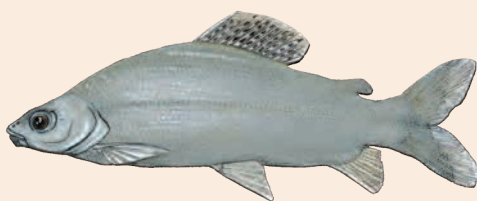# Growth and ontogeny

CHRISTIAN
LÉVÊQUE

Growth is one of the most complex processes for an organism. On the metabolic level, part of the energy consumed will be devoted to increasing its weight, but the proportion of energy used to generate living matter depends on the age of the individuals, their physiological state, their environmental conditions, etc.
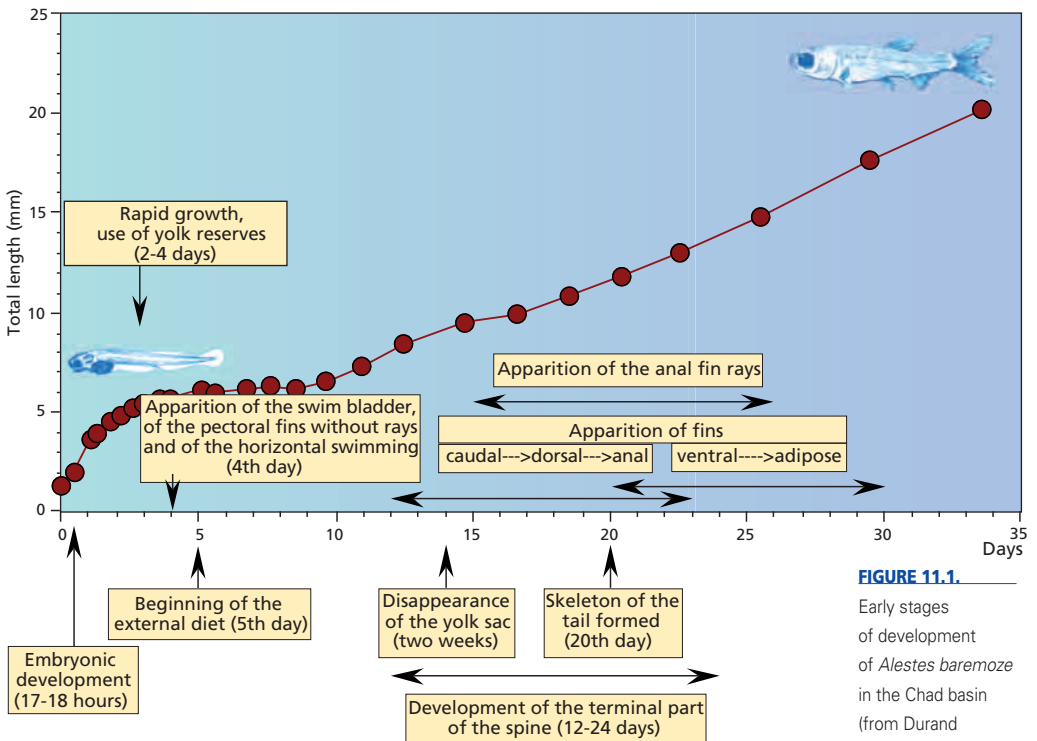
First stages of development

Little is known about the first stages of development in African fishes. A review of literature shows that data is only available for 18 of 74 identified families (Cambray & Teugels, 1988).

ONTOGENY AND MAIN STAGES OF DEVELOPMENT

Ontogeny is the process of differentiation of the different stages of development in the life of an organism. We usually distinguish several periods in the life of a fish. (Balon, 1981, 1984 and 1986):

• the embryonic period which begins with fertilization and is characterized by exclusively endogenous nutrition from the egg yolk;

• the larval period which begins with the progressive but rapid transition from an endogenous food supply to exogenous feeding. This period is characterized by the presence of temporary larval organisms;

• the juvenile period begins when the fins are well-differentiated and when all temporary organs are replaced by final organs. This stage ends with the first maturation of gametes. This is usually a period of rapid growth sometimes characterized by a specific colouration;

• the adult period begins with the first maturation of gametes. It is characterized by a decrease in somatic growth rate;

• finally, there is sometimes a period of senescence.

