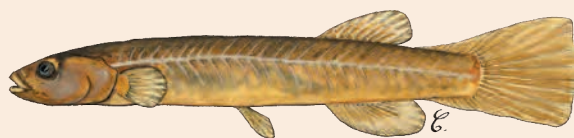# Ethology

YVES FERMON

RÉMY BIGORNE

Ethology calls on a wide range of disciplines including genetics, physiology, ecology, developmental biology, and evolution to converge in an integrated view of the organism, its function, and its interactions with its physical system. Among the vertebrates, bird and mammal behaviour have been the subject of much investigation, whereas fish behaviour is still relatively unknown barring a few exceptions, in particular species that are popular with aquarium enthusiasts. The majority of studies on African fishes focus on two families, the Mormyridae because of their particular means of communication (electric signals), and the Cichlidae, owing to their economic importance and significance in evolutionary science with the "species flocks" in the African great lakes (see box, "History of the ethology of African fishes"; chapter *Diversity of African fish: a heritage of evolution*).

Functions and structure of behaviour

Behaviour is composed of a series of specific actions in response to information, and favourable to sustaining an individual or species. This stimulus may be external (provided by the environment: changes in the physical conditions of the system, presence of a predator or congener, etc.) or internal (provided or possessed by the individual: change in serum hormone levels, etc.) To be efficient, these actions must be spatially and temporally organized. It is therefore necessary to have the response coincide with the stimulus (Guyomarc'h, 1995). Behaviours are generally subdivided into four broad categories (Guyomarc'h, 1995):

• so-called maintenance behaviours (resting phases);

• food behaviours (exploratory strategies, capture, etc.)

• so-called agonistic behaviours (to ward off intra- or interspecific competitors from a territory where the animal feeds and/or reproduces);

• reproductive behaviours (mating, arrangement of spawning site, nest construction, spawning, parental care, etc.).

HISTORY OF THE ETHOLOGY OF AFRICAN FISHES

As early as 1950, Baerends & Baerends von Roon pioneered in the behavioural study of Cichlidae, but the most significant work on Tilapias *sensu lato* was carried out by researchers from the Université de Liège, with Ruwet & Voss (1966), then Voss (1977, 1981). This enabled not just the acquisition of data on systematics, but also led to direct applications in the establishment of fishfarming for this "African carp". At around the same time, Wickler (1962) began studying mimetism in these fishes.

Studies expanded in the 1980s-90s to the fishes of the great lakes: Tanganyika (Kawanabe *et al.*, 1997), Malawi (Ribbink *et al.*, 1983; Hert, 1989), and Victoria (Crapon de Crapona, 1982; Crapon de Crapona & Fritzsch, 1984; Goldschmidt, 1991; Fermon, 1997), as scientists attempted to determine if behaviour was one of the keys to understanding species flocks, as already hypothesized by the preliminary work of Fryer & Iles (1972) and Greenwood

(1991). Investigations continue to this day and focus on sexual selection, colouring patterns, and sex partner selection, territoriality, and male competition (Maan, 2006; Djikstra *et al.*, 2007; Blais *et al.*, 2009; Baldauf *et al.*, 2011; Ding *et al.*, 2014; Sefc *et al.*, 2015, etc.).

Meanwhile, Mormyridae attracted the attention of researchers because of their ability to produce electricity. Initial investigations on these fishes focused mainly on physiological and neurological aspects in order to understand how they produced and used electricity. Later studies showed that discharges could have specific characteristics, also varying according to the social behaviour, physiological state, and sex of the fish, much like the role of songs in birds.

For a full bibliography, the following references can be consulted: Kramer, 1990, 1996; Hopkins, 1986; Moller, 1995; Feulner, 2006; Arnegard *et al.*, 2010).

Functions of behaviour

An organism can act directly on its biotic or abiotic environment. This is a direct action: fleeing a predator, seeking food, building a nest, and so on. These are known as first-order behaviours that contribute directly to the survival or reproduction of the organism.

An organism may also establish a relationship with another animal and influence its behaviour, which implies in this case that there is a form of communication between the individuals present. This is the case of mating or territorial defence. These second-order behaviours thus contribute to:

- the synchronization of individual activity cycles;
- the selection of partner activities;
- the regulation of partner activities and distances;
- the physiological adjustment of interacting individuals;
- psychological or ontogenetic adjustment. The quality of information and the manner in which it circulates in social groups lead to individual differentiation of hierarchies and behavioural styles that prove useful for the smooth function of social structures.

There are obviously relationships between the two types of actions, and it is sometimes difficult to differentiate them, especially since the organs used in these two behavioural categories are often the same. For instance, electrical signals allow Mormyridae to locate themselves in the environment and detect an obstacle or prey (electrolocation), but they are also communication signals between individuals.
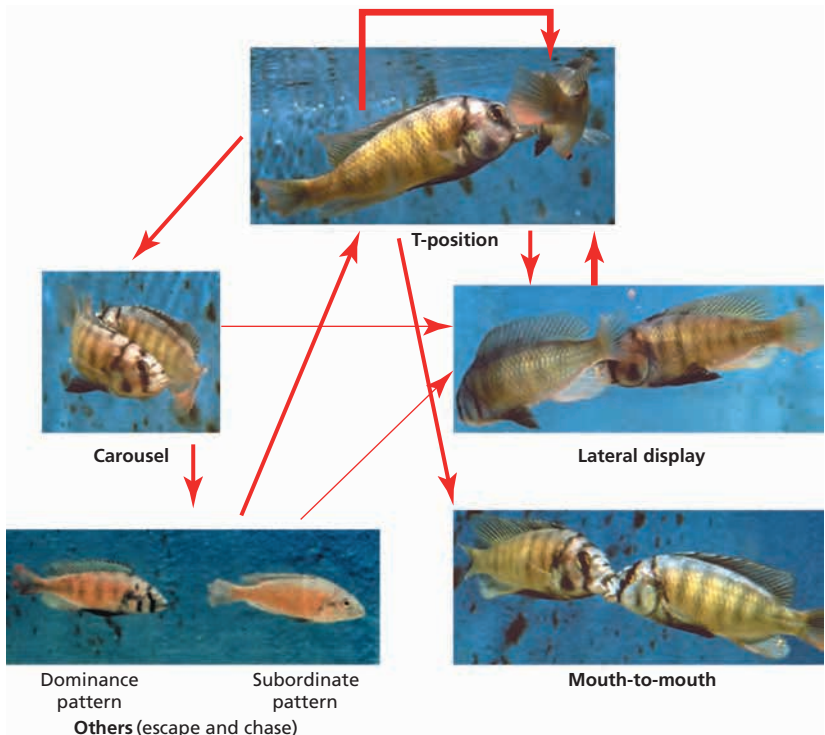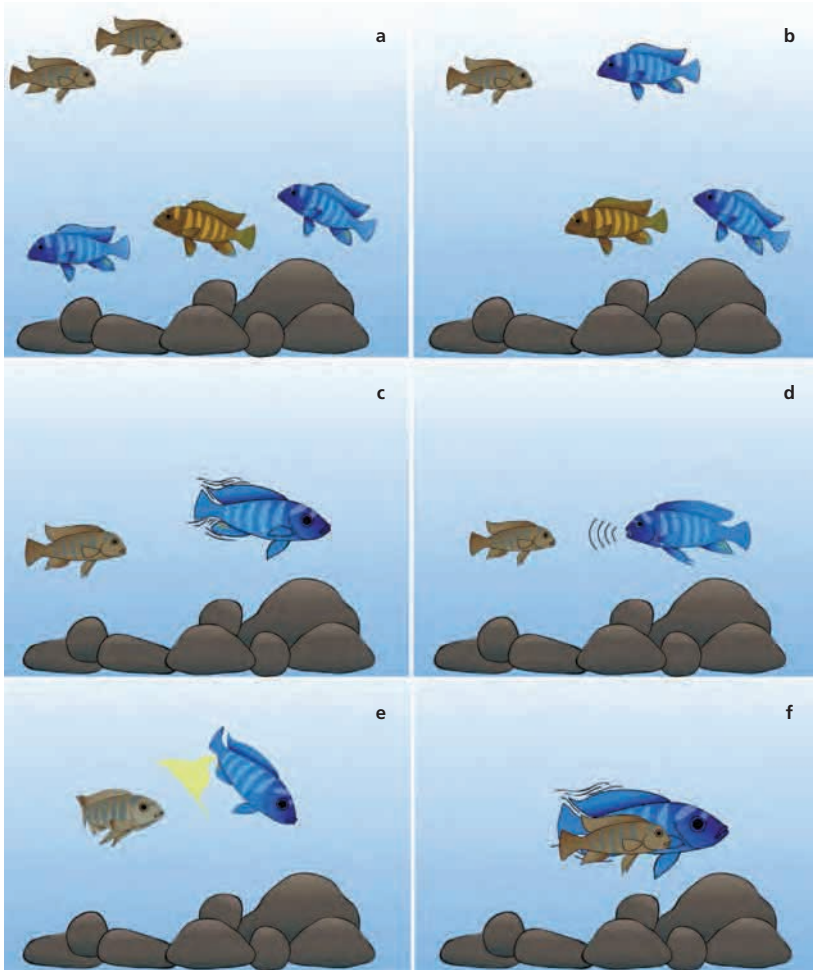
Structure of behaviour

Behaviours have a structure that has well-defined properties and characteristics:

• They are organized in systems: a behaviour is composed of a set of events that are arranged in a gradual or fragmented manner. For a given signal (colour, sound, etc.), a species has one or several structured signalling systems ("repertoires"). For example, in *Haplochromis brownae*, a Cichlidae species endemic to Lake Victoria, fights are ritualized and a given position will be followed by another one in a relatively consistent manner (figure 14.1). A "T-position" will often precede a "carousel" position, which is then often followed by the flight of one of the protagonists, with the loss of its aggressive colouring pattern (Fermon & Voss, 1990).

• They are multimodal: a message may be sent using different types of signals that reinforce or complement each other. For example, in *Haplochromis burtoni*, the aggressiveness of a male is expressed by the association of two components, one locomotor (vertical position) and the other pigmentary (slope of the lachrymal stripe) during fights (Heiligenberg, 1974). This is also the case during the mating ritual in *Maylandia zebra* (Escobar-Camacho & Carleton, 2015) (figure 14.2).

• The structure of behaviour is, in general, highly specific given the intra-specific functional framework. In fights between congeners among Cichlidae, the lateral position is followed by a carousel in *H. brownae*, whereas in *Neolamprologus fasciatus*, it is mainly followed by a face-to-face phase (figure 14.1) (Fermon & Voss, 1990; Busson, 1996).

Fight habits between males of *Haplochromis brownae* (from Fermon & Voss, 1990).

T-position

Carousel

Lateral display

Dominance pattern   **Subordinate pattern**

Mouth-to-mouth

Others (escape and chase)

• They vary gradually. Within a species, the general expression of a behaviour may vary from one individual to another according to age and sex, but also social rank or physiological state. For instance, female *Neochromis greenwoodi* in Lake Victoria take the aggressive colour pattern of males and become territorial during incubation (Witte pers. com.; Fermon, pers. obs.).

Different behavioural signals – communication

Communication is the transmission of signals and information between a sender and a receiver. It takes very diverse sensory channels in the animal kingdom, and we now know that a fish species may use various modes of communication. This is a means of reducing the risks of misinterpreting messages from a single

sensory channel, but it also allows better targeting of the receiver. In aquatic systems that are inhabited by numerous species, it may be indispensable to remain recognizable to one's congeners, if only for reproduction. To the extent that vision is limited at night-time and in murky or plant-rich waters, it is even more necessary to develop other specific modes of communication that can transmit rapid, precise messages. This is the case with electrical signals, sounds, and the olfactory or gustatory perception of chemical messages.

