A Review of Reproduction and Development in the Fork-tailed Catfishes (Ariidae)

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Available data on a number of aspects of reproduction of ariids are presented with emphasis on recent information. Gonad structure, secondary sex characters, spawning movements and behaviour, eggs, development and parental care are discussed. Evolution of buccal incubation as a reproductive strategy is briefly considered.

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INTRODUCTION

The family Ariidae is estimated to comprise 150 species inhabiting freshwater, estuarine and marine environments in tropical and sub-tropical regions throughout the world (McDowall, 1981). Despite unresolved speciation problems, it is apparent that a radiation of ariids has occurred in Australasia; approximately 40 species are known to occur in New Guinea and 18 in Australia (Kailola, 1981).

Ariid reproduction has previously been reviewed by Gudger (1916, 1918, 1919) and Breder and Rosen (1966); the objective of this paper is to complement those earlier surveys by presenting recent information, especially data relating to Australasian species. The information now available indicates that all species practise oral incubation. Gudger (1918), Breder (1935) and Breder and Rosen (1966) dismissed suggestions that gastric incubation and even viviparity were to be found in ariids, although suggestions of these latter modes occasionally still appear in literature (Nikolsky, 1963).

Bancroft (1924) noted a specimen of *Arius australis* with ova in the mouth, but Semon (1899) reported that this species laid eggs (3-4 mm in diameter) in a nest about one metre in diameter, composed of gravel and small stones. This latter observation was repeated by Wiedersheim (1900), Stead (1906), Whitley (1941, 1957), Breder and Rosen (1966) and Balon (1975) but was rejected by Lake and Midgley (1970). The authors consider that Semon's original description resulted from misidentification of the nest of the sympatric freshwater plotosid catfish *Tandanus tandanus,* which builds nests of the type described (Lake, 1978; Merrick and Midgley, 1981).

The 6 parts of this review summarize and attempt to interpret all the available information; detailed published data on reproduction and development in ariids are listed in Table 1. Generic nomenclature, where applicable, follows Wheeler and Baddokwaya (1981), all other epithets listed are those used in individual publications.

LITERATURE DISCUSSION

Gonad Structure

Because of the large and spectacular eggs found in ariids, most gonad descriptions have dealt with the ovaries. Gudger (1919) described the ovaries of *Bagre marinus* in detail; other species for which ovary descriptions have been published are: *A. manillensis*

(Mane, 1929), *A. felis* (Merriman, 1940; Gunter, 1947), *A. heudoloti* (Tobor, 1969), *A. thalassinus* and *A. dayii* (Dmitrenko, 1970, 1974) and *A. dussumieri* (Vasudevappa and James, 1980).

Generally, three size classes of eggs are found in ariid ovaries: (a) large yolky eggs which are the group fertilized at spawning, and which in *A. felis* may have a small (0.5 mm) stellate micropyle present during later stages of maturity (Gunter, 1947), (b) smaller yolky eggs, and (c) small (ca. 1-2 mm) hyaline eggs in vast numbers. Mane (1929), Dmitrenko (1970, 1974) and Vasudevappa and James (1980) detailed diameters of oocyte classes of *A. manillensis, A. thalassinus* and *A. dayii,* and *A. dussumieri* respectively. Mature ovaries may take up most of the body cavity, compressing the stomach and intestine and precluding feeding prior to spawning (Gudger, 1916, 1919; Smith, 1945; Pantulu, 1963; Tobor, 1978), although gonadal development in *A. heudoloti* does not reach this extreme (Tobor, 1969).

Fecundity values (listed in Table 1) are low (14-184), by teleost standards, while mature oocyte diameters are large (9.5-25.0 mm). Several workers have investigated relationships between fecundity and body length, body weight and gonad weight (Pantulu, 1963; Tobor, 1969; Etchevers, 1978; Vasudevappa and James, 1980) but findings have been variable.

Gabaeva and Ermolina (1972) detailed changes in the follicular epithelium of ovum membranes during oogenesis of *A. thalassinus* and observed that the small hyaline oocytes differed considerably from the larger yolky oocytes in the cell structure of the follicular epithelium during the later stages of oogenesis. Stott *et al.* (1980, 1981) provided micrographs of ovarian sections of *A. felis,* together with a general description of histology of both ovaries and testes in this species. The mature testes of ariids are reported to be small, elongated straps which vary little seasonally (Lee, 1937; Tobor, 1969; Bishop *et al.,* 1980) and which in *A. leptaspis* contain small quantities of colourless milt (S. H. Midgley, pers. comm., 1980).

