Reproduction

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The reproductive cycle of a species implies a set of physiological and behavioural processes influenced by various factors in the abiotic and biotic environment. Traditionally a distinction is made between gametogenesis and spawning. Gametogenesis is the physiological process involved in gonad development that leads to the formation of gametes (oocytes and spermatozoa). In tropical regions, gametogenesis is controlled by tiny changes in environmental factors, and its duration varies according to species (Munro, 1990). Spawning is the critical moment of the reproductive cycle, which includes the sequence of events that leads to laying of the gametes (maturation of oocytes, ovulation, spermiogenesis), under the influence of specific stimuli (Billard & Breton, 1978).

Gametogenesis is the longest of these processes. It generally lasts several months, but reproductive success depends to a large extent on the success of a set of behavioural activities. These include the search for partners, parental care before and after spawning, whether or not migration is required to find suitable sites for eggs and larvae, synchronization of spawning with changes in environmental factors, synchronization of the genital products laying, etc. These activities may be accompanied by a set of phenological adaptations, such as the development of secondary sexual characters with regard to morphology or colouring.

The study of the fish reproductive cycle thus requires a multidisciplinary approach that involves ecologists, physiologists, ethologists, and geneticists. Coordinating all these disciplines is not always a straightforward affair, and explains why data is often fragmentary. Yet we need studies that include them if we want to understand the cause-and-effect relationships between environmental factors, physiological processes, and reproductive behaviour of species.

Gonad maturation and fecundity

Reproductive effort is the fraction of absorbed energy that an organism devotes to its reproductive activities. This investment can be partially measured through the amount of material or energy stored in the gonads, keeping in mind that it would also need to add all the energy spent on eggs or larvae care, or on mating displays.

Gonado-somatic index

To describe the growth of gonads in relation to body mass, scientists frequently use the gonado-somatic index (GSI) which is the ratio of gonad weight to body weight excluding gonads:

$$GSI = \frac{GW}{TW - GW}$$

where GW is the weight of the gonads and TW the total weight.

The growth of ovaries during the gonad maturation cycle reflects the growth of oocytes through yolk accumulation. The GSI of mature females varies widely from one species to another. It can reach 20 to 30% prior to spawning in some species, but only remain at a few % in others (tables 10.I and 10.II).

In many tropical species, testes develop much less than ovaries, and for African species, the GSI of mature males rarely exceeds 2% (table 10.I; see also box "Gonado-Somatic Index (GSI)"). While the reasons for such a difference are unknown, males generally reach maturity before females and remain mature longer.

Species	Females	Males
Polypterus bichir	23.4	0.2
Hyperopisus bebe	8.0	0.2
Mormyrus rume	11.8	0.2
Mormyrops anguilloides	7.5	
Marcusenius senegalensis	18.7	0.5
Petrocephalus bovei	21.4	0.4
Hydrocynus forskalii	9.4	2.1
Alestes baremoze	13.4	1.3
Brycinus nurse	26.1	2.0
Brycinus leuciscus	17.0	1.2
Brycinus macrolepidotus	19.8	6.7
Labeo senegalensis	17.2	2.0
Labeo coubie	12.0	0.8
Chrysichthys auratus	27.5	0.7
Schilbe intermedius	23.4	1.1
Schilbe mystus	16.2	
Clarias anguillaris	14.4	
Synodontis schall	16.7	2.1
Synodontis ocellifer	26.3	1.5
Sarotherodon galilaeus	4.8	

TABLE 10.I.

Comparison of female and male gonado-somatic index for different species in the Baoulé River, Upper Senegal in Mali. Maximum observed values quoted for different species (from Paugy, 2002).

The gonado-somatic index is a simple but rough estimate of sexual activity. A more refined assessment of gonad development requires a histological study, such as an investigation into the frequency distribution of oocyte size, provided that the relationship between oocyte size and the physiological state of gonads has been predetermined. The GSI is a good tool for estimating reproductive seasons of species that spawn only once per year or per reproductive season. However, it becomes inexact for species with multiple spawning events, because a low GSI (for instance between 0.5 and 1.5% for *Oreochromis niloticus*)

GONADO-SOMATIC INDEX (GSI)

In the African inter-tropical zone, testes weight is always lesser than that of ovaries (table 10.I). This is also often the case in temperate zone. Thus, in *Gasterosteus aculeatus* (Gasterosteidae), while the GSI of the female reaches or even exceeds 20%, the fully mature male's GSI is below 2% (Wootton, 1984). Nonetheless, in some brackish water species, higher values can be observed. In very favourable conditions, the GSI of male *Fundulus heteroclitus* (Cyprinodontidae) can reach 4.7% (Taylor, 1990). Even higher values can be found in some marine species. The male Arctic cod *Boreogadus saida* (Gadidae) can have testes weighing 10 to 27% of the body weight (Craig *et al.*, 1982).

Theory suggests that testes size (and thus weight) could be linked to the mode of fertilization used by the species. Thus, in the case of "coupling" with partners, the amount of sperm needed is less than in the case of dissemination in the physical system without an actual meeting of the progenitors, as with numerous marine species. In the latter, the chances of an encounter are greater if more sperm is released.

Other "solutions" can be found, such as variations in the sex ratio. When a species lays all its eggs in one instance and leaves them to sink to the bottom, where they become attached on submerged surfaces, a large number of spermatozoa is needed to increase chances of fecundation. Consequently, testes are as developed as ovaries in these species, and males must be at least as numerous as females (high sex ratio). In other cases, meanwhile, spawning is spaced out and eggs float, so spermatozoa found in the same waters can be less abundant. As a result, testes are less developed then ovaries and there can be fewer males than females (low sex ratio). As the reproductive behaviour of tropical species is still poorly known, we cannot yet state if this strategy has been verified in this zone.

In any case, the energy allocated for the constitution of genital products appears to be lower in males than in females.

can characterize very different stages of ovarian maturity, such as a gonad in early maturation (stage 2 according to the scale by Legendre & Écoutin, 1989) or a post-spawning gonad (stage 6). The resulting loss of information can be detrimental, particularly in attempts to correlate the reproductive season with environmental factors involved in the regulation of sexual cycles, and it is advisable to use a gonad maturity scale rather than the GSI for species that spawn several times during a reproductive season (Duponchelle *et al.*, 1999).

Maturity scales allow rapid characterisation of the different developmental states of ovaries and testes. In particular, they take into account the macroscopic appearance of gonads (shape, colour, vascularization, transparency) and the GSI. Such scales have been established for *Alestes baremoze* (Durand & Loubens, 1970), *Schilbe mystus*, *S. uranoscopus* (Mok, 1975) and *Sarotherodon melanotheron* (Legendre & Écoutin, 1989). The maturity scale proposed for the last species has been applied successfully to *Oreochromis niloticus* (Duponchelle & Panfili, 1998, Duponchelle *et al.*, 1998, 1999, 2000a; Duponchelle & Legendre, 2000, 2001) and to numerous *Haplochromis* species (Duponchelle *et al.*, 2000b). It appears to be suitable for the majority of Cichlidae.

Fecundity

The ovaries contain oocytes of different sizes corresponding to the different stages of development. A unimodal distribution suggests single spawning, while polymodal structures suggest that the species under study has multiple spawning events (Albaret, 1982) (figure 10.1). In all cases, absolute fecundity (F) corresponds to the number of mature oocytes found in the ovary immediately prior to spawning. For species with only one annual spawning, F equals total annual fecundity. In species that spawn several times, F is the number of oocytes that will be released in the next spawning event (these oocytes are the largest in size), and annual fecundity is the sum of all oocytes released over the year in successive spawning events.
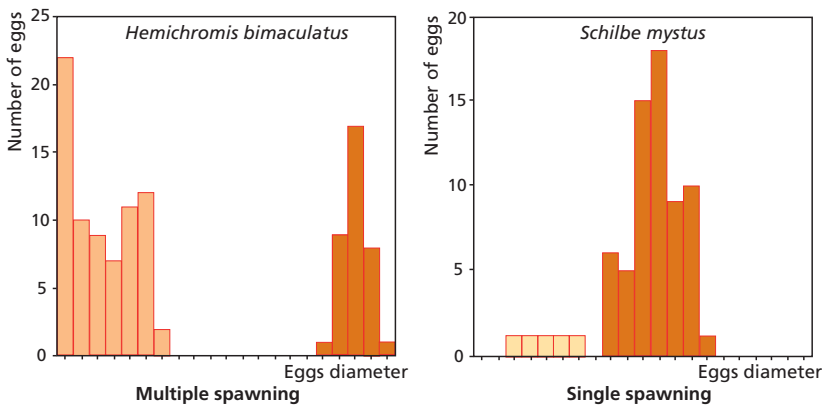

FIGURE 10.1.
Distribution in oocyte diameters of two species from Côte d'Ivoire (from Albaret, 1982).

Brosset (1982) calculated the annual fecundity for three species of Cyprinodontiformes found in the Ivindo River (Gabon). The number of eggs released annually by a female is the same, that is, 200 to 300, regardless of the strategy adopted during the reproductive season: one egg a day in *Diapteron sp.*, 8 to 15 eggs every 8-10 days in *Aphyosemion hertzogi*, 30-75 eggs a month in *Aphyosemion cameronense* and *A. punctatum*.

In the Nothobranchiidae species *Nothobranchius guentheri*, a mature female weighing 1 g produces 20 eggs a day, which represents a reproductive effort equivalent to 27% of its weight in a month. In this case, in a 4-5 month period, the total egg production can be equivalent to the female's weight. This is much higher than the energy investment usually made by species that have single spawning (table 10.II).

To compare the fecundity of fishes of different sizes or from different physical systems, we often calculate the *relative fecundity* which is the number of eggs per unit of body weight, expressed in g or in kg. However, in some species including a lot of Cichlidae, a correlation (generally negative) exists between relative fecundity and female weight (*Sarotherodon melanotheron*, Legendre 1992; *Oreochromis niloticus*, Duponchelle, 1997; Duponchelle *et al.*, 2000a), and we must thus proceed by comparing lines of regression between fecundity and female body weight.

TABLE 10.II.

Selected data on mean female size at first sexual maturity (mm), egg diameter (mm), relative fecundity expressed as number of eggs per kilogram of female body weight, maximum gonado-somatic index (GSI in %) and maximum size observed (MSO in mm) for different African fish species.

