cohen (1989) "If an ecological community is like a city, a web is like a street map of the city: it shows where road traffic can and does go."

A food chain describes the energy transfer through different trophic levels, from producers (vegetation for example) to top consumers. The energy transfers are subject to the laws of thermodynamics: at each link, considerable energy is dissipated from the system in the form of heat. Chain lengths are usually short and include four to five links.

In aquatic environments, there are basically two major types of food chains depending of the main energy source represented by primary producers or detritus:

- grazing food chain: in lakes, the food webs of the pelagic zone are fundamentally based on the primary production by phytoplankton;
- detritus food chain: in contrast, the food webs in the benthic zone are usually based on organic material, including living and dead organisms, imported from pelagic communities, or of allochthonous origin.

In small streams and rivers, the food webs are often heavily dependent on allochthonous organic material, falling into the water or washed in by rains (leaves and terrestrial insects for example). In contrast, in large rivers with a slow flow, the primary production of indigenous origin is more important.

Phytoplanktivore communities

The shortest food chain could be illustrated by simple fish communities feeding on phytoplankton. However, Bowen (1988) pointed out that the majority of African fish do not feed directly on living plant material but depend either on zooplankton or benthic invertebrates for food. True primary consumers only belong to some genera (*Labeo*, *Citharinus*, *Distichodus*, *Tilapia*, *Oreochromis* and *Sarotherodon*), that is to say fewer than 7% of the total species.

The cichlid *Alcolapia grahami* is endemic to Lake Magadi where it feeds on benthic filamentous cyanophytes, insect larvae and copepods. It was introduced in the 1950s into Lake Nakuru to control mosquito breeding. There it is the only fish species, and quickly became one of the major filter feeders exploiting the high standing crops of the cyanobacterium *Spirulina platensis* which provide 95% of its diet.

Phytoplankton, mostly blue-green algae, is very abundant in Lake George. It was mainly consumed by two species, *Oreochromis niloticus* and *Haplochromis nigripinnis*, which largely dominated the fish biomass (Gwahaba, 1975).

Relatively simple trophic webs: pelagic fish communities of East African Great Lakes

The trophic hierarchy among the pelagic fish of East African Great Lakes is relatively simple because few fish species are adapted to the pelagic zone of inland waters. For example, in Lake Tanganyika the trophic web is mainly organized from phytoplankton which is consumed by zooplankton (Coulter, 1991). The latter is the main food of two clupeid species, *Stolothrissa tanganyicae* and *Limnothrissa miodon*, which appear from their diet and life history to be narrowly specialized for pelagic life and are key members of the pelagic food chain, linking planktonic and piscivorous trophic levels (figure 12.10). Juveniles of *Limnothrissa* are zooplanktivores, but adults feed regularly on juvenile and adult *Stolothrissa*. The two clupeids are the prime food for predators, which are essentially two species of *Lates*. An alternative is in a phytoplankton-shrimp-fish food web (figure 12.10).

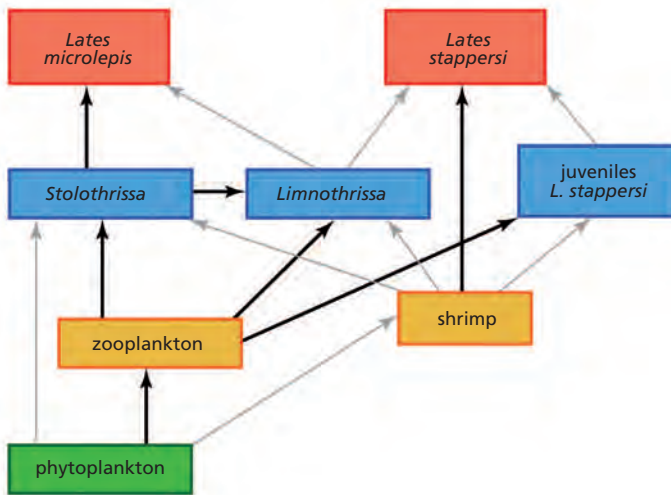


FIGURE 12.10.