Visual signals

Many fishes communicate visually through body movements and/or colour patterns. These visual cues are favoured in certain families such as the Cichlidae or the Cyprinodontiformes.

The position of the body is a signal perceived by other fishes. This mode of communication is used especially during mating rituals or encounters between rivals. Baerends & Baerends van Roon (1950) were the first to propose a nomenclature of positions, for Cichlidae. Some are common to numerous species. For instance, in "lateral" position, a threatened Cichlidae may appear larger if its pelvic and median fins are extended (figure 14.1). Likewise, in "face-to-face" position, the threatened fish turns its head towards the attacker while puffing out its opercles and branchiostegal membranes. Conversely, frightened fish try to make themselves as small as possible by drawing in their fins close to the body. Nonetheless, when drawing up the catalogue of positions, their order of appearance, combination, and length for a given family, specific differences can be noted and may play an important role, in particular as reproductive barriers during mating rituals.

Noble & Curtis were the first to posit in 1939 that the mating ritual of *Hemichromis bimaculatus* did not have a solely ornamental purpose. It was not until the 1960s that scientists truly found evidence of the role of coloured structures in communications between individuals. They found that the colour pattern at a given moment could play an important role in social and/or sexual behaviour. Generally speaking, each fish has a range of predetermined and specific colouring composed of various coloured structures whose overall configuration is characteristic of the species. However, under the effect of internal emotional or physiological factors (such as changes in serum hormone levels) or external environmental factors (presence of a congener, temperature changes, etc.), many species can change their colour pattern (figure 14.3). Pigments are grouped in special cells called chromatophores, which can aggregate or disperse them to the point of changing the animal's appearance almost instantaneously. The characters of the pigmentation and colouring range vary in Cichlidae in close conjunction with reproductive behaviour and parental care (Voss, 1983). In species such as *Tilapia* which are substrate spawners, where partners remain together for a long time and both play a role in defending territory and protecting eggs, colouring range is complex but nonetheless remain very similar in the male and the female. Meanwhile, in Cichlidae where couples only exist during spawning and only one of the two partners cares for the fry (*Oreochromis, Haplochromis, Labeotropheus*, *Pseudotropheus*, etc.), the range of colour patterns is limited but with marked sexual dimorphism. Marks and colouring play an important role
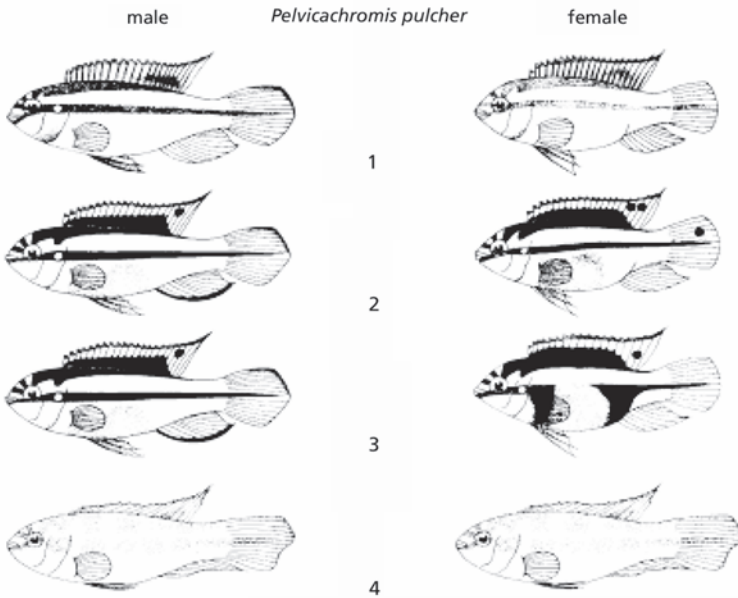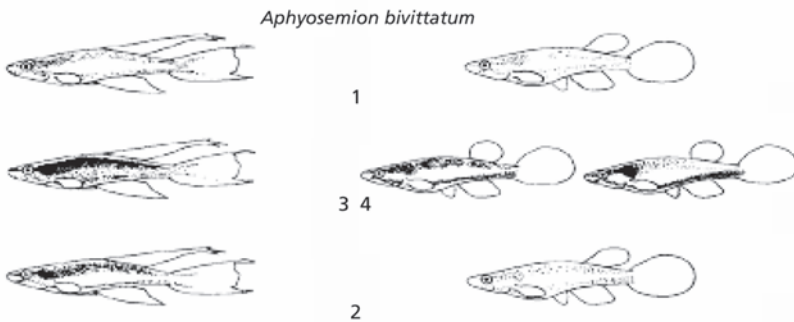
in the social status of Cichlidae. The intensity of the colour red during the mating ritual of *Pundamilia nyererei* in Lake Victoria is correlated with the individual's social status in the group (Dijkstra *et al.,* 2007). In *Neolamprologus pulcher*, results of experiments using familiar and unfamiliar images indicate that individuals are capable of distinguishing familiar from unfamiliar individuals using facial colour patterns (Kohda *et al.*, 2015).

Touch signals

Physical contact may also be a mode of communication. During mating rituals, contact is established between the two partners. In *O. mossambicus*, the male touches the genital papilla of the female to determine the sexual state

of the latter. Similarly, in *Haplochromis* spp., contact with the anal fin of the male by the female is a decisive factor in ejaculation and the fertilisation of eggs in the female's mouth (Wickler, 1962; Hert, 1986; Fermon, 1997). In many Mormyridae it can be observed that manual stimulation leads to a flexion of the anal fin (Kirschbaum, 1987). This reflex may facilitate the fertilisation of eggs by forming a canal for sperm flow.

That said, the line between a communicative act and a fight is often difficult to establish, especially in agonistic situations. For example, in mouth-to-mouth positions in Cichlidae, the two individuals seize and push each other by the jaw. In T-position, one of the protagonists moves its tail to send water towards the head of the other (Baerends & Baerends von Roon, 1950; Fermon & Voss, 1990) (figure 14.1).

Chemical signals

Chemical communication plays an especially important role in the aquatic environment, as water can transmit chemical messages over long distances (Saglio, 1992). Depending on the type of end neurological connections of receptors, there are two major categories of chemical communication: olfaction and taste. Olfactory receptors are located in the nasal cavities. Taste receptors can be found throughout the body, but are generally concentrated in the barbels, filamentary fins, the gill zone and the mouth (Nelissen, 1991).

Fishes are able to react selectively to the perception of substances produced by their congeners, prey, or predators. A substance produced by an animal and perceived by an individual that reacts immediately to it is called a pheromone. Its duration of action is generally transient. We can distinguish *releaser pheromones* that induce an immediate change in the receptor's behaviour from *primer pheromones* that trigger a change in the physiological state of the individual that receives them. The latter category includes the sex pheromones, which influence the appearance and synchronization of male and female reproductive activities. It has thus been shown that female *Haplochromis burtoni* cichlids that are ready to spawn produce chemical signals that stimulate sexual activity in males of their species (Crapon de Crapona, 1980). In experimental conditions, it has been shown that ovulating female *Clarias gariepinus* preferred the waters of male-occupied basins rather than female-occupied ones because of the pheromones produced by the males (Resink *et al.*, 1989). These substances also play an important role in parental care. Experimentally, it has been shown that parents of *Hemichromis bimaculatus* recognize their own young but not those of a heterospecific spawn. Likewise, young are attracted by chemical substances produced by their congeners (Kühme, 1963; 1964). In *Oreochromis mossambicus* (Barata *et al.*, 2007) and *Haplochromis burtoni* (Maruska & Fernald, 2012), the urine of males plays a role in social interrelations.

Chemical substances can also play a role in the detection of prey or congeners. The electric fish *Malapterurus electricus* reacts when it is placed in contact with the mucous of prey or a conspecific. This reaction disappears when taste receptors are severed (Bauer, 1968).

Sound signals

The aquatic system is far from being the "silent world". Fishes are not mute, as people sometimes think, and many species produce sounds. Those produced by catfish of the genus *Synodontis* are familiar to African fisherfolk, who refer to them as "konkon" in certain countries, in reference to the grunts they produce when they are taken out of the water.

There are three broad categories of sound signals:
• strident sounds produced by the friction of teeth (figure 14.4) or fin rays;
• sounds resulting from swimming movements;
• sounds from the swim bladder which acts as a resonating chamber when it is moved by certain muscles.
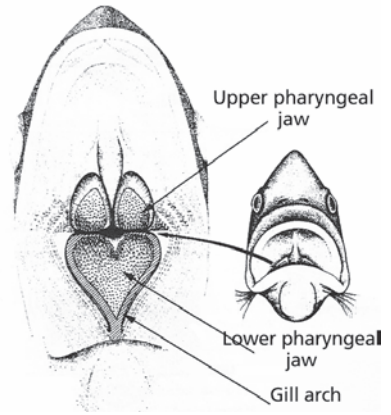
Sound communication in African fish is still poorly understood, but a number of works tend to show that it plays an important role in social relations. For Cichlidae, investigations have been carried out on some 30 species. Cichlidae produce more than one type of sound and use them for social interactions and reproduction. For example, *Hemichromis bimaculatus* can produce and receive sound signals (Rowland, 1978). Nelissen (1978) was able to show in various closely related Cichlidae species in Lake Tanganyika that the use of sound communication varied depending on lifestyle. *Simochromis diagramma* and *S. babaulti*, diurnal fish, had several colour patterns but mostly similar acoustic signals. The exact opposite holds true for *Tropheus moorii*, *T. brichardi* and *T. duboisi* which are nocturnal species. Sound communication may play a role in the recognition of individuals during the mating ritual. Sounds produced by three closely related species in Lake Malawi (*Maylandia zebra*, *M. callainos* and *M.* sp. "zebra gold") differ during mating (Simoes *et al.*, 2006). Meanwhile, it appears that in Cichlidae living in social groups, such as *Neolamprologus pulcher*, there is no sound communication (Pisanski *et al.*, 2015). Some Mormyridae can also produce and detect sound signals whose biological significance is still unclear. It is probable that these signals come from the swim bladder. We have discovered that they play an important role in the reproductive behaviour of *Pollimyrus isidori* and a nomenclature of these signals has been established for this species (Crawford *et al.*, 1986). Territorial males produce grunts, whines, and growls during sexual activity, whereas snapping and hooting sounds are produced during attacking behaviour. The acoustic signals of territorial males may be warning signs for congeners to inform them of the presence and location of reproductive sites. In *Marcusenius macrolepidotus*, it appears that these sounds differ depending on the populations (Lamml & Kramer, 2007).