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Polypteridae							
Polypterus bichir	Mali/Senegal				23.4		Paugy (unpublished)
Polypterus endlicheri	Côte d'Ivoire	320	2.45	15 000	9.2	750	Albaret,1982
Polypterus senegalus	Côte d'Ivoire	185	1.75	50 000	15	505	Albaret,1982
Clupeidae							
Pellonula leonensis	Lake Kainji	30	0.3-0.5		10.5	75	Otobo, 1978a
Sierrathrissa leonensis	Lake Kainji	19	0.1-0.3		12.5		Otobo, 1978a
Notopteridae							
Papyrocranus afer	Côte d'Ivoire	431	3.6	531	2	590	Albaret,1982
Mormyridae							
Brevimyrus niger	Chad	110	1.3-1.5	80 000			Lek, 1979
Gnathonemus longibarbis	Lake Ihema				15		Plisnier *et al.*, 1988
Hyperopisus bebe	Mali	320	1.8	50 000	9	510	Bénech & Dansoko, 1994
Hyperopisus bebe	Nile	300	1.72				Nawar, 1960
Hyperopisus bebe	Mali/Senegal		1.64		8		Paugy (unpublished)
Hippopotamyrus psittacus	Ogun	166	1.48	15 010		240	Adebisi, 1987
Mormyrops anguilloides	Ogun	397	2.4	15 550			Adebisi, 1987
Mormyrops anguilloides	Côte d'Ivoire	210	2.65	11 300	11	1500	Albaret, 1982
Marcusenius furcidens	Côte d'Ivoire	228	1.8	39 250	14.4	286	Albaret,1982
Mormyrus hasselquistii	Côte d'Ivoire	190	1.85	24 300	12	480	Albaret, 1982
Mormyrus kannume	Lake Victoria	183	2.14			1000	Okedi, 1970
Mormyrus rume	Ogun	350	2.16	15 820			Adebisi, 1987
Mormyrus rume	Mali	330	2.2	20 000	8	870	Bénech & Dansoko, 1994
Mormyrus rume	Mali/Senegal		1.57		11.8		Paugy (unpublished)
Marcusenius senegalensis	Ogun	190	1.35	14 670		321	Adebisi, 1987
Marcusenius senegalensis	Mali/Senegal		1.31		18.7		Paugy (unpublished)
Marcusenius ussheri	Côte d'Ivoire	130	1.75	51 800	15.3	305	Albaret, 1982
Petrocephalus bane	Chad	110	1.0-1.2	46 000			Lek, 1979
Petrocephalus bovei	Côte d'Ivoire	67	1.55	91 230	20.4	100	Albaret,1982
Petrocephalus bovei	Chad	70	1.0-1.1	133 000			Lek, 1979
Petrocephalus bovei	Côte d'Ivoire	65		105 900		100	Mérona, 1980
Pollimyrus isidori	Chad	65	1.2	141 000			Lek, 1979
Petrocephalus soudanensis	Côte d'Ivoire	83	1.6	76 440	16.3		Albaret,1982
Hepsetidae							
Hepsetus odoe	Côte d'Ivoire	140	2.3	18 250	8.4	700	Albaret,1982
Hepsetus odoe	Okavango	150	2.7	12 100		279	Merron *et al.*, 1990
Alestidae							
Alestes baremoze	Côte d'Ivoire	175	1.1	224 100	11.5	284	Albaret,1982
Alestes baremoze	Chad	205		231 000		326	Durand, 1978
Alestes baremoze	Côte d'Ivoire	170	1.1	236 000		284	Paugy, 1978
Brycinus imberi	Côte d'Ivoire	65	1	251 000	14.6		Albaret,1982
Brycinus imberi	Zambezi	120		284 000		189	Marshal & van der Heiden, 1977
Brycinus imberi	Côte d'Ivoire	65	0.89	191 000			Paugy, 1980a
Brycinus leuciscus	Mali	30	0.8	250 000	16		Bénech & Dansoko, 1994
Brycinus leuciscus	Mali/Senegal	65	0.9		18.9		Paugy (unpublished)
Brycinus longipinnis	Côte d'Ivoire	46	1.95	166 000	13.5		Albaret,1982
Brycinus longipinnis	Bandama	74		156 000	12.35		Paugy, 1982b
Brycinus longipinnis	Cavally	68		97 000	11.6		Paugy, 1982b
Brycinus macrolepidotus	Ogun	269	1.26	148 650			Adebisi, 1987
Brycinus macrolepidotus	Côte d'Ivoire	180	1.2	182 400	13.8		Albaret,1982
Brycinus macrolepidotus	Côte d'Ivoire	180	1.33	180 000		330	Paugy, 1982a
Brycinus nurse	Côte d'Ivoire	80	1.05	339 000	19.5	218	Albaret,1982
Brycinus nurse	Côte d'Ivoire	80		368 000		218	Paugy, 1980b
Hydrocynus forskalii	Côte d'Ivoire	150	1.05	127 300	6.9	780	Albaret,1982
Micralestes acutidens	Chad	35	0.6	183 000			Lek & Lek, 1977

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TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Distichodontidae							
Ichthyborus besse	Chad	183	0.85	111 500		208	Lek & Lek, 1978a
Cyprinidae							
Barbus spurelli	Côte d'Ivoire	47	0.85	320 000	11.8	87	Albaret,1982
Barbus sublineatus	Côte d'Ivoire	55	0.85	677 000	21.6	100	Albaret,1982
Barbus trispilos	Côte d'Ivoire	50	0.9	449 000	20.2	95	Albaret,1982
Labeo capensis	Vaal River	310		303 000		500	Mulder, 1973
Labeo coubie	Côte d'Ivoire	200	1.25	122 000	8.6		Albaret,1982
Labeo ogunensis	Ogun	185	1.04	233 940		120 ?	Adebisi, 1987
Labeo parvus	Côte d'Ivoire	100	0.95	347 000	19	350	Albaret,1982
Labeo senegalensis	Côte d'Ivoire	175	1	181 500	14.3	550	Albaret,1982
Labeo umbratus	Vaal River	300		410 000		420	Mulder, 1973
Raiamas senegalensis	Côte d'Ivoire	100	1.35	47 700	8.3		Albaret,1982
Bagridae							
Bagrus bajad	Mali	330	1.1	30 000	2.5	720	Bénech & Dansoko, 1994
Bagrus docmak	Nile	200	1.2	36 000		1110	El Sedfy & El Bolock, 1987
Claroteidae							
Auchenoglanis occidentalis	Côte d'Ivoire		2.6	4 150	4		Albaret,1982
Auchenoglanis occidentalis	Mali	100	2	3 000	2.1	480	Bénech & Dansoko, 1994
Chrysichthys auratus	Côte d'Ivoire	140	2.2	11 980	13.2	250	Albaret,1982
Chrysichthys auratus	Mali/Senegal	70	2.3	19 000	27.5		Paugy (unpublished)
Chrysichthys maurus	Côte d'Ivoire	140	2.55	19 700	16.7		Albaret,1982
Chrysichthys maurus	Lekki Lagoon	100	2.2	19 100		510	Ikusemiju, 1976
Chrysichthys nigrodigitatus	Côte d'Ivoire	195	2.9	16 990	19.5	650	Albaret,1982
Chrysichthys nigrodigitatus	Côte d'Ivoire			24 000			Kouassi, 1973
Schilbeidae							
Schilbe mandibularis	Bandama	154	0.95	217 000	9.6	450	Albaret,1982
Schilbe mandibularis	Bandama	175		175 800		389	Lévêque & Herbinet, 1982
Schilbe mystus	Ogun	246	0.87	437 190			Adebisi, 1987
Schilbe mystus	Côte d'Ivoire	100	0.85	253 700	8		Albaret,1982
Schilbe mystus	Côte d'Ivoire	110		228 200		267	Lévêque & Herbinet, 1980
Schilbe mystus	Chad	120		207 000		330	Mok, 1975
Schilbe mystus	Nile			255 000		340	Nawar & Yoakim, 1964
Schilbe niloticus	Mali/Senegal				16.2		Paugy (unpublished)
Schilbe uranoscopus	Chad	180		207 000		360	Mok, 1975
Amphiliidae							
Amphilius atesuensis	Côte d'Ivoire	38	1.7	41 400	11.2	63	Albaret,1982
Clariidae							
Clarias anguillaris	Côte d'Ivoire	235	1.3	62 000	9.6		Albaret,1982
Clarias anguillaris	Mali	150	1.4	180 000	16	1500	Bénech & Dansoko, 1994
Clarias gariepinus	Lake Sibaya	280		36 400		1500	Bruton, 1979a
Clarias gariepinus	Lake Ihema				17		Plisnier *et al.*, 1988
Heterobranchus isopterus	Côte d'Ivoire	255	1.5	122 000	13.8	900	Albaret,1982
Mochokidae							
Synodontis membranaceus	Mali	210	1.1	150 000	10.5	460	Bénech & Dansoko, 1994
Synodontis afrofisheri	Lake Ihema				26		Plisnier *et al.*, 1988
Synodontis eupterus	Volta Lake			28 000		160	Ofori-Danson, 1992
Synodontis ocellifer	Volta Lake			126 000		200	Ofori-Danson, 1992
Synodontis ocellifer	Mali/Senegal		0.81		26.3		Paugy (unpublished)
Synodontis schall	Ogun	291	1.12	96 880			Adebisi, 1987
Synodontis schall	Côte d'Ivoire	150	1.2	156 600	13.6	380	Albaret,1982
Synodontis schall	Volta Lake	200	1.1	179 000		400	Ofori-Danson, 1992
Synodontis velifer	Volta Lake			70 300		290	Ofori-Danson, 1992
Channidae							
Parachanna obscura	Ogun	245	1.33	19 460		400	Adebisi, 1987
Latidae							
Lates niloticus	Chad	520	0.7	86 000	4.5		Loubens, 1974
Cichlidae							
Alticorpus 'geoffreyi'	Lake Malawi	90	2202	4,3	3.9	165	Duponchelle *et al.*, 2000b
Alticorpus macrocleithrum	Lake Malawi	97	3682	5,4	3.6	136	Duponchelle *et al.*, 2000b
Alticorpus mentale	Lake Malawi	160	1330	3,7	4.2	246	Duponchelle *et al.*, 2000b
Alticorpus pectinatum	Lake Malawi	70	3677	5	3.7	136	Duponchelle *et al.*, 2000b
Astatoreochromis alluaudi	Lake Victoria	98	2.9				Goldschmidt & Goudswaard, 1989

TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Aulonocara 'blue orange'	Lake Malawi	48	5548	3,3	3.1	78	Duponchelle *et al.*, 2000b
Aulonocara 'cf. macrochir'	Lake Malawi		2285	1,5	3.2	134	Duponchelle *et al.*, 2000b
Aulonocara 'minutus'	Lake Malawi	42	7525	3,2	3.1	72	Duponchelle *et al.*, 2000b
Aulonocara 'rostratum deep'	Lake Malawi	75	2467			139	Duponchelle *et al.*, 2000b
Buccochromis lepturus	Lake Malawi	160	970	2,7	4	327	Duponchelle *et al.*, 2000b
Buccochromis nototaenia	Lake Malawi	115	2308	2,5	3.5	300	Duponchelle *et al.*, 2000b
Chromidotilapia guntheri	Côte d'Ivoire	60	2.25	8 100	3.4		Albaret,1982
Copadichromis quadrimaculatus	Lake Malawi	100	692	3,4	5.2	149	Duponchelle *et al.*, 2000b
Copadichromis virginalis	Lake Malawi	75	1343	3,5	3.9	123	Duponchelle *et al.*, 2000b
Cynotilapia afra	Lake Malawi	50	2896	5,5	3.8	75	Duponchelle *et al.* (unpublished)
Diplotaxodon apogon	Lake Malawi	88	632	3,6	5.4	129	Duponchelle *et al.*, 2000b
Diplotaxodon argenteus	Lake Malawi	140	360	4	6.9	206	Duponchelle *et al.*, 2000b
Diplotaxodon limnothrissa	Lake Malawi	105	454	3,7	6.3	175	Duponchelle *et al.*, 2000b
Diplotaxodon macrops	Lake Malawi	98	498	3,7	6	134	Duponchelle *et al.*, 2000b
Genyochromis mento	Lake Malawi		2323	3,8	3.7	97	Duponchelle *et al.* (unpublished)
Haplochromis "argens"	Lake Victoria	61	3.4	3 850	4.4	78	Goldschmidt & Witte, 1990
Haplochromis "reginus"	Lake Victoria			6 500		72	Goldschmidt & Witte, 1990
Haplochromis anastodon	Lake Kivu	68	3.5	3 400			Losseau-Hoebeke, 1992
Haplochromis heusinkveldi	Lake Victoria	63	3.6	3 490	5.1	80	Goldschmidt & Witte, 1990
Haplochromis laparogramma	Lake Victoria	55	3.4	3 230	3.9	79	Goldschmidt & Witte, 1990
Haplochromis olivaceus	Lake Kivu	67	3.7	3 100			Losseau-Hoebeke, 1992
Haplochromis paucidens	Lake Kivu	70	3.6	2 500			Losseau-Hoebeke, 1992
Haplochromis piceatus	Lake Victoria	62	3.2	7 210	5.7	74	Goldschmidt & Witte, 1990
Haplochromis pyrrhocephalus	Lake Victoria	59	3.1	5 290	4.4	76	Goldschmidt & Witte, 1990
Hemichromis bimaculatus	Côte d'Ivoire	45	1.2	111 700	7.1	92	Albaret,1982
Hemichromis fasciatus	Ogun	104	1.26	28 740		204	Adebisi, 1987
Hemichromis fasciatus	Côte d'Ivoire	80	1.65	30 000	4.5	204	Albaret,1982
Labeotropheus fuelleborni	Lake Malawi	74	5	1 900			Marsh *et al.*, 1986
Labeotropheus fuelleborni	Lake Malawi	64	1670	4,5	4.4	100	Duponchelle *et al.* (unpublished)
Labeotropheus trewavasae	Lake Malawi		1967	3,4	4	90	Duponchelle *et al.* (unpublished)
Lethrinops argenteus	Lake Malawi	108	2162	5	4	166	Duponchelle *et al.*, 2000b
Lethrinops 'deep water albus'	Lake Malawi	82	3642	4,8	3.5	161	Duponchelle *et al.*, 2000b
Lethrinops 'dw altus'	Lake Malawi	60	4086	4,1	3.3	130	Duponchelle *et al.*, 2000b
Lethrinops gossei	Lake Malawi	92	2087	5,2	4.1	170	Duponchelle *et al.*, 2000b
Lethrinops longimanus	Lake Malawi		1839	4,6	3.7	168	Duponchelle *et al.*, 2000b
Lethrinops macrochir	Lake Malawi		3107	4,2	3.5	150	Duponchelle *et al.*, 2000b
Lethrinops 'minutus'	Lake Malawi		5272				Duponchelle *et al.*, 2000b
Lethrinops 'oliveri'	Lake Malawi	60	4931	4,3	3.3	98	Duponchelle *et al.*, 2000b
Lethrinops polli	Lake Malawi	65	2775	3,9	3.6	120	Duponchelle *et al.*, 2000b
Melanochromis auratus	Lake Malawi	62	4	3 900			Marsh *et al.*, 1986
Melanochromis auratus	Lake Malawi	55	2861	5,3	3.5	76	Duponchelle *et al.* (unpublished)
Melanochromis vermivorus	Lake Malawi	55	2774	5,3	3.8	73	Duponchelle *et al.* (unpublished)
Mylochromis anaphyrmus	Lake Malawi	105	2430	3,3	3.5	164	Duponchelle *et al.*, 2000b
Nyassachromis 'argyrosoma'	Lake Malawi	57	4901	3,9	3.3	97	Duponchelle *et al.*, 2000b
Alcolapia alcalica	Lake Magadi	59	2.8				Coe, 1969
Oreochromis niloticus	Côte d'Ivoire	160	2.55	3 720	2.6		Albaret,1982
Oreochromis niloticus	Mali	135	2.8	4 000	2.8		Bénech & Dansoko, 1994
Oreochromis niloticus	Lake Ihema	187	2		5.2	530	Plisnier *et al.*, 1988
Oreochromis niloticus	Lake Kossou/ Côte d'Ivoire	140	4526	3,3	2.3	252	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Ayamé/ Côte d'Ivoire	125	4367	3,5	2.5	198	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Buyo/ Côte d'Ivoire		4806	3,2	2.2	225	Duponchelle, 1997
Oreochromis niloticus	Lake Sambakaha/ Côte d'Ivoire	106	4738	3,4	2.4	233	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Tine/ Côte d'Ivoire	115	4380	3,4	2.3	357	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Lokpoho/ Côte d'Ivoire	129	3734	3,4	2.5	250	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Solomougou/ Côte d'Ivoire	115	4610	3,8	2.3	255	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a

TABLE 10.II. (CONT.)

Species	Country/basin	1st size maturity	Egg diameter	Relative fecundity	Max. GSI	MSO	Source
Oreochromis niloticus	Lake Korokara-T/ Côte d'Ivoire	105	6324	5	2.3	194	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Oreochromis niloticus	Lake Korokara-S/ Côte d'Ivoire	123	5133	3,8	2.3	252	Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2000a
Otopharynx 'productus'	Lake Malawi		2287				Duponchelle *et al.*, 2000b
Otopharynx speciosus	Lake Malawi		853				Duponchelle *et al.*, 2000b
Pallidochromis tokolosh	Lake Malawi	135	489	3,6	6.8	214	Duponchelle *et al.*, 2000b
Petrochromis polyodon	Lake Tanganyika	134	7.1				Kuwamura, 1986
Petrotilapia 'fuscous'	Lake Malawi	80	1867	4,1	4.1	103	Duponchelle *et al.* (unpublished)
Petrotilapia nigra	Lake Malawi	80	1466	4,1	4.3	104	Duponchelle *et al.* (unpublished)
Placidochromis 'long'	Lake Malawi		4602	2,4	3.1		Duponchelle *et al.*, 2000b
Placidochromis 'platyrhynchos'	Lake Malawi		2662	4,7	3.6	115	Duponchelle *et al.*, 2000b
Protomelas taeniolatus	Lake Malawi	72	3.9	3 000			Marsh *et al.*, 1986
Pseudotropheus 'ag. grey head'	Lake Malawi	55	2914	4,6	3.7	79	Duponchelle *et al.* (unpublished)
Pseudotropheus 'aggressive blue'	Lake Malawi		2213	6,3	4.1	90	Duponchelle *et al.* (unpublished)
Pseudotropheus aurora	Lake Malawi	60	2859	5,5	3.7	80	Duponchelle *et al.* (unpublished)
Pseudotropheus barlowi	Lake Malawi		3162	4,7	3.6	83	Duponchelle *et al.* (unpublished)
Pseudotropheus callainos	Lake Malawi	57	1735	5,3	4.4	83	Duponchelle *et al.* (unpublished)
Pseudotropheus heteropictus	Lake Malawi		2953	4,5	3.6	83	Duponchelle *et al.* (unpublished)
Pseudotropheus livingstonii	Lake Malawi	37	6740	3,9	3.2	63	Duponchelle *et al.*, 2000b
Pseudotropheus tr. 'lilac'	Lake Malawi		2099	4,6	3.8	90	Unpublished)
Pseudotroph. tr. 'orange chest'	Lake Malawi	65	2264	5,1	3.9	88	Unpublished)
Pseudotropheus tr. 'red cheek'	Lake Malawi	65	1677	3,8	3.9	88	Unpublished)
Pseudotropheus tropheops 'blue'	Lake Malawi		2264	4,2	3.7	83	Unpublished)
Pseudotropheus williamsi	Lake Malawi	65	2619	5,4	3.9	87	Unpublished)
Pseudotropheus zebra	Lake Malawi	72	4.2	2 600			Marsh *et al.*, 1986
Pseudotropheus zebra	Lake Malawi	55	2572	5,1	3.9	84	Unpublished)
Pseudotroph. z. 'black dorsal'	Lake Malawi	62	2503	5,4	3.9	86	Unpublished)
Pseudotroph. zebra 'red dorsal'	Lake Malawi	52	2926	5	3.6	89	Unpublished)
Pseudotroh. zebra 'yellow throat'	Lake Malawi		2239	5,1	3.9	86	Unpublished)
Sarotherodon galilaeus	Ogun	284	2.01	3 740			Adebisi, 1987
Sarotherodon galilaeus	Côte d'Ivoire	145	2.3	3 940	2.1		Albaret,1982
Sarotherodon galilaeus	Mali	140	2.6	4 000	4.2	410	Bénech & Dansoko, 1994
Sarotherodon melanotheron	Ebrié Lagoon/ Côte d'Ivoire			1 700	8		Legendre & Écoutin, 1989
Sarotherodon melanotheron	Ebrié Lagoon/ Côte d'Ivoire	176	1757	5,8	4.1	334	Legendre & Écoutin, 1989
Sarotherodon melanotheron	Gambia/Senegal	170	4395	4,9	2.8	220	Panfili *et al.*, 2004a
Sarotherodon melanotheron	Saloum/Senegal	131	5091	8,2	2.8	200	Panfili *et al.*, 2004a
Sciaenochromis alhi	Lake Malawi		2006	4,2	3.9	124	Duponchelle *et al.*, 2000b
Sciaenochromis benthicola	Lake Malawi	100	1271	4,2	4.4	167	Duponchelle *et al.*, 2000b
Simochromis diagramma	Lake Tanganyika	75	5.2		5.5		Kuwamura, 1986
Stigmatochromis 'guttatus'	Lake Malawi	100	1220	3,9	4.5	147	Duponchelle *et al.*, 2000b
Taeniolethrinop. praeorbitalis	Lake Malawi	130	1450	4	4.3	200	Duponchelle *et al.*, 2000b
Taeniolethrinops furcicauda	Lake Malawi	130	1911	1,9	3.4	178	Duponchelle *et al.*, 2000b
Tilapia guineensis	Ebrié Lagoon/ Côte d'Ivoire			20 600	11		Legendre & Écoutin, 1989
Oreochromis macrochir	Lake Ihema	185	2		4	402	Plisnier *et al.*, 1988
Tilapia mariae	Ogun	116	1.41	9 270			Adebisi, 1987
Tilapia moorei	Lake Tanganyika	70	5.7		4.6		Kuwamura, 1986
Tilapia nigra	East Africa	75	2.4	10 400			Cridland, 1961
Coptodon rendalli	Lake Ihema				6		Plisnier *et al.*, 1988
Tilapia tholloni				85 000	14		Peters, 1963c
Coptodon zillii	Côte d'Ivoire	70	1.65	38 600	4		Albaret,1982
Coptodon zillii	Mali	100	1.5	100 000	6.5	285	Bénech & Dansoko, 1994
Coptodon zillii	East Africa	110	1.5	65 500		250	Cridland, 1961
Trematocranus brevirostris	Lake Malawi	50	4577	3,9	3.3	85	Duponchelle *et al.*, 2000b
Trematocranus placodon	Lake Malawi	105	2043	3	3.6	159	Duponchelle *et al.*, 2000b
Xenotilapia longispinnis	Lake Tanganyika	69	3.2				Kuwamura, 1986
Anabantidae							
Ctenopoma kingsleyae	Côte d'Ivoire	115	1.05	103 000	8.7	215	Albaret,1982
Mastacembelidae							
Mastacembelus nigromarginatus	Côte d'Ivoire	150	2.35	19 800	12.5	340	Albaret, 1982

There is an inverse relationship between the number of eggs released at each spawning event and the size of the oocytes. Very prolific species that produce small eggs mostly belong to the Cyprinidae, Alestidae, and Schilbeidae families. Most are pelagic species, and are often migratory. Species producing a few large eggs mainly belong to the Bagridae, Mormyridae (which only possess the left gonad), and Cichlidae families. For the latter, substrate layers (*H. bimaculatus, H. fasciatus,C. zillii*) have smaller and more numerous eggs than mouth brooding species (*S. galilaeus, O. niloticus*).

Mouth brooders generally have a limited number of large eggs, as shown in the results obtained for various Cichlidae species of the African great lakes (table 10.II).

Relationships between fecundity and length or weight of females

The fecundity of a species is most often a function of the size of the females. The larger they are, the more eggs they lay. It is customary to determine the relationship between fecundity and size of females, expressed either by length (often the standard length) or weight (table 10.III).

The relationship is generally $F = a\ SL^b$.

Reproductive strategies

Each individual possesses a set of biological characteristics related to reproduction that are the heritage of evolution and phylogeny. The reproductive strategy of a fish species in a given environment is indeed a set of biological traits such as age and size at first reproduction, fecundity, gonad development and gamete size, reproductive behaviour including the existence of parental care, reproductive season, etc.