Balon (1985; 1990) distinguishes two broad types of ontogenic trajectories. In the indirect development or "altricial" model, eggs are generally small and produced in large numbers. They yield small, underdeveloped young larvae with only a small volume of yolk that is not sufficient for producing the final phenotype. These young larvae must feed rapidly on small particles to complete their development and are highly vulnerable during this period. The Alestidae *Alestes baremoze* is a good example of this type of fish (Durand & Loubens, 1971) (figure 11.1), as are *Clarias gariepinus* (Bruton, 1979a) and *Heterobranchus longifilis*.

FIGURE 11.1.

Early stages of development of *Alestes baremoze* in the Chad basin (from Durand & Loubens, 1971).

In the direct development ("precocial") model, fishes produce a limited number of large eggs with a large amount of yolk, which allows the embryo to develop to an advanced stage. This shortens or eliminates the larval period, and juveniles are already well-formed and thus less vulnerable when they start seeking an external diet. *Labeotropheus*, a Cichlidae mouth-brooder from Lake Malawi, is a good example of this type of fish that releases a large juvenile (14% of adult size) only 31 days after fertilization (Balon, 1977) (see box "First stages of development in *Labeotropheus*"). *Cyphotilapia frontosa* illustrates an even more advanced style, as embryos already start consuming an external diet even while in the buccal cavity where they still have a yolk reserve (Balon, 1985).

FIRST STAGES OF DEVELOPMENT IN *LABEOTROPHEUS* (FROM BALON, 1977)

*L*abeotropheus is an endemic Cichlidae in Lake Malawi.
It is a mouth-brooder for eggs and juveniles.
Just after spawning, 30 to 50 oval-shaped eggs (3 mm in diameter and 4.4 mm long) are immediately collected in the mouth by females.
They are fertilized in the oral cavity of the female which is almost completely filled by eggs.

The eggs are incubated for 6 days before hatching. At birth, juveniles have a large yolk sac and stay in the oral cavity where they develop and acquire their main morphological structures (skeleton, fins, etc.). The yolk sac is absorbed 21-22 days after fertilization, but embryos stay in the oral cavity of the female up to the 31st day. At this age, they are very well-formed, autonomous, large (approximately 15 mm, i.e., 14% of the adult size) and begin their exogenous foraging.

There are, of course, intermediate modes between the two broad styles discussed above. *Pollimyrus isidori* (table 11.I) is an example.

TABLE 11.I.

Comparative characteristics in the development of some African fish species.
References. 1: Durand & Loubens, 1971; 2: Cambray, 1985; 3: Bruton, 1979; 4: Legendre & Teugels, 1991; 5: Kirshbaum, 1987; 6: Balon, 1977; 7: Balon, 1985. Gonado-somatic index (GSI)

Species	Altricial development				Intermediate development	Precocial development	
	Alestes baremoze	*Barbus trevelyani*	*Clarias gariepinus*	*Hetrobranchus longifilis*	*Pollimyrus isidori*	*Labeotropheus trewavasae*	*Cyphotilapia frontosa*
References	1	2	3	4	5	6	3
Egg size (mm)	1-1.3	1.5	1.6-1.9	1.5-1.8	2	3 x 4.3	5.6x4.0
Egg number	x 10,000		x 10,000	x 100,000	120	30-50	
GSI	9 %		7-10 %	20-23 %			
Parental care	no	no		no	nest protected (male)	mouth-brooder (female)	mouth-brooder (female)
Embryonic development	< 1 day	2.8 days	1 day	1 day	3 to 4 days	6 days	5 days
Exogenous diet	5 days	?	3-4 days	3 days	15 days	25-30 days	14 days
Size (mm)	6 mm	7 mm	6.2 mm	10 mm TL	8 mm	15 mm	15 mm
Disappearance of the yolk sac	12 days	11.5 days	3 days	3-4 days	14 days	21 days	
Size (mm)	7 to 8	7.1	6.2		8	13-14	
End of larval time	30 days	50-60 days	14 days ?		40 days		feeding
Size	17.5 mm	20 mm	12.1 mm		15 mm		oral cavity
Juvenile freedom						31 days	54 days
Size						15 mm	23 mm LT

Growth estimation

Growth can be estimated using changes in size or biomass in a given time interval. It corresponds to the organism's energy intake that is not used for maintaining metabolism.