Electrical signals

Many organisms are sensitive to electrical field deformations (including *Xeno-mystus nigri* and *Papyrocranus afer,* in African fishes), but few are capable of generating electricity themselves. Yet in African fresh waters, certain fish families have developed an electro-sensory system that is complex enough to play an
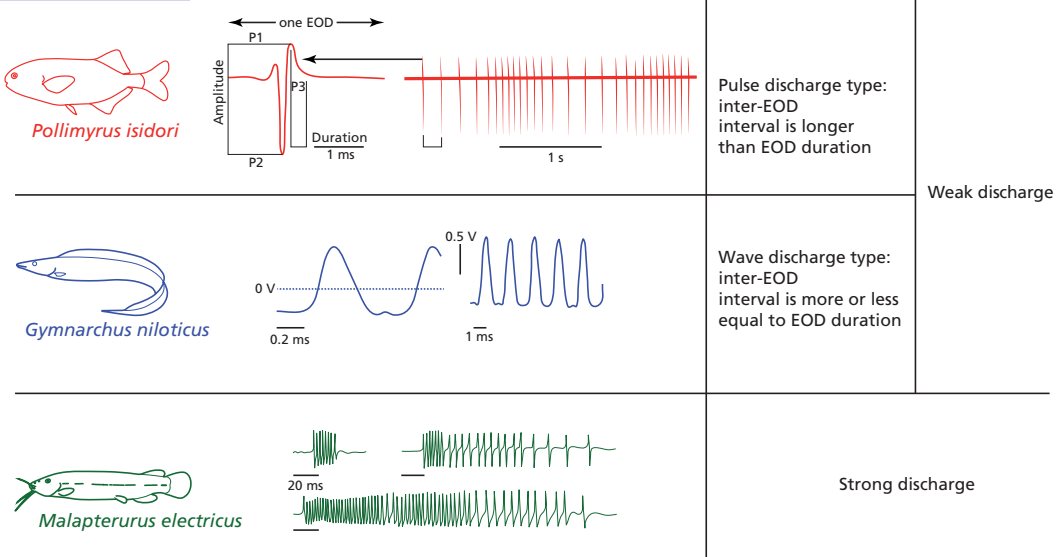

Upper pharyngeal jaw

Lower pharyngeal jaw

Gill arch

FIGURE 14.4.

Pharyngeal jaws of *Oreochromis mossambicus* (from Lanzing, 1974). The friction of the jaws produces a sound.

essential behavioural role and be a favoured means of communication. This is the case of so-called weakly electric fish that emit, almost constantly, discharges of several tenths of a volt to one volt. Depending on the rhythm of the discharges, we can distinguish species that emit pulses (Mormyridae, around 250 species) or waves (Gymnarchidae, a single species, *Gymnarchus niloticus*) (figure 14.5). In both cases, modified muscle cells (electrocytes), found in the caudal peduncle in Mormyridae or spreading from it in Gymnarchidae, are responsible for producing electricity (figure 14.6). The resulting electric field is directed from the tail to the head. Electrical signals are received and analysed by a highly sensitive receptor system. These electroreceptors, innervated by nerve fibres from the lateral line, can be found on the peripheral parts of the body (stomach and back), but are more numerous in the head (figure 14.6).

One of the functions of this electro-sensorial system is to allow the animal to orient itself in its environment. The fish is informed of an obstacle's existence by the deformation it induces in the electric field. This electrolocation can be used to advantage in hunting and detecting prey (von der Emde, 1990). The system also plays an important social role, particularly in Mormyridae. The fish's discharges are imperceptible to humans, but they can be recorded and visualised using an oscilloscope. This allowed researchers to discover the enormous range of electrical signals, in form as well as frequency and rhythm. The characteristics of the electrical discharge may form a veritable specific signature allowing congeners
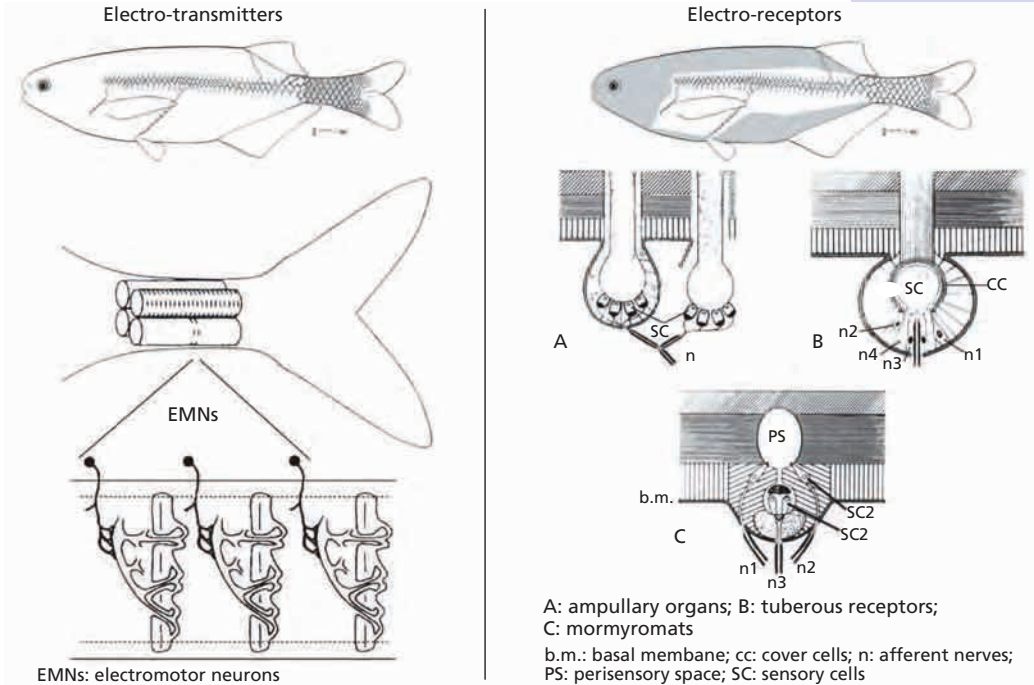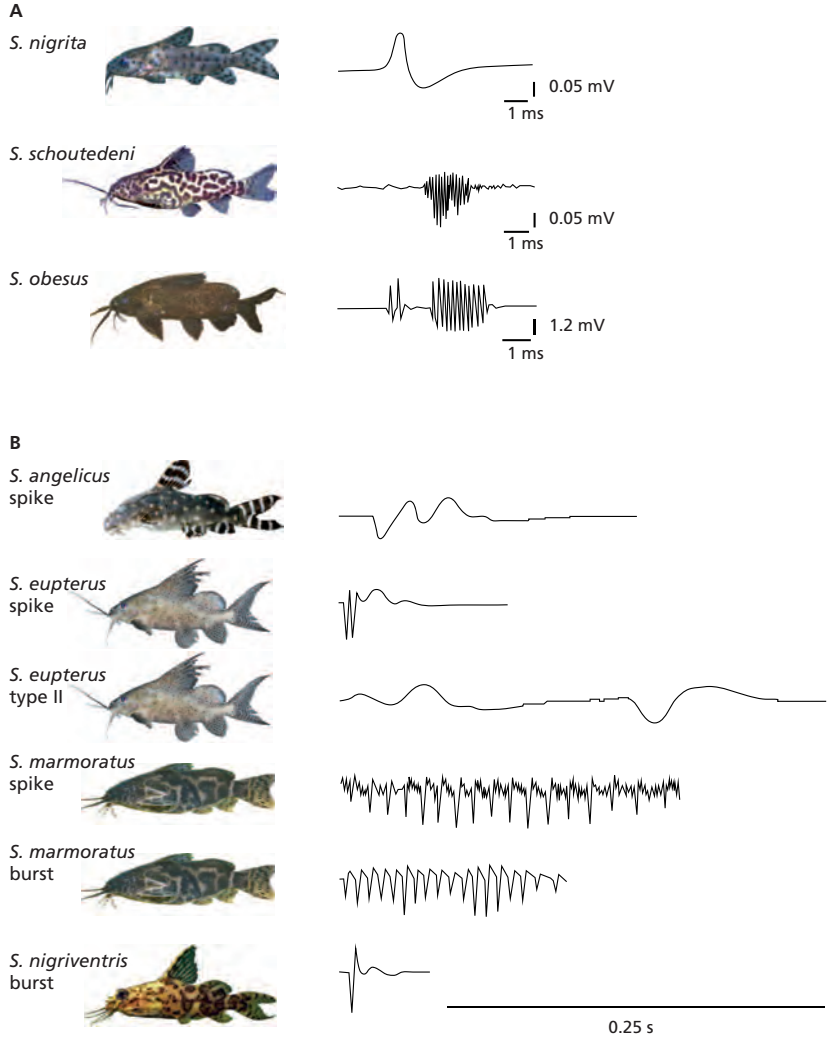
Electro-transmitters

Electro-receptors

EMNs

EMNs: electromotor neurons

A: ampullary organs; B: tuberous receptors;
C: mormyromats
b.m.: basal membane; cc: cover cells; n: afferent nerves;
PS: perisensory space; SC: sensory cells

to recognize each other. This may be used in systematics to distinguish morphologically similar species (Hopkins, 1981; Crawford & Hopkins, 1989; and chapter *Taxonomy and Systematics*). The characteristics of signals may also vary according to sex or the physiological state of individuals within the same species. Fishes can thus transmit information on their aggressiveness, sexual maturity, or their respective hierarchical rank. Interruptions in the discharge rhythm most often indicate a sign of submission. Meanwhile, accelerations in rhythm are often correlated with attacking behaviour, and dominant individuals often emit discharges more rapidly (Kramer, 1974; 1978; Kramer & Bauer, 1986). Many Mormyridae live periodically or constantly in shoals, and continuously exchange information to maintain the spatial and social structure of the group (Moller, 1976; Squire, 1981; Serrier, 1986; Graff, 1986, 1989; Moller *et al.*, 1989). One can imagine that when hundreds of individuals from different species of electric fish cohabit, there must undoubtedly be a genuine electrical "cacophony". In these conditions, how can one perceive the messages of a congener without any risk of transmission jams? Electroreceptors in fact have filtering capabilities that are comparable to those of auditory receptors. Moreover, they have maximal sensitivity for electrical stimulations whose components, in frequency and phase, correspond precisely to those of the species's discharges. It was recently discovered (Hagedorn *et al.*, 1990; Baron *et al.*, 1994) that fishes other than Mormyridae and Gymnarchidae were capable of emitting weak electrical discharges. This is the case of several catfish of the genera *Clarias* or *Synodontis* (figure 14.7). The range for discovery undoubtedly still remains open in this field (see also box "Electrical fish history").

A

S. nigrita

0.05 mV
1 ms

S. schoutedeni

0.05 mV
1 ms

S. obesus

1.2 mV
1 ms

B

S. angelicus spike

S. eupterus spike

S. eupterus type II

S. marmoratus spike

S. marmoratus burst

S. nigriventris burst

0.25 s

Alongside these weakly electric fish, there are others that can generate high-intensity discharges. They are represented in Africa by the family Malapteruridae, which has 18 species. In *Malapterurus*, electrocytes develop from the pectoral muscles and are found over nearly the entire body surface. Production of electricity is intermittent and in salvos (figure 14.5) that include one or several bursts of discharges. A salvo can thus last up to 30 seconds and contain over 1,000 discharges. The amplitude of the latter varies with the size of the fish and can reach 350 volts in an individual measuring 50 centimetres in length. It is a fearsome weapon, but *Malapterurus* does not appear to limit the use of its electric potential to attacking prey or defending itself. A typology of discharge salvos emitted by *Malapterurus* classifies them into five categories (Moller, 1995). Four are directly linked to predatory or protective activities. A fifth

Highly electric fish have fascinated humans since ancient times. Representations of *Malapterurus electricus* are painted on Egyptian tombs in Saqqara. It was considered the "protector of fish" and any fisherman that felt its discharge was supposed to free his entire catch. Ancient Arabs called it "thunder fish" or "trembler fish". Closer to Europe, the Jesuit Nicolao Godigno recounted in wonder in 1615 how dead fish were brought back to life when they were placed in contact with a freshly caught *Malapterurus*. Depictions of Mormyridae (*Petrocephalus*, *Mormyrus* and *Marcusenius*) have also been identified in fishing scenes on the bas-reliefs of tombs in Giza and Saqqara (figure 14.8). There was even a cult devoted to *Mormyrus*. However, as the fish emits discharges that are imperceptible to humans, one would be hard-pressed to attribute this veneration to the fish's electric characteristics.