But an individual can also develop tactics, which are in fact variations on the typical reproductive schema of the species, to adapt to changes in environmental factors. This adaptive behaviour to special ecological conditions is intended to ensure the survival of the species, as we have already seen. This is the case for instance of *Oreochromis niloticus* in artificial reservoirs in Côte d'Ivoire, whose reproductive characteristics (reproductive season, size at first sexual maturity, fecundity, egg size, etc.) vary from one year to another depending on environmental conditions (Duponchelle & Panfili, 1998; Duponchelle *et al.*, 1998, 1999 et 2000a).

Main modes of reproduction

Most fishes are oviparous. Oocytes and sperm are released into the water and fecundation takes place immediately. There are also cases of intra-buccal fecundation, particularly in Cichlidae.

Depending on the demographic strategies implemented by fishes and the ecological adaptations to certain physical systems, we can distinguish different

TABLE 10.III.

Relationships between fecundity (F) and standard length (SL in mm) or weight (W in g)
for different African fish species.

Species	F *vs* SL	F *vs* W	Source
Mormyridae			
Marcusenius ussheri	F = 80 SL - 9742	F = 45 W + 592	Albaret, 1982
Petrocephalus bovei	F = 55 SL - 3335	F = 105 W - 180	Albaret, 1982
Hepsetidae			
Hepsetus odoe	F = 172 SL - 41581	F = 59 W - 14250	Albaret, 1982
Hepsetus odoe	F = 10.8 SL - 803.0		Merron *et al.*, 1990
Alestidae			
Alestes baremoze	F = 657.4 SL - 117813.5	F = 323 W - 19122	Durand, 1978
Alestes baremoze		F = 288 W - 7078	Paugy, 1978
Alestes baremoze	F = 391 SL - 51456	F = 253 W - 1884	Albaret, 1982
Brycinus imberi	F = 6994.6 SL - 73028.3		Marshall & van.der Heiden, 1977
Brycinus imberi	F = 176.7 SL - 11768.6	F = 186 W + 140	Paugy, 1980a
Brycinus imberi	F = 328 SL - 24686	F = 356 W - 2800	Albaret, 1982
Brycinus longipinnis	F = 119 SL - 6633	F = 224 W - 540	Albaret, 1982
Brycinus longipinnis (Bandama)	F = 124.3 SL - 6834.6	F = 323 W - 1295	Paugy, 1982b
Brycinus longipinnis (Cavally)	F = 70 SL - 3818.9	F = 108 W - 151	Paugy, 1982b
Brycinus macrolepidotus	F = 814 SL - 137900	F = 195 W - 1980	Albaret, 1982
Brycinus macrolepidotus	F = 812.8 SL - 138120	F = 187 W - 1460	Paugy, 1982a
Brycinus nurse	F = 448.6 SL - 34638	F = 423 W - 2406	Paugy, 1980b
Brycinus nurse	F = 491 SL - 39871	F = 450 W - 3967	Albaret, 1982
Hydrocynus forskalii	F = 1325 SL - 319084	F = 187 W - 25065	Albaret, 1982
Micralestes acutidens	F = 19.93 SL - 539	F = 0.23 W - 70.3	Lek, 1978
Cyprinidae			
Barbus ablabes	F = 122 SL - 5266	F = 258 W + 413	Albaret, 1982
Barbus kimberleyensis	F = 0.222 SL^3 - 495.2		Gaigher, 1976
Barbus sublineatus	F = 534 SL - 27819	F = 958 W - 1849	Albaret, 1982
Barbus trispilos	F = 150 SL - 6325	F = 439 W + 87	Albaret, 1982
Labeo capensis	F = 1220 SL - 367774	F = 518 W - 214717	Mulder, 1973
Labeo parvus	F = 721 SL - 69461	F = 424 W - 5933	Albaret, 1982
Labeo umbratus	F = 1324 SL - 381914	F = 625 W - 215164	Mulder, 1973
Bagridae			
Bagrus docmak	F = 617 SL - 278389	F = 43 W - 16827	El Sedfy & El Bolock, 1987
Claroteidae			
Chrysichthys maurus	F = 45 SL - 5265	F = 18 W + 138	Albaret, 1982
Schilbeidae			
Schilbe mandibularis	F = 353 SL - 44425	F = 157 W + 5970	Albaret, 1982
Schilbe mystus	F = 1.5 SL - 185.1	F = 207 W - 1292	Lévêque & Herbinet, 1980
Schilbe uranoscupus	F = 528 SL - 98770	F = 250 W - 7475	Mok, 1975
Amphiliidae			
Amphilius atesuensis	F = 3.8 SL - 104	F = 40 W + 2	Albaret, 1982
Mochokidae			
Synodontis schall		F = 201 W - 7841	Albaret, 1982
Synodontis schall		F = 174.9 W + 5784	Ofori-Danson, 1992
Cichlidae			
Alticorpus 'geoffreyi'	F = 2.4365 SL - 171.76	F = 1.7836 W + 28.037	Duponchelle *et al.*, 2000b
Alticorpus macrocleithrum	F = 3.6323 SL - 259.3	F = 3.3229 W + 14.744	Duponchelle *et al.*, 2000b
Alticorpus mentale	F = 2.4897 SL - 211.7	F = 0.9359 W + 63.115	Duponchelle *et al.*, 2000b
Alticorpus pectinatum	F = 2.2238 SL - 114.87	F = 3.2395 W + 12.796	Duponchelle *et al.*, 2000b
Aulonocara 'blue orange'	F = 1.0608 SL - 33.755	F = 3.3845 W + 9.6689	Duponchelle *et al.*, 2000b
Aulonocara 'cf. macrochir'	F = 1.5397 SL - 87.623	F = 1.6714 W + 18.2	Duponchelle *et al.*, 2000b
Aulonocara 'rostratum deep'	F = 2.6948 SL - 191.6	F = 2.3872 W + 1.3981	Duponchelle *et al.*, 2000b
Buccochromis lepturus	F = 4.7556 SL - 768.67	F = 0.9143 W + 22.481	Duponchelle *et al.*, 2000b
Buccochromis nototaenia	F = 1.9659 SL - 105.22	F = 0.8115 W + 96.468	Duponchelle *et al.*, 2000b
Chromidotilapia guntheri	F = 2.6 SL - 64	F = 3.4 W + 25	Albaret, 1982
Copadichromis quadrimaculatus		F = 0.684 W - 0.8577	Duponchelle *et al.*, 2000b

TABLE 10.III. (CONT.)

Species	F *vs* SL	F *vs* W	Source
Cynotilapia afra	F = 0.6252 SL - 17.179	F = 1.9679 W + 6.3959	Duponchelle *et al.* (unpublished)
Diplotaxodon apogon		F = 0.6738 W - 1.0371	Duponchelle *et al.*, 2000b
Diplotaxodon argenteus	F = 0.306 SL - 11.866	F = 0.3006 W + 6.1836	Duponchelle *et al.*, 2000b
Genyochromis mento	F = 1.6346 SL - 94.359	F = 2.203 W + 0.8898	Duponchelle *et al.* (unpublished)
Labeotropheus fuelleborni	F = 0.6331 SL - 21.182	F = 1.1687 W + 7.7613	Duponchelle *et al.* (unpublished)
Labeotropheus trewavasae		F = 2.857 W - 15.549	Duponchelle *et al.* (unpublished)
Lethrinops argenteus	F = 2.5193 SL - 185.09	F = 1.7255 W + 21.72	Duponchelle *et al.*, 2000b
Lethrinops 'deep water albus'	F = 2.8885 SL - 178.91	F = 2.8411 W + 22.771	Duponchelle *et al.*, 2000b
Lethrinops gossei	F = 2.2518 SL - 147.31	F = 1.6832 W + 19.458	Duponchelle *et al.*, 2000b
Lethrinops longimanus	F = 2.7948 SL - 225.41	F = 2.9578 W - 43.716	Duponchelle *et al.*, 2000b
Lethrinops macrochir	F = 3.6833 SL - 267.1	F = 2.7129 W + 12.68	Duponchelle *et al.*, 2000b
Lethrinops 'oliveri'	F = 1.7657 SL - 72.585	F = 4.5704 W + 3.0726	Duponchelle *et al.*, 2000b
Lethrinops polli	F = 1.5365 SL - 83.52	F = 2.5654 W + 2.6796	Duponchelle *et al.*, 2000b
Mylochromis anaphyrmus	F = 2.7755 SL - 194.73	F = 1.9783 W + 25.864	Duponchelle *et al.*, 2000b
Nyassachromis 'argyrosoma'	F = 0.9259 SL - 29.05	F = 3.2835 W + 10.481	Duponchelle *et al.*, 2000b
Oreochromis niloticus	F = 111.92 SL - 993.64	F = 2.91 W + 277.7	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 53.507 SL - 308.55	F = 2.52 W + 164.4	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 129.9 SL - 1254	F = 3.64 W + 197.1	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 85.852 SL - 695.1	F = 3.61 W + 103.3	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 116.2 SL - 1095	F = 2.59 W + 337.2	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 81.871 SL - 633.54	F = 2.01 W + 368.6	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 122.43 SL - 1156.2	F = 3.14 W + 260.5	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 77.809 SL - 504.14	F = 3.78 W + 152.5	Duponchelle *et al.*, 2000a
Oreochromis niloticus	F = 99.584 SL - 775.71	F = 2.69 W + 317.8	Duponchelle *et al.*, 2000a
Otopharynx 'productus'		F = 2.8372 W - 7.8469	Duponchelle *et al.*, 2000b
Otopharynx speciosus	F = 3.547 SL - 452.51	F = 1.0452 W - 25.644	Duponchelle *et al.*, 2000b
Pallidochromis tokolosh	F = 0.7106 SL - 78.13	F = 0.5496 W - 4.5233	Duponchelle *et al.*, 2000b
Petrotilapia 'fuscous'		F = 2.1274 W - 6.1381	Duponchelle *et al.*, (unpublished)
Placidochromis 'long'	F = 1.333 SL - 57.675	F = 6.8445 W - 12.583	Duponchelle *et al.*, 2000b
Placidochromis 'platyrhynchos'		F = 1.8798 W + 14.85	Duponchelle *et al.*, 2000b
Pseudotropheus 'aggressive blue'	F = 1.0151 SL - 46.016	F = 1.7042 W + 6.5604	Duponchelle *et al.* (unpublished)
Pseudotropheus callainos		F = 1.1263 W + 5.8628	Duponchelle *et al.* (unpublished)
Pseudotropheus heteropictus	F = 0.9346 SL - 34.827	F = 4.0141 W - 10.079	Duponchelle *et al.* (unpublished)
Pseudotropheus livingstonii	F = 3.1033 SL - 128.38	F = 6.4275 W + 1.2343	Duponchelle *et al.*, 2000b
Pseudotropheus tr. 'lilac'	F = 0.7236 SL - 23.059	F = 1.4092 W + 9.8755	Duponchelle *et al.* (unpublished)
Pseudotropheus tr. 'red cheek'	F = 0.6259 SL - 22.07	F = 2.0579 W - 4.9336	Duponchelle *et al.* (unpublished)
Pseudotropheus tropheops 'blue'	F = 1.6927 SL - 89.196	F = 3.596 W - 17.192	Duponchelle *et al.* (unpublished)
Pseudotropheus williamsi	F = 1.8937 SL - 104.3	F = 3.0137 W - 5.8688	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra	F = 0.8112 SL - 27.739	F = 1.9246 W + 6.6811	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'black dorsal'	F = 1.4866 SL - 74.477	F = 1.7705 W + 9.2223	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'red dorsal'	F = 0.9901 SL - 36.543	F = 2.1674 W + 6.981	Duponchelle *et al.* (unpublished)
Pseudotropheus zebra 'yellow throat'	F = 1.1536 SL - 53.814	F = 2.3995 W - 1.8984	Duponchelle *et al.* (unpublished)
Sarotherodon melanotheron	F = 0.0008 LF 2.449	F = 1.72 W -15.0	Legendre & Écoutin, 1989 (unpublished)
Sarotherodon melanotheron	F = 2.7238 LF - 160.01	F = 1.948 W + 119.08	Panfili *et al.*, 2004a
Sarotherodon melanotheron	F = 2.8459 LF - 156.76	F = 2.111 W + 128.11	Panfili *et al.*, 2004a
Sciaenochromis alhi	F = 2.4762 SL - 200.07	F = 4.4172 W - 55.843	Duponchelle *et al.*, 2000b
Sciaenochromis benthicola	F = 1.0481 SL - 74.232	F = 1.264 W - 0.3265	Duponchelle *et al.*, 2000b
Stigmatochromis 'guttatus'	F = 1.1159 SL - 87.92	F = 1.4769 W - 8.0045	Duponchelle *et al.*, 2000b
Taeniolethrinops praeorbitalis	F = 2.0847 SL - 135.28	F = 0.9672 W + 74.587	Duponchelle *et al.*, 2000b
Tilapia guineensis	F = 0.1458 LF 1.9899	F = 18.61 W + 2018.0	Legendre & Écoutin, 1989 (unpublished)
Coptodon zillii	F = 49 SL - 2987	F = 28 W + 610	Albaret, 1982
Trematocranus placodon	F = 1.5364 SL - 62.449	F = 1.2303 W + 50.512	Duponchelle *et al.*, 2000b
Mastacembilidae			
Mastacembelus nigromarginatus	F = 8.4 SL -1468	F = 187 W + 67	Albaret, 1982

