Review

Reproductive biology of the neotropical armoured catfish *Hoplosternum littorale* (Siluriformes - Callichthyidae): a synthesis stressing the role of the floating bubble nest

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Abstract – The most distinctive feature of the reproductive biology of *Hoplosternum littorale* is the building and guarding of an elaborate floating bubble nest. Reproduction starts at the age of one year. Males grow to a larger size than females and, during the breeding season, they develop fat deposits in the pectoral fin and an elongated recurved pectoral spine that often assumes a reddish colour. Analysis of gonadal development and surveys of nesting in swamps show that initiation of reproduction is associated with the onset of the rainy season. Males start building the nest at night, and spawning takes place around noon the day after. Most nests are built in newly flooded swamps, especially in open water in the peripheral area of the swamp. A minimum distance of 10 m between nests is usually observed. The floating bubble nest consists of a dome of plant material supported by oxygen-rich foam produced by the male. Diameter and height of the nest average 30 and 6 cm, respectively. The nest is the centre of a territory that is vigorously defended by the male, using its enlarged pectoral spine, against conspecific and heterospecific intruders. The number of nests that did not acquire spawns (48 %) suggests a strong competition among males for females. There are indications that the female drinks the sperm and that fertilization takes place after the sperm has passed through her digestive tract. *Hoplosternum littorale* is a multiple spawner. Investment in reproduction is high in females since they can spawn up to 14 times during a 7-month breeding season and each spawn consists of 6 000 to 9 000 eggs. On average, two to four females spawn simultaneously, resulting in an average number of 20 000 eggs per nest. Incubation of the eggs takes two to three days depending on the temperature in the nest. Despite intense predation pressure on eggs and larvae, the guarding behaviour of the male extends for only one or two days after hatching. In the hypoxic water of tropical swamps, the main function of the floating bubble nest appears to be to provide oxygen to the developing eggs by lifting the eggs above the water surface while protecting them from desiccation. Other functions of the nest may be protection of the brood against predators, temperature regulation, identification of the centre of the territory and synchronization of reproductive activities. We suggest that *H. littorale* may be a useful model for the study of the reproduction of tropical freshwater fish in hypoxic environments. © Ifremer/Elsevier, Paris

Tropical swamps / hypoxic environment / reproduction / foam nest / fecundity / multiple spawning / parental care / Siluriformes / *Hoplosternum littorale* / Guianas

Résumé – Biologie de la reproduction de l'atipa *Hoplasternum littorale* (Siluriformes, Callichthyidae). Rôle du nid de bulles. Une caractéristique biologique essentielle de l'atipa est la construction d'un nid de bulles et d'herbes à la surface de l'eau. L'étude du rapport gonado-somatique (GSI) et le suivi des nids construits dans les bassins et les marais ont montré que la maturité sexuelle est atteinte dès l'âge de 1 an et que l'entrée en reproduction de l'atipa coïncide avec le début de la saison des pluies. Il existe un dimorphisme sexuel marqué. Ce sont les mâles, plus gros que les femelles, qui initient la construction du nid la nuit. La ponte ayant lieu le lendemain vers 12 h 00. La plupart des nids (30 cm de diamètre et 6 cm de hauteur) sont construits dans des zones fraîchement inondées, en bordure des marais. Le plus souvent espacés d'une dizaine de mètres, ils sont constitués d'un dôme d'herbes reposant sur un tapis de bulles produit et entretenu par le mâle. Centre d'un territoire, chaque nid est défendu agressivement par un mâle contre tout intrus (y compris les femelles qui viennent d'y pondre) ; l'importante proportion de nids sans ponte (48 %) suggère d'ailleurs une forte compétition entre les mâles pour la reproduction. Il est possible que la fertilisation des œufs n'ait lieu qu'après que le sperme bu par la femelle ait traversé la totalité du tube digestif. L'atipa est un poisson à pontes fractionnées. L'investissement

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des femelles dans la reproduction est important, puisqu'il peut atteindre 14 pontes comprenant de 6 000 à 9 000 œufs au cours d'une saison de reproduction s'étendant sur 7 mois. En moyenne, ce sont de deux à quatre femelles qui pondent environ 20 000 œufs dans chaque nid construit par un mâle. Selon la température dans le nid, l'incubation des œufs dure de 2 à 3 j et malgré une forte préda- tion sur les œufs et les larves, le comportement de garde du mâle ne s'étend pas au-delà de 48 h après l'éclosion. Dans les eaux hypoxiques des marais tropicaux, le rôle essentiel du nid d'herbes et de bulles serait de placer les œufs dans un milieu oxygéné au- dessus de la surface de l'eau, tout en les protégeant du dessèchement. D'autres fonctions possibles du nid sont mises en évidence : la protection de la descendance contre les prédateurs, la régulation de la température d'incubation, la matérialisation du centre d'un territoire et la synchronisation des activités de reproduction. En conclusion, nous suggérons que ce poisson constitue un modèle inté- ressant pour l'étude de la reproduction des poissons tropicaux d'eau douce vivant dans des milieux hypoxiques. © Ifremer/Elsevier, Paris

Marais tropicaux / milieu hypoxique / reproduction / nid de bulles / fécondité / pontes fractionnées / soins parentaux / Siluriformes / Hoplosternum littorale / Guyanes

1. INTRODUCTION

Hoplosternum littorale [23] ('tamuata' in Brazil, 'atipa' in French Guiana, 'hassar' in Guyana, 'kwikwi' in Suriname, 'cascadu(ra)' in Trinidad, 'busco' or 'cur- rito' in Venezuela) is a valuable resource extensively fished in the deltas of the Amazon [67] and the Orinoco [49]. In French Guiana, Suriname and Trin- idad, *H. littorale* is an extremely popular food fish and trials for its culture have been conducted [26, 39, 45, 55, 56].

Hoplosternum littorale is a medium-sized armoured catfish of the family Callichthyidae. Growth is rapid with 3 day-old larvae reaching a weight of 12 g in 45 days [26]. Adults measure 16–30 cm (total length) and weigh 100–300 g; males may exceptionally reach 450 g [54]. The diet of *H. littorale* consists mainly of benthic invertebrates and detritus [46, 72]. Callichthyid catfish can be distinguished from all other fish by their body armour consisting of two longitudinal rows of bony plates covering each side of the body [7, 25, 62]. Of the six genera composing the family Callichthyidae (*Aspidoras, Brochis, Corydoras, Callichthys, Dianema* and *Hoplosternum* [14, 22], but see [58, 65]), *Corydo- ras* is the best known as it includes many species of interest to aquarists.

Living in tropical standing waters along with other fish species like *Aequidens* (*Krobia*) sp., *Astyanax* sp., *Crenicichla* sp., *Electrophorus electricus, Gymnotus carapo, Hoplerythrinus unitaeniatus, Hoplias mala- baricus, Lepidosiren paradoxa, Polycentrus schom- burgki, Serrasalmus* sp. and *Synbranchus marmoratus* [17, 42, 48], *H. littorale* is widely distributed in the neotropics. A detailed examination of collecting local- ities in South and Central America [45] revealed that *H. littorale* is not found in rainforest creeks and clear- water rivers draining the Precambrium Guyana and Brazilian Shields, where water is extremely poor in dissolved minerals. *Hoplosternum littorale* is restricted in its distribution to the swamps of (sub)tropical South America and the floodplains of Amazonian white- water rivers originating in the Andes.

The aquatic environment of tropical swamps and floodplains is characterized by low levels of dissolved oxygen and markedly seasonal conditions caused pri- marily by fluctuations in rainfall [16, 28, 38, 70]. In such an hypoxic environment, *H. littorale* has devel- oped morphological, physiological and behavioural adaptations: the building of a floating bubble nest [17, 20, 41, 44, 68], synchronous air breathing [10; see also 36], two functional hemoglobin components [19, 71], and secondary intestinal respiration [17; see also 30]. The respiratory air probably passes through the intes- tine [17] as it does in related callichthyid catfish [30].

