Larval development and reproductive strategies of Central Amazon fishes

A Thesis submitted to the University of Stirling

for a degree of Doctor of Philosophy

by

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ABSTRACT

Larval development and reproduction of 19 species of Central Amazonian fish (five cichlids, two siluriforms, one osteoglossiform and 11 characiforms) were studied over two years. Most species spawn during the flooding season. The cichlids, the siluriforms and two species of characiform are nest spawners, reproducing in the littoral areas of the floodplain. The osteoglossiform is a mouth-brooder. The remaining characiforms spawn in the river channels and show no parental care. Two main strategies explain 90% of the variability of reproductive traits found among the 19 species. The first strategy is used by riverine spawners (characiforms). They have high fecundity, high to very high reproductive expenditure (calories per spawn per wet weight of female) and spawn once a year during a short season. Their eggs vary in size from 0.06 to 0.3 mg and have intermediate to high calorific value.

The second strategy is used by the cichlids and two species of characiforms. They have low fecundity, low reproductive expenditure, long spawning season, multiple spawnings per season and some of them show parental care. Their eggs vary in size from 0.4 to 1.2 mg and have an intermediate calorific content. The other three species show distinct combinations of reproductive traits, but have as common feature a high reproductive expenditure, a short annual spawning season and parental care.

Patterns of larval development are correlated with egg size and adult spawning sites. Egg size explained most of variability of larval body size at hatching, pectoral fin bud, eye pigmentation, jaw formation, swim bladder inflation, onset of swimming, first feeding and maximum size attained with exclusively endogenous feeding. The pattern of blood

circulation of the larvae was correlated with the spawning sites. Larvae of riverine spawners are small, utilize yolk efficiently and are relatively resistant to starvation. Newly hatched larvae of riverine spawners seem to be very sensitive to physico-chemical conditions of the floodplain lakes, but by the first feeding stage they develop some resistance to the low availability of oxygen. Larvae of littoral spawners are large, utilize yolk less efficiently, and seem to be resistant to low concentrations of oxygen. The resistance of larvae to oxygen deficiency is correlated with the development of the larval respiratory system.

It is suggested that egg size of riverine spawners was selected to optimize the distance of the dispersal of the larvae in a range of floodplain lakes. Conversely, egg size of floodplain spawners seemed to be selected to optimize larval survival in the spawning lake. The results are further discussed in relation to life history models.

1 INTRODUCTION

In the life cycle of a species reproduction is the link that ensures the continuation of the species. For species to exist, reproduction has to provide individuals that will successfully continue the cycle. The most vulnerable part of this cycle is the embryonic and larval period, since eggs and larvae experience higher mortality than the subsequent life stages (Gulland, 1988). Fishes have extremely diverse ways of reproducing and combinations of several reproductive traits can be found in this group. Wootton (1984) defines the reproductive strategy of a species as "the complex of reproductive traits that a fish will attempt to manifest to leave offspring". The strategies evolve in response to the environment and they are assumed, therefore, to be adaptive. Species are, however, linked to an evolutionary history, (Southwood, 1988; Caswell, 1989), that may impose constraints on these responses. The reproductive strategies of a sympatric species may converge to give common patterns. Wootton (1984), analyzing the strategies of Canadian freshwater fishes, found the 162 species could be clustered in a limited number of patterns. This and several other cases (Stearns, 1977) suggest that there is an order in the diversity of combinations of reproductive traits. The search for the processes behind the patterns its a more complex task, since similar patterns can be created by different processes (Berry, 1989; May, 1989).

Under an adaptationist framework natural selection should maximize reproduction and all other activities related to its success (Krebs and Davies, 1978). Conclusions on the processes (i.e. adaptive significance) responsible for the reproductive traits can be realized by correlations between reproductive strategies and the environment

(Potts and Wootton, 1984). This approach is based on the assumption that animals living in a common habitat are likely to have evolved particular strategies that improve their fitness in that environment, and therefore common patterns should occur (Southwood, 1988). The main problem of this method is that the strategies have both a phylogenetic component (Southwood, 1988; Caswell, 1989) and a physiological component (e.g size) (Miller, 1979; Partridge and Harvey, 1988) that may also explain the pattern. Interpreting how closely related species respond to different environments may help in avoiding this problem (Krebs and Davies, 1978). Finally, analysis of the adaptive convergences can also produce insights into the power of such pressures (Wootton 1984; Dando, 1984).

The processes leading to particular reproductive strategies can also be analyzed by using models based on the demographic and the optimization theories (Ware, 1982; Krebs and Davies, 1978; Horn, 1978). Most of those models approach reproduction as part of the life history strategy and with the assumption that reproduction competes with somatic growth. Two important predictions are derived from the models (Stearns, 1976; Partridge and Harvey, 1988). Firstly, the number of breeding seasons of a species is positively correlated with the juvenile/adult mortality ratio (Cole, 1954; Stearns, 1976; Horn, 1978). Secondly, breeding organisms, at each age, should maximize the difference between the number of young gained by current spawning and those lost through the death or lowered fecundity of the parent. Experimental tests have not always confirmed these predictions. Reznick and Endler (1982) showed that increased predation pressure on the parents results in higher fecundity, more spawnings and earlier maturity. A main caveat of these tests is that the observed effect may be the result of phenotypic plasticity instead

of the expression of different genotypes (Stearns, 1980; Partridge and Harvey, 1988; Caswell, 1989).