reproductive modes or styles. The general classification proposed by Balon (1975 and 1990), based on the degree of parental care (ethology) and reproductive sites (ecology) is generally accepted. The author identifies three broad sets within which there are etho-ecological subsets, regardless of the phyletic origin of the species (table 10.IV):

• fishes that do not guard their eggs once these have been released, among which we can distinguish fishes that lay eggs on open substrates or those that provide a modicum of protection by concealing them. These are generally fishes that are highly fecund and have an indirect form of development;

• fishes that guard their eggs in nests, either on pre-selected or pre-constructed substrates. These species generally have a few relatively large eggs, to which they provide different forms of parental care;

• fishes that bear their eggs for at least part of the embryonic period. In external brooders, the eggs are carried on the body surface or in the mouth, or in structures that open out. In internal brooders, the eggs are fertilized and transported within the body.

Each etho-ecologic section includes different reproductive guilds, of which we provide only a few examples (table 10.IV). These guilds are based on a combination of morphological, behavioural, and ecological characteristics.

TABLE 10.IV.
Simplified classification of reproductive styles in fish (from Balon, 1975).

NON-GUARDERS	**Open substrate spawners**	
	pelagic spawners	*Stolothrissa*
		Limnothrissa
		Alestes
		Lates
		Ctenopoma spp
	plant spawners	Small alestids and cyprinids
		Epiplatys, *Aphyosemion*
	rock and gravel spawners	*Opsaridium microlepis*
	Brood hiders	
	Annual fishes	*Nothobranchius*
GUARDERS	**Clutch tenders**	
	plant tenders	*Polypterus*
	rock tenders	many cichlids
	Nesters	
	froth nesters	*Hepsetus odoe*
		Microctenopoma spp.
	hole nesters	many cichlids
		some mormyrids
		Protopterus
	sand nesters	*Tilapia* spp.
		Tanganyikan lamprologine cichlids
	plant material nesters	*Gymnarchus niloticus*
		Heterotis niloticus
BEARERS	**External brooders**	
	mooth brooders	*Oreochromis spp.*
		Sarotherodon spp
		all haplochromines
	pouch brooders	freshwater pipefishes
	Internal live bearer	some asian poeciliids

An estimate of the proportion of different eco-ethological guides in African continental waters reveals a much higher number of guarders and bearers in the East African great lakes, which are characterized by relatively predictable physico-chemical systems. Meanwhile, a large percentage of non-guarder species are found in the rivers and wet zones, which have less predictable physical systems (Bruton & Merron, 1990).

To complete the reproductive guilds, we should also take into account the frequency of spawing and the period(s) during which spawning occurs. This usually takes place when the environmental conditions are, in principle, most conducive to the survival of eggs and larvae, and many species have a seasonal reproductive cycle. It is nonetheless possible to distinguish several options in reproductive behaviour (table 10.V).

Type of fecundity	Seasonality	Examples	Migratory behaviour / parental care
"big-bang"	once in the lifetime	*Anguilla*	long distance migrations, no parental care
total spawners	highly seasonal	*Alestes*	anadromous migrations
(very high fecundity)	(generally throughout the flood)	*Labeo*	open water spawners
		Schilbe	no parental care
partial spawners	throughout the flood	many cyprinids	
		Clarias	
		Protopterus	bottom nester
		Heterotis	egg garders
		Gymnarchus	floating nest (plant material)
		Hepsetus	floating nest (foam)
		anabantids	
small brood spawners	sometimes throughout the year	*Tilapia*	nest constructors and parental behaviour
(low fecundity)	sometimes throughout the flood	*Sarotherodon*	mouth brooders
	during the filling of ponds	*Nothobranchius*	annual species with resting eggs

One very rare behaviour is the "big bang" (Lowe-McConnell, 1987) which, like in eels, consists of reproducing once in a lifetime and then dying.

Several species, meanwhile, have a single short reproductive period every year. This is the case for many riverine species that practice reproductive migrations and spawn at the beginning of or during the flood, when conditions are optimal for juveniles that can find shelter and food in the flooded plains. This periodic strategy does include risks tied to climate variability and variations in flooding, making it difficult to predict the optimal period for reproduction. The species in question often release a very large number of eggs, and are sufficiently long-lived to reproduce for several consecutive years, thus minimizing the consequences of climate-related variations on the recruitment.

For other species, the reproductive season is spread out over the year. Scenarios differ depending on the group. Either individuals of a given species do not reach maturity at the same time, or eggs are spawned in batches at more or less

regular intervals. This strategy tends to minimize the risks of a single spawning that may occur at an unfavourable period, and tends to benefit species with short lifespans.

Finally, other species spawn practically throughout the year. Most of these multiple spawners provide parental care, like the Cichlidae. Although a full reproductive cycle cannot be completed in 24 hours, certain phases follow a daily cycle. In particular, spawning can take place at certain hours, as has been observed in many fishes such as *B. macrolepidotus* which appears to reproduce before dark (Paugy, 1982a)

Cichlidae belonging to the genera *Tropheus* and *Simochromis* that live in the same habitats in Lake Tanganyika (between rocks, a few metres depth) and feed on Aufwuchs do not spawn at the same time of day. The former spawn early in the morning, while the latter spawn during daylight (Nelissen, 1977). Differences in spawning activity rhythms can contribute to limiting interspecies competition.

In the Nothobranchiidae *Nothobranchius guentheri*, reproductive behaviour follows a day-long cycle (Haas, 1976b). Reproductive activity is low very early in the morning, but increases 2.5 hours after dawn and reaches a peak 6 hours after dawn before waning.

The influence of lunar cycles has also been identified in the reproductive behaviour of certain fish species. The proportion of females ready to spawn among Lake Victoria *Oreochromis niloticus* is higher during the full moon than during the new moon (Okorie, 1973). In the Ethiop River in Nigeria, which has particularly clear waters, there is a marked synchronization of *Tilapia mariae* spawns with the lunar cycle, as 85% of spawning occurs during the last quarter of the lunar cycle, that is, between 0 and 6 days before the full moon (figure 10.2). Spawning before the full moon could contribute to improving larval survival owing to more efficient parental guarding during moonlit nights (Schwanck, 1987).
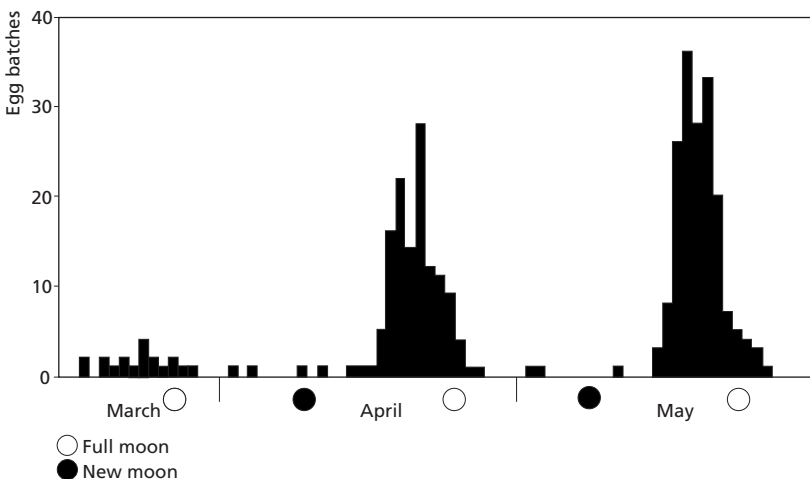
Synchronization between reproduction and changes in the environment

Reproduction in fishes is a cyclic phenomenon, synchronized in many species, with seasonal environmental fluctuations that have an impact on fish physiology, as they can stimulate or inhibit certain stages of gametogenesis or spawning. Both are controlled by endocrine processes that are influenced by environmental factors such as temperature, photoperiod, rainfall, etc. Each species or species group can react differently to the environmental factors that affect their physiological rhythms.

This synchronization between the reproductive cycle and predictable changes in the environment is an adaptive process. As they evolved, fishes adapted their sexual cycle in order to reproduce at periods most favourable to the survival of their eggs. How did fishes program their reproductive cycle? What factors are responsible for gonad maturation in such a way that species are ready to spawn when conditions are favourable for the survival of eggs and larvae, thus granting them a selective advantage? We are still far from knowing the answers to all these questions, even though we suspect certain ecological factors of playing an important role, as reproduction is a complex phenomenon in which several abiotic factors are involved. In all likelihood, the chronology of the reproductive cycle is in fact a compromise between stimuli from different sources. Gametogenesis thus starts several months before spawning season, when conditions are not yet favourable to the survival of the young. Whatever the case, the synchronization of the reproductive cycle with environmental changes confers an adaptive advantage to species.

Single spawning species

Several authors have attempted to identify which factors in the physical system were involved in triggering maturation as well as spawning.