The building and guarding of an elaborate floating bubble nest (*figure 1*) is one of the most distinctive fea- tures of the reproductive biology of *H. littorale*. Described for the first time by Vipan in 1886 [68], this behaviour has recently raised much interest [20, 27, 44, 50]. On the assumption that predation and the availability of oxygen are the main factors determining the mode of reproduction in fish, Balon created the 'aphrophilic reproductive guild' for fish that build and guard a floating bubble nest [5]. The aphrophils include fish of widely different geographical distribu- tion that are only distantly related to each other [44]: Belontiidae (*Betta, Colisa, Macropodus*) and the syn- branchiid eel *Monopterus alba* in Asia, *Ctenopoma* (Anabantidae), *Polycentropsis* (Nandidae) and *Hepse- tus odoe* (Hepsetidae) in Africa, and Callichthyidae (*Callichthys, Dianema* and *Hoplosternum*) and the electric eel *Electrophorus electricus* [2] in South America.

Recent research on *H. littorale* in fish ponds in French Guiana [e.g., 27–29, 39,50] and in natural hab- itats in Suriname [e.g., 44–48] has considerably increased our knowledge on this fish. There currently exists more information on *H. littorale* than for a vast majority of neotropical fish. Here, we provide a syn- thesis of the present state of knowledge of the repro- ductive biology of *H. littorale* then consider the function of the floating bubble nest and identify topics in need of future research.

2. THE TIMING OF REPRODUCTION

2.1. Age at first maturity

On Trinidad, spawning of *H. littorale* is restricted to a contracted rainy season in June-August [61]. Males and females usually attain sexual maturity after one
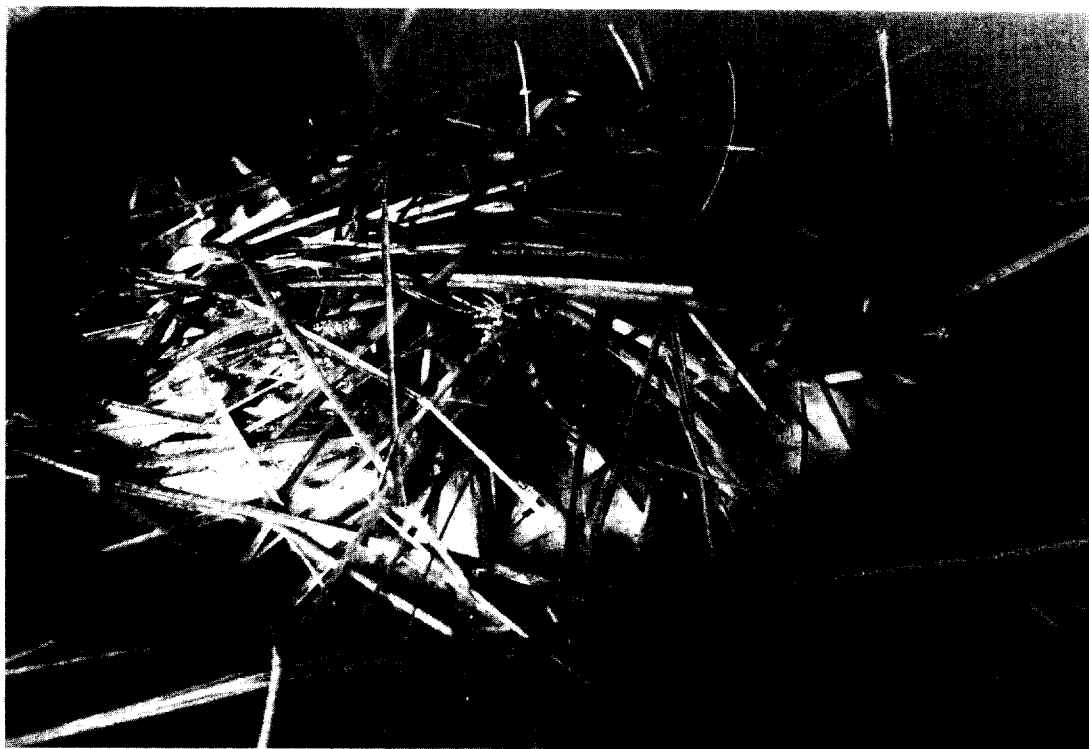
Figure 1. Photograph of a large floating bubble nest of *H. littorale*.

year and were ready to reproduce during the following rainy season. In ponds of French Guiana, nesting and spawning commonly occurred in 1 year olds; spawning has also been observed in fish no older than 9 months [50].

2.2. Seasonality of reproduction

Seasonality in tropical environments is caused primarily by fluctuations in rainfall [38, 63, 70]. The annual reproductive cycle of *H. littorale* has been studied by analysis of the Gonado-Somatic Index (GSI) in Trinidad [61], French Guiana [28] and Brazil (Marajo island, Para; [67]), and by recording the appearance of nests in Trinidad [61], Venezuela [41] and Suriname [47]. Maximum GSI values of female *H. littorale* (12–15 %) were found in the first months of the rainy period immediately succeeding the main dry season (July in Trinidad; December-January in French Guiana; January-February in Brazil). The time-lag between gonad maturation in Trinidad, French Guiana and Marajo (Brazil) was related to the annual translation of the Intertropical Convergence Zone [28], suggesting that the synchronization between peak GSI values and peak rainfall is a general phenomenon in *H. littorale*.

Although maximum GSI values occurred in the first months of the rainy season, the building up of the gonads was always associated with the latter part of the dry season, prior to the onset of rain [28]. The large

visceral fat deposits characteristic of adult *H. littorale* in the first months of the dry season [46, 72] are probably used in the development of the gonads. The high GSI values in the last months of the dry season show that neither rainfall nor a rise in water level can account for the initiation of vitellogenesis in *H. littorale*.

Hyder [31] and Schwassmann [60] suggested that the onset of rainfall could trigger final oocyte maturation and initiate spawning in tropical fish. Possible spawning cues associated with rainfall are changes in water chemistry, especially a decrease in conductivity [34], and changes in water level. In *H. littorale*, nest building and spawning could be induced in the laboratory by reducing the conductivity of water [57]. Increasing the water level in the tanks without any change in conductivity had no effect on nest building. However, field studies of nesting in *H. littorale* in Suriname [47] and Trinidad [61] showed that nest construction only took place when rainfall was sufficient to raise the water level in the swamps by approximately 30 cm. We suggest that *H. littorale* needs this minimum water depth in the swamp to gain access to its spawning sites.

The swamps in Suriname are usually flooded twice each year and nesting of *H. littorale* peaked during both rainy seasons of January-February and April-June [47]. Interestingly, analysis of GSI showed that in French Guiana, spawning of *H. littorale* probably did not take place in the April-June rainy season, although rainfall data indicated that the water level in the

swamps was suitable for nesting [28]. Mol [47] suggested that, following the first flooding of the swamps after the main dry season of September-November, environmental conditions for the newly hatched larvae (water quality, food, competition, predation) deteriorate with continuing inundation of the swamps. When environmental conditions were kept favourable in experimental fish ponds in French Guiana, nests of *H. littorale* were observed from January until June [50]. In Suriname, rainfall is not reliable in the January rainy season [63], and a reproductive strategy based on a single breeding season in January (as observed in French Guiana) risks the total failure of reproduction in years with deficient rainfall.

2.3. Diel pattern of nest construction, spawning and hatching

According to Vipan [68], the first to describe the building of a floating bubble nest by male *H. littorale* in his aquarium, construction of the nest started at night and was finished the next day. In swamps, nests were also built during the night [44, 61]. In experimental fish ponds, nest building started between 20:00 and 24:00 hours ([39], Hostache, pers. obs.).

Vipan [68] mentioned spawning of *H. littorale* in his aquarium on the day following the night of nest construction. In the swamps of Trinidad [61] and Suriname [44], spawning of *H. littorale* occurred around noon. In fish ponds in French Guiana, 52 % of spawnings occurred between 11:00 and 13:00 hours [51]. Where feeding and locomotor activity of *H. littorale* is restricted mainly to night and twilight hours [9, 10], it is of interest to note that spawning occurred during the day. Surinamese fishermen are well acquainted with the timing of spawning of *H. littorale* and catch both male and female(s) during the act of oviposition by positioning a bottomless basket over the nest as soon as they notice the nest shaking [44].