Patterns of reproductive strategies of fish communities and groups have also been explained by larval survival. Miller (1979, 1984) has suggested that the reproductive strategies of the gobioids and other small teleosts are largely determined by their size and the predictability of the environment for larval food. The non seasonal circumstances of tropical climates favour several spawnings per season. In circumstances when there is a predictable supply of food for the larvae, such as in temperate seas, gobioids show larger egg size, few spawnings per season, planktonic larvae, and a match between spawning season and the production cycle. Cushing (1975) suggests that the larval season in temperate climates should match the peaks of primary and secondary production in the sea. This would maximize the availability of food for the larvae. Hempel and Blaxter (1967) suggest that *Clupea harengus*, a species with year-round spawning, has adapted its fecundity and egg size to the availability of food and to the predation pressure on the larvae. Populations spawning in the winter and spring have lower fecundity and larger egg size than summer spawners. Barlow (1981), analyzing the spawning strategies of coral reef fishes, found that large species usually have small planktonic eggs and high fecundity. Small species produce large eggs and planktonic larvae, or large eggs usually accompanied by parental care. Dando (1984) studied the reproduction of estuarine fishes. He argued that estuaries show rapidly fluctuating conditions that are not ideal for egg development. Most species spawning in the estuaries usually have demersal eggs and/or adhesive eggs, so preventing them from being flushed towards the sea. Lowe-McConnell (1987), surveying the literature on tropical freshwater fishes, grouped

the species according to main patterns of reproduction. One group of fishes has high fecundity and one spawning per year during a short or extended season. A second group has intermediate fecundity, an extended spawning season and multiple spawning. A third group is aseasonal, with low fecundity and multiple or one spawning per season. However, she made few comments about the relationship between these traits and the constraints and adaptations of the larvae to the spawning and nursery sites.

Embryonic and larval development is characterized by dramatic morphological, anatomomical, ecological and physiological changes (Blaxter, 1986; Moser *et al*, 1984; Rombough, 1988). The body increases up to 10^3 times in size, while organs and body structures are formed. Some species develop special larval structures for this period, such as the spines found in marine larvae or the cutaneous circulatory systems found in some freshwater larvae (Balon, 1985; Blaxter, 1988; Rombough, 1988). The energetic cost of development and growth, and also the maintenance of the new tissue, is provided by the yolk, initially. The amount of yolk available and the efficiency of its use, therefore, should be linked to the extent of larval development (Sinervo and McEdward, 1988) and growth before the switch to exogenous feeding. Conversely, a minimum amount of yolk should be available to develop the larvae to a successful start of feeding. The influence of the amount of yolk on larval survival has been demonstrated in marine and freshwater larvae. Larvae from large eggs have a longer period between first feeding and the "point of no return" (Hunter, 1981) and are larger at first feeding (Blaxter, 1988). The egg size is, therefore, related to larval survival. Survival is a main component of fitness and factors related to it are important for an analysis of reproductive strategy.

The fish community of the Central Amazon offers a good opportunity to study the relationship between larval development and adult reproduction. In a small area of 100 km^2, there are several species with distinct reproductive patterns and styles of larval development. The habitats available for the larvae have opposite characteristics. On one side there is the floodplain with its lakes. They are highly productive areas, but due to fluctuations of temperature and dissolved oxygen can be considered to be physico-chemically adverse. Conversely, the river has extremely low production, but is physico-chemically stable. The larvae and the reproductive patterns of the species are developed between these two environments. These opposite situations may permit an inference of the constraints of larval development on reproductive strategies.

The present study compared the patterns of reproductive strategies and the larval development of 19 species from the central part of the Amazon floodplain. The main objective of the study was to understand how both aspects of the life history are interrelated and what correlates and "trade-offs" arise from this relationship.

Additionally to the academic interest of this study, its results also can be extended to fisheries and aquaculture, since most of the species studied have high commercial importance (Petrere, 1989). Knowledge on the reproductive strategies has been suggested as important to a better understanding of stock and recruitment relationships (Ware, 1982; Garrod and Horwood, 1984).

