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Alternative life-history strategies of catfishes

Michael N. Bruton

J.L.B. Smith Institute of Ichthyology, Private Bag 1015,
Grahamstown 6140, South Africa.

Present address: *Two Oceans Aquarium, P.O. Box 50603,*
Waterfront 8002, Cape Town, South Africa.

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Abstract

Siluriformes, as well as Characiformes and Cypriniformes, are a diverse and widespread group of Ostariophysan fishes, but Siluriformes have a probable ancestral benthic feeding habit. They have a unique suite of morphological, physiological, ecological and behavioural traits that equip them to succeed in freshwaters but only to a limited extent in the sea. They are typically, non-aggressive stalking predators that hunt at night or in turbid water using primarily nonvisual sense organs, although there are many exceptions. The modification of the Weberian apparatus for sound production has probably resulted in some loss of buoyancy control. Catfishes are represented in all the different breeding guild categories and exhibit diverse and sometimes bizarre breeding methods. Catfishes tend towards the altricial end of the altricial-precocial life-history continuum. Only two families (Ariidae and Plotosidae) have successfully colonised the sea; physiological constraints and strong competition from Elasmobranchii and Actinopterygii fishes are probable reasons, and it is notable that the two families that have succeeded have precocial life histories that are more suited to highly competitive environments.

Keywords: Catfish, morphology, ecology, behaviour, physiology, breeding guild, life-history, adaptations.

Stratégies comportementales des poissons-chats.

Résumé

Les Siluriformes, de même que les Characiformes et les Cypriniformes ont un organe de Weber ; ils constituent un groupe diversifié et largement répandu avec un comportement alimentaire ancestral probablement benthique. Ils présentent une remarquable combinaison de caractéristiques morphologiques, physiologiques, écologiques et comportementales qui leur permet de se développer efficacement dans les eaux douces mais de façon beaucoup plus limitée en milieu marin. Bien qu'il existe de nombreuses exceptions, il s'agit généralement de prédateurs peu agressifs qui se nourrissent de nuit ou en eau turbide, utilisant principalement leurs organes sensoriels non visuels. La modification de l'appareil de Weber, impliqué dans la production de sons, s'est vraisemblablement accompagnée d'une perte partielle du contrôle de la flottabilité. Les poissons-chats sont représentés dans toutes les guildes reproductives et mettent en œuvre des modalités de reproduction variées et parfois inhabituelles. En ce qui concerne les stratégies démographiques, les poissons-chats tendent à se situer à proximité du pôle « altricial » du continuum « altricial-précoce ». Seules deux familles (Ariidae et Plotosidae) se sont bien adaptées en milieu marin ; les contraintes physiologiques et la forte compétition avec les poissons Elasmobranches et Actinoptérygiens en sont des causes probables. Il est remarquable, de ce point de vue, que les deux familles trouvées en mer présentent des stratégies démographiques de type « précoces » qui sont plus adaptées dans des milieux où la compétition est importante.

Mots-clés : Morphologie animale, écologie, comportement, reproduction, adaptations.

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INTRODUCTION

The aim of this paper is to provide an ecological classification of catfishes. There are two kinds of ecological classifications, one based on ecomorphology and feeding guilds, which defines a species interrelationships with other species, and the other based on breeding guilds, which defines how a species maximises its contribution to its species gene pool and to future generations. Both will be used in this preliminary treatment. Examples in these classifications are drawn mainly from Breder and Rosen (1996), Balon (1975), Burgess (1989), Nelson (1994) and Paxton and Eschmeyer (1994).

What is a catfish?

Catfishes are highly diverse ostariophysan fishes with a probable ancestral benthic habit. They evolved in the Cretaceous/Ecocene epoch about 70 million years ago and are essentially Tertiary fishes like most euteleosts. Ancestral ostariophysans originated before the break-up of Gondwanaland and then evolved in both the New and Old Worlds.

Catfishes are commonly found in freshwaters on all continents, except Antartica, and are especially abundant in the tropics of South America, Africa and Asia. They are the only ostariophysans to have penetrated the sea but they have done so to a limited extent. Catfishes have a characteristic but highly varied morphology which has to some extent restricted their ecological niches but has also provided them with the basic equipment to dominate benthic habitats in many freshwater ecosystems. Representatives of only a few genera have occupied pelagic habitats.