In the Niger basin, Bénech & Ouattara (1990) investigated the role of various environmental factors in the ovarian growth of *Brycinus leuciscus* by comparing the reproductive cycle in different natural conditions (different flood periods) between the sites of Mopti and Niamey. In Mopti, gametogenesis begins in week 20 at the same time as the climate changes induced by the movement of the intertropical front. The same thing occurs in Niamey in week 22. In both stations, the start of gonad development occurs once the water temperature has attained a maximum (29°C) in week 19, and water conductivity has stopped increasing with the appearance of the first rains. The gonado-somatic index reaches its peak in week 30 in Mopti, after which spawning begins and continues up to week 39. In Niamey, meanwhile, ovarian growth appears to be interrupted in week 22, then restarts again six to nine weeks later to reach a peak in week 35, with spawning occurring until week 45. In both sites, gonad development coincides with a decrease in conductivity after a period of warming and the start of the flood. Spawning occurs as water rises, a few weeks before the water level reaches its peak. It is nonetheless difficult to establish precisely which factor is responsible for triggering the different reproductive processes.
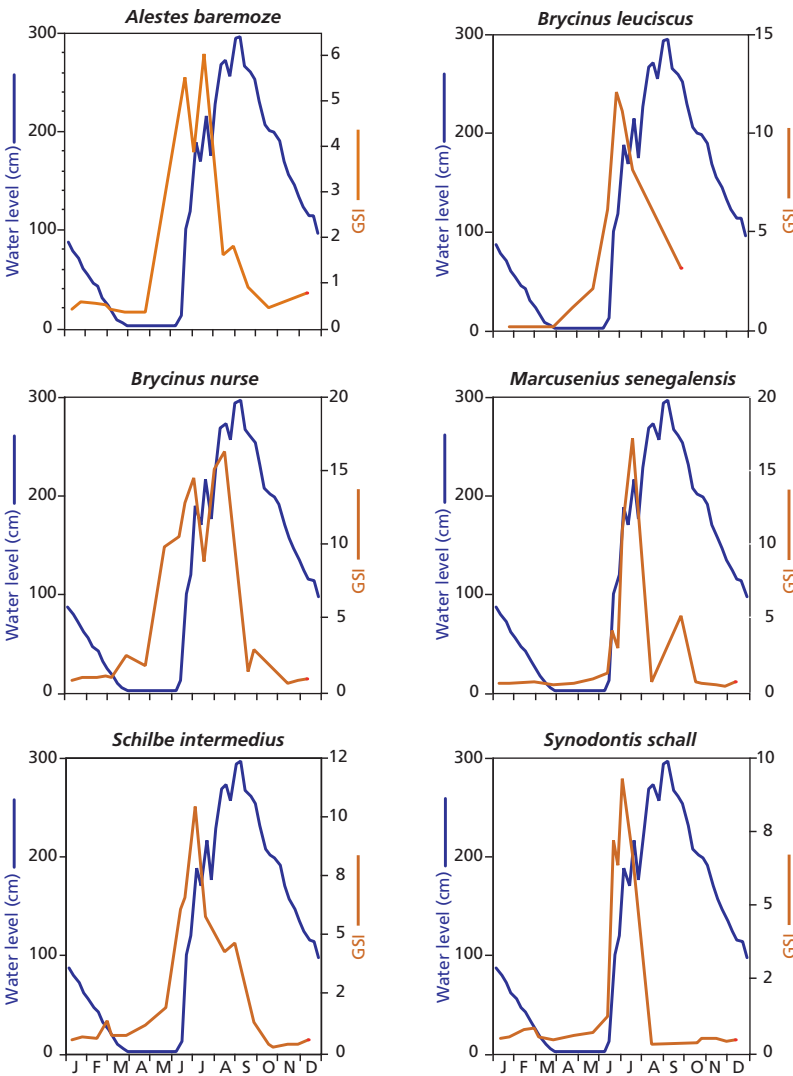
In aquarium conditions, Kirshbaum (1984) triggered Mormyridae gonad maturation by diminishing water conductivity, simulating rainfall, and increasing the water level, all factors identical to those that appear to be involved for *B. leuciscus*.

What stimuli trigger spawning? In large tropical rivers, the hydrological regime (or, to be precise, the set of climatic conditions prevailing at the start of the flood) appears to be the main regulator of reproduction. For many species, spawning coincides with the flood and can occur from the start of the flood up to its peak, but rarely during the recession. As such, most of the species present in the Baoulé (upper course of the Senegal) reproduce before the flood (figure 10.3), and this phenomenon has been seen in numerous species in various physical systems (Bénech & Quensière, 1985; Munro, 1990).

However, reproduction and flood are not always synchronized, which casts some doubt on the true role of this factor. In the Okavango delta, the flood occurs in the dry season, during winter months, as the flood wave takes a while to go from southern Angola via the Okavango River. In these conditions, *Hepsetus odoe* spawns in summer, with activity reaching a peak when waters are low (Merron *et al.*, 1990), which appears to indicate that the flood is not the primary stimulus triggering spawning in this species. A comparable situation exists in Lake Chad, where the lake floods in winter (December-January), several months after the flood peaks in the Chari River (September). Yet reproduction in most species takes place during the rainy season (July-August) which immediately follows the hot season (Bénech & Quensière, 1985). There are exceptions to this trend, as in *Brycinus macrolepidotus* and *Hydrocynus forskalii* of the 'Sahelo-Sudanian' basins found in the same latitudes. It is moreover customary in numerous equatorial species which indivudually have a single annual spawn, but without a precise spawning period when the entire population is considered. *Brycinus imberi* (figure 10.4) and *B. longipinnis* of the Côte d'Ivoire basins demonstrate such behaviour (Paugy, 1980a and 1982b).
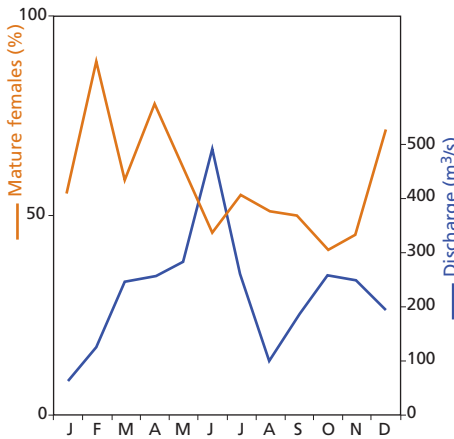
Multiple spawning species

For species that have a reproductive period spread out over time (interval spawning or spawning throughout the year), it is rather difficult to identify the factors influencing the reproductive cycle (Jalabert & Zohar, 1982). This is especially the case for Cichlidae, which are theoretically capable of reproducing uninterruptedly in equatorial regions, though with a tendency to seasonal behaviour depending on latitude. In the Ébrié lagoon (Côte d'Ivoire), lagoon Tilapias (*Sarotherodon melanotheron* and *Tilapia guineensis*) reproduce throughout the year without displaying any clear seasonal variation in the intensity of sexual activity (Legendre & Écoutin, 1989). A high proportion of maturing fishes is observed throughout the year. However, in populations reared in parks in the lagoon, the sexual activity of *S. melanotheron* decreases significantly during the rainy season, from June to September (see box "Spawning frequency in cichlids"). Meanwhile, the sexual activity of *Oreochromis niloticus* shows marked seasonality in artificial reservoirs of Côte d'Ivoire, with a more spread-out season in the centre and south of the country than in the small agro-pastoral reservoirs of the north (Duponchelle *et al.*, 1999). In both north and south, periodicity of the reproductive season is nonetheless regulated by the photoperiod (see box "Influence of photoperiod on the reproductive cycle of cichlids"). On the

other hand, in *O. niloticus*, fecundity rates are correlated with trophic availability in Côte d'Ivoire's artificial reservoirs. The highest fecundity rates are recorded when chlorophyll *a* concentrations are at their highest, just before the flood (Duponchelle *et al.*, 2000a).

SPAWNING FREQUENCY IN CICHLIDS
(FROM LEGENDRE & ÉCOUTIN, 1989)

In the lagoons of Côte d'Ivoire, where the two species reproduce throughout the year, the interval between two spawns is about two weeks in *Sarotherodon melanotheron*, and around three weeks in *Tilapia guineensis* (figure 10.5). Nonetheless, the frequency of spawning appears to be less regular in *T. guineensis,* which can go for nearly four months without spawning.
For both species, the frequencies provided are averages that should be adapted, as relative frequency varies according to the seasons as shown in the figure below, where it is clear that a minimum is reached in both species during the rainy season, that is, June-July.
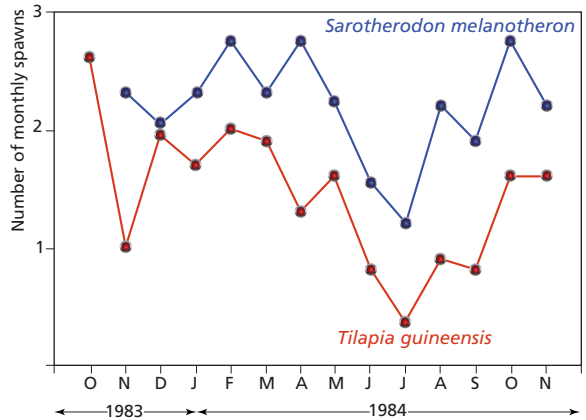
FIGURE 10.5.

Seasonal changes in the spawning frequency for *Sarotherodon melanotheron* and *Tilapia guineensis* in concrete tanks (redrawn from Legendre & Écoutin, 1989).

Several observations appear to reveal the existence of reproductive seasonality that is linked to the abundance of available food. In most of the zooplanktophagous haplochromines of Lake Victoria, there is a small proportion of mature females throughout the year, but there is a peak in reproductive activity during the dry period (June-October) when plankton production is highest owing to the mixing of waters (Goldschmidt & Witte, 1990). This situation is comparable to that of Lake Malawi where the zooplanktophagous 'utaka' spawn between March and July, when the waters mix (Iles, 1960).

A recent study in Lake Malawi confirmed that the reproductive season for these species occurs between March and December, with an additional peak of activity in December. These periods of sexual activity correspond to the ones where plankton production is highest (Duponchelle *et al.*, 2000b). Meanwhile, for the 37 other benthic or pelagic species studied that do not belong to the 'utaka' group, no correspondence has been found between the reproductive season and the annual cycles of temperature, photoperiod, oxygen concentration (for deep water species), conductivity, or phytoplankton abundance. Some species are capable of reproducing throughout the year, while others do so during well-defined seasons, regardless of the depth they inhabit. It appears

INFLUENCE OF PHOTOPERIOD ON THE REPRODUCTIVE CYCLE OF CICHLIDS

The influence of the photoperiod on the regulation of fish reproductive cycles is well-known in temperate systems, but it is often neglected in tropical and sub-equatorial environments where it remains relatively constant.

Yet in the artificial reservoirs of Côte d'Ivoire, the periodicity of the *Oreochromis niloticus* reproductive cycle is strongly correlated with the annual cycle of the length of day (figure 10.6). Analyses have shown that among the various environmental factors (precipitation, variations in water level, water temperature, chlorophyll *a* concentration) that are potentially involved in the regulation of the reproductive cycle of this species, photoperiod is the only factor that contributes significantly to the model.

Indeed, it accounts for 66 to 85% of the variation in reproductive seasonality, depending on the reservoir (Duponchelle *et al.*, 1999).

A good correlation was also observed with the annual cycle of chlorophyll *a* concentrations (used as an indicator of trophic availability), or with water temperature.

However, in experimental conditions, with optimized regular feeding, reproductive activity ceased when the photoperiod decreased (Baroiller *et al.*, 1997; Desprez & Mélard, 1998), even in optimal temperatures. These various results, in both natural and experimental conditions, led to the following hypothesis.

The reproductive season in Tilapias could be controlled at two levels: an upper level, controlled by a constant astronomical factor (photoperiod) which determines the periodicity of the reproductive season, and a lower level, regulated by the combination of different environmental variables (temperature, precipitation, availability of resources, etc.) which affect the inter-annual variations of reproductive duration and intensity (Duponchelle *et al.*, 1999).
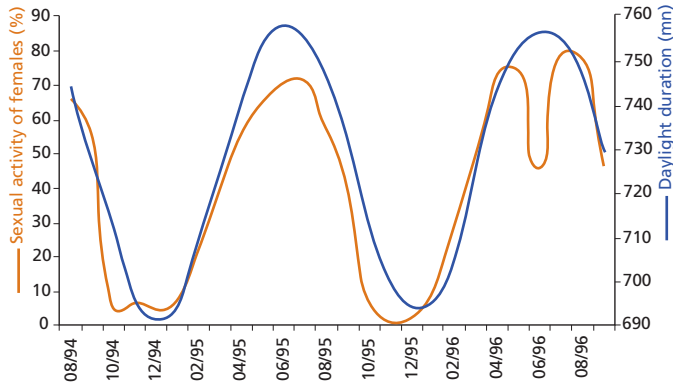
FIGURE 10.6.