There is a great deal of literature on growth estimation methods, and researchers agree that it is difficult to determine the age of tropical fish. Marks on bony structures are harder to read and interpret than on temperate fishes (Mérona *et al.*, 1988). Nonetheless, certain investigations have shown that growth marks generally coincide with drops in temperature, which often occur during low water periods. In some cases, growth marks can be associated with gonad maturation which generally follows a long period of fasting. Formation of marks on bony structures is thus the result of various physiological disturbances, and it is necessary to determine which ones are at play for a given species.

Determination of growth and age were long considered key elements for models of fish stock dynamics. As a result, a large number of growth curves were calculated for African fishes (Mérona *et al.*, 1988), but most did not attempt to account for the relationships between growth and other biological parameters. Consequently, many of these results are of limited use to understand species biology.

Growth models

Annual growth can be described as an asymptotic curve, and the most widely used is von Bertalanffy's model (1938). It is based on bioenergetic principles, with the hypothesis that growth rate is equal to the difference between the anabolic rate and the catabolic rate. The von Bertalanffy model is expressed as the equation:

$$Lt = L_\infty \left\{ 1 - e^{-K(t-t_0)} \right\}$$

where L_∞ is the asymptotic length, Lt fish length at age t, K is a constant that describes the rate of growth, and t_0 is the hypothetical time at which size is zero.

Similarly, fish weight at time t is given by the equation:

$$Wt = W_\infty \left\{ 1 - e^{-K(t-t_0)} \right\}$$

While von Bertalanffy's model provides us with a smooth annual growth curve, growth is not a continuous process. At times there are long periods in a year during which growth stops or is sharply reduced. In other words, growth can take place during rather short periods. For instance, 75% of the growth of young *Oreochromis andersoni* and *O. macrochir* in the Kafue River occurs during the six weeks of peak water levels (Dudley, 1972). During the dry season, growth is very slow but does not stop (Kapetsky, 1974).

Welcomme & Hagborg (1977) proposed a growth model for fishes in flood zones, which takes into account a rapid initial increase in length followed by a slower growth period. In the formula $L_{t+t'} = L_t + G (e^{t'})$, the values of L_t for successive years are the same as the ones provided by the von Bertalanffy model, but growth during the year is calculated for each week. This gives a growth curve that is a more accurate representation of what happens on the field.

Growth in length and weight gain are not always correlated. Weight gain includes the creation of fat reserves, for instance, or gonad development, phenomena that do not necessarily involve an increase in length (table 11.II).

TABLE 11.II.

Some growth data about African fish (from Mérona *et al.*, 1988.
S: sex (m: male, f female, t: sexes blended);
L: length (TL: total length; SL: standard length; FL: fork length);
M: size at first maturation; A: average longevity (years);
AMS: average maximal size; MSO: maximal size observed;
L_∞, K and t_0: parameters of the von Bertalanffy equation.

Species	Sex	Locality	L	M	A	AMS	MSO	L_∞	K	t_0
Mormyrus rume	t	Niger-Benue	TL	425	6,0	785		2 048	0.071	- 0.483
Petrocephalus bovei	t	Côte d'Ivoire	SL	65	2,5	95	110	99	1.104	- 0.203
Hepsetus odoe	m	Lake Liambezi	FL	200		305	370	307	1.712	- 0.237
Hepsetus odoe	f	Lake Liambezi	FL	250	5,0	413	470			
Hydrocynus vittatus	m	Lake Bangweulu	FL	390	8,0	605		796	0.266	- 0.337
Hydrocynus vittatus	f	Lake Bangweulu	FL	390	11,0	689		740	0.229	- 0.145
Alestes baremoze	m	Chad	SL	180	5,0	231	285	252	0.696	- 0.243
Alestes baremoze	f	Chad	SL	205	6,0	263	326	292	0.518	- 0.318
Bagrus meridionalis	m	Lake Malawi	TL	340	11,0	607	890	1 048	0.092	+ 0.017
Bagrus meridionalis	f	Lake Malawi	TL	360	17,0	832	970	1 092	0.091	+ 0.017
Oreochromis niloticus	t	Lake Mariut	TL		5,0	376		426	0.460	+ 0.541
Coptodon zillii	m	Niger	TL	200	6,0	300	320	310	0.531	+ 0.226
Coptodon zillii	f	Niger	TL		6,0	269		274	0.603	+ 0.252
Lates niloticus	f	Chad	SL	24				953	0.191	- 0.749

Length-weight relationships and coefficient of condition

The relationship between fish length and weight takes the form:

$$\log W = \log a + b \log L$$

where W is the weight, L the length, a and b are constants.