Secondary Sex Characters

Sexually dimorphic pelvic fins have been found in *B. marinus* (Merriman, 1940), *A. felis* (Lee, 1931, 1937), *A. australis* (Whitley, 1941, 1957) and *A. leptaspis* (Bishop *et al.,* 1980). In these cases the female pelvic fins were longer and more rounded than those of the male. In addition, the pelvic fin base is broader in females than in males (P. Kailola, pers, comm., 1982). Breder (1935) reported that Hubbs found no sexual dimorphism in *A. aquadulce.*

The development of a hook-like thickening on the inner dorsal surface of the pelvic fins of female ariids appears to be closely associated with the reproductive cycle, as these 'claspers' (Smith, 1945) increase in size as the breeding season progresses and are resorbed following spawning (Lee, 1937). These secondary modifications are found in the genera *Arius* (Mane, 1929; Hardenberg, 1935; Lee, 1931, 1937; Smith, 1945; Dmitrenko, 1970; Morley, 1981), *Hemipimelodus* (Smith, 1945), *Potamarius* (Hubbs and Miller, 1960), *Selenaspis* (Luengo, 1973), *Brustiarius, Cochlefelis* and *Nedystoma* (P. Kailola, pers. comm., 1982) but are absent in *Bagre marinus* (Gudger, 1916) and *Cinetodus froggatti* (P. Kailola, pers. comm., 1982). The degree of maximum development and the shape of the claspers appears to vary between species (P. Kailola, pers. comm., 1982).

Mane (1929), Lee (1937) and Smith (1945) suggested that the claspers were used to hold the eggs as they were extruded and the male picked them up one at a time from the basket thus formed. Hardenberg (1935) suggested that the male attached himself to these hooks in order to fertilize the eggs internally or at the moment they were extruded. However, there is no record of any specializations necessary for internal fertilization amongst ariids, nor of any corresponding developments of the pelvic fins

of the male which would enable such attachment. Dmitrenko (1970) suggested that these fin modifications assist in holding the egg mass close to the urogenital orifice as further oocytes are extruded.

Gudger (1916) considered the distension of the branchial region of incubating male *B. marinus* to be a secondary sex character developed prior to spawning, since he took several specimens of this species with enlarged buccal cavities which were not carrying eggs. However, Breder and Rosen (1966) suggested that these fish may have released or lost their offspring and that the enlarged buccal cavity may thus be the result of, rather than a modification for, carrying a large volume of eggs or young. Lee (1937), Dmitrenko (1970) and Luengo (1973) noted similar changes in the branchial region of several other ariid species.

Other reported changes associated with breeding are reductions in tooth patches and changes in the structure of the oral epithelium. Willey (1910) found that male *A. falcarius* brooding eggs had greatly reduced tooth patches compared to females and non-incubating males. Thistlethwaite (1947) found that the oral epithelium of female *A. felis* contained no goblet cells, while that of non-brooding males contained scattered goblet cells in the surface layer. During the brooding process the proportion of goblet cells in the oral epithlium increased sharply, as did folding of the epithelium, reaching a peak approximately midway through the egg development period. As Di Conza (1970) found serum immunoglobulins to be present in *A. australis* mucus secretions, modifications to the oral epithelium, apparently associated with increased mucus production during buccal incubation, may have an important protective role in maintaining eggs and larvae.

Migrations

Little detailed information is available on movements of ariid populations: however, among estuarine and marine species anadromous movements associated with breeding have been reported in *A. felis* (Lee, 1937; Gunter, 1947; Harvey, 1972a, b), *Osteogeneiosus militaris* (Pantulu, 1963) and *A. heudoloti* (Tobor, 1969). *A. australis* shows a marked seasonal pattern of abundance in estuarine creeks in southern Queensland (Ellway and Hegerl, 1972; Stephenson and Dredge, 1976; Quinn, 1980) which may be related to its breeding season. Two references refer to movements in freshwater species: Mane (1929) reported that *A. manillensis* began schooling in deep water in Laguna de Bay at the beginning of the breeding season, and newly-released juveniles migrated to shallower portions of the lake, close inshore; Roberts (1978) suggested that *A. acrocephalus* may move upstream into highland habitats of the Fly River to spawn.