Food web of the pelagic fish community of Lake Tanganyika (from Coulter, 1991). Heavy arrows for major food preference, grey arrow for secondary food preference.

It is interesting to highlight that the pelagic food web of Lake Tanganyika is marine in nature: the primary grazer is a diaptomid copepod just as in many productive marine systems, and the primary planktivores (Clupeidae) are also of marine origin, as are the main predators, *Lates*, which also belong to a family of marine origin (Hecky, 1991).

In Lake Kivu, the pelagic food web is relatively simple including the introduced zooplanktophage *Limnothrissa miodon* (from Lake Tanganyika), the microphytophage *Haplochromis kamiranzovu*, the micropredator *Raiamas moorei* (feeding on insects but also on juvenile fish), and the piscivore *Haplochromis vittatus* (Ulyel, 1991).

Trophic webs can sometimes change without necessarily becoming more complicated. A striking example can be seen in Lake Victoria. In some zones, after the introduction of *Lates niloticus*, the stock of *Haplochromis spp.* which

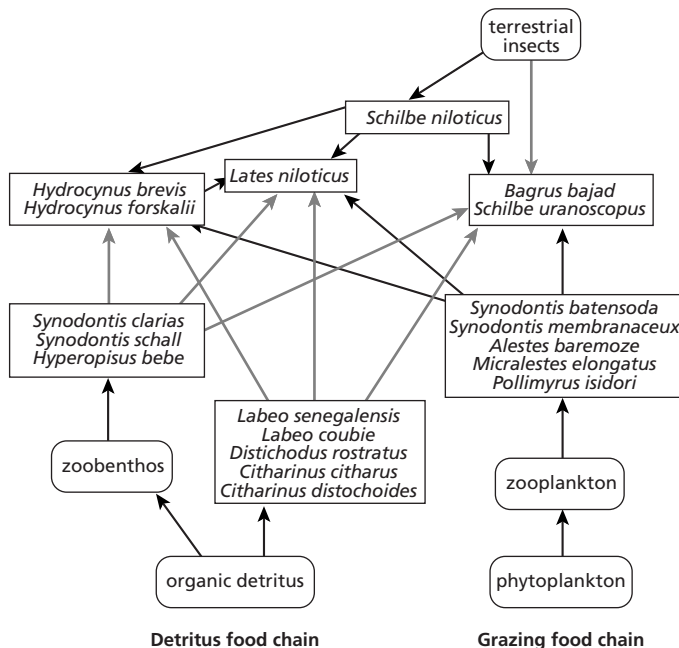
served as the essential food for predators has almost totally disappeared (Ligtvøet & Witte, 1991). Since then, although certain species still exist, they are no longer the major prey, and the predator, which now often exhibits cannibalistic behaviour, feeds almost exclusively on a single Cyprinidae species (see chapter *Fish communities in East African rift lakes*).

More complex food webs of shallow lakes

In Lake Chad, before the drought of the early 1970s, trophic webs – including in free waters – were much more complex than in the pelagic zones of the great lakes owing to the shallowness of the waters. Lauzanne (1976 and 1983) distinguishes two closely intertwined chains in the open waters of Lake Chad. The first one, planktonic, starts with phytoplankton, and the second one, benthic, is partly of detritic origin. The planktonic network leads to planktivorous Alestidae (*Micralestes acutidens*, *Brycinus nurse*, *Alestes baremoze*), Mochokidae (*Synodontis membranaceus*, *Synodontis batensoda*), and Mormyridae (*Pollimyrus isidori*). In turn, these fishes are prey to several predator species (figure 12.11) that consume relatively few of the species from the detritivore and benthic chain (see also box “Ecopath”). Therefore, as in Lake Tanganyika, zooplanktivorous fishes serve as the main food source of *Lates* and *Hydrocynus*. Similar results were obtained in Lake Turkana (Hopson & Ferguson, 1982).