The exact time of hatching of the larvae of *H. littorale* is variable, depending on the nest temperature during incubation. However, in the swamps of Suriname hatching usually occurred late in the morning or in the afternoon of the third day after oviposition ([44]; *figure 2*). In fish ponds, an average energy of 1 400 to 1 450 °C·h is needed for hatching [27].

3. THE SITE OF REPRODUCTION

The lack of (or limited) mobility of eggs and early free-living stages of fish makes them vulnerable to both unfavourable abiotic conditions and attack by predators. Consequently, the nature of the spawning site and the nest determine to a large extent the intensity and nature of the hazards that eggs and larvae encounter [53, 74]. Foremost among the potential hazards for early stages of fish are lack of oxygen, siltation, infection, temperature extremes, and predation [5, 53, 74]. The floating bubble nest itself is important

in providing oxygen to the eggs by positioning the eggs above the water surface as well as protecting them from other hazards.

Prior to spawning, most neotropical swamp fish move laterally from their dry season habitat of creeks, canals or deep pools into flooded swamps [38, 42]. In Surinamese swamps, nests of *H. littorale* were not constructed at random, but built at apparently preselected sites within the fish's habitat: most nests were observed in newly flooded swamps and only a few were built in deep canals [47]. The swamps provide abundant food and space for young fish [38, 70], and possibly a habitat with reduced predation pressure [48]. Within the swamp habitat, nests were especially abundant in shallow, open water at the edge of emergent vegetation in the peripheral area of the swamp [47]. Dense stands of emergent aquatics like *Typha* or *Eleocharis* in the central region of the swamp were avoided as nesting habitat. In fish ponds [51] and rice fields (Mol, pers. obs.), nests of *H. littorale* were often observed near the dikes and attached to a clump of grass. In natural swamps and in ponds, nests were generally built at a minimum distance of 10 m from each other [44, 51], but in rice fields nests were sometimes found at a distance of only 3 m from each other [44].

4. SECONDARY SEXUAL CHARACTERS

Males *H. littorale* grow to a larger size than females [26, 41, 61, 72]. A striking sexual dimorphism in the pectoral fins of *H. littorale* exists during the breeding season (rainy season), when males *H. littorale* develop an elongate, recurved pectoral spine (*figure 3*) [25, 41, 61, 67, 72]. In addition, the male pectoral spine may assume a reddish colour at that time [41, 61] and thick fat deposits may develop in the pectoral fin ([72], pers. obs.). Although most growth of the pectoral spine occurs in the first 4–5 months after hatching, osteogenesis is enhanced in a specific region of the male pectoral spine at the end of the dry season [8]. The enlarged pectoral spine is used as a weapon by males during the defence of the floating bubble nest [72].

5. REPRODUCTIVE BEHAVIOUR

5.1. Nest construction

The behaviour of male and female *H. littorale* during courtship, nest building, spawning and parental care was described in some detail by Gautier et al. [20] after observations in aquariums. The floating bubble nest is constructed by the male, but females may (or may not [61]) stimulate the male during nest building. The process of nest building begins with the production of bubbles at the water surface by the male. Females may also add some bubbles to the nest under construction [1, 20, 61]. Observations of the production of foam by males differ among authors. Lowe-McConnell [37] observed that bubbles were expelled

from the anus and worked into the nest with the pelvic fins with the male swimming inverted (ventral side directed to the surface) below the water surface. Singh [61] also noted that a few bubbles were extruded from the anus, but these were generally not directed towards the nest. Both Singh [61] and Andrade and Abe [1] held that the foam in the nest was produced by first gulping air and then producing bubbles through both operculi. According to Gautier et al. [20], bubbles were produced through the mouth. The fact that amylase activity (110 units·L^{-1}, n = 2; Mol, unpubl. data) has been detected in the foam of nests of *H. littorale* might throw some light on this question.

In the next stage of the process, the male adds plant materials to the bubbles at the water surface [1, 20]. Using vigorous lateral strokes of his tail fin, males first create upward water currents that lift plant materials from the bottom of the tank [20]. The plant material is then carried to the water surface using the extended pectoral fins, the spine held perpendicular to the body [20]. Once arrived at the water surface, the body is inverted and the plant material is placed in the nest. At the same time, the male adds bubbles to the nest to keep the plant material floating.

Descriptions of the nests of *H. littorale* in the Paraguayan Chaco [17], the Venezuelan llanos [41] and the swamps of Trinidad [61] and Suriname [44] differ only in minor details. The nest of *H. littorale* consists of a dome of dead or dying plant material, particularly grasses (e.g., *Hymenachne amplexicaulis*, *Paspalum repens*), *Typha* sp., *Thalia* sp., filamentous algae and floating aquatics (e.g., *Azolla*, *Pistia*, *Salvinia*, Lemnaceae) (*figures 1*, *3*). Fresh grass is occasionally used as nest material, prompting Singh's [61] question as to how such materials might have been cut. Filamentous nest materials are preferred and these are firmly knitted together in the nest by the male. The mass of eggs is positioned in the centre of the nest under the dome of plant material. The thickness of the plant cover is 2 to 3 cm. Diameter and height of the nest average 30.0 ± 5.0 cm (mean ± SE) and 6.0 ± 0.4 cm, respectively [44]. Below the eggs and covering the whole of the underside of the nest is a mass of foam, which keeps the nest in shape and floating on the water surface. The eggs are positioned above the water surface (*figure 3*) and not in contact with the oxygen-depleted swamp water. The diurnal fluctuation of dissolved oxygen was 0.5–3 mg·L^{-1} in the swamp water and 6.5–7.5 mg·L^{-1} in nest foam [44].

5.2. Territorial defence

Male *H. littorale* vigorously defend the area around their nest from both conspecific and heterospecific intruders [17, 41, 44]. Although feeding and locomotor activity are mainly nocturnal in non-breeding *H. littorale* [9, 10], territorial defence is maintained both day and night (Mol, pers. obs.). Once spawning has been completed, the male also attacks females that have deposited their eggs in the nest [20, 61, 68]. The

aggressive attack of *H. littorale* consists of a rapid propulsion of the body in forward direction followed by a sharp lateral turn, resulting in an abrupt contact between the pectoral spine and the intruder [72]. This swimming motion also causes the rough outer surface of the spine to be dragged across the target producing significant abrasion. After each attack, the male immediately returns to his accustomed position below the nest and starts to patrol the area surrounding it [20].

Territoriality in fish is often associated with a limited availability of spawning sites [6] and an increased probability of paternity for male guards [52, 66]. In *H. littorale*, the defence of the nest territory has also been associated with the protection of the brood against predators [47, 72]. Although defence of nests that did not contain eggs has been observed occasionally in Surinamese swamps (Mol, unpubl. data), the aggressive guarding behaviour of the male is much more pronounced after eggs have been deposited in the nest. With 74.5 % of the nests containing eggs, it was possible to catch the guarding male with a scoop-net by provoking an attack by stirring the water surface alongside the nest with a small stick [44]. By measuring the maximum distance from the nest where an attack could still be provoked, it was possible to define the territory of *H. littorale* as a circle with a radius of 57 ± 7 cm (mean ± SE) and the nest as its center [44]. Preliminary results with marking of nest-guarding males suggested that males did not maintain their territory throughout the breeding season; although on one occasion, a male constructed two successive nests at the same spot using the same nest materials [44]. The guarding behaviour of males is only extended for 1–2 days after hatching.

5.3. Courtship and mating

Courtship probably functions in species recognition, mate choice, mutual orientation to the spawning site, and synchronization of the activities of males and females [74]. Since males *H. littorale* strongly defend their floating bubble nest against intruders, courtship may also serve to minimize aggressive interactions towards potential mates [33]. Gautier et al. [20] give a detailed account of the courtship and mating in *H. littorale* based on aquarium observations of isolated male-female couples. Although they describe courtship as the formation of a male-female couple, it should be noted that in nature, several females spawn simultaneously in one nest [44]. Here, we define simultaneous spawning as sequential spawning with multiple females.