When growth is isometric, that is, when the fish shape does not change with growth, b is equal to 3. A value below 3 indicates that weight gain is inferior to increase in length. The opposite holds true if b is above 3 (table 11-III).

TABLE 11-III.

Length-weight relationships of some African fish species.

Constant values: a and b.

Species	log a	b	Range size (mm)	Geographical origin	Source
Polypetridae					
Polypterus senegalus	4.556	2.760	375	Nile	Hickley & Bailey, 1986
Mormyridae					
Hyperopisus bebe	5.972	3.370	400	Nile	Hickley & Bailey, 1986
Marcusenius furcidens	4.459	2.785	75-225	Côte d'Ivoire	unpublished
Marcusenius senegalensis	4.951	3.040	75-205	Côte d'Ivoire	unpublished
Marcusenius ussheri	4.342	2.746	20-235	Côte d'Ivoire	unpublished
Mormyrus cashive	5.074	3.010	585	Nile	Hickley & Bailey, 1986
Mormyrus rume	4.389	2.706	20-430	Côte d'Ivoire	unpublished
Petrocephalus bovei	4.533	2.907	30-120	Côte d'Ivoire	unpublished
Arapaimidae					
Hetrotis niloticus	4.973	3.030	880	Nile	Hickley & Bailey, 1986
Hepsetidae					
Hepsetus odoe	5.460	3.258	90-290	Côte d'Ivoire	unpublished
Alestidae					
Hydrocynus forskalii	4.714	2.943	75-275	Côte d'Ivoire	unpublished
Hydrocynus forskalii	4.781	2.930	470	Nile	Hickley & Bailey, 1986
Alestes baremoze	4.875	2.987	30-250	Côte d'Ivoire	unpublished
Alestes dentex	4.485	2.790	360	Nile	Hickley & Bailey, 1986
Brycinus nurse	4.492	2.935	30-210	Côte d'Ivoire	unpublished
Brycinus nurse	4.464	2.900	155	Nile	Hickley & Bailey, 1986
Brycinus imberi	4.616	3.031	28-153	Côte d'Ivoire	unpublished
Brycinus macrolepidotus	4.554	2.940	23-308	Côte d'Ivoire	unpublished
Brycinus macrolepidotus	4.513	2.880	315	Nile	Hickley & Bailey, 1986
Brycinus longipinnis	4.792	3.115	42-104	Côte d'Ivoire	unpublished
Micralestes acutidens	4.628	2.960	48	Nile	Hickley & Bailey, 1986
Citharinidae					
Citharinus citharus	4.357	2.910	310	Nile	Hickley & Bailey, 1986
Citharinus latus	4.369	2.950	430	Nile	Hickley & Bailey, 1986
Ichthyborus besse	5.993	3.133	185	Chad	Durand *et al*., 1973
Ichthyborus besse	5.486	3.270	185	Nile	Hickley & Bailey, 1986
Nannocharax fasciatus	4.786	2.994	30-52	Côte d'Ivoire	unpublished
Distichodontidae					
Distichodus rostratus	4.576	2.950	670	Nile	Hickley & Bailey, 1986
Cyprinidae					
Barbus trispilos	4.238	2.766	27-72	Côte d'Ivoire	unpublished
Labeo coubie	4.178	2.825	60-305	Côte d'Ivoire	unpublished
Labeo niloticus	4.448	2.890	390	Nile	Hickley & Bailey, 1986
Labeo parvus	4.311	2.888	40-205	Côte d'Ivoire	unpublished
Labeo senegalensis	4.471	2.934	35-275	Côte d'Ivoire	unpublished
Raiamas senegalensis	4.791	2.995	40-150	Côte d'Ivoire	unpublished
Bagridae					
Bagrus bajad	4.696	2.890	530	Nile	Hickley & Bailey, 1986

TABLE 11-III. (CONT.)