In the early 1950s, H. Lissmann paved the way for the study of weakly electric fish. During an expedition in Ghana, he noticed that the rivers were teeming with "live" electricity (Lissmann, 1951). Ample proof was provided by dipping two copper wires connected to an amplifier, and hearing the crackling sound that testified to the electric activity of fishes.

FIGURE 14.8.

Amulet of *Oxyrhynchus* (bronze), Graeco-Roman period (332 B.C. -337 A.D.), Egypt (© Musée des Confluences, Lyon/P. Ageneau).

is only used during confrontations with congeners (Rankin & Moller, 1992). But to the extent that this type of discharge only concerns one of the congeners (be it the dominant or the dominated), it is difficult to determine if it has any real value as an element of communication, or if it only reflects the individual's degree of agitation. Yet observations in laboratory conditions (Kastoun, 1971, 1972; Rankin, 1984; Rankin & Moller, 1986, 1992, among others) suggest that when they are associated with other sensory systems (gustatory, olfactory, and chemical), the electrical discharges of *Malapterurus* play a role in inter- and intraspecies relationships.

Ecology and behaviour

Reproductive, social, and feeding behaviours cover the active attitudes of fishes and their adaptation to external constraints in order to ensure their survival and propagation.

Reproductive behaviour

To ensure the best possible reproductive success, fishes employ diverse strategies that are coded genetically. These are expressed as often complex sexual and reproductive behaviour.

Sexual selections and competitions

Most fishes do not actively seek out sexual partners. However, in species where such a choice is made, it is generally the female who does the choosing, and it may be based on a quest for immediate or material benefit in order to increase the chances of gene dispersion and preservation. This generally manifests as active selection based for instance on the best builders or protectors (selecting the male with the largest nest, in *Mchenga eucinostomus* (McKaye, 1983); selecting a large partner, in *Sarotherodon* (see box, "Small females for large males")).

In the search for benefits tied to the genetic potential of the partner ("choosing good genes"), males generally sport brilliant colours that are designed to attract females. The most colourful ones have greater success, as in mouth brooding Cichlidae, especially in lakes Malawi and Victoria (McKaye, 1991). The same dimorphism is seen in Nothobranchiidae (figure 14.9). In Cichlidae, some secondary sex characteristics play a very important attractive role during the mating ritual. These are decoys such as the ocellae on the anal fin of Haplochromines, or spots on the pelvic fins of *Cyatopharynx* or *Ophthalmotilapia* (figure 14.10). In *Pelvicachromis taeniatus*, the length of the pelvic fin and the colour pattern in females could play a role in the choice of male (Baldauf *et al.,* 2010; Baldauf *et al.,* 2011). An investigation of the genetic analysis of male colour patterns and the choice of females in the Cichlidae of Lake Malawi, *Maylandia zebra* and *M. benetos*, suggests that (i) several non-additive genetic factors influence melanistic factors; (ii) the choice of sexual partner can be controlled by at least 1 or 2 non-additive genetic factors; the choice of the female from the second generation of hybrids is not influenced by the male's efforts to court her (Ding *et al.*, 2014). An analysis of the colour pattern and the female's choice indicates that these two traits are physically linked. The electrical signals in Mormyridae may play a similar role as that of colouring. A study of two closely related sympatric species of *Campylomormyrus*, *C. rhynchophorus* and *C. compressirostris*, showed that the length of the EOD could be one of the elements of reproductive isolation (Feulner *et al.*, 2009).

FIGURE 14.9.

Examples of sexual dimorphism in the colour pattern in two species of Nothobranchiidae (Photo M. Chauche, Revue française d'Aquariologie).

male   female

Aphyosemion coeleste

Fundulopanchax sjostedti
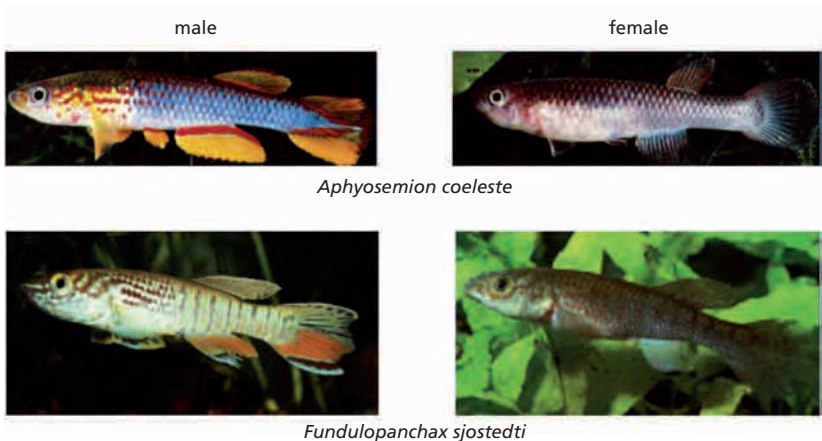
SMALL FEMALES FOR LARGE MALES

In mouth brooders, the number of eggs that can be incubated depends on the size of the oral cavity, and thus the size of the parent providing this form of care. In *Sarotherodon melanotheron*, a paternal incubator, small males cannot efficiently incubate all the eggs laid by a female of similar size, as these would occupy 90% of their oral cavity. During growth, the volume of the oral cavity increases more rapidly in males than the spawn volume does in females. Hence it is only after a given size that the male can care for all the eggs laid by a female, even a small one (Legendre & Trébaol, 1997). Females that pair off with larger males thus ensure the efficacy of incubation.
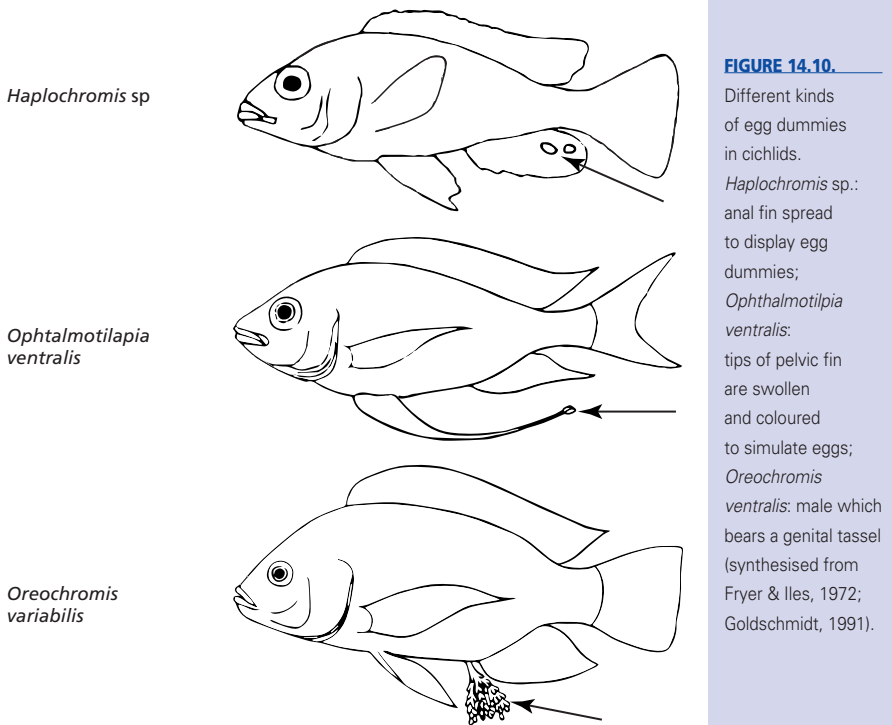

Haplochromis sp

Ophtalmotilapia ventralis

Oreochromis variabilis

FIGURE 14.10.

Different kinds of egg dummies in cichlids. *Haplochromis* sp.: anal fin spread to display egg dummies; *Ophthalmotilpia ventralis*: tips of pelvic fin are swollen and coloured to simulate eggs; *Oreochromis ventralis*: male which bears a genital tassel (synthesised from Fryer & Iles, 1972; Goldschmidt, 1991).

As they make their choice, females must also consider other constraints, such as the risk of forced fasting, or competition for food at the very least. In *Tropheus moorii,* an endemic Cichlidae in Lake Tanganyika, the female will feed in the male's territory a few days prior to reproduction (Yanagisawa & Nishida, 1991). The wealth of resources in the male's territory can thus become an important factor. That said, the female's desire for good-quality territory reinforces competition between males and male reproductive success (Hermann *et al.,* 2015). The choice is also limited by the attitude of the members of the opposite sex. A territorial male can spend time chasing off intruders, and other individuals can sneak in and fertilize the eggs already laid by the female present in the territory, as occurs in *Pseudocrenilabrus philander* (Ribbink & Chan, 1989). Among the Cichlidae '*Lamprologus' lemairii*, the females enter nests formed by crevices

in the rocks, and the male passes in front of the opening to fertilize the eggs. Parasite males attempt to fertilize the eggs. But males that reproduce in nests with smaller openings have greater reproductive success (Ota *et al.,* 2014). In species that have harem structures, a single male monopolises all the females, as is the case with *Ctenochromis horei* in Lake Tanganyika (Ochi, 1993a). The choice of females is thus very limited and can lead to significant competition. In some colonies of shell-dwelling fishes, nearly all aggressive interactions between females are regulated by the male. This is the case in *Neolamprologus ocellatus*, where the polygamous male guards the snail shells that will serve as shelter and spawning sites for females (Walter & Trillmich, 1994). The most common intraspecific reproductive competition between males involves conflicts related to the defence of territories (see section below, "Social life, Conflict, and Cooperation").

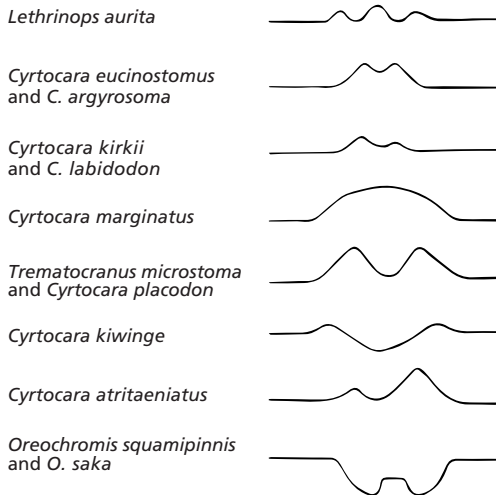### From reproduction to parental care

The majority of reproductive systems, from monogamy to polygamy, can be found in African fresh water fishes (see box, "Different reproductive systems").

Many species select a spawning site either directly on the substrate – the most usual case – or in the water, with no visible barriers, for a number of pelagic species. In the former case, on or around the spawning site, some species build nests. They have a twofold role: to attract females by their shape, size, and arrangement (figure 14.11), and to protect eggs and larvae. They can be guarded by the parents.

There is a wide variety of nests in fishes. Some are constructed depressions as with *Heterotis niloticus* or consist of burrows, as with *Protopterus annectens*. Floating nests are a fairly common form in physical systems presenting a risk

FIGURE 14.11.
Major forms of sand-scrape nests in Cichlids of Lake Malawi (from Fryer & Iles, 1972; McKaye, 1983 and McKaye & Stauffer, 1988).