Pair formation in *H. littorale* is closely associated with the building of the bubble nest and consists of the following components [20]:

– parallel swimming of male and female,

– male and female facing each other (barbels make contact),

– stimulation of the flanks of the male by the female,

– swimming to the surface by male and female and production of first bubbles at the location of the future nest,

– adding further bubbles to the nest under construction.

In Surinamese swamps, 48 % of the nests never acquire eggs [47, 50]. Thus, in nature, nest building seems to precede courtship and the last two components may either not occur during courtship or involve a completed nest. The high percentage of nests that did not acquire spawns in swamps [47] and in fish ponds [50], suggests a strong competition among males for females.

The behavioural sequence culminating in spawning and fertilization of the eggs is initiated by female *H. littorale* stimulating the flanks of the male [20]. After repeated stimulation, the male accepts the contact of the mouth of the female with his genital opening and the "T" position is formed [14, 20]. While in the "T" position, the female collects the sperm in her mouth. After a few seconds, the female descends to the bottom of the tank where she stays motionless for 30–60 s, head up, her body at a 45° angle from the horizontal plane. Next, the female swims to the nest, turns upside down, and, plunging her abdomen in the foam of the nest, starts to deposit small batches of eggs while spreading her pelvic fins and shaking her abdomen [20]. The whole sequence of actions is repeated several times until spawning is completed.

There is some controversy as to when and where the eggs are fertilized in *H. littorale*. Until recently it has been assumed that fertilization took place when the female simultaneously releases the sperm (held in her mouth) and the eggs (held between her pelvic fins) in the foam nest [20]. However, Kohda et al. [35] have shown that in the callichthyid *Corydoras aeneus* females directly drink sperm from the male's genital opening and that the sperm passes through the intestine before it is discharged together with the eggs into the 'pouch' formed by the pelvic fins. This unique reproductive behaviour ensures that the eggs are fertilized with maximum efficiency in an enclosed space by the non dispersed sperm. In *H. littorale*, the female rests approximately 30–60 s on the bottom of the tank after drinking the sperm and we suggest that this may be the time it takes for the sperm to travel through the intestine from the mouth to the anus.

5.4. Parental care

In teleost fish, the construction and defence of a nest occurs in many families [12, 53]. All species belonging to the aphrophilic reproductive guild [5] continue parental care after construction of the floating bubble nest and spawning [44]. This additional parental care always includes guarding and maintenance of the nest and sometimes removal of eggs infected with micro-organisms and defence of newborn larvae. In the subfamily Callichthyinae (*Callichthys*, *Dianema*, *Hoplosternum*) parental care is by the male [44]. Male *H. littorale* tends their nest during the three days of egg incubation (*figure 2*). In Surinamese swamps, males regularly supplied fresh foam to the nest [44]. When the guarding male was removed from the nest, the nest flattened out on the water surface and the eggs rapidly deteriorated after coming into contact with the hypoxic swamp water [44]. A 24-hour observation revealed that guarding and maintenance of the nest occurred day and night (Mol, unpubl. data).

In spite of the vulnerability of the larvae to aquatic predators [48], male *H. littorale* extended their guarding behaviour for only one or two days after hatching [50]. The guarding of the 10 000–23 000 larvae that hatch from one nest [41, 44, 61] may not be feasible, the more so as the larvae need to disperse in order to avoid food depletion at the nest site. Two days after hatching, the yolksac is completely absorbed [40, 46, 56] and the larvae start feeding on exogenous food.

6. FECUNDITY

When discussing the fecundity of fish, it is important to take into account the pattern of egg development and spawning [3, 74]. In total spawners, females shed all the eggs that they will spawn in a breeding season over a very short time interval. Maximum GSI values just prior to spawning are often high in such fish (20–30 %). Other species are batch spawners ('partial' or 'multiple' spawners): the eggs are spawned at intervals throughout the breeding season and maximum GSI values of spawning females vary from 2–14 %. Tropical freshwaters include numerous batch spawners [38], among them *H. littorale* [50, 61]. The number of eggs that a female spawns over a definite time period depends on both the number of eggs per spawning and the number of spawnings [3]. Following Wootton [74],
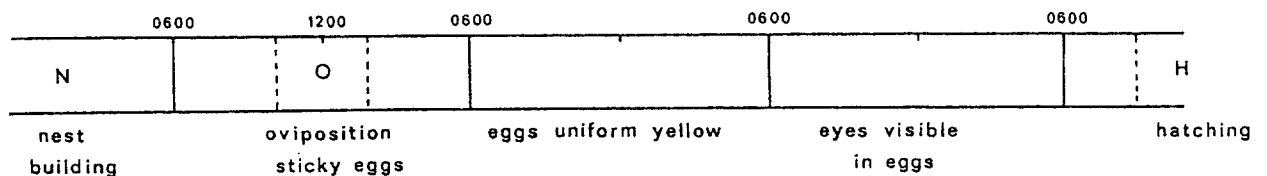
0600	1200	0600	0600	0600	
N		O				H
nest building	oviposition sticky eggs	eggs uniform yellow	eyes visible in eggs		hatching

Figure 2. Time schedule of nest building, spawning and hatching in *H. littorale* in Surinamese swamps ([44] reprinted with kind permission of Kluwer Academic Publishers).

we distinguished batch fecundity, breeding season (annual) fecundity, and lifetime fecundity.

6.1. Batch fecundity

In fish ponds, *H. littorale* can spawn more than ten times during a 6-month breeding season [50]. The number of eggs produced per spawning is difficult to determine in the field as several females spawn simultaneously in one nest [41, 44]. Batch fecundity of *H. littorale* has been estimated in nature by counting the number of ripe ova in the ovaries [41, 44] and in fish ponds by counting the number of eggs per spawning in couples isolated in cages [50].

In determining the batch fecundity of *H. littorale*, Machado-Allison and Zaret [41] and Mol [44] distinguished ripe ova (diameter 1–1.2 mm) from immature eggs (diameter < 1 mm). Estimates of fecundity that do not distinguish between ripe and immature ova [61, 67] are difficult to interpret. In teleosts, the relationship between batch fecundity (*F*) and fish length (*L*) typically takes the form: $F_{batch} = a.L^b$ [3]. When fitting the data presented by Machado-Allison and Zaret [41] and Mol [44] to this model, the relationship between fecundity and standard length in *H. littorale* is described by $F = -1.59.L^{2.49}$ (n = 54, r = 0.524, *P* < 0.0001). With isolated pairs in fish ponds, females weighing on average 90 and 207 g produced 6 675 and 9 200 eggs per spawning, respectively [50]. Approximately 6 900 ripe ova were counted in the ovaries of 100 g females from Surinamese swamps [44].

6.2. The number of eggs and spawnings per nest

The average number of eggs per nest of *H. littorale* was 10 200 (2 000–22 800) in Trinidad [61], 17 100 (5 600–55 300) in Venezuela [41] and 23 340 (3 888–51 981) in Suriname [44]. In fish ponds, nests contained 16 350 (1 135–61 760) eggs [50]. Taking into account the mean batch fecundity of *H. littorale*, it may be estimated that on average 2–4 females spawn in a nest [41, 44]. Up to 8 females may have spawned in a nest with 60 000 eggs. In ponds, 49 % of the nests contained eggs that were spawned by at least 2 females [50].

When the nests of *H. littorale* are compared to the nests of the closely related *H. thoracatum* and *Callichthys callichthys*, some striking differences become evident [44]. Although the nests of all three species usually received their eggs from more than one female, only nests of *H. littorale* show the eggs always at the same developmental stage. The life span of the nests of *H. littorale* was also relatively short and varied little compared to thoses of *H. thoracatum* and *C. callichthys*. Mol [44] concluded that in nests of *H. littorale*, spawning (and hatching) occurred simultaneously, while in nests of *H. thoracatum* and *C. callichthys* eggs were spawned continuously over several days. The observation that Surinamese fishermen often catch both the male and several females during oviposition,

by placing a bottomless basket over the nest when they notice the nest shaking, reveals that spawning by multiple females is really simultaneous in *H. littorale* [44].