Catfishes, with at least 2 584 species (Teugels, 1996), are one of the most diverse orders of fishes, with only the Cypriniformes and the Perciformes (the latter possibly polyphyletic) being more diverse. The largest catfish families are the locariids (651 species) and the pimelodids (323 species), both of the neotropics.

The most primitive catfishes are thought to be the two species of *Diplomystes*, which are the only extant siluriforms with a toothed maxillary (Teugels, 1996). While it is difficult to allocate directionality to ecomorphological attributes, it has been suggested that the benthic shovelling, suction-feeding mode of *Diplomystes* in ancestral. Bagrids, such as *Bagrus ubangensis* Boulenger, 1902, may also be close to the generalised catfish form.

MORPHOLOGICAL, ECOLOGICAL AND BEHAVIOURAL CHARACTERISTICS OF CATFISHES

Catfishes have characteristic ecomorphologies that define their potential life-history styles:

Morphological and physiological characteristics

1. Catfishes have a wide range of body shapes but the generalised form is a sub-cylindrical body with flattened ventrum, as in the claroteid *Auchenoglanis occidentalis* (Valenciennes, 1840). Somes species have highly divergent shapes for a specialised life style, such as the anguilliform clariid *Channalabes*, whereas others are laterally compressed like the pelagic schilbeid *Schilbe intermedius* Ruppel, 1832.

2. Catfishes have a predominant suction feeding or gulping mode of feeding which is made possible by their large bucco-pharyngeal volume and large mouth, as in the mochokid *Chiloglanis bifurcus* Jubb and Le Roux, 1969.

3. The absence of large, incisiform teeth. The teeth are usually small and villiform and present in bands on the premaxillary, vomerine, mandibular and pharyngeal jaw bones. The teeth are primarily used to retain the prey in the mouth rather than to catch or lacerate it. Although some catfishes have become pelagic piscivores, such as *Schilbe*, they do not have the dental genetic component to have developed incisiform teeth like some characins, such as *Hydrocynus vittatus* Castelnau, 1861.

4. Reduction in the number of elements in the cranial skeleton compared with other ostariophysans. In most catfishes the maxilla is reduced to a small articulatory support for the maxillary barbel. The reduction of the maxilla means that catfishes are not able to protrude their mouths, unlike many cyprinids and other fishes.

5. Dorso-ventral flattening of the head to form a flat shovel or scoop which is used for bottom grubbing or uprooting plants. The flattened head may possibly also be used as a hydrofoil. This condition is well shown in species of *Chaca* (Chacidae).

6. The bones of the head are typically fused or strongly sutured to form a well-ossified cranial box, as in doradids and clariids. The selective advantage of the cranial box is unknown, but it may be related to the ancestral shovelling mode of feeding or to protection from aerial predators in shallow water. In some catfishes, such as the gill parasite *Vandellia*, the head bones are less ossified.

7. Lack of scales, which has facilitated sinuousity. The tough, mucus-covered scaleless skin is used for cutaneous respiration to supplement aquatic respiration in many species. Numerous species of South American catfishes, such as the callichthyids, have armour plating on the head and scutes on the body.

8. Many catfishes are nocturnal and have well-developed non-visual sense organs, especially the senses of touch (through the barbels and tactile organs on the mouth and skin), as in pimelodids, doradids and amphiliids. The barbels are essential for detecting food in the blind cave catfish *Clarias cavernicola* Trewavas, 1936, and other troglodytes. Catfishes typically also have well-developed senses of

taste, hearing, vibration detection (using the octavolateralis system) and electroreception. The electric catfish, *Malapterurus electricus* Gmelin, 1789, has a unique and powerful electrical organ derived from the muscles which can generate up to 600 volts, three times more than electric rays.

9. A well-developed Weberian apparatus in association with a reduced swimbladder. This arrangement has improved their sense of hearing and their sound-producing repertoire, which is very important for interspecific communication in a group of fishes that frequently lives in low visibility water or is active at night. Squeakers of the genus *Synodontis* make a variety of sounds by moving the pectoral fin bases over a corrugated bone facet.