Spawning

Generally ariids have a single annual spawning corresponding to the beginning of the wet season in tropical species (P. Kailola, pers. comm., 1982), and spring in sub-tropical species (Table 1). However, there is evidence of biannual spawning in *A. caerulescens* although fish may be observed in reproductive condition throughout the year (Gonzalez, 1972; cited by Warburton, 1978). No detailed analyses of environmental stimuli on spawning in ariids have been published although Dmitrenko (1970, 1974) notes that *A. thalassinus* and *A. dayii* breed at surface water temperatures of 25 to 28°C, while Lake (1978) reported that *A. leptaspis* commenced spawning when water temperatures exceeded 26°C. Spawning season duration varies but can be up to seven months in the case of *A. heudoloti* (Tobor, 1969). Etchevers (1978) observed that older female *A. spixii* have a more protracted breeding season than younger females. Gonadal development may be extremely rapid, the bulk of development taking place in the few months prior to spawning (Merriman, 1940; Ward, 1957; Etchevers, 1978; Bishop *et al.,* 1980).

TABLE 1

Summary of Published Reproductive Data for the Family Ariidae

Genus and Species	Spawning		Mature oocyte diameter: Range (Mean)	Fecundity[1]: Range (Mean)	Buccal Incubation			Source(s)
	Sites, Movements	Season, Locality			Period	No. eggs in mouth	Development Notes[2]	
Arius								
A. caelatus			11-15 mm ovulated			33-68 (2 spec.)		Sekharan & Mojumder, 1974
A. dussumieri	-	Annual: Dec-Mar, Peak activity Feb; India	13-17 mm	105-184 (141)				Vasudevappa & James, 1980
A. felis	Coastal bays, salinities down to 13.6%	Annual: Jun-Jul; East coast U.S.	12-14 mm 14-18 mm ovulated	40-62	6-8 wks	Usually 10-30, Max. 48	Young at release: 40-49.5 mm. Begin feeding while in mouth	Lee, 1937; Merriman, 1940; Gunter, 1947; Ward, 1957
A. gambiensis			10-20 mm (13.5 mm)	70-90 (78)		15-22	Max. size found in mouth: 100 mm. Begin feeding while in mouth	Tobor, 1978
A. heudoloti	Migration to breeding grounds in Nov, depart Aug.	Annual: Nov-Jun, Peak activity Mar-Apr; Nigeria	10-19 mm	22-45	7 wks	Max. 20	Young at release: 90 mm. Begin feeding while in mouth	Tobor, 1969
A. jella			9.5-11.5 mm (10.5 mm)	ca.50	8 wks	Usually 30-40		Chidambaram, 1941
A. leptaspis	Freshwater billabongs; 26°C	Annual: Nov-Dec; Australasia	11.9-15.7 mm (13.8 mm)	26-70 (42)	8 wks	1-62 (28)	Incubated egg dia. 14.0 mm. Max. size found in mouth 60 mm.	Bishop et al., 1980; Lake, 1978
A. maculatus		Annual: Jul; Java	12 mm	~19-22		Usually 25-35		Hardenberg, 1935
A. manillensis	Freshwater lake: School at start of breeding season, disperse afterwards	Annual (4 spawning runs): Feb-May; Philippines	10.75 mm		8 wks		Young at release: 30-44 mm	Mane, 1929; Aldaba, 1931
A. sagor			11-12 mm			39 (+ 4 larvae) -48 (2 spec.)		Smith, 1945

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A. spixii		Annual: Jul-Oct; Venezuela		14-38			Young at release: 42-44 mm	Luengo, 1973; Etchevers, 1978
A. thalassinus /*A. dayii*[3]	*A. thalassinus* 20-60 m depth over silt substratum; 25-28°C	Annual: Jun-Aug; (*A. thalassinus*); Nov-Mar (*A. dayii*); Arabian Sea.	15-20 mm Usually 16 mm	160, in 4 batches; each batch 23-67		1-47	Young at release: 64 mm. Each male incubates a single batch of eggs	Dmitrenko, 1970, 1974; Al-Nasiri and Hoda, 1977
Bagre B. marinus	Over mud substratum	Annual: May-Jun; East Coast U.S.	15-25 mm Usually 19-20 mm	25-68	9 wks	1-55 Usually 10-30	Egg weight 3.5 g; Young at release: 9.0 g, 85-100 mm	Gudger, 1916, 1919; Merriman, 1940
Nedystoma N. dayi	Freshwater		10 mm			20 (1 spec.)		Roberts, 1978
Ostegeneiosus O. militaris	Lower estuarine areas, after migration up estuaries in late winter, Jan-Feb.	Annual: Mar-May; India	9.8-12.0 mm (10.45)	18-63				Pantulu, 1963
Selenaspis S. herzbergii			9.5-11.0 mm	54 (1 spec.)				Luengo, 1973
Sciadeichthys S. proops						20-28	Young at release: 69-73 mm	Luengo, 1973