6.3. Multiple spawnings and breeding season fecundity

The observation that 15 % [44] to 21 % [41] of the ova in the ovaries of female *H. littorale* were immature (< 1.0 mm) suggests that *H. littorale* is a batch spawner. The number of spawnings during a breeding season is probably determined by environmental factors such as food availability, pH and changes in water level. Information on the number of spawnings per breeding season is difficult to obtain in the field, but a study with isolated couples of *H. littorale* in fish ponds [50] gives a good idea of the number of spawnings that females can achieve in one breeding season. One-year old females (90 g), reproducing for the first time, produced on average 6.6 spawnings per female per breeding season (December to August). One female even produced 14 spawnings. The average time interval between two successive spawnings of a female was 10.4 days. A second group of larger females (age unknown; average weight 207 g) produced on average 5.2 spawnings per female per breeding season. Three females of this group spawned 10 times and one female 14 times. The average time interval between two successive spawnings was 14.8 days. Pooling the results from both groups, female *H. littorale* spawned on average 5.5 times in a breeding season.

In their experiment with isolated pairs in fish ponds, Pascal et al. [50] also determined the breeding season fecundity. Each morning, the new spawns were removed from the nest and weighed. The number of eggs was determined for each spawn by dividing the weight of the spawn by the weight of an individual egg (3.7 mg, n = 55; [50]). The breeding season fecundity was determined by the total weight of the spawns that were produced during the 6-month breeding season. In one breeding season, females weighing 100 g and 200 g spawned 48 600 eggs (n = 7) and 91 900 eggs (n = 3), respectively.

Male *H. littorale* not only mate with several females in each nest, but also construct several nests per breeding season. The latter point is illustrated by the experiments of Pascal et al. [50] with isolated pairs and by preliminary observations of marked males in Surinamese swamps [44].

6.4. Lifetime fecundity

Lifetime fecundity depends on breeding season fecundity and life span. The longevity of *H. littorale* in nature was estimated at 4 years [61]. If female *H. littorale* spawn 48 600 eggs in their first year and 91 900 eggs in their second, third and fourth year [50], the lifetime fecundity may amount to 324 300 eggs.

7. PARENTAL INVESTMENT AND ALLOCATION TO INDIVIDUAL PROGENY

The allocation of time and material resources to reproduction differs among males and females in *H. littorale*. Males must allocate resources to the development of the enlarged pectoral spine, the testes, sperm production and to the building and defence of the floating bubble nest. In addition, males spend approximately five days at nest building and guarding of eggs and new-born larvae (*figure 2*). In fish ponds, males weighing 290 g at the start of the breeding season lost 9 % of their initial weight during the 6-month breeding season, while males weighing 185 g lost only 0.4 % of their initial weight [50].

The main investment of females in reproduction consists of the production of eggs (size, energy content and rate of turnover of the ovaries). The production of eggs per breeding season by female *H. littorale* may amount to 170–180 % of the body weight [50]. These values may be compared to production of eggs in other batch spawners: 50 and 250 % in *Gobius paganellus* and in *Pomatoschistus microps*, that spawn twice and six times per breeding season, respectively [43], 120–200 % in *Hyphessobrycon pulchripinnis* [15], and 200–300 % in *Gasterosteus aculeatus* [73]. However, it should be noted that Pascal et al. [50] weighed spawned (hydrated) eggs (diameter 1.82 mm, [44]), while investment in gonads is determined by the weight (and chemical composition) of the mature ova prior to spawning (diameter 1.2 mm, [41]). In fish ponds, females weighing 89 and 207 g lost 9.7 and 23 %, respectively, of their initial body weight during a 6-month breeding [50]. The major weight loss of females during the breeding season attests to the large investment in reproduction that is characteristic of batch spawners [15].

The way in which the material in the female gonad is divided into a few large eggs or many small eggs is important to the new-born larvae. Large eggs generally produce large larvae which have a better chance of survival than small larvae [3, 69]. Allocation of material resources to individual progeny is governed by the contribution of the female to the fertilized egg, and this is reflected in the size and the quality (chemical composition) of the egg. The diameter of the fertilized egg of *H. littorale* is 1.5 mm according to Machado-Allison [40] and 1.82 mm according to Mol [44]. The weight of the eggs is 3.7 mg according to Pascal et al. [50] and 3.2 mg according to Mol [44]. The chemical composition of the fertilized eggs of *H. littorale* was 12.52 ± 0.62 % protein (wet weight basis; mean ± SD, n = 10), 1.95 ± 0.38 % lipid (n = 8) and 1.00 ± 0.20 % ash (n = 5; Mol, unpubl. data). New-born yolksac larvae (free embryos) measure about 6 mm TL (total length) and weigh 2.5 mg (Mol, unpubl. data; see also [40, 56]).

## 8. THE FUNCTION OF THE FLOATING BUBBLE NEST

The complex reproductive behaviour of *H. littorale* revolves around the building and guarding of the floating bubble nest. Nests of fish have a number of important functions [50], some of which are not necessarily improved by the structure of the floating bubble nest. The nest may function as a focal point of territorial activity, a site for attracting mates and a spawning site. The nest may also stimulate ovulation in females, increase the probability of paternity and facilitate multiple spawning and parental care.

In the animal kingdom, foam nests are built by insects [59], frogs [18], and fish [5, 44]. Richards and Davies [59] suggest that the foam of insect foam nests protects eggs and nymphs from predation by lizards and birds and from desiccation in the sun. The foam nest of frogs is associated with a progressive evolutionary trend towards terrestriality and the avoidance of aquatic predators of eggs and larvae [24]. Eggs of amphibians (and fish) lack the protective amnion membrane and calcareous shell that prevent desiccation of reptiles and birds' eggs in arid terrestrial environments. By providing a humid environment for the amphibian egg, the foam nest makes deposition of the eggs out of the water possible [18, 24]. The hardening of the outer surface and the high viscosity of the foam may also protect the frog eggs from terrestrial predators. The main function of the foam nests of fish is probably the supply of oxygen to the developing eggs [17, 44], but other functions have also been proposed [5, 27, 41, 44].