10. A very varied fin array that has allowed catfishes to leave their ancestral benthic habitat, colonise pelagic and epipelagic habitats and adopt different feeding modes. Many loricariids have extensive fins whereas the silurid *Ompok* species swims using undulating waves along its anal fin. The presence of sharp spines on the dorsal and pectoral fins of many catfishes is characteristic. An adipose fin is present in 22 of the 33 families of catfishes (Nelson, 1994).

11. Limited osmoregulatory capacity, except in the ariids and plotosids.

12. Catfishes probably have the greatest range of sizes within any order of bony fishes (ca 14 mm-5 m). The spiny dwarf catfishes in the genus *Scoloplax* (Scoloplacidae) from the neotropics (some with a maximum size of 14 mm TL) are among the smallest catfishes.

Amongst the largest catfishes are the wels *Silurus glanis* Linnaeus, 1758, of Europe (> 5 m and 330 kg), the pangasiids *Brachyplatystoma filamentosum* Lichtenstein, 1819 (> 3 m) and *Pangasianodon gigas* Chevey, 1931, of the Mekong River (3 m and 300 kg). Many catfish species exceed 2 m, such as the clariid *Heterobranchus longifilis* Valenciennes, 1840, of Africa and the pimelodid *Sorubimichthys planiceps* Agassiz, 1829 of South America.

Ecological and behavioural characteristics

1. Catfishes are predominantly primary freshwater fishes. Their limited penetration of the sea is nevertheless evidence of their greater adaptability compared with other ostariophysans and many other primary freshwater fish groups. Interestingly, the marine plotosids and ariids are the only ostariophysan fishes in the freshwaters of Madagascar, Australia and New Guinea.

2. Catfishes have a very wide habitat range in freshwater, but many show a preference for shallow, relatively capricious, running water environments. Many inhabit large open waters, such as callichthyids, whereas others inhabit cave lakes, such as *Clarias cavernicola*. There are many cave-dwelling or troglodytic catfishes; in Brazil Trajano (1991) found that all except one of the troglodytic fishes were catfishes (the other is a characin).

3. There is a predominance of catfishes in the New World, especially in the neotropical zone (Nelson, 1994). Of the approximately 2 584 species of catfishes, about 1 680 species (64 %) in 14 families live in South America.

4. Catfishes exhibit the full range of reproductive styles from non-guarding, open-substrate spawning madtoms (Ictaluridae) to mouthbrooding ariids and internally fertilising woodcats.

5. Catfishes are typically thigmotactic, which is typical of benthic fishes with predominantly tactile sense organs, and are typically negatively buoyant partly as a result of their reduced swimbladder and heavy, bony head.

6. Catfishes typically have wide trophic niches with wide niche overlaps between them. Some of their more specialised feeding modes include scale eaters, parasites, blood suckers, urinophiles (the candiru, *Vandellia* species, is the only vertebrate parasite of man), wood eaters, blind bottom-foraging cave dwellers, plankton pluckers and many benthic foragers.

7. Catfishes are predominantly defensive rather than offensives fishes. For instance, mochokids of the genus *Syndontis* have a triangle of sharp spines which they can lock in place to prevent a predator from swallowing them. Others, such as *Pimelodus pictus* Steindachner, 1876 (Pimelodidae), form shoals to confuse their predators.

8. Many catfishes, such as *Amphilius uranoscopus* Pfeffer, 1889, are relatively independent and asocial fishes compared to other ostariophysan and many acanthopterygian fishes. Exceptions include the pelagic schooling groups (ariids, plotosids and pimelodids, Loiselle, 1988) and some species in various families that live in small groupe, *e.g. Phractura* and *Doumea* species (Amphiliidae).

9. On the other hand, some catfishes, such as *Clarias gariepinus* Burchell, 1822, *C. ngamensis* Castelnau, 1861, and *Heterobranchus longifilis* (all Clariidae), use social hunting tactics (Bruton, 1979*b*).

11. Catfishes typically have low species interdependencies, with few mutualisms or symbioses and little resource defence (but see below).