1. Sample sizes are variable — where an estimate is based on a very small sample, the sample size is given.
2. Unless otherwise stated lengths are assumed to be total length.
3. A number of observations of the reproductive biology of *A. thalassinus* (Dmitrenko, 1970) were later found to be based on two species, *A. thalassinus* and *A. dayii* (Dmitrenko, 1974); thus it is uncertain to which species quantitative information refers.

No details of spawning behaviour in ariids are available but a few general observations have been recorded. Atz (1958) noted that spawning in *A. felis* was apparently preceded by females vigorously chasing the males. Gudger (1916) and Gunter (1947) noted that stripped female *B. marinus* and *A. felis* extruded clumps of oocytes, both yolky and hyaline, which were held together by an adhesive substance which broke down when exposed to water for a few hours. Similar clusters were reported by Chidambaram (1941) and Smith (1945). Gudger (1918) quoted a report of *A. felis* depositing the egg mass in a depression in sand where it was fertilized and then picked up by the male. Dmitrenko (1970, 1974) found similar clusters of oocytes of *A. thalassinus* and *A. dayii* on the substratum of the Arabian Sea and postulated that the function of the positively buoyant hyaline eggs was to prevent the egg mass sinking into the silt before it could be ingested by the male. As several males of these two species were found to have stomach contents which included empty follicular membranes and hyaline eggs, Dmitrenko further suggested that males swallowed the egg mass. He postulated that the adhesive denatured under enzyme action, and that mature eggs were then regurgitated to the buccal cavity. However, it is difficult to accept that the fertilized eggs would remain undamaged by either the stomach enzymes or regurgitation process. Sekharan and Mojumder (1974) observed that unfertilized oocytes in an egg mass carried by *A. caelatus* decomposed soon after spawning.

Most authors have reported a single spawning per season; however, Mane (1929) and Dmitrenko (1970) found egg classes corresponding to separate spawning runs in *A. manillensis* and *A. thalassinus* respectively, although this observation for the latter species appears to have been due to some taxonomic confusion (Dmitrenko, 1974). Merriman (1940) suggested that *A. felis* may be polygamous, as individual fecundity exceeds the number of eggs generally carried by a single male, but Dmitrenko (1970, 1974) found *A. thalassinus* and *A. dayii* to be apparently monogamous.

Development

All published reports, with one exception, note that the male carries the eggs and larvae; Mane (1929) reported that in a sample of 250 *A. manillensis* a single female was found to be carrying eggs. Assessing numbers of eggs held orally is difficult as carrying males often drop or swallow eggs when captured (Gudger, 1916, 1918; Lee, 1931; Breder, 1935; Luengo, 1973); this phenomenon at least partly explains the wide range of mouth egg counts recorded (1-68). Lake and Midgley (1970) found 123 eggs in the mouth of a male ariid from the Dawson River, Queensland; however, the specific identification of this specimen is now uncertain. Generally, all the eggs or juveniles are at the same stage of development, although Smith (1945) found a male *A. sagor* carrying a newly-spawned egg mass as well as four postlarvae 40 mm in length, suggesting that some individuals may incubate more than one brood per season.

During the incubation period the male does not feed; the stomach shrinks greatly and contains only a small quantity of mucus (Willey, 1910; Gudger, 1918, Hardenberg, 1935; Lee, 1937, Merriman, 1940; Chidambaram, 1941; Smith, 1945; Tobor, 1969, 1978; Luengo, 1973; Bishop *et al.*, 1980). Lee (1937) noted that the testes of male *A. felis* carrying eggs were much more developed than those of non-carriers. Recorded incubation periods range from 6 to 9 weeks and during the latter part of the carrying period the young may commence feeding on plankton (Merriman, 1940; Tobor, 1969, 1978). Gudger (1918) and Luengo (1973) reported observations of young leaving the male's mouth for short periods and returning when alarmed, a behaviour pattern also observed in other mouthbrooders (Oppenheimer, 1970; Merrick and Green, 1982). The size of young at release varies from 30 to 44 mm for *A. manillensis* (Mane, 1929) to 85 to 100 mm for *B. marinus* (Gudger, 1918).