8.1. Oxygen supply to the eggs

Bagenal and Braum [4] consider oxygen, temperature and waterflow, ecological features of fundamental importance for the development and survival of fish eggs. There is a close relationship among these parameters. In mountain streams with a strong current, oxygen is continuously supplied to the developing eggs (e.g., salmonids). In standing waters, fish can create a current over their eggs by fanning their fins (e.g., cichlids). In tropical swamps, high temperatures and decaying organic materials create an hypoxic environment [16]. Most, if not all, fish that construct floating bubble nests live in tropical, oxygen-depleted standing waters [44]. The floating bubble nest of *H. littorale* supplies oxygen to the eggs by lifting them (specific gravity > 1.0, [44]) out of the hypoxic swamp water and into the air ([44]; *figure 3*). The foam and the thick cover of plant materials keep the eggs moist. Removal of the guarding male results in the flattening of the nest on the water surface and deterioration of the eggs after contact with oxygen-depleted swamp water [44]. The oxygen-rich foam, regularly replaced with fresh foam by the guarding male, may also function as an oxygen reservoir for the eggs since dissolved oxygen concentrations in the swamp water (0.5–3 mg·L^{-1}) are well
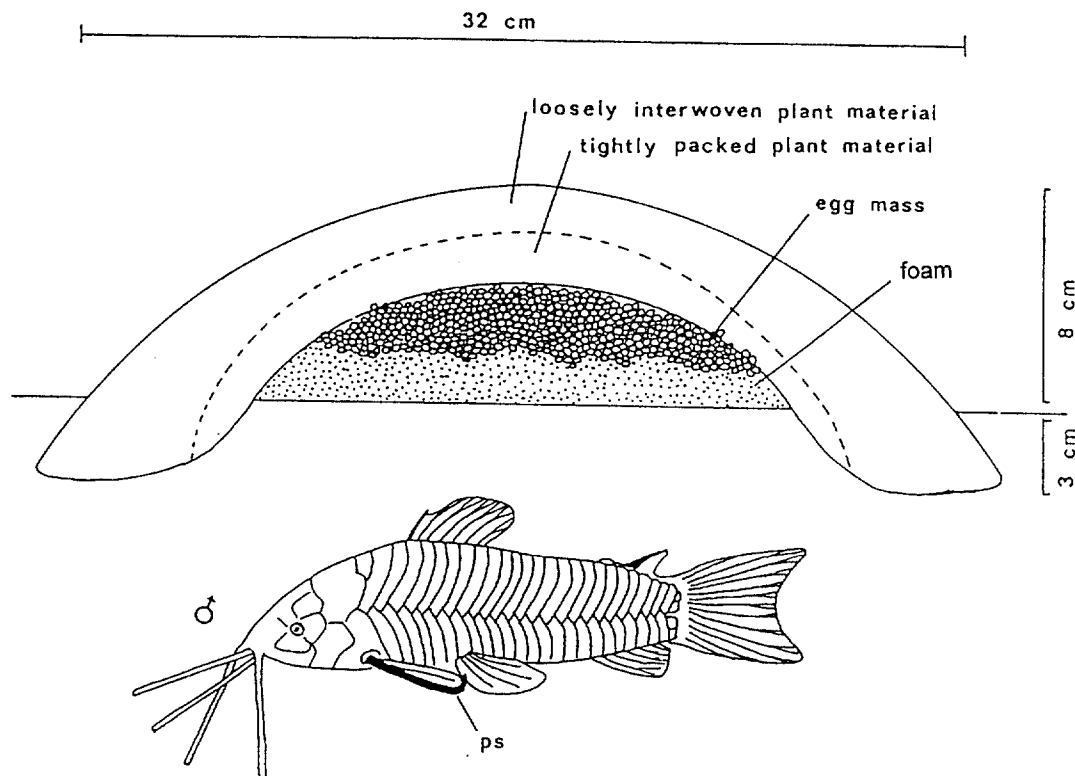
Figure 3. Drawing of a cross-section through a *H. littorale* nest. Also shown is the guarding male (not drawn to scale) with an enlarged ski-like pectora spine (ps), (Mol [44] reprinted with kind permission of Kluwer Academic Publishers).

below oxygen concentrations in nest foam (6.5–7.5 mg·L^{-1}) [44].

8.2. Thermal properties of the bubble nest

Using conical incubators with a continuous supply of oxygen, Hostache et al. [27] found that the minimum hatching time of eggs of *H. littorale* (36.4 h) was associated with an incubation temperature of 33.6 °C, but that a constant temperature of 38 °C proved lethal to the developing eggs. When temperatures in the nest of *H. littorale*, in the swamp water around the nest and in the air above the nest were measured during a 24-hour period, it appeared that the diurnal fluctuation of the temperature in the air was, to some degree, dampened by the nest [44]. However, in fish ponds emptied of aquatic vegetation, very high nest temperatures were recorded in daytime resulting in diurnal fluctuations of up to 11 °C [27]. The average incubation time of 51 h recorded in the ponds was also relatively short compared with the 72 h incubation in Surinamese swamps ([44]; *figure 2*). The aquatic vegetation surrounding the nest in the swamp and the large quantities of nest material used in nature can probably account for the dampening of extreme temperatures. However, Gorzula [21] demonstrated a cooling effect of the foam of leptodactylid frogs' nests and stressed the role of this foam in the dampening of extreme temperatures in nests

exposed to intense sunlight. If exposure to temperatures above 36 °C is lethal to eggs [27], prevention of such extreme temperatures, common to swamps, seems important. In addition to cooling the nest in daytime, the foam may also keep the nest temperature from falling at night, hence speeding up the development of eggs.

The brooding effect of the structure of *H. littorale*'s nests, as revealed by the high nest temperatures measured in ponds [27], could accelerate the embryonic development in eggs and be responsible for the shifts in sex-ratios recorded in ponds [29, 39].

8.3. Protection against predators

Balon [5] states that two factors play a leading role during embryonic development of fish eggs: predation and the availability of oxygen. The potential impact of 24 aquatic predators on early stages of *Hoplosternum* was large in Surinamese multi-predator swamps [48]. Aquatic invertebrates (snails, water bugs, Odonata nymphs) and small fish are important predators of eggs and larvae. Odonata nymphs are also important predators of *H. littorale* larvae in fish ponds of French Guiana [26]. All fish nests guarded by one or both parents probably offer some protection against predation, but the structure of the floating bubble nest of *H. littorale* does not necessarily improve this protective function.

The floating bubble nest places terrestrial predators, such as egrets and snakes, in a favourable position to prey upon the eggs (observations of Surinamese fishermen). The foam of *H. littorale* nests do not have the stickiness and consistency of frog nest's foam (Mol, pers. obs.) and probably does not offer protection against predators. Although the rich invertebrate fauna of the nests of *H. littorale* [44] indicates that some potential egg predators are not effectively expelled from the nest (e.g., *Pomacea* snails), densities of Odonata nymphs and water bugs were substantially lower in the nest than in the surrounding floating vegetation [44]. The violent attacks of the guarding male against any animal or object nearing the nest probably prevent egg predation by fish predators.

8.4. Properties of the foam in relation to microbial growth

Balon [5] suggested that the foam produced by fish of the aphrophilic reproductive guild may attract micro-organisms on which the larvae can feed. Braum [11] discusses the detrimental effect of fungi and bacteria on fish eggs. Duellman and Treub [18] mention experimental evidence of growth-inhibiting properties of frog nests' foam. The observation that eggs of *H. littorale* deteriorate after the male was removed from the nest [44] did raise the question of whether an attack by micro-organisms, made possible by the absence of protective foam, caused the decay of eggs. However, no antimicrobial properties of the foam of *H. littorale* against nine species of bacteria and two species of fungi were found [44].

It is possible that the foam nest attracts micro-organisms in the way decaying nest material certainly does. Whether the newly hatched larvae of *H. littorale* feed on this microflora is controversial. *H. littorale* larvae do not start feeding before the yolksac is consumed (two days after hatching [40]) and by that time, foam is no longer present at the nest site and the larvae have dispersed from the nest. The stomach content of 4 days old larvae of *H. littorale* in Surinamese swamps consisted mainly of Rotifera (21.2 %) and microcrustacae (71.15 %) [46]. On the other hand, observations of the feeding behaviour of larvae suggested that micro-organisms are a main component of the diet of larval stages in this species [61].

8.5. Concealment of previous spawns

Machado-Allison and Zaret [41] pointed out that the structure of the foam nest allows the male to conceal the presence of previously deposited eggs from courting females. However, concealment of previous spawns seems irrelevant to male *H. littorale* as multiple spawnings take place simultaneously in the nest.

8.6. The nest as a centre of reproduction in space and time

Territoriality in fish is associated with a limited availability of spawning sites [6] and certainty of paternity for male guarders [52, 66]. In the expanded environment of neotropical swamps, spawning sites do not seem to constitute a limited resource. Certainty of parternity is more likely to be related to territoriality in *H. littorale* since several trends in the reproduction of this fish seem to value the assurance of paternity : external fertilization, spawning of several females in the nest guarded by a single male, multiple spawning, and access to reproduction limited to a fraction of the male population. In addition, territoriality contributes to maximizing the occupation and exploitation of resources in flooded swamps, since it promotes the rapid dispersion of the species in a new expanding environment.

The nest is probably also essential in synchronizing spawning in time, especially when several females spawn simultaneously. Initiation of nest building by males the day before spawning, may provide a stimulus for final oocyte maturation. In species where territorial guarding causes a segregation of sexes during reproduction, it can be expected that males stimulate ovulation in females when they start building the nest [64]. In *H. littorale*, the existence and sensory modality (visual, chemical, etc.) of such a stimulus have yet to be studied.

9. CONCLUSION

We hope to have shown that *Hoplosternum littorale* can be used with profit to study the reproductive biology of fish. The elaborate floating bubble nest is easily observed in its natural habitat, thus providing good opportunities for field work. Because *H. littorale* can also be raised and induced to reproduce in ponds and indoor tanks, detailed laboratory studies are possible. Eggs of *H. littorale* may be incubated outside the nest in conical incubators if a continuous flow of oxygenated water is provided. Early maturity, high fecundity and a 7-month breeding season assure a continual and large pool of larvae.