12. Sound production is common in both sexes of many catfishes and usually involves the vibration of the swimbladder as a result of the stridulation of the pectoral spines. Vocal catfishes include the talking catfish (Doradidae) and banjo catfishes (Aspredinidae) but also ariids, callichthyids, clariids, bagrids and chacids.

Thus, in summary, a catfish is a relatively non-aggressive predator that needs to approach its prey closely, usually under cover of darkness or in turbid water and using primarily non-visual sense organs, before it can capture the prey using the sink-suck method and small villiform teeth. Specialised means of prey detection or predator avoidance may be used. The modification of the Weberian apparatus for sound production has resulted in some sacrifice in buoyancy control. Foraging near a substrate probably increases hunting success.

BREEDING GUILDS OF CATFISHES

The breeding guild categories of fishes were defined by Balon (1975). Unlike may orders of fishes, catfishes are found in all three major breeding guild categories, *i.e.* non-guarders, guarders and bearers. Breeding guilds may be regarded as genotypic alternate states over evolutionary time from generalised to specialised types.

Non-guarders

The most generalised state involves scattering the gametes on open substrata (including open water) and exercising no parental care. These non-guarders produce a large number of small eggs and invest little energy in each young.

(a) The most primitive group, the *egg scatterers*, includes schilbeids, such as *Pareutropius* species, which scatter adhesive eggs on plants and do not guard them; some clariids, such as *Heterobranchus longifilis*; callichthyids, such as *Corydoras pygmaeus* Knaack, 1966, which cups its ventral fins together to form and inseminating basket and scatters the adhesive eggs among plants (Jockel, 1988); some silurids, such as sheatfish *Parasilurus* species, which scatter their eggs over plants; the bagrid *Mystus armatus* Day, 1865, which scatters large numbers of small eggs on the substrate.

The sharptooth catfish *Clarias gariepinus* in a egg scatterer which awaits suitable environmental conditions before spawning. Gonadal maturation is associated with increasing water levels, temperatures and photoperiod. Spawning occurs during the summer, usually on dark nights after rain. The fecundity is very high (30 000 – > 80 000 eggs). There is a massive aggregation of catfish before spawning, and courtship is preceded by aggressive encounters between males. Mating takes place between isolated pairs in shallow water among inundated plants. There is no parental protection of the young except by the careful choice of a spawning site and time. Early development is rapid and semi-direct with an abbreviated larval stage (Bruton, 1979*a*).

(b) The second group of non-guarders, the *brood hiders*, includes some callichthyids (such as *Corydoras, Brochis* and *Aspidorus* species, which prepare but do not guard nesting sites on plants); some loricariids which attach their eggs individually to rocks in deep potholes or under leave; some plotosids, such as *Plotosus lineatus* Thunberg, 1787, which deposit their eggs in crevices, and some mochokids, such as *Synodontis*, which lay their adhesive eggs on prepared sites on rocks or logs but do not guard them.

One of the most bizarre methods of breeding in any fish was recently discovered by Kohda *et al.* (1995) in the callichthyid *Corydoras aeneus* Gill, 1858. In this species the male courts the female by presenting his abdomen to her and the female fish responds by attaching her mouth to the male's genital opening and drinking the sperm. The sperm passes rapidly through her intestine and is discharged together with the eggs into a pouch formed by the female's pelvic fins. There the eggs are mixed with the sperm and inseminated. The ability of *Corydoras* species to practise intestinal breathing may have facilitated the evolution of sperm drinking. This mode of insemination has not been found in any other animals but probably occurs in several catfish species; the females of at least 20 *Corydoras* species are known to adopt the "T" position and place their mouths against the male's genital opening (Sakurai *et al.*, 1985).

Guarders

Guarders make a greater parental investment in the young than non-guarders, both by producing larger but fewer eggs but also by protecting the young. Aristotle was the first to observe that a silurid species guards its brood of eggs.

(a) *Substratum choosers* include some silurids, such as *Silurus glanis*, which lay their adhesive eggs on cleaned patches on plants or leaf litter where they are guarded and fanned by the male, some bagrids which lay adhesive eggs on plants, and some loricariids, such as *Rineloricaria* species.