Species	log a	b	Range size (mm)	Geographical origin	Source
Clatoteidae					
Chrysichthys maurus	4.391	2.862	30-205	Côte d'Ivoire	unpublished
Clarotes laticeps	4.561	2.940	400	Nile	Hickley & Bailey, 1986
Auchenoglanis biscutatus	4.573	2.990	375	Nile	Hickley & Bailey, 1986
Clariidae					
Clarias gariepinus	4.432	2.750	78	Nile	Hickley & Bailey, 1986
Schilbeidae					
Schilbe mandibularis (M)	4.535	2.804	30-230	Côte d'Ivoire	unpublished
Schilbe mandibularis (F)	4.648	2.869	30-230	Côte d'Ivoire	unpublished
Schilbe intermedius	5.541	3.312	26-305	Côte d'Ivoire	unpublished
Schilbe niloticus	5.323	3.150	350	Nile	Hickley & Bailey, 1986
Mochokidae					
Synodontis schall (youngs)	3.793	2.562	35-105	Côte d'Ivoire	unpublished
Synodontis schall (adults)	4.969	3.149	105-200	Côte d'Ivoire	unpublished
Synodontis schall	5.021	3.200	330	Nile	Hickley & Bailey, 1986
Synodontis bastiani	4.362	2.837	30-205	Côte d'Ivoire	unpublished
Synodontis clarias	5.501	2.420	290	Nile	Hickley & Bailey, 1986
Synodontis frontosus	4.543	3.000	285	Nile	Hickley & Bailey, 1986
Amphiliidae					
Amphilius atesuensis	4.242	2.703	20-54	Côte d'Ivoire	unpublished
Nothobranchiidae					
Epiplatys spilargyreius	3.987	2.420	36	Nile	Hickley & Bailey, 1986
Latidae					
Lates niloticus	4.669	3.018	100-799	Lake Chad	Loubens, 1974
Lates niloticus	4.479	2.945	100-799	Chari	Loubens, 1974
Lates niloticus	4.474	2.930	1280	Nile	Hickley & Bailey, 1986
Cichlidae					
Hemichromis bimaculatus	4.217	2.885	16-93	Côte d'Ivoire	unpublished
Hemichromis fasciatus	4.601	3.061	32-150	Côte d'Ivoire	unpublished
Hemichromis fasciatus	4.281	2.900	145	Nile	Hickley & Bailey, 1986
Hemichromis letourneuxi	4.388	2.960	63	Nile	Hickley & Bailey, 1986
Oreochromis niloticus	4.463	3.040	400	Nile	Hickley & Bailey, 1986
Oreochromis niloticus	1.055	2.990	Long. totale	Lake Turkana	Harbott & Ogari, 1982
Chromidotilapia guntheri	4.366	2.971	29-125	Côte d'Ivoire	unpublished
Sarotherodon galilaeus	4.158	2.906	25-180	Côte d'Ivoire	unpublished
Sarotherodon galilaeus	4.216	2.950	255	Nile	Hickley & Bailey, 1986
Sarotherodon galilaeus	1.055	3.010	Long. totale	Lake Turkana	Harbott & Ogari, 1982
Haplochromis loati	4.295	2.870	70	Nile	Hickley & Bailey, 1986
Coptodon zillii	4.205	2.924	20-170	Côte d'Ivoire	unpublished
Coptodon zillii	4.405	3.020	210	Nile	Hickley & Bailey, 1986
Mastacembelidae					
Mastacembelus nigromarginatus	5.111	2.775	55-175	Côte d'Ivoire	unpublished

The index K, also called the coefficient of condition, is the relationship between body weight (W in g) and length (L in cm):

$$K = \frac{W}{L^3}$$

This coefficient does not change with length if growth is isometric, which is rarely the case. In many species, however, there may be a variation in body shape or weight during growth, depending for instance on the reproductive cycle or the availability of food. The coefficient of condition makes it possible to monitor the fish's weight. It is thought to be a good instrument for comparing the overall physiological state of populations during a seasonal cycle or between basins with different ecological conditions.

Longevity, size and growth

An important characteristic of fishes is that growth never stops during their lifetime but only slows down with age or size, unlike in mammals and birds. One thus cannot associate an absolute average size to a species and, instead, the maximum size observed (MSO) is most often mentioned. Another characteristic is the great variability in growth at an individual level as well as at the level of populations living in physical systems with different ecological characteristics (food, space, temperature, competition, etc.).