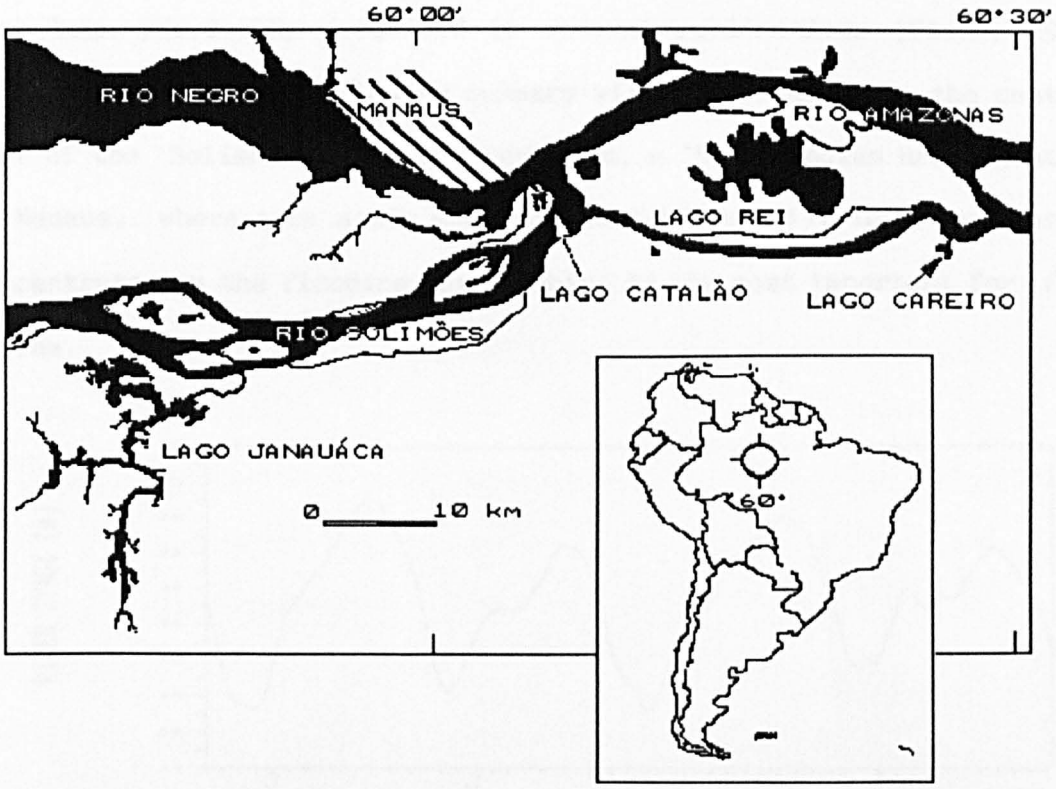


Figure 1 Map of the study area showing the main sampling sites.

Studied area

The Amazon basin drains an area of 5.7 million km^2. Its main river, the Solimões/Amazonas, cuts the north of South America from the Andes to the Atlantic ocean. The river runs on a bed of quaternary sediments eroded from the Andes (Irion, 1989). The system is dynamic, having its main characteristics varying in a long term basis as well as in seasonal cycles. In the long term, the water currents continuously change the landscape by shifting the river channels along their perpendicular axis (Mertes, 1985; Salo and Rasanen, 1989). This modifies not only the river channel, but also the floodplain lakes and islands. Seasonal changes in the water level causes alterations in the available habitats for all aquatic biota, including fish larvae.

General information about the basin and its characteristics have been previously described in several publications (Sioli, 1984; Welcomme, 1985). The following summary will focus mainly on the central part of the Solimões/Amazonas floodplain, a ~50 km radius area, centred in Manaus, where this study was conducted (Figure 1). This description concentrates on the flooding season which is the most important for fish larvae.

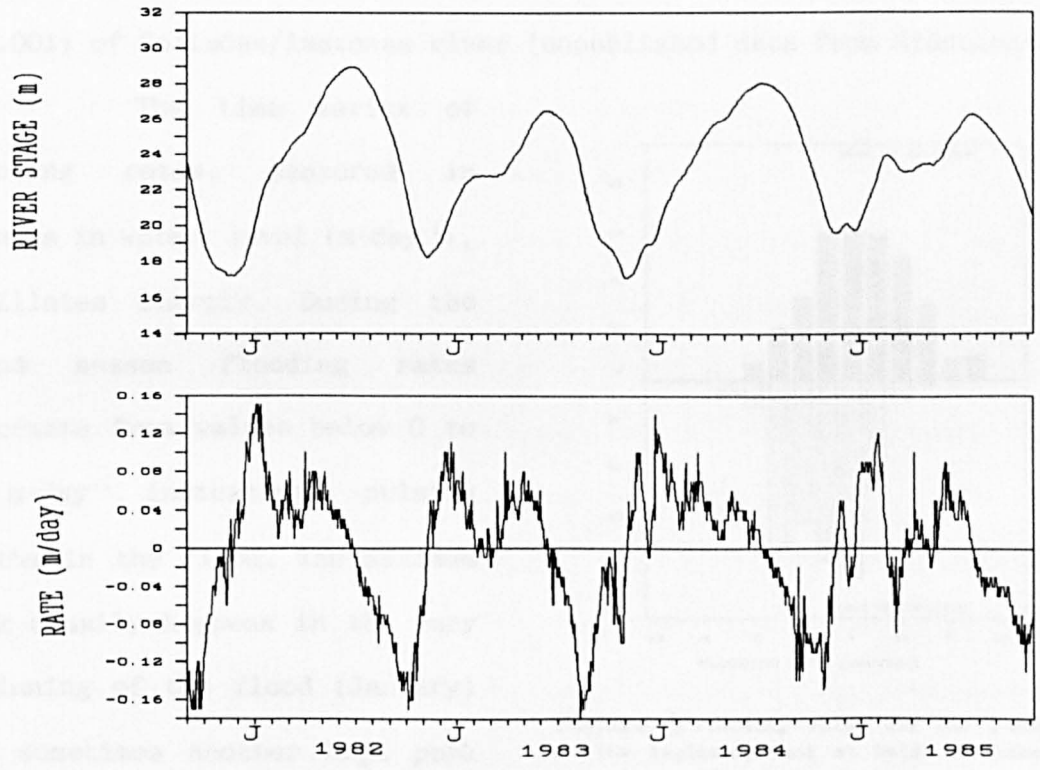


Figure 2 Time series of water level and flood rate measured at Manaus harbor (J= January).