(b) *Nest spawners:* in *Silurus aristotelis* Gill, 1906 and *Ictalurus nebulosus* Lesueur, 1819 (the males construct and guard a simple nest in the sand. The male armoured catfish *Hoplosternum littorale* Hancock, 1828 makes a remarkable foam nest similar to that of hepsetids and some anabantids. The female expels several eggs into a basket formed by her pelvic fins and carries them to the nest where she deposits them among the bubbles. The male adds more bubbles and they guard the nest for up to four weeks (Schehr, 1988; Ramnarine, 1990; Mol, 1993).

The Lake Malawi bagrid *Bagrus meridionalis* Gunther, 1893, a nest guarder, shares the guarding and feeding of its young with a cichlid, often a *Cyrtocara* species. The cichlid parent actively deposits its young into the catfish's nest and then defends the periphery of the nest from predators. The catfish remains in the middle of the nest where it defends its own young. When cichlids are present the catfish young survived over 80 % longer than when the cichlids were absent. Shared, interspecific brood care, as shown by these species, is apparently rare (McKaye, 1985, 1986).

It has also been found that *B. meridionalis* feeds its young trophic eggs (unfertilised, degenerate eggs) in a similar way to some birds, sharks and social insects. The male also feed the young by disturbing the sediments in the nest and exposing invertebrates or by bringing mouthfuls of sand and invertebrates into the nest from outside (McKaye, 1985, 1986). Eggs accounted for > 90 % of the mass of food in the stomachs of the young. The females appear to gain more by investing in eggs to feed the young which allows them to grow faster, rather than by depositing more fertilised eggs. This is clear evidence of the benefits of a more precocial life style in a biotically saturated environment like Lake Malawi.

Guarders also include fluviatile, freshwater ariids which bury their eggs in a mound of gravel; some doradids which make a nest of leaves; an Australian freshwater plotosid *Tandanus tandanus* Mitchell, 1838 which nests in gravel or sand in streams, the nest is guarded and fanned by both parents whereas in other plotosids the nest is only guarded by the male; some ictalurids which make nests in sand or gravel or use natural cavities that are guarded by one or both parents; some heteropneustids that spawn in pits prepared and guarded by both parents. In the Asian clariids *Clarias batrachus* Linnaeus, 1758, and *C. macrocephalus* Gunther, 1864 the males make and guard nests in muddy bottoms or stream banks among vascular plants. *C. batrachus* produces 2 000 to 15 000 fry. Somes loricariids deposit their eggs in holes in the banks of swamps whereas others clean a nest on a rock which is guarded by both parents. The bagrid *Pelteobagrus fulvidraco* Richardson, 1845, excavates nest burrows 9-14 cm deep in the bottom and the male guards the eggs whereas in the airsac catfish *Heteropneustes fossilis* Bloch, 1794, the male and female excavate a simple nest and guard the eggs (in a sticky ball) and the embryos. In pimelodids, such as *Sorubim* species, the parents dig a shallow nest beneath driftwood and guard the nest and in some *Bunocephalus* species (Aspredinidae) the male excavates and guards a nest in which the eggs have been deposited after the female carries them in a basket formed by her pelvic fins. A pair of dwarf bagrids (*Lophiobagrus* species) has been observed digging a pit under a pile of rocks and guarding the 30-40 eggs until they hatch. There are unconfirmed reports that the electric catfish *Malapterurus electricus* and the talking catfishes (Doradidae) are also nest guarders.

Bearers

Bearers make the greatest investment in their young and play a low number, high investment game. They also exert considerable control over the environment in which their young develop.

There are several groups of external bearers:

Transfer brooders include some callichthyids, such as *Callichthys* and *Corydoras* species, in which the females carry the spherical eggs in their fins during a prolonged search for a suitable place to attach them, possibly to remove them from predators that were attracted to the spawning site.