Longitudinal section of different forms of sand-scrape nests

Longitudinal section and overview of a nest built by a male of *Otopharynx heterodon*

Lethrinops aurita

Cyrtocara eucinostomus and *C. argyrosoma*

Cyrtocara kirkii and *C. labidodon*

Cyrtocara marginatus

Trematocranus microstoma and *Cyrtocara placodon*

Cyrtocara kiwinge

Cyrtocara atritaeniatus

Oreochromis squamipinnis and *O. saka*
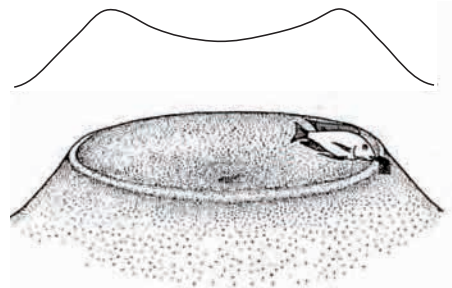
Different reproductive systems

Polygamy

As males are capable of producing enough gametes for reproduction more often than females are, polygyny is frequent. While males do not provide parental care, a territorial structure is often found in polygamous males. This is the case of fishes living in harems (such as *Neolamprologus pulcher* (= *brichardi*) (von Siemens, 1990). When males protect the eggs, they can take care of several broods and thus reproduce with several females. This appears to be the case in the Mormyridae *Pollymirus isidori*. In Cichlidae maternal mouth brooders, the females can simultaneously incubate eggs fertilized by several partners (*Mchenga eucinostomus* of Lake Malawi) (Mc Kaye, 1983).

Monogamy

Monogamous species generally practice biparental care. After the spawning event, both parents remain associated throughout the period when the young need to be cared for. A good number of Cichlidae species, including the Tilapia (except *Oreochromis* and *Sarotherodon*), the Lamprologini, are monogamous and in some cases fishes mate for life. A study of *Neolamprologus caudopunctatus* has shown that genetically, the young come from the same couple (Schaedelin *et al.,* 2015). This is also the case for other species such as *Bagrus meridionalis* in Lake Malawi (Mc Kaye *et al.*, 1994).

Alternative strategies of males: satellite males or dominant males

Strategies can vary depending on the age of the individual: for instance, a large male of a species can stake out a reproductive territory to attract females.

Meanwhile, a smaller male of the same species can adopt another tactic by taking on the colour pattern of a female and attempting to fertilize eggs during the mating ritual between a female and a territorial male. There is an intermediate stage with semi-territorial fishes that attempt to attract females, but in an occasional manner. Their territory is hence located outside the customary substrate for the species. This strategy has been observed in mouth brooding Cichlidae species such as *Pseudosimochromis curvifrons* and *Pseudocrenilabrus philander* (Kuwamura, 1987; Ribbink & Chan, 1989).

Other strategies

There are only a few known examples of sex change in African fishes. Cases of male-to-female sexual inversion have been observed in a brackish water fish, *Polydactylus quadrifilis* (Loubens, 1966). The converse may happen occasionally in some Cichlidae. In certain Cichlidae of Lake Victoria and particularly in *Neochromis greenwoodi*, some individuals possess functional gonads of both sexes while exhibiting the full set of external male characteristics (Fermon, pers. obs.). Simultaneous hermaphroditism (where male and female gonads are functional at the same time), known only in reef fishes, and sexual and asexual reproduction, observed in *Rivulus* and the Poeciliidae, have not been seen in African fishes.

of anoxia. This is the case for nests of *Gymnarchus niloticus* built using plants. Mormyridae nests are also built using plant matter. 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*. In some Cichlidae such as *Cyatopharynx furcifer* of Lake Tanganyika and *Mchenga eucinostomus* of Lake Malawi, structures similar to bird "leks" are observed. These are large surfaces or arenas where territorial males are found, and where they build their nests according to the hierarchy of the individuals, from the edges towards the centre (McKaye, 1983; Rossiter & Yamagishi, 1997).

On the spawning site, many species engage in a mating ritual (figures 14.12 to 14.14) whose specificity serves as a reproductive barrier and the role of which is to optimize egg fertilisation. These rituals, often highly complex, call several types of signals into play. Their structure and duration depend on the type of parental care provided by the species, as well as external factors to which the partners are subjected. For example, in mouth brooding Cichlidae such as Haplochromines, the females lay a small series of eggs (3 to 6) that they immediately take into their mouths, where fertilisation takes place; in *Oreochromis*, the female lays a large number of eggs that will be fertilized in part onsite, then, later, in the female's mouth. It is thought that, for Haplochromines, the speed at which eggs are taken into the mouth is essential because of the number of potential predators that may eat the eggs (Trewavas, 1993). They may also be the victim of "cuckoo" fish (see box, "Cuckoo fish"). In the Gobiidae *Glossogobius callidus*, the male prepares the nest and is joined by the female after a few days. The sticky eggs are adhered to the roof. After spawning, the male enlarges the opening and chases away the female. The male does not feed himself throughout the entire period of caring for the young (Wasserman *et al.*, 2015).
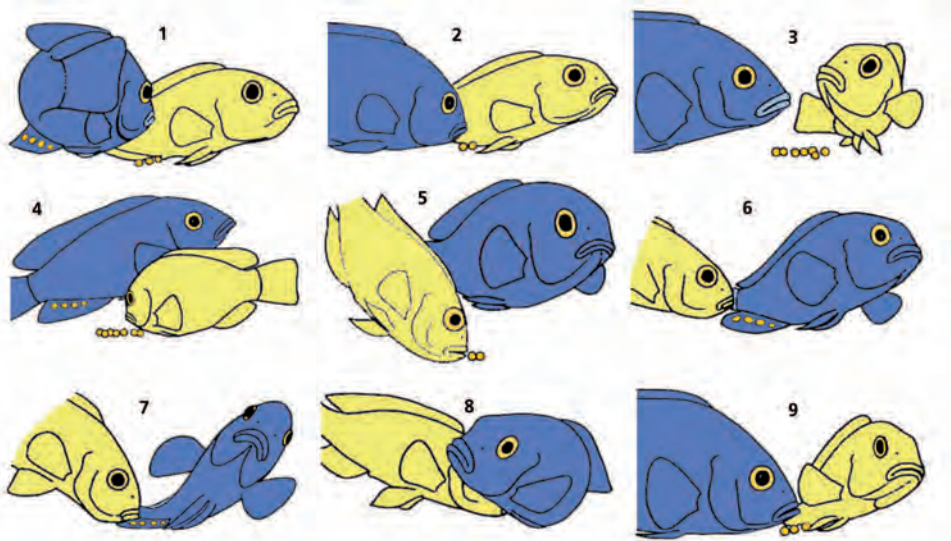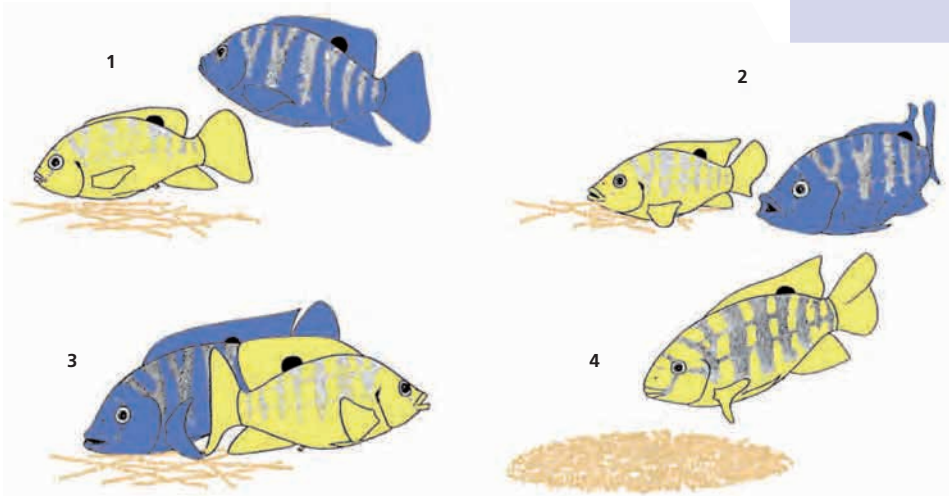

FIGURE 14.12.

Courtship and spawning in *Haplochromis burtoni*, a Lake Tanganyika cichlid.
The male is in blue and the female in yellow. 1: At the culmination of courtship the female begins to extrude eggs and the male is in close attendance; 2: egg laying continues; 3: A small batch of eggs having been laid, the female quickly turns; 4: the female prepares to take the newly laid eggs into her mouth, before the male has fertilized them; 5: the female quickly collects the eggs into her mouth; 6: the male extends his anal fin to reveal the eggs dummies "painted" on it and displays it before the female; 7: attracted and deceived by the egg dummies the female attempts to collect them and thereby brings her mouth, now containing eggs, into close proximity with the genital aperture of the male, which discharges sperm;
8: attempted collection of the egg dummies and fertilisation continue; 9: the female begins to lay another batch of eggs. The whole sequence is repeated several times until the mouth is filled with fertilized eggs (redrawn from Fryer & Iles, 1972).

FIGURE 14.13.

Courtship and spawning in *Coptodon zillii*, cichlid from West Africa.

The male is in blue and the female in yellow.

1: the female prepares to deposit a row of eggs on the cleaned surface where spawning has already begun.

The male stands by;

2. the female begins to lay. The male prepares to follow;

3: the female leaves the site, after spawning and the male, following the same course across,

fertilizes the newly laid eggs;

4: the female, now darker than when spawning, guards and aerates eggs

(redrawn from Fryer & Iles, 1972).
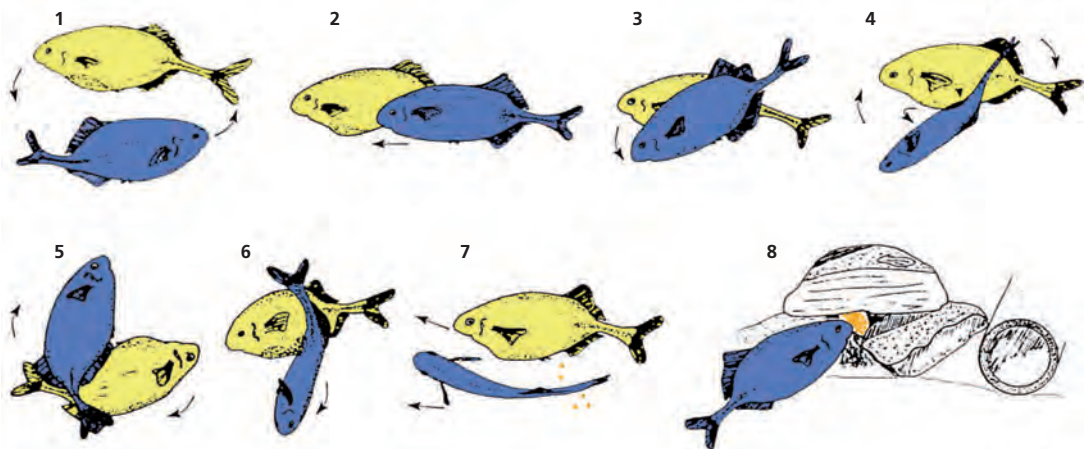
FIGURE 14.14.

Courtship and spawning in *Pollimyrus isidori*, mormyrid from West Africa.