We can posit that the larger a fish, the older it is. If this is the case, there should be a relationship between characteristic growth parameters and a parameter expressing maximum age or size. This indeed holds true, and there is a significant relationship between the maximum size observed (MSO) in wild populations and estimated lengths at 1 year (L1) and 2 years (L2) (Legendre & Albaret, 1991) (figure 11.2). They are, respectively, L1 = 0.205 MSO + 45.57 and L2 = 0.333 MSO + 63.86 for 58 value pairs. These models have been validated experimentally using 6 farmed species.
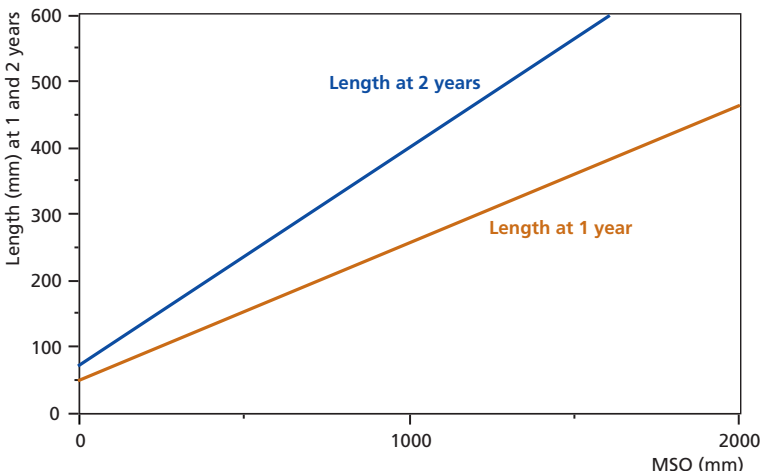
FIGURE 11.2.
Relationship between the maximum size observed (MSO in mm) and the length at 1 and 2 years old for various fresh- and brackishwater African fish species. (data from Legendre & Albaret, 1991).

These results show the existence of a strong positive correlation between the MSO and lengths L1 and L2, which indicates that fishes with a high MSO have a higher growth rate than fishes with a lower MSO.

The ratios L1/MSO and L2/MSO indicate that African fishes reach about a third and then half their maximum size at the end of the first and the second year, respectively (Legendre & Albaret, 1991). These observations agree with the results obtained by de Mérona (1983) who underscored a similar relationship between the asymptotic length, $L\infty$, and the coefficient K of the von Bertalanffy equation: $\log K = 2.186 - 1.048 \log L\infty$ which can be simplified to $K = 153/L\infty$. In order to apply this relationship to field data, de Mérona (1983) also established an empirical relationship between $L\infty$ and the maximum average size (MAS) of the population, which is the average value (or mode) of the largest individuals observed in the population: $L\infty = 1.248$ MAS. The combination of these two ratios allows a rough estimate of the growth curve of African fishes (Mérona *et al.*, 1988), which serves as a quick model for estimating growth. Data available for African fishes appear to show that fishes in tropical regions do not grow faster than those in temperate zones, contrary to common belief, but this would merit further investigation.

If the above results highlight general trends, it should be nonetheless recalled that there is high inter-species variability as well as large differences between populations of the same species living in different hydrographic basins. That said, the MSO remains a practical tool for rapid assessment of growth rates in the absence of other data.

Size and age at first maturity

Puberty is an important event in the life of an animal, and is accompanied by a reduction in somatic growth. Sexual maturation is costly in terms of energy. The reserves accumulated up to that point are used for gonad development, gamete production, development of secondary sex characteristics, etc.

As a result, there are potential conflicts in energy use between:
• continued growth of the individual, who could then produce more eggs;
• immediate production of descendants, which is another type of demographic strategy.

The age at which the fish reaches sexual maturity thus has evolutionary implications. In stable populations, it is believed that the age at first reproduction evolved in order to maximize reproductive success throughout the fish's lifetime. The average size at first reproduction, defined as the size class in which at least 50% of the individuals are mature, is often mentioned. This average size may vary depending on the type of physical system and may not be the same for both sexes (see table 11.II).

Do fishes reach sexual maturity at a given age or size? This question was the object of much discussion but is probably not highly relevant after all, as fishes mature within an age or size range that is probably defined by the combined influence of genetics and environment. For some cichlid species living in different physical systems, growth and age or size at first maturation, as well as MSO, can also be very different (Noakes & Balon, 1982). For *O. niloticus*,

the size at first maturation may vary from 140 mm to 390 mm in the natural environment, and for *C. zillii* and *O. mossambicus*, this size can go from 70 and 45 mm respectively in an aquarium, and 135 and 300 mm in a lake or reservoir (table 11.IV).