It should be noted that terrestrial invertebrates that fall on the open waters of Lake Chad, sometimes tens of kilometres from the coast, play an important role in the diets of a few species such as *Schilbe niloticus*, which on several occasions has been observed to have stomachs full of crickets. This observation has also been made, to a lesser degree, in *Schilbe uranoscopus* and *Bagrus*

FIGURE 12.11.
Food webs
in the open waters
of Lake Chad
(modified from
Lauzanne, 1983).



bajad. Similar observations on the diet of *Schilbe niloticus* have been made in Lake Albert (Worthington, 1932). *S. niloticus* plays an important role in the diet of other predators in Lake Chad, and in a way represents the main link of a third trophic chain, one that connects external sources to top predators.

Prior to the introduction of *L. niloticus*, certain areas on the edge of Lake Victoria provided an example of a relatively complex trophic web.

ECOPATH

It is often useful to quantify the energy transfers that occur, rather than limiting oneself to a simple description of a trophic web, in order to obtain a partial (by level) or general appraisal that takes all the supposed players into account.

An initial attempt to model this led to the creation of the first "ECOPATH" programme (Polovina & Ow, 1983 ; Polovina, 1984 and 1985).

A new version of the initial attempt was recently proposed under the name "ECOPATH II" (Christensen & Pauly, 1993 ; Pauly *et al.*, 1993), which resurrected the initial model and simplified it to include only easily-obtained parameters, in order to characterize the relative consumption of different fish populations as faithfully as possible.

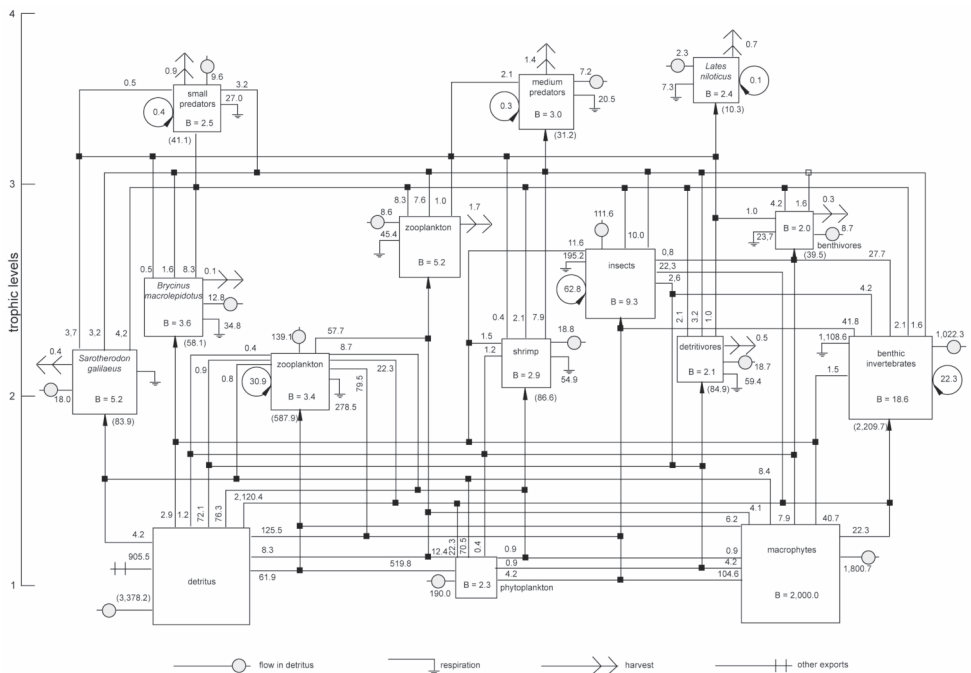
As an example, we present below the modelling of a relatively complex web: Lake Chad

(Palomares *et al.*, 1993) (figure 12.12).

This model estimates total biomass to be 26 t. km⁻², a reasonable figure when compared with the value for total captures, estimated at 6.4 t. km⁻². Likewise, the relative dominance of species (*B. macrolepidotus* and zooplanktivores) is quite consistent with previous observations (Durand, 1983). Nonetheless, this model should not be considered universal, as it only reflects the "normal" period of Lake Chad's evolution; neither can it be applied to other systems of the ecoregion.

FIGURE 12.12.

Ecopath II: model of Lake Chad during the "normal" period (from Palomares *et al.*, 1993).



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The Inland Water Fishes of Africa

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