The water level, the main physical influence on the shape landscape, fluctuates in a stable yearly cycle. The minimum level occurs in October/November and the maximum level in June/July (Figure 2). The difference between the two levels averages 12 m, but varies from year to year. In a 80 years period, the minimum and maximum differences between

low and high water levels were ~6 m and ~16 m, respectively (Junk, 1989). This variation in the flood is caused by fluctuations in the rainfall througout the drainage basin. The rainy season at the study zone usually starts in November/December. Rainfall is highly localized and local rainfall has little effect on the overall shape of the river stage (water level of the river) (Figure 2), but it does affect the inflow of water to the floodplains lakes (Junk, 1973; personal observation). River stage in Manaus is linearly correlated with discharge data ($r=0.92$; $N=15$; $p<0.001$) of Solimões/Amazonas river (unpublished data from Hidrologia).

The time series of flooding rates, measured in changes in water level ($m \cdot day^{-1}$), oscillates sharply. During the flood season flooding rates fluctuate from values below 0 to 0.1 $m \cdot day^{-1}$, indicating a pulsing rhythm in the flood. The maximum peak usually happens in the very beginning of the flood (January) and sometimes another high peak occurs in April/May (Figure 2). The average flooding rate was higher at the first three months of the flood, if compared with the second three months ($t= 6.9$; $D.F.= 712$; $p<0.0001$) during the 1982-1985 period. The second three months period also had a frequency of zero or negative flooding rates 3 times higher than the first period (Figure 3).

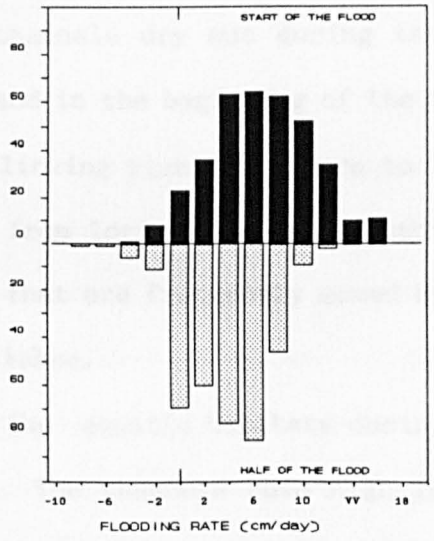


Figure 3 Flooding rates for the 3 months at the beginning and at half of flooding season during 1982-1985 in Amazon river.

Welcomme (1985) classified the major habitats of river systems by morphological, chemical and physical characteristics into two

types: river channels and floodplain habitats. River channels (the lotic component) are divided into two other habitats: the main channel (the river) and small channels (linking the river to the floodplain). Floodplains (the lentic component) are divided into several habitats, but the most important in the area studied are the floating meadows (grassland), the lakes and the flooded forest. In the Amazon system all these habitats can be considered to be ephemeral, except for the main river channel. The latter has stable characteristics throughout the year, except for the river flow velocity, which varies from 1.0-1.6 $m \cdot s^{-1}$, and river depth that changes with water level according to sites (unpublished data from Hidrologia). Several small channels dry out during the low water season, behaving like lake grassland in the beginning of the flood and finally changing back to a channel linking river or rivers to lakes at high water season, i.e. they switch from lotic to a lentic habitat. Transmutations also occur with meadows that are frequently moved by the wind from one side to the other of the lakes.

The main characteristics of the aquatic habitats during the flooding season are listed in Table 1. The channels have high levees when closed to the river (but progressively change to something more similar to a lake when water currents slow down) with open water and littoral parts. The latter can be outlined by meadows or flooded forest. However, the water current speed in the channel is faster than in the lakes. The flow in the channels during the flood is not unidirectional and when the water level in the lake is increased by a local rainfall the flow can reverse or stop, an effect that also has been reported by Junk (1973). This alteration of the flow is certainly responsible for the variability in dissolved oxygen and temperature in the channels. The lakes vary in depth with water oscillation. Some are continuously

Table 1 Summary of the characteristics of the main habitats of Central Amazon floodplain during the flood period.

HABITAT	TYPE	DEPTH	T C	OXYGEN % SATURATION	CURRENT SPEED(cm·s^{-1})	REF.
M.channel	open water	surface	28-29	60-65	85-100	1,2
M.channel	littoral	surface	28-31	30-80	30-	2,3
M.channel	littoral	bottom	28-29	50-60	-	2,3,9
Channel	open water	surface	28-29	55-65	-	2,3
Channel	open water	bottom	27-28	45-55	-	2,3
Channel	littoral	surface	28-34	-	10-15	3
Lake	open water	surface	28-32	0-102	1-5	1,4,5,6
Lake	open water	bottom	27-28	0-65	-	1,4,5,6
Meadow	littoral	surface	28-37	0-104	-	7,8
Meadow	littoral	bottom	28-30	0-56	-	7,8

M.channel= main channel; Months codes follow: 1=January; 2=February; etc; 1= Fisher and Parsley, 1979; 2= Araujo-Lima, 1984; 3= Junk, 1973; 4= Schimdt, 1973; 5= Melack and Fisher, 1983; 6= McIntyre and Melack, 1984; 7= Tundisi et al, 1984; 8= This study; 9= include measurements taken in the strands of aquatic grasses.

connected to the river, others are connected only after a certain water level. In daytime an epilimnion is formed in which oxygen is produced due to algal photosynthesis, but below a depth of 3.5 m oxygen levels are reduced and above the sediments values close to zero are common. At night time the thermocline depth rises and oxygen levels close to the surface can also drop dramatically. The winds play an important role in the lakes, affecting the depth of thermocline and affecting stratification if depth is less than 3.5 m (Melack and Fisher, 1983). In the meadows the situation is more radical, as the fauna and flora of the roots utilized most oxygen at night. Little data are available for flooded forests, but oxygen fluctuations are expected to be less stressful compared with the meadows, since water circulation is better in this habitat. Meadows receive plenty of light and the plant community is dominated by roots and stalks of grasses and other shrubs, while flooded forests are shaded by the trees and are dominated by branches of small trees and trunks of large trees. Large inflow from the river seems to affect oxygen

concentrations in lakes as well and it was noticed that high flood rates improve water conditions at least in areas close to the river.