Correlation between photoperiod and the reproductive seasonality of *Oreochromis niloticus* in small agropastoral reservoirs of Côte d'Ivoire (adapted from Duponchelle *et al.*, 1999).

that the reproductive modalities observed in these species, most of which feed on benthic invertebrates, are probably influenced by variations in the abundance of their preferred prey (Duponchelle *et al.*, 2000b). This also appears to be the case for species confined to rocky zones or 'mbunas' (Marsh *et al.*, 1986). These authors have noted that ten Cichlidae species, sexually active throughout the year, living in rocky physical systems, had a peak of reproductive activity during the spring (August-October) and a second one in early autumn (February-March), but were less active during cold periods (May-June). The spring peak coincides with significant algal development, whereas the autumn peak corresponds to a large biomass of epilithic algae.

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It was also highlighted in the pelagic Clupeidae of Lake Tanganyika, *Limnothrissa miodon* and *Stolothrissa tanganicae*, which reproduce throughout the year, that the main period of juvenile production coincided with the period of maximum plankton development (Coulter, 1970). It appears that the maximum spawning period varies according to the lake's regions, in relation to zooplankton production (Chapman & Well, 1978).

In other cases, it is difficult to provide an interpretation based on food availability. For the three Tilapias endemic to Lake Malawi, which have a well-defined reproductive period (Lowe McConnell, 1987), *Oreochromis saka* and *O. lidole* spawn in shallow waters before the beginning of rains (October-November), in the hottest period of the year. Meanwhile, *O. squamipinnis* spawns during the rainy season (December-February) in deeper waters.

Flexibility of the spawning season

A species's spawning season can change if the conditions in the physical system change as well. This is the case for instance if a dam is built on a river. Thus, *Pellonula leonensis* (Clupeidae) which reproduces during the dry season in the Volta River, spawns all year round in Lake Volta. Likewise, *Physailia pellucida* (Schilbeidae), which spawns after the rainy season in rivers, also spawns throughout the year in the lake (Reynolds, 1974).

Other species use different strategies depending on geographic region, and thus according to climatic zones. Thus, all populations of *Brycinus imberi* (Alestidae) reproduce during the flood in the Zambezi (tropical regime) (Marshall & van der Heiden, 1977), while communities in Côte d'Ivoire (equatorial or subtropical regime) reproduce throughout the year with no specific synchrony with the flood regime (Paugy, 1982b). Moreover, potential fecundities differ significantly. We thus note that Ivorian individuals that may find more favourable conditions at some point in the year are individually less fecund than specimens from the Zambezi. There is thus a reproductive strategy adapted to the local conditions of the physical system.

Adaptive strategies

In some species, it has been noted that egg size is relative to parental size. In *Sarotherodon melanotheron* for example, the average weight of eggs is less than 5 mg for females weighing 50 g, but can reach 20 mg for 200 g females (Peters, 1963). A significant relationship between female size and egg size has also been observed in Lake Victoria Haplochromines (Glodschmidt & Witte, 1990). On the other hand, no relationship between egg size and female size was observed in *Oreochromis niloticus* in Côte d'Ivoire (Duponchelle *et al.*, 2000a), nor in 39 species of *Haplochromis* in Lake Malawi (Duponchelle *et al.*, 2000b).

The number and size of oocytes can also vary within the same species, and for individuals of the same size. Peters (1963) showed, for instance, that in laboratory conditions, a female *S. melanotheron* can produce either a large number of small eggs or a small number of large eggs. In the lagoons of Côte d'Ivoire, we have also noted that for females measuring 180-220 mm, the

average weight of oocytes was 28 mg in the lagoon (F = 329 eggs per spawn and per female), from 15 to 18 mg in 'acadja' parks (F = around 500 eggs), and only 12 g in intensive-breeding fish parks (F = 726 eggs) (Legendre & Écoutin, 1989). Nonetheless, regardless of the spawning technique, the relative weight of gonads in relation to body weight remained the same, which suggests that the ovarian quantity generated during the reproductive cycle is a specific constant. That said, while this character is the least variable in *Oreochromis niloticus*, some inter-population and intra-population differences in successive years have been reported in Côte d'Ivoire (Duponchelle *et al.*, 2000a).

In Senegal, *S. melanotheron* populations show different reproductive and growth characteristics depending on the salinity of the estuaries they are in (Panfili *et al.*, 2004a). In the saltiest physical systems, size at first sexual maturity is smaller, relative fecundity is higher, oocytes are smaller, and growth slower. The most marked changes are observed in hyperhaline conditions (> 60 psu). Similar observations have been made in *Ethmalosa fimbriata* (Panfili *et al.*, 2004b). In this Clupeid species, the lack of genetic differentiation in the studied populations suggests that variations in reproductive and growth traits are not due to genetic isolation. Rather, they are probably phenotypic responses to marked fluctuations in salinity (Panfili *et al.*, 2004b).

CHANGES IN CICHLID REPRODUCTION INDUCED BY ENVIRONMENT

To test if the reproductive differences observed between *Oreochromis niloticus* populations from various artificial reservoirs in Côte d'Ivoire were induced by the environmental conditions encountered or if they had a genetic basis, two approaches were adopted:

• Fishes from two of the monitored reservoirs in Côte d'Ivoire, whose reproductive characteristics were among the most pronounced, were captured, marked, and placed in the same environment for five months. At the end of this period, they were sacrificed and their reproductive characteristics were compared.

• At the same time, the genetic characterisation of 300 specimens from each of the two populations was carried out using microsatellite markers.

No genetic difference was found between the two populations. After sharing the same environment for five months, no difference was found in the reproductive characteristics of the two populations.

Fecundity and oocyte size, which were very significantly different in their respective physical systems, were identical in the communal pond (figure 10.7). This led to the conclusion that the differences in reproduction observed between the two populations in natural conditions were a phenotypic response to their different environments. (Duponchelle *et al.*, 1998).
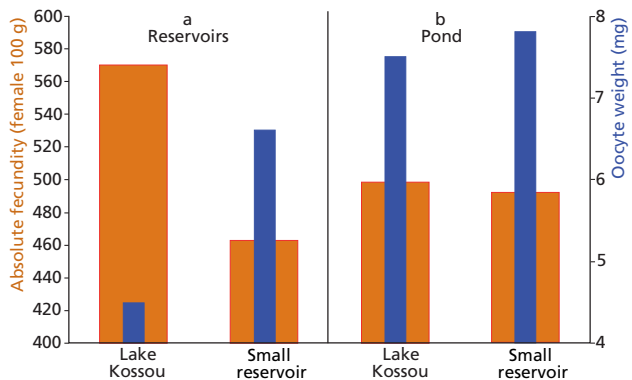

FIGURE 10.7.

Reproductive characteristics (fecundity and oocyte weight) of two populations of *Oreochromis niloticus* females in their respective reservoirs of origin in Côte d'Ivoire (a) and after 5 months of rearing in communal pond (b) (adapted from Duponchelle *et al.*, 1998).

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In *Oreochromis niloticus*, marked variations in size at first sexual maturation (Duponchelle & Panfili, 1998), reproductive season (Duponchelle *et al.*, 1999), fecundity and egg size (Duponchelle *et al.*, 2000a) have been observed between populations of different artificial reservoirs in Côte d'Ivoire. Significant variations in reproductive characteristics have also been observed within each population over successive years. Genetic analyses and experiments in controlled environments (see box "Changes in cichlid reproduction induced by environment") have shown that the reproductive differences observed in the reservoirs were phenotypic responses to variations in the environmental conditions encountered (Duponchelle *et al.*, 1998).

The remarkable plasticity of the reproduction of *S. melanotheron* and *O. niloticus* depending on environmental conditions are illustrations of adaptive strategies that can be developed by Cichlidae. While the mechanisms involved in the regulation of their reproductive cycles have not yet been identified, a few elements can serve as a starting point. Vitellogenesis takes place very rapidly in Cichlidae. In *O. niloticus*, for example, a full gonadal cycle lasts 27 days on average and can be as short as 15 days in non-incubating females (Tacon, 1995). The rapidity of their gonadal cycle thus allows Cichlidae to adapt their reproductive characteristics very quickly in reaction to changes in their environment (see box "Rapid phenotypic changes in Nile tilapia, *Oreochromis niloticus*").

RAPID PHENOTYPIC CHANGES IN NILE TILAPIA, *OREOCHROMIS NILOTICUS*   DUPONCHELLE & LEGENDRE, 2001

In Côte d'Ivoire, one of the major characteristics of certain artificial lakes is the presence of a large number of dead tree stumps.
To find out if the resulting spatial structure can influence the reproductive characteristics of *Oreochromis niloticus*, fishes from the same parents were placed for two months in concrete tanks with three different types of spatial organization:

• bare concrete tanks serving as controls;

• tanks with a sand-covered bottom;

• tanks with an artificial reef created from concrete blocks.

After two months, analysis of the fishes showed that Tilapias were capable of adapting to the organization of their living space by modifying their living traits. Females had lower fecundity in the tanks with reefs than in the control tanks (figure 10.8). An opposing trend was noted for egg size. These results also suggest that spatial organization, through the increase in the number of shelters and nesting sites, exercises a greater influence on Tilapia reproduction than the intrinsic quality of the spawning substrate does.

Even more significantly, it is the first time than an experiment demonstrated such a swift adaptive response in fishes. It occurred within one to two reproductive cycles, that is, around four to six weeks for the species (Duponchelle & Legendre, 2001).
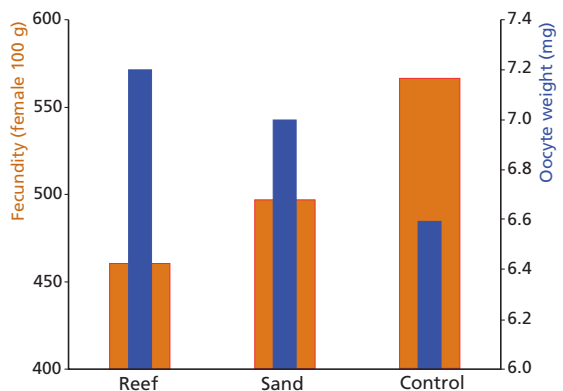

FIGURE 10.8.

Fecundity of *Oreochromis niloticus* females and mean oocyte weight depending on rearing environment.
For clarity, values were equated for 100 g standard females (redrawn from Duponchelle & Legendre, 2001).

Parental care

Parental care refers to any assistance provided by parents whith the purpose of ensuring better survival of eggs after fecundation. Such assistance may range from the construction of nests to the brooding of eggs and fry, including egg ventilation to ensure oxygenation or to remove silt.

Only 22% of teleost families (Blumer, 1982), especially ones with freshwater presence, provide a form of parental care. Care is more often provided by males (11% of teleost families) than by females (7% of families), while biparental care is seen in 4% of families (Sargent & Gross, 1992) (see box "Types of parental care").

TYPES OF PARENTAL CARE

Parental care in fishes takes many forms:
• guarding eggs and larvae by chasing off other fishes and predators,
• construction and maintenance of a nest,
• incubation of eggs and larvae in the mouth or gill cavity,
• transport of eggs from one site to another, generally in the mouth,
• cleaning of spawning sites,
• ventilation of eggs using fins to ensure better oxygenation and remove deposited sediments.

It has been suggested that parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990) or densely-populated systems characterized by significant predation on eggs and juveniles. Such parental care practices helped reduce hazards, but this theory ought to be backed by observations. The main function of parental care is to protect the young from predators and a wide variety of behaviours exist in substrate brooders and mouth brooders.