Chidambaram (1941) noted that embryos of *A. jella* hatched head-first through a tear in the egg membrane, and Fowler (1942) concluded that secretory cells in the epidermis of the head region of *A. felis* embryos were responsible for the thinning of the embryonic membrane just prior to hatching. Hatching generally takes place approximately mid-way through the incubation period (Merriman, 1940; Chidambaram, 1941).

Evolution of Reproductive Strategies

Gudger (1918) and Breder (1935) speculated on the evolution of buccal incubation as a reproductive mode in siluroids. Both authors suggested that buccal incubation evolved from a nest-building mode as seen in modern ictalurid catfishes. The nest-building *Ictalurus nebulosus* may rearrange its eggs by 'mouthing' the egg mass and may even retain the eggs in the mouth for short periods (Breder, 1935). Such an evolutionary trend, from nesting to oral incubation, is seen in the Cichlidae (Oppenheimer, 1970; Balon, 1977). It has also been suggested that territorial behaviour, such as nest guarding, may pre-adapt a species for the evolution of male parental care by optimizing the level of paternity (Werren *et al.*, 1980).

The evolution of parental care in fishes has generally resulted in decreased fecundity and increased egg size (Oppenheimer, 1970), and this is particularly evident in the Ariidae. The ariids are also notable for the length of time the eggs and young are retained — generally 6 to 8 weeks — which is far longer than is found in most other mouthbrooders (Oppenheimer, 1970; Merrick and Green, 1982).

The advantages of buccal incubation involve minimizing mortality in the vulnerable egg and larval stages by optimizing physiological conditions (e.g. water temperature, dissolved oxygen) and by limiting predation during incubation as well as after release due to the production of large well-developed offspring (Oppenheimer, 1970; Lowe-McConnell, 1975). An example of physicochemical influences on oral incubation was noted by Harvey (1972a, b) who found incubating male *A. felis* with embryos in salinities from 8.33 to 12.78 p.p.t., while those brooding larvae were found in salinities from 16.66 to 28.32 p.p.t.; Harvey suggested that this was a response to limited salinity tolerances of the embryo until kidney development could cope with osmoregulation in higher salinities.

Balon (1977) noted that the buccal cavity may often be an oxygen deficient environment due to the limited amount of water movement possible when much of the mouth is blocked by eggs. Recent evidence suggests that the evolution of bright yellow, orange or red eggs, commonly found in fishes with well-developed parental care strategies, may be due to the use of the carotenoid pigments in endogenous oxygen metabolism (Nikolsky, 1963; Balon, 1977, 1979).

The mode of reproduction found in ariids is undoubtedly an important aspect of their success in fluviatile, estuarine and marine environments. Buccal incubation does not necessitate specific substrata or water quality criteria as the mobile adults are able to select the environmental conditions necessary for developing eggs and larvae. This feature, in addition to apparently wide physiological tolerances, has enabled ariids to colonize a wide range of habitats in tropical and sub-tropical regions.

CONCLUSIONS

Whilst further information is required on all aspects of ariid reproduction and development, this survey summarizes data on 28 species representing 11 genera. From the current knowledge a number of general points can be drawn to form the basis for future detailed investigations, either of individual species or groups.

Ariids are dioecious, oviparous and possess paired functional cystovarian gonads of an unlobed hollow type. Sexual dimorphism is confined to pelvic fin structural differences and seasonal changes in the oral epithelium of the male and the 'claspers' of the female.

Anadromous and limnodromous movements associated with breeding have been observed in several species. Most ariids have a single annual spawning associated with the wet monsoon (tropical species) or spring (sub-tropical species); the few water temperatures reported during the spawning season have ranged from 25° to 28°C.

The external fertilization involves small numbers of large demersal eggs together with large numbers of small non-functional eggs apparently laid in clusters onto the substratum. Development is protracted; buccal incubation, undertaken by the male, may continue for up to 9 weeks before the offspring are released as well-developed, actively feeding juveniles.

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