Species	Locality	Size at maturation (mm)	Maximal size (mm)	Longevity (years)
Coptodon zillii	Lake Kinnereth	135	270	7
	Egypt, ponds	130	250	
	Lake Naivasha	90		
	aquarium	70		
Oreochromis mossambicus	Lake Kariba	300	390	8
	South Africa		390	11
	Sri Lanka	150	340	
	Egypt		300	7
	Hong Kong	165	310	4
	aquarium	45		
Oreochromis niloticus	Lake Turkana	390	640	
	Lake George	280	400	
	Lake Albert	280	420	
	Lake Edward	250	360	
	Lake Baringo	180	360	
	Egypt	200	330	9
	Buhuku lagoon	140	260	

Size and age at maturation are thus influenced by the environmental conditions in which the fish grows. Thus, most Tilapias are known for their capacity to reproduce at a smaller size when they are in an environment that does not fully suit them. For four wild populations of *O. mossambicus* living in small pools of water with different sets of environmental characteristics, the age at first maturity varies from 1 to 3 years, and the size at first maturity ranges from 118 to 236 mm for females (James & Bruton, 1992) (table 11.V).

Habitat	SL 50 % maturity (mm)	Maximal SL (mm)	Weight (g) at SL 50 %	Age (years)	Average size of layings (nb of eggs)	Average size of eggs	Average number of eggs / g
Kowie lagoon							
males	223	289	410	3+			
females	212	262	345	3+	2662	2.9	4.27
Rufanes pond							
males	110	281	40	1+			
females	118	250	49		376	2.4	6.92
Lake Bradshaw							
males	168	266	170	2+			
females	186	246	239	2+	1374	2.8	2.63
Lake Mill Farm							
males	265	356	842	2+			
females	263	359	820	2-3+	3113	3.5	3.32

For Cichlidae, changes in the size at first maturity (SFM) are also influenced by fishing pressure. In Lake George, for instance, intensive fishing is thought to have led to the decrease in the SFM of *Oreochromis niloticus* from 27.5 cm TL in 1960 to only 20 cm in 1972 (Gwahaba, 1973). Likewise, in Lake Turkana, the SFM of *O. niloticus* went from 39 cm in the 1950s to only 29.6 cm in the 1970s (Harbott & Ogari, 1982).

There are many other examples of variations in age or size at first maturity for a single species. But the reasons for the shift from a demographic tactic favouring growth to another one favouring early reproduction have not yet been identified in a convincing manner. Diet-related factors are often mentioned. In fact, field data have shown that Tilapias in poor physiological condition have a strong tendency to reproduce at a smaller size than those in better condition. Such a phenomenon has been observed for *Oreochromis niloticus* in different African lakes (Lowe, 1958), and for *Sarotherodon melanotheron* in the lagoons of Côte d'Ivoire (Legendre & Écoutin, 1996) (figure 11.3).