There remains a number of important questions related to the reproductive biology of *H. littorale*:

– Do all males take part in reproduction, and how is female choice related to male characters like body size, colour and size of the pectoral spine, and size of the nest and territory?

– Is the description of courtship, based on aquarium observations involving a single pair, accurate when in nature several females spawn simultaneously?

– How are resources partitioned in time between growth and reproduction?

– How is sperm transported to the eggs to accomplish fertilization? If it passes through the intestines [35], how is the rapid passage (25 cm in 30–60 s)

achieved? Has intestinal sperm transport evolved to accommodate 'transfer brooding' described in callichthyids such as *Callichthys* and *Corydoras*, 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 spawning sites) [13], or to avoid negative effects of low-pH swamp water on sperm mobility [32], or for other reasons?

Other physiological characteristics of *H. littorale*, not reviewed here, such as intestinal air breathing [9, 30] and thermosensitivity of sex determination [29] make this fish an interesting biological model. From the perspective of aquaculture, these features suggest that it is possible to rear *H. littorale* in oxygen-depleted water (seasonal pools or cages in swamps) and modify the sex ratio in favour of males that grow faster.

Acknowledgements

REFERENCES

[1] Andrade D.V., Abe A.S., Foam nest production in the armoured catfish, J. Fish Biol. 50 (1997) 665–667.

[2] Assunção M.I., Schwassmann H.O., Reproduction and larval development of *Electrophorus electricus* on Marajo Island (Para, Brazil), Ichthyol. Explor. Freshw. 6 (1995) 175–184.

[3] Bagenal T.B., Aspects of fish fecundity, in: Gerking S.D. (Ed.), Ecology of freshwater fish production, Blackwell, Oxford, 1978, pp. 75–101.

[4] Bagenal T.B., Braum E., Eggs and early life history, in: Bagenal T.B. (Ed.), Methods for assessment of fish production in fresh waters, 3rd ed., Blackwell, Oxford, 1978, pp. 165–201.

[5] Balon E.K., Reproductive guilds of fishes: a proposal and definition, J. Fish. Res. Board Can. 32 (1975) 821–864.

[6] Baylis J.R., The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection, Environ. Biol. Fishes 6 (1981) 223–251.

[7] Bhatti H.K., The integument and dermal skeleton of Siluroidea, Trans. Zool. Soc. London 24 (1938) 1–102.

[8] Boujard T., Meunier F.J., Croissance de l'épine pectorale, histologie osseuse et dimorphisme sexuel chez l'Atipa, *Hoplosternum littorale* Hancock, 1828 (Callichthyidae, Siluriforme), Cybium 15 (1991) 55–68.

[9] Boujard T., Keith P., Luquet P., Diel cycle in *Hoplosternum littorale* (Teleostei): evidence for synchronization of locomotor, air breathing and feeding activity by circadian alternation of light and dark, J. Fish Biol. 36 (1990) 133–140.

[10] Boujard T., Moreau Y., Luquet P., Entrainment of the circadian rhythm of food demand by infradian cycles of light-dark alternation in *Hoplosternum littorale* (Teleostei), Aquat. Living Resour. 4 (1991) 221–225.

[11] Braum E., Ecological aspects of the survival of fish eggs, embryos and larvae, in: Gerking S.D. (Ed.), Ecology of freshwater fish production, Blackwell, Oxford, 1978, pp. 102–131.

[12] Breder C.M., Rosen D.E., Modes of reproduction in fishes, Natural History Press, Garden City N.Y., 1966, 941 p.

[13] Bruton M.N., Alternative life-history strategies of catfishes, in: Legendre M., Proteau J.P. (Eds.), The biology and culture of catfishes, Aquat. Living Resour. (special issue) 9 (1996) 35–41.

[14] Burgess W.E., Family Callichthyidae (armored catfishes), in: An atlas of freshwater and marine catfishes, T.F.H. Publications, Neptune City, 1989, pp. 326–367.

[15] Burt A., Kramer D.L., Nakatsuru K., Spry C., The tempo of reproduction in *Hyphessobrycon pulchripinnis* (Characidae), with a discussion on the biology of "multiple spawning" in fishes, Environ. Biol. Fishes 22 (1988) 15–27.

[16] Carter G.S., Beadle L.C., The fauna of the swamps of the Paraguayan Chaco in relation to its environment. I. Physico-chemical nature of the environment, Zool. J. Linn. Soc. 37 (1930) 205–258.

[17] Carter G.S., Beadle L.C., The fauna of the swamps of the Paraguayan Chaco in relation to its environment. II. Respiratory adaptations in the fishes, Zool. J. Linn. Soc. 37 (1931) 327–368.

[18] Duellman W.E., Treub L., Biology of amphibians, McGraw-Hills, New York, 1986, 670 p.

[19] Garlick R.L., Bunn H.F., Fyhn H.J., Fyhn U.E., Martin J.P., Noble R.W., Powers D.A., Functional studies on the separated hemoglobin components of an airbreathing catfish, *Hoplosternum littorale* (Hancock), Comp. Biochem. Physiol. 62 (1979) 219–226.

[20] Gautier J.Y., Planquette P., Rouger Y., Étude éthologique de la relation mâle-femelle au cours du cycle de reproduction chez *Hoplosternum littorale*, Rev. Ecol. Terre Vie 43 (1988) 389–398.

[21] Gorzula S.J., Foam nesting in leptodactylids: a possible function, Br. J. Herpetol. 5 (1977) 657–659.

[22] Gosline W.A., A revision of the neo-tropical catfishes of the family Callichthyidae, Stanford Ichthyol. Bull. 2 (1940) 1–29.

[23] Hancock J., Notes on some species of fishes and reptiles from Demerara presented to the Zoological Society by Joly Hancock, Zool. J. 4 (1828) 240–247.

[24] Heyer W.R., The adaptative ecology of species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae), Evolution 23 (1969) 421–428.

[25] Hoedeman J.J., Notes on the ichthyology of Surinam (Dutch Guiana). The catfish genera *Hoplosternum* and *Callichthys*, with key to the genera and groups of the family Callichthyidae, Beaufortia 1 (1952) 1–11.

[26] Hostache G., Vallat P., Tessier C., Maîtrise du cycle d'élevage de l'atipa, Nature Guyanaise 4 (1990) 33–41.

[27] Hostache G., Pascal M., Kernen M., Tessier C., Température et incubation chez l'atipa, *Hoplosternum littorale* (Teleostei, Siluriforme), Aquat. Living Resour. 5 (1992) 31–39.

[28] Hostache G., Pascal M., Planquette P., Saisonnalité de la reproduction chez l'atipa, *Hoplosternum littorale* (Siluriforme, Teleostei), par l'analyse de l'évolution du rapport gonado-somatique, Aquat. Living Resour. 6 (1993) 155–162.

[29] Hostache G., Pascal M., Tessier C., Influence de la température d'incubation sur le rapport mâle : femelle chez l'atipa *Hoplosternum littorale* (Hancock, 1828), Can. J. Zool. 73 (1995) 1239–1246.

[30] Huebner E., Chee G., Histological and ultrastructural specialization of the digestive tract of the intestinal air-breather *Hoplosternum thoracatum* (Teleost), J. Morphol. 157 (1978) 301–328.

[31] Hyder M., Gonadal and reproductive patterns in *Tilapia leucosticta* (Teleostei: Cichlidae) in an equatorial lake, Lake Naivasha (Kenya), J. Zool. (London) 162 (1970) 179–195.

[32] Iwanatsu T., Effects of pH on the fertilization response of the medaka egg, Dev. Growth Differ. 26 (1984) 533–544.

[33] Keenleyside M.H.A., Diversity and adaptation in fish behaviour, Springer-Verlag, Berlin, 1979, 207 p.

[34] Kirschbaum F., Reproduction of the weakly electric fish *Eigenmannia virescens* (Rhamphichthyidae, Teleostei) in captivity. I. Control of gonadal recrudescence and regression by environmental factors, Behav. Ecol. Sociobiol. 4 (1979) 331–355.