Primary production in the Central Amazon is concentrated in the littoral areas of the channels where aquatic grass grows abundantly and in the lakes and their littoral areas where phytoplankton, periphyton and higher plants are congregated.

Phytoplankton production in the channels is less than 3% of lake production and estimates of zooplankton biomass show similar ratios (Fisher and Parsley, 1978; Wissmar *et al*, 1981). Planktonic primary production in the floodplain lakes is strongly linked to flooding regime. Water from the river floods the lakes, bringing nutrients into the floodplain (Forsberg *et al*, 1988). As sedimentation proceeds with distance from the river and light penetration increases, phytoplankton primary production also increases (Fisher and Parsley, 1979). The highest values of planktonic primary production (Schimdt, 1973), as well as the highest biomass of zooplankters (Marlier, 1967; Robertson and Hardy, 1984) are reached at the low water period just before the flood, but peaks of biomass of rotifers have been noticed in the beginning of the flood (Robertson and Hardy, 1984). However, some authors have reported that zooplankton density in the lakes is negatively correlated with the sediment suspended in the inflowing waters of the Solimões/Amazonas river (Fisher and Parsley, 1979; Carvalho, 1984). This suggests that these organisms avoid this water. On the meadows, which are the feeding habitats of the juvenile fishes (Araujo-Lima and Hardy, 1987; Bayley, 1988), the peak of density of zooplankters larger than 200µm was found from May to December (Junk, 1973). The average density of cladocera plus copepoda in the beginning of the flood (January and February) varied from 9 to 77 $ind \cdot l^{-1}$, roughly 4 to 70% of peak values. However, the

density of potential food is larger than those values if the zooplankton smaller than 200 µm are also considered, as well as other organisms like insect larvae and ostracods.

Primary production from higher plants reaches the system directly through seeds eaten by fish or indirectly by insects or through the detrital food chain, as in the case of siluriforms (Araujo-Lima et al, 1986), but its importance to fish larvae is unknown. Dense fauna of invertebrates have been described for the floating meadows (Marlier, 1967; Junk, 1973). However, some preliminary data failed to show any link between zooplankters of these habitats, an important food for young fish larvae (Araujo-Lima *et al.*, 1986; Araujo-Lima and Hardy, 1987) and carbon from higher plants, as described by Carvalho (1984), suggesting that zooplankton in the macrophytes are also supported by algal production.

2 MATERIALS

2.1 Samples for reproduction analyses

Adult individuals of *Hoplias malabaricus*, *Heros* sp, *Potamorhina altamazonica*, *P. latior*, *Psectrogaster rutiloides*, *P. amazonica*, *Semaprochilodus insignis*, *S. taeniurus*, *Prochilodus nigricans*, *Eigenmannina melanopogon* and *Pterigoplichthys multiradiatus* (Table 2) were sampled with stationary gill nets in Lago do Rei, Lago do Catalão, Lago do Janauaca and drifting gill nets at Rio Amazonas and Rio Solimões.

The sampling frequencies were every two months between May and November and at least once a month between December and April of

Table 2 Taxonomic list of the species studied.

SPECIES	FAMILY	ORDER
Semaprochilodus insignis	Prochilodontidae	Characiformes
Semaprochilodus taeniurus		
Prochilodus nigricans		
Eigenmannina melanopogon	Curimatidae	
Potamorhina altamazonica		
Potamorhina latior		
Psectrogaster rutiloides		
Psectrogaster amazonica		
Brycon erytropterum	Characidae	
Colossoma macropomum	Serrasalmidae	
Mylossoma duriventre		
Metynnis sp		
Piaractus brachypomus		
Hoplias malabaricus	Erythrinidae	
Hoplosternum littorale	Callichthydae	Siluriformes
Pterigoplichthys multiradiatus	Loricariidae	
Astronotus ocellatus	Cichlidae	Perciformes
Cichla monoculus		
Crenicichla sp		
Heros sp		
Mesonauta insignis		
Osteoglossum bicirrhosum	Osteoglossidae	Osteoglossiformes

1987 and 1988, except in Lago Janauaca where only one sample was taken in December 1988.

2.2 Samples for developmental studies

The eggs of *Eigenmannina melanopogon* (one spawn), *Semaprochilodus insignis* (one spawn), *Potamorhina latior* (five spawns), *P. altamazonica* (one spawn) and *Psectrogaster amazonica* (one spawn) were obtained from artificial fertilization of gametes stripped from ripe fishes captured with drifting gill nets in Rio Solimões in 1986 and in 1988-1989, respectively. The eggs were incubated in a field laboratory using river water and the newly hatched larvae were

transported to the laboratory in plastic bags enriched with oxygen and packed in styrofoam box.

The eggs of *Prochilodus nigricans* (one spawn), *Piaractus brachypomus* (one spawn) and *Colossoma macropomum* (two spawns) were obtained from fishes which spawned at the Aquaculture Department of INPA in 1988.