The male is in blue and the female in yellow. 1: the female advances into the male's region;

2: the male arrives alongside of the stationary female; 3: the male becomes coupled Vent-to-Vent;

4: then the male turns laterally; 5: as both fish pivot around each other; 6: in one complete rotation;

7: during spawning the rotation is deleted and the sequence runs from (4) to (7) when the eggs are laid;

8: the male then quickly picks up the eggs in his mouth and places them into the nest

(redrawn from Bratton & Kramer, 1989).

CUCKOO FISH

FIGURE 14.15.
Development of a brood parasitic squeaker (*Synodontis multipunctatus*) in mouth-brooding cichlid fishes in Lake Tanganyika
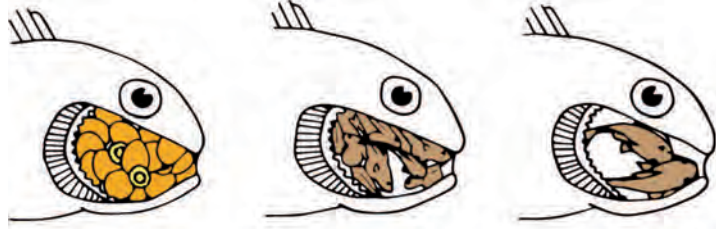
The behaviour of certain fishes recalls that of the cuckoo, which places its eggs in the nest of another species that will take care of them as it does its own eggs.

The catfish *Synodontis multipunctatus*, endemic to Lake Tanganyika, is a parasite to several mouth brooding Cichlidae species (Sato, 1986) (figure 14.15). This *Synodontis* spawns while a Cichlidae couple are engaged in their mating ritual. The eggs, which are of the same size as the host's eggs, are then taken by the female at the same time as its own eggs, and incubated in the same way.

However, the eggs of *S. multipunctatus* develop faster and the yolk sac is resorbed three days after hatching. The hungry larvae begin to feed on the embryos and larvae of its host.

This particular strategy allows the "cuckoo" fish to exploit its host twice over, by using the parent as shelter and the larvae as a food source.

This type of behaviour has also been observed in the Cichlidae of Lake Malawi (Ribbink, 1977) where *Nimbochromis polystigma* and *Serranochromis robustus* incubate eggs of another species, *Copadichromis chrysonotus*. At least 15 species of Cichlidae in Lake Malawi incubate the embryos of other species in their mouths, and it has been observed that "broods" can contain juveniles of 2 or 3 other species (Ribbink *et al.*, 1980).

The direct or indirect risks of predation can be reduced by caring for the young. Such behaviour is not very widespread in African freshwater fishes. When it exists, it can take various forms, including:

• constructing and maintaining a nest,

• guarding eggs and larvae,

• incubating eggs and larvae in the mouth or gill cavity,

• fanning eggs with fins to ensure better oxygenation and remove deposited sediments,

• feeding the young.

Such care is most often provided by the male, then, in decreasing order of frequency, by both parents, then by the female.

In the Cichlidae, there are two large groups of fishes that provide care to their young (see box, "Different reproductive styles in cichlids"):

• substrate spawners keep their eggs on a surface and watch over the young until they are self-sufficient;

• mouth brooders transport their offspring in the mouth, from the time of spawning until they are self-sufficient. There are paternal, maternal, and biparental brooders. Intermediate cases also exist, wherein the female carries the eggs in the mouth then the male protects the fry along with the female. This is the case of the Cichlidae *Perissodus microlepis* (Yanagisawa & Nshombo, 1983).

The distribution of tasks between the two parents is sometimes well-established. In shell-dwelling Cichlidae, the male defends the territory while the female watches over the young. *Neolamprologus mondabu* feeds on benthic animals on the sandy surface, but also unearths prey by moving its body and fins vigorously. The young also feed on the benthos on the substrate surface, but only using the first technique. Feeding by digging represented 30% of feeding activity in adult females. That said, parental females fed less frequently than non-parental females. The young are gathered together in the pit and feed intensively, which suggests that parental females dig for their young (Ota & Kohda, 2014). In *Pelvicachromis taeniatus*, parents adjust the care according to the vulnerability of the young. However, parents with a poor quality brood showed a more significant reduction in care than parents with good quality broods. The result suggests that parents adjust their care to the quality of the brood, and takes into account the theory of parental investment. Moreover, mothers of high quality fry were much more aggressive towards their partners than mothers of low quality ones (Thünken *et al.*, 2010). In *Bagrus meridionalis*, the parents share the task of feeding the young; the female gives them eggs and the male collects small benthic invertebrates. When fighting off predators, the female attacks the intruder while the male stays with the young. As they grow, the risk of predation decreases and parents spend more effort in feeding them (McKaye *et al.*, 1994).

Social life, conflict and cooperation

A fish comes into contact with congeners and heterospecifics in its physical system. Such contact creates relationships that are often conflictual in nature and related to defending space. This territoriality may be temporary or lifelong (lithophilic Cichlidae of Lake Malawi). There are different types of territories (breeding or home range) that may overlap. In *Tropheus duboisi*, the male defends a large area against males of the same species (reproductive territory) while tolerating other species (Yanagisawa & Nishida, 1991; Yanagisawa, 1993). Within that area, it also defends a smaller space where it feeds (home range), and finally, a small surface which serves as a spawning site. In *Gnathochromis pfefferi*, a Cichlidae of Lake Tanganyika, the home range is different from the breeding territory. Males occupy their reproductive territory in the morning and feed in the living area in the afternoon (Ochi, 1993b) (figure 14.18).

In the goby Cichlidae of Lake Tanganyika that lives in rocks in shallow depths, *Eretmodus cyanostictus*, individuals with the poorest competitive capacity ignore the high quality habitats which are also most in demand. Habitat quality and individual size are correlated. Rockier territories are preferred by both sexes in the absence of competition, and smaller fishes prudently occupy vacant territories of lesser quality (Taborsky *et al.*, 2014).

Conflicts can lead to actual fights that nonetheless remain highly ritualized to avoid killing one of the protagonists, at least in a specific framework. In schooling fish, a hierarchy emerges. For example, in the "leks" of *Mchenga eucinostomus*, subordinate males are found in the periphery while dominant ones are in the centre (McKaye, 1983).

DIFFERENT REPRODUCTIVE STYLES IN CICHLIDS

Substrate spawners

The sticky eggs are deposited on a hard surface. Depending on the species, this may be hidden (crevices in rocks, snail shells) or an open substrate (pits in the sand or in the mud) (figure 14.16).
The eggs are then fertilized and hatched after a few days, during which both parents generally guard the eggs attentively.
When the fry can swim freely, they remain grouped closed to the substrate as the parents watch over them.

Mouth brooders

The eggs of mouth brooders are larger but less numerous than that of substrate spawners. In most cases, eggs are deposited on a substrate, often prepared by the male.
In some pelagic species, eggs may be released directly into the water. There are three broad categories of mouth brooders (figure 14.17):

• *maternal mouth brooders* constitute the most common system. Spawning takes place on a substrate, 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. Incubation lasts until the young 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.

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

• *biparental mouth brooders* are also a rare case in Cichlidae. In most of the *Chromidotilapia* the two parents split the fry.
There are also species wherein the female begins incubation, which is later taken up by the male. This is the case for the goby Cichlidae of Lake Tanganyika, *Tanganicodus irsacae* and *Eretmodus cyanostictus*.

FIGURE 14.16.

A pair of *Coptodon zilli* guarding a clutch of eggs which the female (in yellow) is cleaning (from Fryer & Iles, 1972).
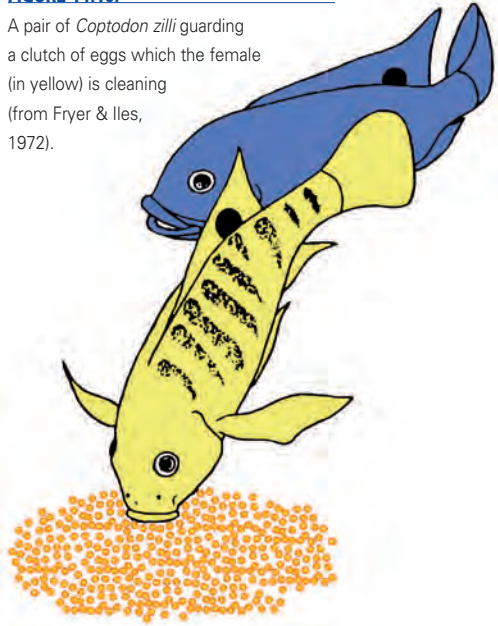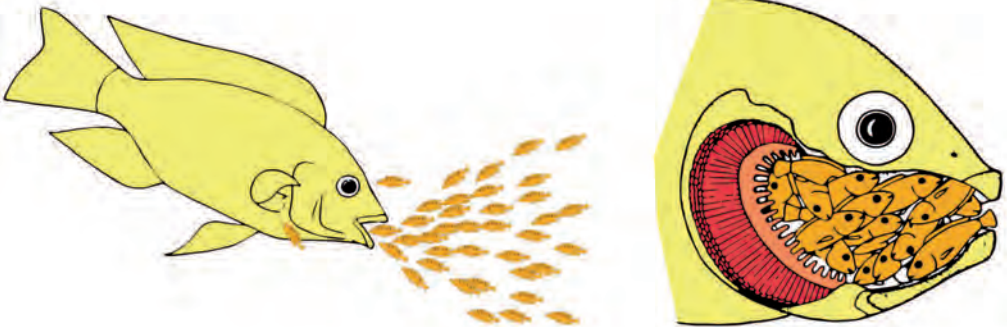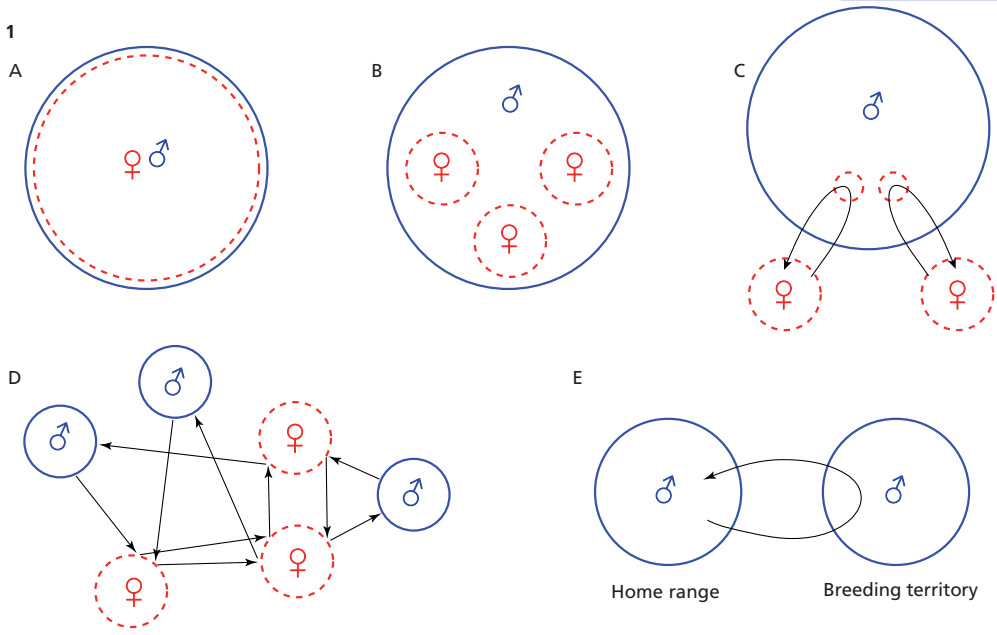

FIGURE 14.17.