In *skin brooders* the eggs are carried while attached to the ventral surface of the body, as in some *Bunocephalus* species (Bunocephalidae), *Loricaria* species (Loricariidae) and *Aspredo* species (Aspredinidae). *Aspredo* develops a spongy skin on its ventrum; the females then roll onto their eggs once they have been fertilised and the eggs adhere to the skin. After some time a cup with a stalk envelopes each egg and permits gas and nutrient exchange. In some aspredinids the female develops spongy tentacles on her belly to which the eggs are attached during incubation.

Pouch brooders include some loricariids in which a pouch or marsupium is formed by the enlarged and everted lower lip of the males.

Mouthbrooding catfishes are primarily estuarine or marine forms. In all ariids the males mouthbrood the eggs and young and may carry out buccal feeding of the young. Juveniles up to 100 mm TL have been collected from male's mouths. In *Hemipimelodus* species the ovigerous females have large pads on their ventral fins which hold the recently extruded eggs until they are fertilised and taken into the mouth by the male.

In the southern African marine catfish *Galeichthys feliceps* Valenciennes, 1840 (Ariidae) the eggs are about 16 mm in diameter and the average brood size is 49. Hatching occurs at an advanced developmental state after 75-80 days, when branchial and fin differentiation are complete. Exogenous feeding begins in the adult's buccal cavity shortly after hatching. The young are released as juveniles after 140 days at a length of 54 mm (Tinley and Hecht, 1993).

In the Australian ariid *Arius graeffi* Kner and Steindachner, 1866, the maximum brood size is 83. Brooding lasted 6-8 weeks with hatching in 4-5 weeks. Juveniles are released at a length of 59 mm TL. The branchial region of the males becomes distended to accommodate the brood and the oral epithelium thickens to cover the palatine tooth patches. The number of young produced may be less than the fecunditiy as the males swallow or drop young (Rimmer and Merrick, 1983).

Although most mochokids are non-guarding, lithophilous brood hiders, at least one species of squeaker, *Synodontis multipunctatus* Boulenger, 1898, an endemic of Lake Tanganyika, is a brood parasite that deposits its eggs in such a way that they are picked up and brooded by maternal mounthbrooding cichlids, mainly in the genera *Ophthalmotilapia* and *Cyphotilapia*, especially *C. frontosa* Boulenger, 1906, (Finley, 1988). This occurs despite the fact that the squeaker's eggs are very different from those of the cichlid, being white as opposed to yellow and less than half their size. To add insult to injury, the *Synodontis* embryos, which are faster growing and larger, use the cichlid embryos as their first source of food. This "cuckoo" behaviour is especially remarkable in that it is interordinal and also across different breeding guild categories (non-guarding to external bearing). Furthermore, aquarists have even induced *S. multipunctatus* to be a brood parasite of Lake Malawi cichlids in aquaria. Is the only *Synodontis* species in Lake Malaxi, *S. njassae* Keilhack, 1908, also a brood parasite?

The selection pressure for the evolution of intra- and interspecific brood care (brood parasitism) may be a reduction in predation on the parent's offspring due to the presence of foreign young (McKaye, 1985). In Lake Malawi the bagrid *Bagrus meridionalis* Gunther, 1893, guards cichlid young within its nest, with the foreign young being kept on the periphery of the nest.

Internal bearers exert nearly full control over the developmental environment of the young. There are no truly viviparous catfishes, as far as we know, but internal fertilisation has been recorded in auchenipterids and ageneiosids with the aid of a gonopodium and sperm storage in the ovaries. After fertilisation the ova are spawned externally. This is a simple form of partial ovoviviparity that is not classified by Balon (1975).

Internal fertilisation has been reported in some woodcats *Parauchenipterus* species (Auchenipteridae). The male has an intromittent organ formed by the modified anal fin rays which insert sperm in a gelatinous plug into the oviduct of the female, where it may be stored for two to four weeks. The fertilised eggs are then scattered over the substrate. These species are therefore ovoviviparous. Internal fertilisation has also been reported in a doradid and in an astroblepid.

While accurate figures are not available for the number of catfish species in each breeding guild category, it is apparent that they have adopted a wide range of breeding options. In fishes in general, about 80 % are non-guarders, 15 % are guarders and 5 % are bearers (Breder and Rosen, 1966); catfishes are probably close to these proportions with perhaps a higher proportion of guarders and a lower number of bearers.