FIGURE 11.3.
Relationships between the mean weight of a 200 mm TL specimen and the size at first maturity (from Legendre & Écoutin, 1996). TL: total length; FL: fork length. *Oreochromis niloticus* populations from several African aquatic environments (data from Lowe, 1958). *Sarotherodon melanotheron* from Côte d'Ivoire (from Legendre & Écoutin, 1996).
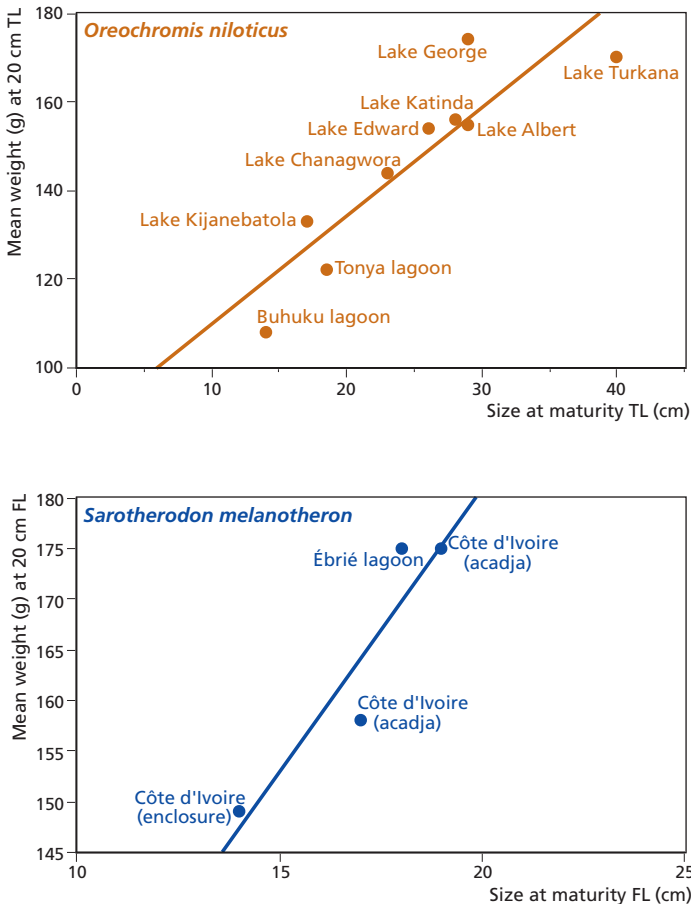
Dwarf populations

The existence of dwarf populations that reproduce at much smaller sizes than those customarily observed has also been found in non-cichlid fishes.

In Lake Chad, *Brycinus nurse dageti* is a dwarf population of *Brycinus nurse nurse* and the two species coexist in the lacustrine environment (Bénech & Quensière, 1985). Likewise, in Lake Turkana, *Brycinus nurse nana* is also a dwarf population of *B. nurse* (Paugy, 1986). There are also dwarf populations of *Schilbe niloticus* in Lake Chad (Bénech & Quensière, 1985) and of *Ethmalosa fimbriata* in some bays of the Ébrié lagoon in Côte d'Ivoire (Albaret & Charles-Dominique, 1982). These phenomena have not been well explained to date. The cline detected in *Schilbe mandibularis* (Lévêque & Herbinet, 1982) that leads to dwarf populations in Liberia has not been explained either.

A distinctive aspect of dwarfism is that of "stunted" populations: fishes are not small for their age, but old for their size (Noakes & Balon, 1982). These populations have an accelerated ontogeny which manifests as very early sexual maturity. Thus, *Coptodon zillii* which usually reaches sexual maturity at around 2 or 3 years and a size of 200-300 mm can become mature in a few months at a size below 100 mm when it is introduced into small pools (Fryer & Iles, 1972). In a hot spring, Hecht & Zway (1985) observed a population of *O. mossambicus* in which the largest individual was a male measuring 105 mm SL, while the smallest mature female measured 35 mm SL at one year of age. This "stunting" phenomenon has been observed in nature when shallow lakes dry out, or when small pools are isolated from the main water mass. In Lake Turkana, where *O. niloticus* is mature at an average size of 280 mm TL, it has been observed that populations living in springs isolated from the lake reproduced at 80 mm TL (Harbott & Ogari, 1982). Here, the mechanisms at play are not well-identified either.

Environmental conditions and growth characteristics

Most species have developed a type of demographic strategy matching a habitat that is favourable to them, as they live there and have adapted to it. Nonetheless, when some species find themselves in worse conditions, they can modify their reproductive behaviour, sometimes within large margins.

The phenotypic plasticity of *Oreochromis mossambicus*, which is found in a large variety of habitats, is well known. Its level of investment in the protection of eggs and young varies depending on the conditions of the physical system. By studying four populations living in physical systems that differed greatly in their abiotic and biotic characteristics, James & Bruton (1992) showed that the species is able to shift from its usual mode of direct development to an indirect one when the conditions of the habitat are more drastic. The populations of the Kowie lagoon and of Mill Farm lake become mature at a length around 70% of their maximum size, which is typical of Cichlidae living in stable physical systems and who have an indirect mode of development. The population in the Rufanes pool, meanwhile, showed early maturity and smaller eggs, characteristics typical of an indirect mode of development. Populations in Rufanes and Lake

Bradshaw, habitats presenting more difficult conditions, are much more fecund than the others. Generally speaking, when all the biological characteristics are taken into account, there is a shift from a direct development style in Mill Farm lake to an indirect one in Rufanes pool.

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