To any alert, young cichlids rush into the mouth of their mother (redrawn from Fryer & Iles, 1972).

1

2

Species	male			female		
	H R	B T	C T	H R	B T	C T
monogamous						
Neolamprologus toae	● ?	●	●	● ?	●	●
Neolamprologus tretocephalus	● ?	● ?	●	● ?	● ?	●
Xenotilapia flavipinnis	●	●	●	●	●	●
polygamous						
Neolamprologus furcifer	○			●		●
Neolamprologus mondabu	●	●		●		●
Neolamprologus savoryi	●	●		●		●
Altolamprologus compressiceps	● ?	●		○		○
Lamprologus callipterus		○				○
Gnathochromis pfefferi	○	○				
Lobochilotes labiatus	○			○		

FIGURE 14.18.

Types and arrangement of the territories of benthic cichlids of Lake Tanganyika
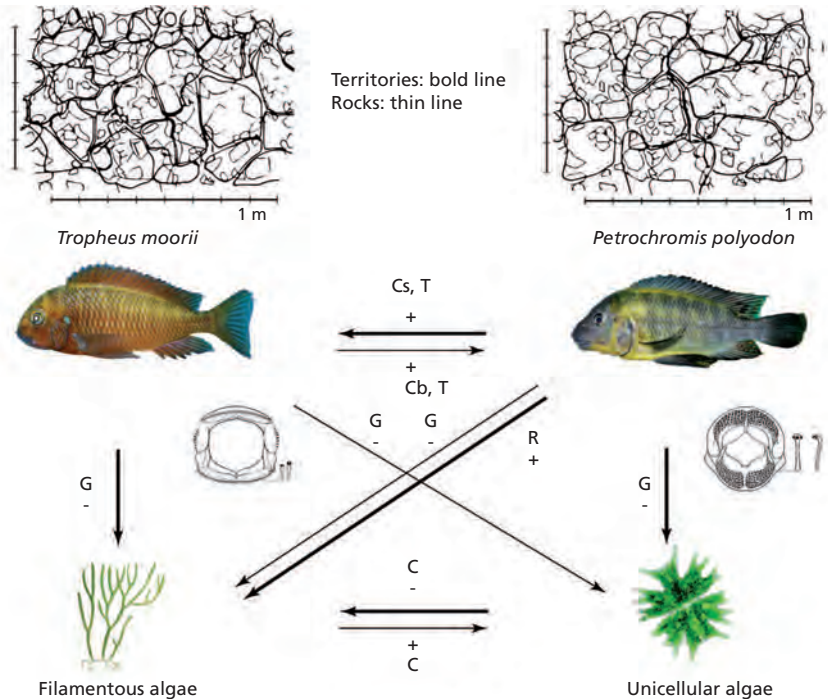(redrawn from Yuma & Kondo, 1997).

1. A: monogamous species. Male and female protect a multifunctional territory (home range and breeding territory); B: species in harem-like social structure. The male protects a breeding territory which includes several females; C: Polygamous species. The male protects a breeding territory which includes several breeding sites. The females have home ranges outside of the male territory. Females meet the male only during the reproduction period; D: polygamous species. Each male or female has a small territory. Males visit only neighbouring females; E: polygamous species. The male has two multifunctional territories; a breeding territory where it lives during the morning and a home range where it feeds during afternoon. Females, non-territorial, meet the male only during the mating. Then they go away with eggs in their mouth.

2. open circles: monofunctional territory; filled circle: multifunctional territory; HR: home range; BT: breeding territory; CT: young care territory.

Forms of cooperation can exist alongside these conflictual situations. This is the case in some colony-forming Cichlidae which accept young from other broods. In *Neolamprologus pulcher (= brichardi),* the young are monitored by their parents and young subdominants. These "helpers" clean the clutches while the dominants feed on eggs. The behaviour of these helpers normally shifts towards a dominant model as they grow. This change may be slowed down or even prevented if the continued presence of eggs requires them to continue providing care (Siemens von, 1990). If a male breeder is removed, it is replaced by a male from outside the group in 71% of cases. Meanwhile, a female breeder will only be replaced by an outsider female in 15% of cases. The helpers increase the frequency of cooperative behaviour when a female is removed, but not when a male breeder is removed (Stiver *et al.*, 2006). This system exists in other Cichlidae hidden substrate spawners. The care provided by helpers can however be completely different. There have even been cases of symbiosis and/or mutualism between heterospecifics, as in lithophilic Cichlidae communities in Lake Tanganyika. The home ranges of *Tropheus moorii*, a grazer of filamentous algae, and *Petrochromis polyodon*, which feeds on unicellular algae, overlap. It appears that the latter species, when grazing, levels out obstacles by removing sand. It is followed by *T. moorii* which has been observed removing ectoparasites from the body of *P. polyodon*. (Takamura, 1983) (figure 14.19).

There are also associations between species based on their diet. For example, researchers have observed *Tropheus moorii* individuals grazing on algae being closely followed by carnivorous *Neolamprologus leleupi* (Takamura, 1984). The

FIGURE 14.19.

Interaction between two rock-dwelling cichlids of Lake Tanganyika, *Tropheus moorii* and *Petrochromis polyodon* (from Takamura, 1997). +: positive action; -: négative action; Cs: cleaning of debris deposited on the grazing surface; Cb: cleaning of the body; T: protection against intruders of the common territory area; G: grazing; R: protection against competitors; C = competition. By grazing unicellular algae, *P. polyodon* promotes the development of the filamentous algae which feed *T. moori.* The thickness of arrows is proportional to the action's intensity.

Territories: bold line
Rocks: thin line

Tropheus moorii — 1 m

Petrochromis polyodon — 1 m

Cs, T +
+ Cb, T
G G
- -
R +
G - G -
C -
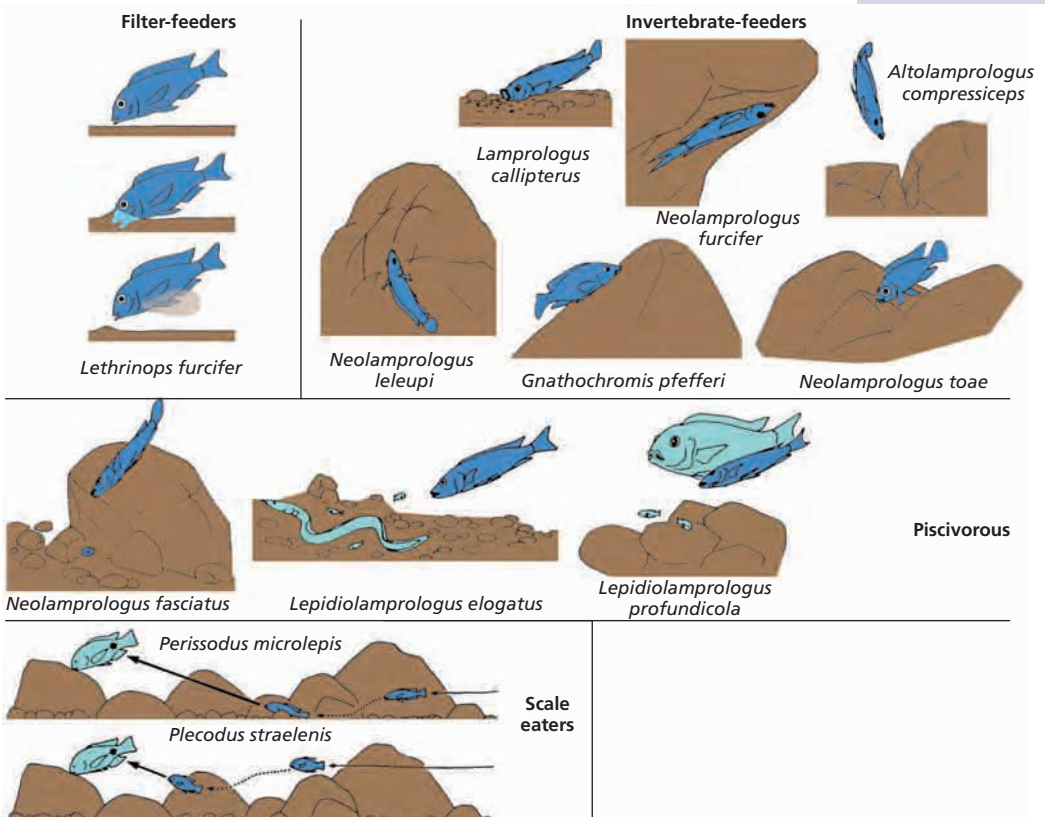+ C

Filamentous algae

Unicellular algae

latter appear to take advantage of *T. moorii*'s grazing to capture the shrimp that have been disturbed by such activity. In these cases, only one of the species benefits from the association, while the other enjoys no advantage. There are also mutually beneficial situations, as in the scale-eating fishes of genus *Perissodus*. An individual is more successful in its attacks in the close presence of a congener using a different hunting strategy (Hori, 1997), as the prey's attention is focused on the presence of the other predator. Such situations have also been observed in piscivores (Hori, 1987).

Survival: eat or be eaten

Among the many examples of trophic adaptations that we might name, the most remarkable are those observed in the Cichlidae of the African great lakes. All food types found in the lakes have been used by these fishes, often with the needed morphological and behavioural adaptations. For instance, in molluscivorous fishes, there are oral shellers/crusher species and pharyngeal crusher species. Meanwhile, epilithic algae grazers employ different strategies. Some rip the algae from the rocks, while others crop them (figure 14.20). There are also special adaptations, such as scale eaters and cleaner fishes that feed on the parasites found on other fishes.

FIGURE 14.20.

Feeding behaviour in some cichlids from the Great Lakes of East Africa (from Fryer & Iles, 1972 and Kawanabe *et al.*, 1997).

Filter-feeders

Invertebrate-feeders

Altolamprologus compressiceps

Lamprologus callipterus

Neolamprologus furcifer

Lethrinops furcifer

Neolamprologus leleupi

Gnathochromis pfefferi

Neolamprologus toae

Piscivorous

Neolamprologus fasciatus

Lepidiolamprologus elogatus

Lepidiolamprologus profundicola

Perissodus microlepis

Scale eaters

Plecodus straelenis

Fishes often organize in groups for more efficient access to resources. This is the case for daily migrations (see chapter *Diversity of fish habitats*). Such groupings may also underlie more aggressive strategies. For example, they allow fishes to feed in zones that are already occupied as territories by congeners or other species. As the resident fish cannot chase off all the intruders, the others have access to the resource. This holds true for the young and females of many epilithic algae grazers.

Hunting strategies are varied in predators. The electric fish *Malapterurus electricus* uses the discharges it can produce to attack prey. *Nimbochromis livingstonii* "plays dead" to attract prey. Mimetism allows some fishes to approach prey more easily (McKaye, 1981). The scale-eating Cichlidae *Corematodus taeniatus* and *C. shiranus* of Lake Malawi have the same colouring as their prey (Fryer & Iles, 1972), a tactic also used by *Lepidiolamprologus mimicus* in Lake Tanganyika (Schelly *et al.,* 2007). Fin-eating Distichodidae (Roberts, 1990), *Eugnathichthys eetveldii* and *E. macrotelorepis*, have the same caudal colour pattern as their preys (*Synodontis decorus* and *Mesoborus crocodilus*). The Clariidae *Channallabes apus*, which lives in muddly bottoms, can feed on dry ground (van Wassenbergh *et al.,* 2006).