The eggs of *Hoplosternum littorale* (five spawns) were obtained from natural spawns found in recent flooded margins of Lago do Catalão, Lago do Rei and Lago do Careiro in 1989. The whole nests were transported in well ventilated box where the air temperature was kept at ~29 °C. Since there are two sympatric species, and due the difficult of sampling the parents, the identity of the eggs were confirmed at the laboratory using cytogenetic techniques (J. Rabelo, personal communication).

Ten eggs of *Osteoglossum bicirrhosum* (one spawn) were obtained from the mouth of one male captured in Lago do Janauaca in 1989. The eggs were transported to Manaus in plastic bags enriched with oxygen and packed in a styrofoam box.

The eggs of *Cichla monoculus* (five spawns), *Astronotus ocellatus* (three spawns), *Heros* sp (two spawns), *Crenicichla* sp (one spawn) and *Mesonauta insignis* (one spawn) were obtained from natural spawns found in the flooded forests of Lago do Catalão and Lago do Rei in 1988-1989. The spawning were identified by the observation and capture of the guarding parents prior to removal of the egg clusters. The spawnings were carefully removed with part of the substrata and transported to Manaus.

The eggs of *Hoplias malabaricus* (one spawn) were obtained from a natural spawning found in a very shallow area of the margin of

Lago do Catalão in 1989. The identification of the egg clutch was achieved by observing one of the guarding parents.

The eggs of *Pterigoplichthys multiradiatus* (two spawns) were obtained from nests found in the margins of Lago do Catalão and Lago do Careiro in 1989. The nests were found by diving on the banks (1-2 m deep) from where guarding parent and the egg clutches were carefully removed and transferred to the laboratory.

All egg clutches were transported to the laboratory in 100 l plastic box isolated with styrofoam. The box water was constantly renewed and temperature was kept at ~29 °C.

Eggs and larvae of *Metynnis sp*, *Semaprochilodus taeniurus* and *Mylossoma duriventre* were obtained from preserved samples collected in 1984-1985.

3 METHODS

3.1 Reproduction analyses

3.1.1 Time of spawning

The sampled fishes were measured to the nearest mm (standard length) and weighed wet to nearest 0.1 g. The ovaries were examined and ranked by stage of maturity following Vazzoler (1981). The time of spawning was estimated by the seasonal analysis of the occurrence of mature plus ripe females captured.

3.1.2 Type of reproduction

The type of reproduction was defined as the number of spawnings per individuals per spawning season (year). It was

analyzed by the technique of frequency distribution of oocyte diameter for *Psectrogaster amazonica*, *Potamorhina latior*, *Pterigoplichthys multiradiatus* and *Heros sp* and by histological analyses of the mature and spent ovary for *Eigenmannina melanopogon* and *Potamorhina altamazonica*.

Each analysis used 5-10 individuals of each species, selected on the basis of maturity stage and availability. After measuring and staging the females, the mature ovaries were extracted, wet weighed and kept in Gilson's fluid for 1-3 months. Once the oocytes were separated from the ovary tissue, they were thoroughly rinsed in 70% alcohol, and kept in this medium for later measurement of their diameters. The diameters of the oocytes were measured with a stereomicroscope to the nearest 0.1 mm. The modal groups of the distribution of diameters were separated by the program MIX (MacDonald and Pitcher, 1979).

Five to ten maturing and spent individuals of *Eigenmannina melanopogon* and *Potamorhina altamazonica* were selected for histological analyses. The preparation of the samples for histology followed the standard technique for haematoxylin-eosin staining.

3.1.3 Fecundity and reproductive expenditure

Fecundity was assumed to be the total number of ripening oocytes in a female prior to the next spawning season (Bagenal, 1978). Fecundity per season was considered to be the number of eggs produced per season (year). Ripening oocytes were considered

to be the most advanced modal group in the distribution of oocyte diameter of mature females and the number of spawnings per season was considered to be the maximum number of modal groups of maturing oocytes.

The measurements were made in two steps. First, the samples were examined by stereomicroscope to estimate the size of the mature oocytes and secondly, the whole sample was fractionated by size using a mesh and the mature oocytes only were counted by an electronic particle counter (photoelectric). The counter was set to be sensitive only to particles with diameter ≥0.4 mm to avoid contamination with ovarian tissue.

Table 3 Parameters of the linear regression of the numbers of oocytes estimated by the counter on the actual numbers of oocytes in the sample.

PARAMETER	ESTIMATE	STANDARD ERROR	T VALUE	PROB. LEVEL
Intercept	0.8374	28.3343	0.0296	0.9769
Slope	0.9910	0.0212	45.0746	<0.0001
r^2	0.9946			

Range: 50-3000 eggs; Slope= 1 ($p< 0.05$); N= 14; Oocytes of more than one species.

The counter was checked against small samples with known numbers of oocytes. The ratio between the oocytes actually present in the samples and those counted was not statistically different from one (t test; $p<0.05$) and the line describing the relationship passed through the origin (Table 3).

For most species the fecundity was estimated from five to ten females. Since this study had a comparative aspect, fecundity had to be standardized per fish weight. To test whether

the standardization was valid, more detailed analysis of the relation between fecundity and body weight was made with three species: *Prochilodus nigricans*, *Psectrogaster rutiloides* and *Osteoglossum bicirrhosum*. This procedure used more than 20 measurements per species.

Reproductive expenditure was calculated multiplying the relative fecundity by the average amount of calories per egg.