Substrate brooders keep their spawn on or near a substrate and watch over their youngs until they are independent, while mouth brooders transport their youngs in the mouth from spawning until they are also independent. There are paternal, maternal, and biparental incubators (see box "Incubation period for cichlids").

The number of eggs that can be incubated in the mouth varies depending on species and individual size. In *O. macrochir*, females measuring 300-350 mm LS incubate up to 800 eggs (Marshall, 1979). Similar values have been observed in the paternal mouth brooder *S. melanotheron* (Legendre & Écoutin, 1989).

The practice of parental care is fairly widespread in African fishes (Blumer, 1982) and particularly in Cichlidae (Keenleyside, 1991). Many Cichlidae substrate brooder species are widely distributed in north and west Africa, and several species are also present in Lake Tanganyika, while the majority of mouth brooder Cichlidae species (over 70% of Cichlidae) are limited to the East African great lakes (see box "Biparental mouth brooder").

INCUBATION PERIOD FOR CICHLIDS

Substrate brooders

The sticky eggs are deposited on a hard surface, fertilized, and hatch a few days after the two parents guard the eggs with great vigilance. Eggs are smaller but more numerous than in mouth brooders. After hatching, the young larvae are hidden in a hole or in vegetation. When they can swim freely, they remain grouped near the substrate under the watchful eye of the parents.

Mouth brooders

There are three broad categories:

• *maternal mouth brooders* constitute the most common system. Spawning takes place on a substrate often prepared by the male, and the non-sticky eggs, released individually or in small batches, are rapidly taken into the mouth by the female. The male releases its sperm as the female collects the eggs, or fertilizes them in the mouth. The female then incubates the eggs until they are fully independent. In some cases, the female abandons them from time to time in order to feed, then takes them back again into the mouth. This behaviour has been observed in numerous Cichlidae in the East African lakes;

• *paternal mouth brooders* are found in only a few species. It is the case for *Sarotherodon melanotheron*;

• *biparental mouth brooders,* that is, mouth brooding by both parents from spawning until the young are independent, is also rare in Cichlidae. It has been observed in *Sarotherodon galilaeu*s.

There are of course many variants for each type of mouth brooding.

The number of eggs that can be incubated depends on the size of the oral cavity. For *S. melanotheron*, a paternal mouth brooder, the number of eggs that can be incubated in relation to the number of eggs released depends on the size of the male compared with the female. It has indeed been shown that the volume of the male's oral cavity increases faster with the male's size than the size of the spawn with the female's size (Legendre & Trébaol, 1993). As a result, smaller males cannot incubate all the eggs released by a female of the same size, as they would occupy 90% of the oral cavity. Incubation is thus more successful when females pair off with larger males.

BIPARENTAL MOUTH BROODER

*X*enotilapia spiloptera is an endemic Cichlidae species in Lake Tanganyika that is a biparental mouth brooder (Konings, 1992).

The species forms shoals but, as the reproductive season approaches, each shoal separates into several couples that seek a rocky habitat.

The couple is established by repeated courtship between the male and the female, and then settles in a small territory about 30 cm in diameter that is defended against other fishes.

A few days prior to spawning, there is a noticeable increase in mutual courtship, and a slight change in colour pattern.

At the time of spawning, the female cleans the site and deposits a few eggs. The male, which usually waits behind her about 3 cm above the substrate, then positions himself above the eggs and fertilizes them. The female waits for the male to go away then takes the fertilized eggs in her mouth.

After a brief pause during which the male chases off intruders, the female swims to the substrate again, waits for the male to position himself behind her, and releases a new series of eggs. The spawn may have 40 eggs, but it appears that quantity depends on the buccal capacity of the female.

The first nine or twelve days after spawning, the female incubates the embryos and does not eat. After this period, the larvae are transferred to the mouth of the male, which incubates them for another ten days. At the end of incubation, the male releases the fry in the territory defended by both parents. In the first few days, the youngs can seek shelter in the male's mouth, but they generally remain on the substrate and navigate within the territory. Youngs measure around 1.5 cm at the time of release, and it takes two years for them to reach the adult size of 10 cm.

There are a few exceptions such as *Oreochromis* and *Sarotherodon*. The paternal mouth brooder *S. melanotheron* is a species common to all brackish waters along the West African coast, while the biparental mouth brooder *S. galilaeus* is widely distributed in the north of tropical Africa.

Fishes build nests

A form of protection for eggs and larvae is to place them in a nest that may or may not be guarded by the parents. There is a wide variety of nests in fishes. Some are constructed depressions as with *Heterotis niloticus*) (see box "Nest of *Heterotis niloticus*"), or consist of burrows, as with *Protopterus annectens* (see box "Nest of *Protopterus annectens*"). Floating nests are a fairly common form in physical systems presenting a risk of anoxia. This is the case for nests of *Gymnarchus niloticus* built using plants, and Mormyridae nests that are also built using plant matter (see box "Nest of *Gymnarchus niloticus*"). In *Pollimyrus petricolus*, a species endemic to Niger, males actively guard the nest built from decomposing roots and branches of *Echinocloa stagnina*, which allows development of micro-invertebrates that serve as food for their young. Floating foam nests are also built by *Hepsetus odoe.*

NEST OF *HETEROTIS NILOTICUS*

The nests of *Heterotis niloticus* are built in herbaceous vegetation.
They are comparable to small basins measuring about 1.2 m in diameter, with a slightly excavated centre located at a depth of about 30 cm.
The bottom is bare and flat.
The compact rims are about 20 cm thick at the top and projects slightly above the water surface.
They are constructed using plant stems that have been removed from the centre of the nest. Parents stay near the nest once the eggs have been released.

Eggs are fairly small (2.5 mm in diameter) and orange.
They hatch about two days after release.
Youngs have long, dark red gill filaments that extend outside the gill cover.
They rapidly form a shoal around 30 cm in diameter occupying the centre of the nest.
On the fifth or sixth day, they leave the nest, still in a dense shoal, and under the protection of the parents (Svensson, 1933).
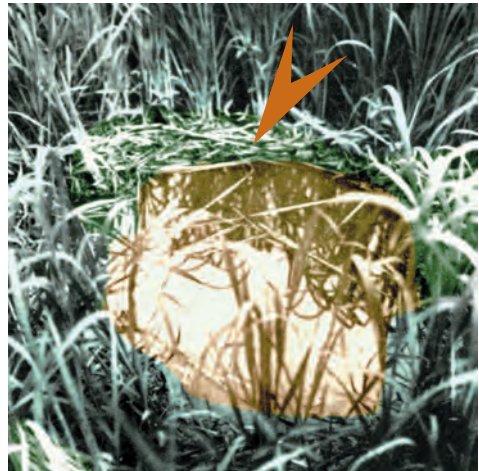
NEST OF *PROTOPTERUS ANNECTENS*
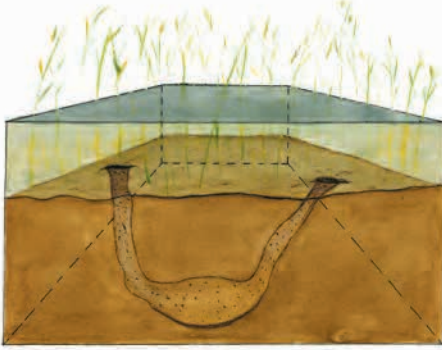
The lungfish burrows into the bottom to reproduce. Nests are generally built in shallow areas covered by herbaceous plants. The most common type is a U-shaped tube with two openings, one measuring 20 to 30 cm in diameter and the other 10 to 15 cm only. The nest is about 40 cm deep and the internal diameter is identical to that of the smaller opening. It contains a larger chamber (20-30 cm in diameter) containing the eggs and larvae.

There is some variability in nest shape. Some may have three openings, while others may be constructed on the bank and have only one.

The male guards the nest until the youngs have left it. He also ventilates the water inside the nest.

It has been observed that eggs inside the nest may be of different sizes. It is thus possible that the nest may be used by more than one female, or if not, that the female has intervals in spawning.

NEST OF *GYMNARCHUS NILOTICUS*

*G*ymnarchus niloticus is only found in the Nilo-Sudanian zone. It can reach a length of 1.60 m, and its pale yellow spherical eggs are very large (9 to 10 mm in diameter).

In the Niger floodplain, during the flood, *Gymnarchus* builds a floating nest in prairies of burgu millet (*Echinocloa stagnina*, also named hippo grass) submerged in depths of 1.5 to 2.2 m. The nest is formed from burgu millet stalks that are 2 to 3 m long, cut at the base and folded in on each other to define a cavity of about 50 cm length by 20 cm width. It forms a sort of floating pouch that measures

around 150 cm by 80 cm and floats on the surface of the water. The parents enter the nest through a tunnel and deposit about a thousand eggs. Hatching is thought to take place some five days later, and the young leave the nest after 18 days, when the yolk sac has been completely resorbed. When they hatch from the egg, youngs have external gills that extend out of the brachial cavity, but they are quickly resorbed.

Parents are never far from the nest in order to protect it from other fishes, particularly lungfish which appear to have a liking for *Gymnarchus* eggs (Daget, 1952).

Origin and evolution of parental care

Fishes that do not provide parental care lay a large quantity of small eggs that are dispersed in the pelagic environment. This is the case for many species belonging to the Clupeidae, Alestidae, Cypriniformes, etc. families. In running water, these eggs drift downstream and the larvae colonize fluvial annexes where they find both food and shelter. There is little chance that pelagic eggs need to withstand anoxic conditions, but they are exposed to much predation. This reproductive mode may represent ancestral conditions. Encouraging dispersion could increase the chances of survival in an unstable environment.

Reproduction by dispersion does not encourage the development of parental care, and it is possible that during evolution, some species found it more advantageous to recognize and select sites that were conducive to spawning. This is especially true for freshwater habitats that are very temporally and spatially heterogeneous, with some of the biotopes less favourable to egg development than others. In reality, many species that do not practice parental care do not lay their eggs at random, but deposit them among plants, in gravel, in holes, etc.

Once favourable habitat has been identified and regularly used, there may be an adaptive advantage to staying there, which is the key step in the appearance of territorial behaviour as well as site preparation and defensive behaviour, in order to monopolise the sites that are most favourable to reproduction.

Substrate brooding, which is seen in both riverine and lacustrine species, is considered an ancestral behaviour in Cichlidae. Their very adhesive eggs, compared with those of mouth brooders, tend to support the hypothesis of a more ancient origin on the phylogenetic level.

Mouth brooding, meanwhile, is more specialized and more recent. It probably derives from an ancestral substrate brooding behaviour in which the act of taking the eggs in the mouth to transport them from one site to another could have become a fixed component of reproductive behaviour. The adaptive advantage is that it keeps embryos away from predators and limits competition for reproductive sites. We may also see a means of escaping the need for a substrate to reproduce, when benthic space is highly sought after (Balon, 1978).

In the beginning, among substrate brooders, parental care was probably provided by both parents. Mouth brooding evolved independently in phylogenically distant groups such as Ariidae, various Anabantidae, Arapaimidae, and Cichlidae. For the great majority of Teleosts, the male is most often the mouth brooder (Blumer, 1982). In Cichlidae, meanwhile, the female provides the care, and this investment may be an innovation in this family (Stiassny & Gerstner, 1992). In some haplochromines of Lake Malawi, it has been observed that mouth brooding can last until the young reach a length of 3 cm (Turner, 1994; Duponchelle *et al.*, 2000b). This long period of parental care given to the young after spawning, as observed in Cichlidae, is also unusual in teleost fishes.

A special case is that of species whose parents place the eggs in floating nests made from plants or foam (for instance *Hepsetus odoe*). This behaviour may be

interpreted as an adaptation to development in anoxic waters (as eggs are placed on the better-oxygenated water/air interface) but may also be considered an adaptation to an unstable environment.

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Diversity, Ecology and Human Use

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