ALTERNATIVE LIFE-HISTORY STYLES

Superimposed on the breeding guilds (genotypic states) outlined above are phenotypic states whereby a fish can alter its life-history style within a generation or generations in response to the environment. These alternative life-history styles form an altricial to precocial continuum that is a response of fishes, within each breeding (or feeding) guild, to changing internal and external environmental conditions (Balon, 1981; Bruton, 1989).

Altricial fishes produce small, incompletely developed young at first exogenous feeding with a long larval stage and are typically generalists capable of surviving in unstable, uncrowded environments in which they are mainly subject to density-independent mortality (Balon, 1981; Bruton, 1989; Flegler-Balon, 1989). Precocial forms produce large eggs and well-developed young at first exogenous feeding have an abbreviated or no larval stage (direct development) and are typically specialists that are best able to survive in a stable, crowded environment in which they are mainly subject to density-dependent mortality. The mechanism for changing from one phenotypic state to another is the alteration in the relative timing of key developmental events *e.g.* size at first exogenous feeding (Flegler-Balon, 1989).

Fish species in highly competitive, biotically harsh environments are hypothesized to be more precocial *i.e.* to make a large parental investment in each of a few young which are larger when they first come into contact with the external environment *i.e.* to have advanced breeding styles with extensive parental care (Bruton, 1989).

There is little information on the phenotypic options adopted by catfishes, but *Mystus macropterus* Bleeker, 1870 (Bagridae) appears to be a relatively precocial non-guarder as it has large eggs (2.8-3.2 mm) a sustained period (6-7 days) of mixed feeding (exogenous and yolk) and shows early differentiation of organs during the larval period. Troglodytic catfishes, and cave-dwelling fishes in general, show delayed sexual maturity, low egg number and increased longevity and have a K-selected life style or are precocial (Trajano, 1991).

Research on the phenotypic options adopted by catfishes is an important priority as an understanding of this aspect of their life histories will shed light on their ecology, breeding biology and early development, and will have wide application in the conservation, aquaculture and management of catfishes.

Why have catfishes not succeeded in the sea?

There are two families of marine catfishes, the ariids with about 149 species, many of which live in freshwaters, and the coral catfishes or plotosids, with about 32 species (Teugels, 1996). Marine catfishes therefore comprise only 7 % of all catfishes, and the question arises: Why has this group, which has been so successfull in freshwater, not penetrated marine environments with any great success?

Physiological constraints on their ability to osmoregulate may be the explanation. Alternatively, chondrichthyan and acanthopterygian fishes may already have colonised most inshore, benthic habitats by the time the catfishes competed for niches on the edge of the sea. Small, benthic sharks and rays may already have created all the benthic-feeding niches in shallow, marine environments before the catfishes were able to compete for them.

Alternatively, the answer may lie in the life-history styles of the two groups that have succeeded. The ariids have one of the most advanced breeding modes of any catfishes. They produce a few, large eggs, have intensive parental care and are very precocial. This breeding style allows ariids to compete successfully in a biotically harsh environment, such as the edge of the sea. In contrast, plotosids are among the few social, pelagically shoaling catfishes, and have successfully mimicked the behaviour of many successfull marine perciforms.

Why are catfishes so successful in freshwaters?

In contrast to the sea, many freshwaters are harsh, variable and relatively shallow water bodies, often with low visibility. Catfishes, by way of their wide range in sizes, wide trophic niches, well-developed non-visual sense organs and altricial to precocial breeding guilds, are able to take advantage of most opportunities offered in inland waters.

Their wide variety of species and life-history options have also made them suitable for both extensive and intensive aquaculture as long as the right species are chosen. It also seems likely that aquaculturalists will be able to manipulate the ecophenotype of catfishes in an altricial or precocial direction with particular reference to the timing of ontogenetic events, as has been done with cichlids, salmonids and sturgeons (Bruton, 1989), in order to optimise growth rates or final size, whichever is the highest priority. An understanding of the life-history styles of catfishes, and their phenotypic ranges, should greatly improve the aquacultural efficiency of these amazing fishes, and also contribute to our knowledge of their natural history.

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