[35] Kohda M., Tanimura M., Kikue-Nakamura M., Yamagishi S., Sperm drinking by female catfishes: a novel mode of insemination, Environ. Biol. Fishes 42 (1995) 1–6.

[36] Kramer D.L., Graham J.B., Synchronous air breathing, a social component of respiration in fishes, Copeia (1976) 689–697.

[37] Lowe-McConnell R.H., The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish, Zool. J. Linn. Soc. 45 (1964) 103–144.

[38] Lowe-McConnell R.H., Ecological studies in tropical fish communities, Cambridge University Press, Cambridge, 1987, 382 p.

[39] Luquet P., Boujard T., Planquette P., Moreau Y., Hostache G., The culture of *Hoplosternum littorale*: state of the art and perspectives, in: Advances in tropical aquaculture, Aquacop-Ifremer, Paris, 1989, pp. 511–516.

[40] Machado-Allison A., Aspectos sobre la historia naturel del "Curito" *Hoplosternum littorale* (Hancock, 1828) (Siluriformes-Callichthyidae) en el bajo llano de Venezuela: desarrollo, alimentacion y distribucion espacial, Acta Cient. Venez. 37 (1986) 72–78.

[41] Machado-Allison A., Zaret T.M., Datos sobre la biologia reproductiva de *Hoplosternum littorale* (Siluri-

formes-Callichthyidae) de Venezuela, Acta Cient. Venez. 35 (1984) 142–146.

[42] Mago F.M.L., Estudios preliminares sobre la ecologia de los peces de los llanos de Venezuela, Acta Biol. Venez. 7 (1970) 71–102.

[43] Miller P.J., The tokology of gobioid fishes, in: Potts G.W., Wootton R.J. (Eds.), Fish reproduction strategies and tactics, Academic Press, London, 1984, pp. 119–153.

[44] Mol J.H., Structure and function of floating bubble nests of three armoured catfishes (Callichthyidae) in relation to the aquatic environment, in: Ouboter P.E. (Ed.), The Freshwater ecosystems of Suriname, Kluwer Academic Publishers, Dordrecht, 1993, pp. 167–197.

[45] Mol J.H., Effects of salinity on distribution, growth and survival of three neotropical armoured catfishes (Siluriformes-Callichthyidae), J. Fish Biol. 45 (1994) 763–776.

[46] Mol J.H., Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes, J. Fish Biol. 47 (1995) 788–807.

[47] Mol J.H., Reproductive seasonality and nest-site differentiation in three closely related armoured catfishes (Siluriformes: Callichthyidae), Environ. Biol. Fishes 45 (1996) 363–381.

[48] Mol J.H., Impact of predation on early stages of the armoured catfish *Hoplosternum thoracatum* (Siluriformes-Callichthyidae) and implications for the syntopic occurrence with other related catfishes in a neotropical multi-predator swamp, Oecologia 107 (1996) 395–410.

[49] Novoa D., A pesqueria del busco curito (*Hoplosternum littorale*) en el delta del Orinoco in: Novoa D. (Ed.), Los recursos pesqueros del Rio Orinoco y su explotacion, Corporacion Venezuelana de Guyana, Caracas, 1982, pp. 151–161.

[50] Pascal M., Hostache G., Tessier C., Vallat P., Cycle de reproduction et fécondité de l'atipa, *Hoplosternum littorale* (Siluriforme) en Guyane Française, Aquat. Living Resour. 7 (1994) 25–37.

[51] Pascal M., Hostache G., Tessier C., Choix du lieu d'implantation du nid et de l'heure de la ponte chez l'atipa, *Hoplosternum littorale* (Siluriforme, Callichthyidae), Cybium 19 (1995) 143–151.

[52] Perrone M., Zaret T.M., Parental care patterns in fishes, Am. Nat. 113 (1979) 351–361.

[53] Potts G.W., Parental behaviour in temperate marine teleosts with special reference to the development of nest structures, in: Potts G.W., Wootton R.J. (Eds.), Fish reproduction: strategies and tactics, Academic Press, London, 1984, pp. 223–243.

[54] Puyo J., Poissons de la Guyane Francaise, Office de la Recherche Scientifique Outre Mer (Orstom), Paris, 1949, 280 p.

[55] Ramnarine I.W., A field trial of semi-intensive culture of the cascadura, *Hoplosternum littorale* (Hancock, 1828), Trop. Agric. (Trinidad) 71 (1994) 1–4.

[56] Ramnarine I.W., Larval culture, development and growth of the cascadu, *Hoplosternum littorale* (Hancock 1828; Callichthyidae), Aquaculture 126 (1994) 291–298.

[57] Ramnarine I.W., Induction of nest building and spawning in *Hoplosternum littorale*, J. Fish Biol. 47 (1995) 555–557.

[58] Reis R.E., Revision of the neotropical catfish genus *Hoplosternum* (Ostariophysi: Siluriformes: Callichthyidae), with the description of two new genera and three new species, Ichthyol. Explor. Freshw. 7 (1997) 299–326.

[59] Richards O.W., Davies R.G., Imm's general textbook of entomology, 10th ed., Chapman & Hall, London, 1977, 1354 p.

[60] Schwassmann H.O., Time of annual spawning and reproductive strategies in Amazonian fishes, in: Thorpe J.E. (Ed.), Rhythmic activity of fishes, Academic Press, London, 1978, pp. 187–200.

[61] Singh T.B., The biology of the cascadura *Hoplosternum littorale* Hancock 1834 (sic!) with reference to its reproductive biology and population dynamics, PhD thesis, Univ. West Indies, Trinidad, 1978, 298 p.

[62] Sire J.Y., Meunier F., Boujard T., Étude de la croissance des plaques osseuses dermiques d'*Hoplosternum littorale* (Siluriformes, Callichthyidae) à l'aide du marquage vital, Cybium 17 (1993) 273–285.

[63] Snow J.W., The climate of northern South America, in: Schwerdtfeger W. (Ed.), Climates of Central and South America, Elsevier, Amsterdam, 1976, pp. 295–379.

[64] Stacey N.E., Control of the timing of ovulation by exogenous and endogenous factors, in: Potts G.W., Wootton R.J. (Eds.), Fish reproduction: strategies and tactics, Academic Press, London, 1984, pp. 207–222.

[65] Teugels G.G., Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview, in: Legendre M., Proteau J.P. (Eds.), The biology and culture of catfishes, Aquat. Living Resour (special issue) 9 (1996) 9–34.

[66] Trivers R.L., Parental investment and sexual selection, in: Campbell B. (Ed.), Sexual selection and the descent of man, Aldine, Chicago, 1972, pp. 36–179.

[67] Tuma Y.S., Contribuiçao para o conhecimento da biologia do tamuatá *Hoplosternum littorale* (Hancock, 1828) Eigenmann & Eigenmann, 1888 (Pisces, Callichthyidae), da Ilha de Marajó, Pará-Brasil, Bol. da FCAP (Belem) 10 (1978) 59–76.

[68] Vipan J.A., On the nesting of a South American siluroid fish *Callichthys littoralis* in this country, Proc. R. Soc. London (Zoology) 22 (1886) 330–331.

[69] Ware D.M., Relation between egg size, growth, and natural mortality of larval fish, J. Fish. Res. Board Can. 32 (1975) 2503–2512.

[70] Welcomme R.L., Fisheries ecology of floodplain rivers, Longman, London, 1979, 317 p.

[71] Willmer E.N., Some observations on the respiration of certain tropical freshwater fish, J. Exp. Biol. 11 (1934) 283–306.

[72] Winemiller K.O., Feeding and reproductive biology of the currito, *Hoplosternum littorale*, in the Venezuelan llanos with comments on the possible function of the enlarged male pectoral spines, Environ. Biol. Fishes 20 (1987) 219–227.

[73] Wootton R.J., Fecundity of the three-spine stickleback, *Gasterosteus aculeatus* (L.), J. Fish Biol. 5 (1973) 683–688.

[74] Wootton R.J., Ecology of teleost fishes, Chapman & Hall, London, 1990, 404 p.