3.2 Development analyses

3.2.1 Culture methods

Rearing systems. Three different systems were used to rear the eggs and larvae. The first system, used from January to April 1988, consisted of two separated 50 l plastic tanks lagged with styrofoam, with a closed system water circulation. The water was aerated and had a renewal rate of 30% day^{-1}. This system supported two batches of 200 individuals to be reared at any one time. The system had the temperature controlled with thermostats and heaters and had a light/dark cycle of 13/11 h. Dissolved oxygen, checked every day with a YSI probe, was always higher than 80% saturation.

The second system, used after November 1988, consisted of a row of five 8 l aquaria, linked to 1000 l reservoir (Figure 4), with a closed water circulation system. The water was sterilized with ultra-violet radiation and the renewal rate was 20% $week^{-1}$. The water flowed through the aquaria and was then pumped from the last aquarium back to the reservoir. The connection between each aquarium was covered by 300 µm mesh. This system supported five batches of up to 500 individuals to be

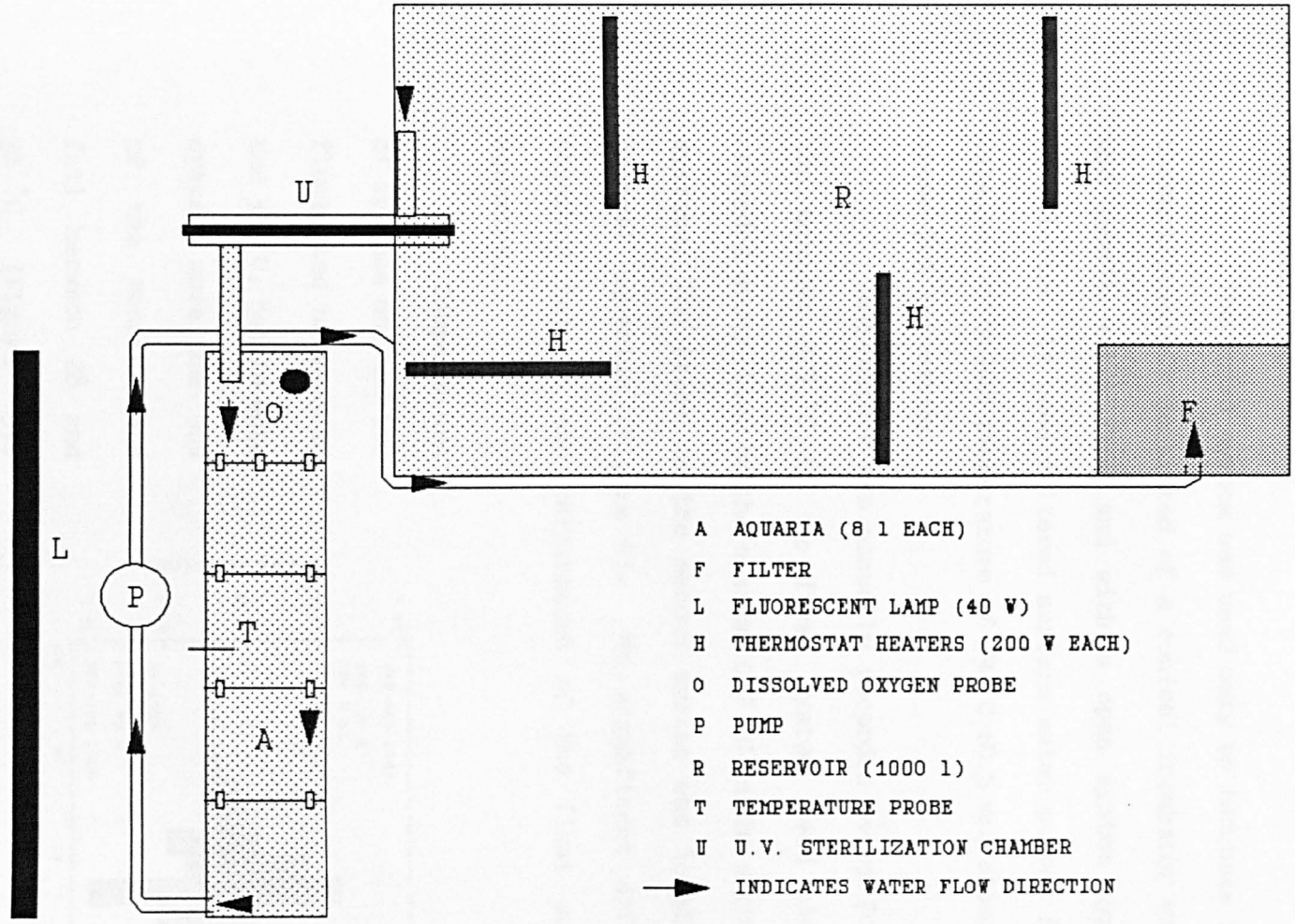


Figure 4 System used to rear the larvae after December 1988.

reared at any one time. Temperature was controlled by thermostats and heaters and had a light/dark cycle of 13/11 h. Dissolved oxygen, checked every day with YSI probe, was always higher than 80% saturation.

The third system was used only to incubate free eggs of characiforms. It consisted of a conical incubator with constant and gentle water flow and with a open system type of water circulation. It used filtered surface water pumped from Lago do Catalão, which had temperature of 29 °C ±0.5 and dissolved oxygen above 70% saturation.

Temperature was manually recorded every four hours to the nearest 0.5 °C in the first system and electronically recorded every hour to the nearest 0.2 °C in the second and third systems. The probe in the second system was localized in the central aquarium (Figure 4). No significant difference was observed between the temperature of the first and the last aquarium.