External factors also have a large influence on species behaviour. In the Cichlidae *Astatoreochromis alluaudi*, there is a relationship between gill surface area and morphological changes in jaws depending on the amount of dissolved oxygen in the habitat (Binning *et al.*, 2010). The two Haplochromines *Haplochromis pyrrhocephalus* and *H. tanaos*, whose populations were drastically cut owing to the ecological changes in Lake Victoria, showed visual adaptations in relation to these changes but also adaptations in the size of prey (van der Meer *et al.,* 2012; van Rijssel *et al.*, 2015). In the Cyprinidae *Barbus neumayeri*, there does not seem to be an adaptation to the anoxia in the physical system, but there has been a drop in energy-intensive activities such as the feeding rate (Barrow & Chapman, 2006).

Ontogenetic development of behaviour

The previous paragraphs have shown us that an animal possesses a whole range of behaviours, very often specific, that address various types of situations. Very little research has been devoted to determine the true extent of learning. That said, several hypotheses have been proffered on the appearance and expression of behavioural patterns throughout a fish's life. They depend in part on the nature and development of sensory (recognising and analysing a message) and motor (responding to a message) organs used. In this sense, the chronology of development is more important than age. In Cichlidae, the faster transition to free swimming allows the young of substrate spawners to develop behaviours earlier than their mouth brooder counterparts. However, acquiring an organ's functions is not sufficient for achieving the final expression of some behaviours. Behavioural patterns change throughout the development of the young fish, and interactions between parents and juveniles play a primordial role. Initially, the young of *Pseudocrenilabrus multicolor* tend to stay

close to the mother hide in her mouth in case of danger, even when they can swim freely. As they grow older, they become capable of actively avoiding larger fishes (Mrowka, 1987).

Parent-offspring interactions can be varied. The hypothesis of imprinting (Barlow, 1983; Colgan, 1983) designates the process of the same name that can take place between young of the same brood and their parents. Several authors (Kop & Heuts, 1973; Russock & Schein, 1977, 1978) have shown that young and their parents are capable of recognizing each other, at the very least as a species but perhaps also as individuals, as a result of their association when parental care was being provided. When young *Haplochromis burtoni* raised with other Cichlidae reach maturity, they initially ignore their conspecifics whereas they develop sexual behaviours towards members of their entourage of adoption (Sjolander & Ferno, 1973; Crapon de Crapona, 1982).

Relationships with parents often end with signal interruptions or changes at the end of the development of young. In the Mormyridae *Pollymirus isidori* where only the male provides parental care, it has been observed that young remain close to the nest until the electric signals they discharge match those of adults (see box, "Existence of a juvenile discharge in *Pollimyrus isidori* and acquisition of a second adult discharge"). At that point, the father chases them from the nest.

EXISTENCE OF A JUVENILE DISCHARGE IN *POLLIMYRUS ISIDORI* AND ACQUISITION OF A SECOND ADULT DISCHARGE
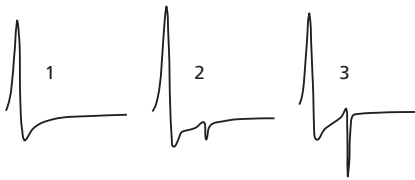

FIGURE 14.21.
Development of EOD in *Pollimyrus isidori*.
Examples of waveforms to illustrate the gradual transition from larval to adult EOD.
1. EOD in larva;
2: in juvenile a second "adult" EOD appears;
3: in adult EOD the second discharge persists and the amplitude increases.

It appears that all Mormyridae species possess a larval electric organ that is then replaced by the adult organ located in the caudal peduncle (figure 14.21).
In *Pollymirus isidori*, the larval organ is located on the trunk and the electrocytes forming it extend from the opercles to the posterior part of the dorsal and anal fins.

Larval electrical discharge
The larval discharge appears eight days after eggs are fertilized. Its amplitude grows rapidly during the first 10-15 days until it reaches a plateau (approximately 10 mV). It remains at this amplitude for about sixty days.

Appearance of the adult electric discharge
Meanwhile, in general after the forty-eighth day, the adult discharge appears with a lag of 0.7 ms to the larval discharge.

Persistence of two types of electric discharges
The two discharges will coexist for some forty days.
During this period, the amplitude of the larval discharge decreases gradually, while that of the adult discharge increases rapidly until it reaches about a hundred mV somewhere around the sixty-eighth day.
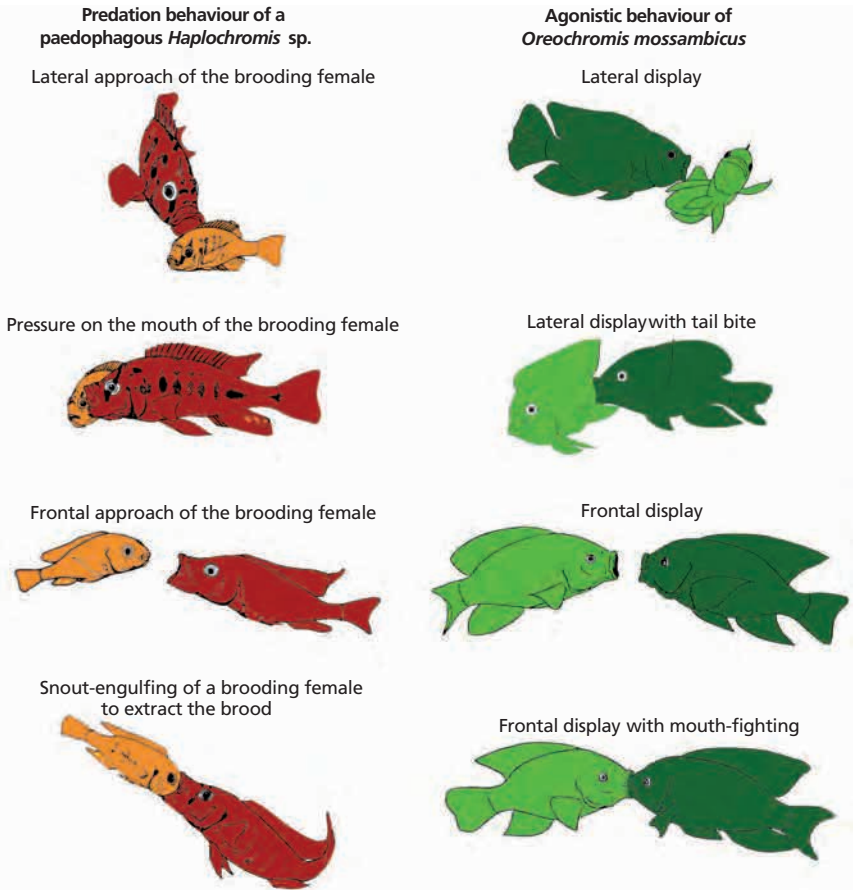(from Westby & Kirschbaum, 1978)

Evolution and behaviour

The variation of a behaviour type can change the selective value of a species and lead to a phylogenetic development. Below we analyse examples of evolution in which behavioural changes played a major role.

Evolution of feeding mechanisms

The hundreds of Cichlidae species in the Lake Victoria basin all came from a single ancestral form that probably had a generalist diet. Since that time, eleven trophic groups diversified, each of which has a distinct bucco-pharyngeal morphology and a set feeding behaviour. Did changes in feeding behaviours lead to morphological changes, or the contrary? The first hypothesis is generally supported, when taking into account the disparity between morphological appearance and genetics, as well as the presumed speed of speciation (Sage *et al.*, 1984). Morphological differentiations may not be related to speciation events, but occur after them. According to this model, morphological differentiation would result from a behavioural mechanism that would involve the

FIGURE 14.22.

Comparison between the predation behaviour of a paedophagous *Haplochromis* sp. and the fight behaviour between males of *Oreochromis macrochir* (based on Ruwet & Voss, 1966 and Wilhelm, 1980).

Predation behaviour of a paedophagous *Haplochromis* sp.

Lateral approach of the brooding female

Pressure on the mouth of the brooding female

Frontal approach of the brooding female

Snout-engulfing of a brooding female to extract the brood

Agonistic behaviour of *Oreochromis mossambicus*

Lateral display

Lateral display with tail bite

Frontal display

Frontal display with mouth-fighting

intra-population spread of a new feeding behaviour, via social learning, that appeared in some members of the population. If this type of behavioural transmission exists, it is possible that it could be transmitted to other species. There are also convergent morphological adaptations tied to a specific behaviour. For instance, in the three African great lakes, certain species have hypertrophied lips that allow them to feed more easily in crevices.

Certain feeding strategies could have evolved from a social component. We can cite the case of paedophagous fishes in Lake Victoria (figure 14.22) whose method is to force open the mouths of incubating female Cichlidae in order to extract the brood.

Phylogeny of parental care behaviour

It has been suggested that parental care developed in fishes occupying physical systems characterized by their spatial and temporal unpredictability (Wootton, 1990).

Fishes that do not provide parental care lay a large number of small eggs that are dispersed in the pelagic system. This is the case for many species belonging to the Clupeidae, Alestidae, and Cypriniformes families. This mode of reproduction could represent ancestral conditions, since one increases the chances of survival in an unstable environment by favouring dispersion. However, there is higher pressure from predators. In fact, many species that do not practice parental care do not lay their eggs at random, but deposit them in plants, gravel, or holes. It is indeed advantageous to recognise and select sites that are favourable to the brood. When the favourable habitat is identified and used regularly, there may be an adaptive advantage to staying there, which is the decisive stage for the appearance of site preparation and defence behaviour, in order to monopolise those that are most favourable to reproduction.
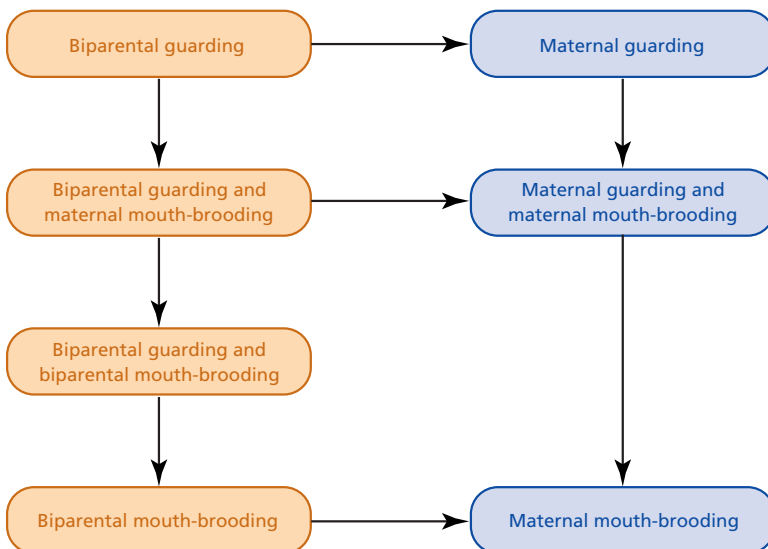

FIGURE 14.23.
Most likely steps of parental care systems of cichlid fishes in Lake Tanganyika (redrawn from Kuwamura, 1997).

Of the freshwater species practicing parental care, the habits observed in Cichlidae are among the best known. From parental care on the substrate, considered an ancestral behaviour (Stiassny & Gerstner, 1992), several possibilities can lead to mouth brooding, a more recent behaviour. Taking eggs into the mouth to transport them from one site to another could have become a permanent component of reproductive behaviour (figure 14.23). The adaptive advantage is in keeping embryos safe from predators and limiting competition for reproductive sites. One may also see there a means of freeing oneself from the need for a substrate, when there is intense competition for available benthic space (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.

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