Temperature of systems one and two fluctuated between 26 and 32 °C, but in both systems more than 90% of the measurements fell between 28 and 31 °C (Figure 5). Results below or above this range were caused mainly by power failure.

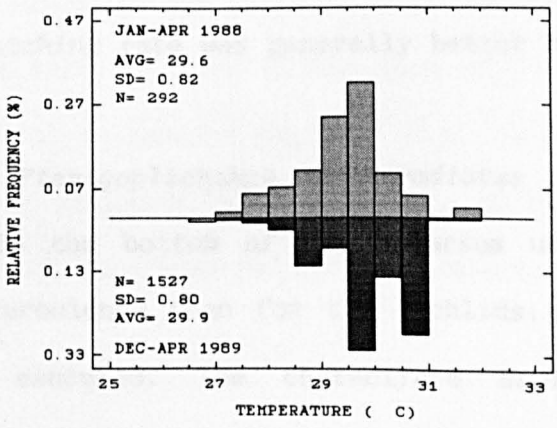


Figure 5 Temperature variation in the rearing tanks.

Rearing techniques. Semi-buoyant characiform eggs were incubated following standard methods for cyprinids and transported to the aquaria after hatching.

The siluriform *Hoplosternum littorale* has floating nests that were incubated on floating and dry glass dishes, covered with wet Nylon gauze in 100% humidity environment. Other techniques were also tried, such as incubating the eggs in very shallow and highly oxygenated water, or inside mesh envelopes just touching the water surface, but dry incubation showed the best results. When hatching started larvae were removed to a nylon mesh located in a very shallow position in the aquaria, where they remained for a while before dispersing down into the aquaria. The hatching rate was not measured.

Cichlid eggs were incubated together with their substrata. The substrata were deposited at the bottom of aquaria and the eggs were artificially fanned with a vent of recirculated water, necessary for successful incubation. After hatching the substrata were removed. Hatching rate was generally better than 50%.

The siluriform *Pterigoplichthys multiradiatus* egg clutches were incubated in the bottom of the aquarium under aeration, but with less turbulence than for the cichlids. The hatching rate was not measured. The characiform *Hoplias malabaricus* egg clutches were incubated as *P. multiradiatus*. The hatching rate was not measured.

The larvae were kept together until the onset of first feeding, when they were split into two batches. The first batch

comprised 80% of the population and was kept without feeding for the experiments. The second batch received food every day and was kept in separate mesh containers (volume= 7 cm^3; mesh width= 100 μm) in the last aquaria as a control group for the experiments.

The food consisted of live zooplankton caught in the fish ponds of Aquaculture Department of INPA with a plankton net of 100 μm mesh. It consisted, mainly, of several species of rotifers, Cladocera and nauplii and copepodite stages of Copepoda. It was fractionated by sieving to sizes from 100-150 μm and larger than 150 μm to match the gape of larval mouth. In general the characiforms received the smaller size fraction while the other groups the larger one.

3.2.2 Measurements and observations of events

The terminology of early life history stages used was a very general one. Egg period accounts for the interval from activation to hatching, larval period from hatching to the loss of larval characters (finray complement, squamation etc) and juvenile from loss of larval characters to maturity. Embryo was used to refer to larval body before hatching. Developmental stages were referred to the feature in question.

Morphological data. Sampling frequency was, at least every 12 h for eggs and newly hatched larvae and thereafter every 24 h. Sampling consisted of: measuring egg diameter and larval/embryo

length, age, checking for certain morphological characteristics and preserving with subsamples of 15-20 individuals with 4% formalin for later weighing and other analysis. Observations were made on 20 live eggs or anesthetized larvae (MS222; ~50 $mg \cdot l^{-1}$) with a stereomicroscope at magnification up to 160X. The individuals were randomly chosen from the aquaria. The number of samples (spawning batches) per species used for the developmental observations are listed in Appendix A.

The main morphological characteristics observed were:

(1) Appearance of red blood cells in circulatory system, as estimated by a pink colouration in the heart region.

(2) Extent of eye pigmentation.

(3) Presence of functionaljaw, considered to be any moving and articulated jaw, able to close the mouth completely.

(4) Presence of swim bladder. Any swim bladder with a vertical axis larger than 10 µm.

(5) Presence of pectoral fin bud. Any bud longer than 10 µm.

(6) Presence of caudal, anal and dorsal rays. After the first ray was stained with Alcian blue.

(7) The pattern of blood circulation. Special attention was paid to describe the main blood circulation in the trunk of the larvae, as perceived by movement of blood components.

Weighing. Dry weight measurements were made to an accuracy of 1 µg after two days in an oven at 60 °C. Measurements were made on preserved samples and the data were later corrected to fresh weight. Three to ten individuals were pooled and all measurements were done in triplicate. The eggs were weighed after dissecting

off the chorion and the yolk sacs and embryo bodies were weighed separately after dissection. Moisture contamination of the samples during weighing were found to be negligible (<1%).

Variation of weight within the species were measured in four species, whose batch numbers exceed four (*P. latior*, *H. littorale*, *C. monoculus* and *A. ocellatus*).

Larval length and egg volume and surface area. Larval length was measured from the snout to the tip of notochord or urostyle (when present).

Egg volume and surface were estimated from:

$$\text{Volume} = 4 \cdot \pi \cdot a \cdot b^2 \cdot 3^{-1}$$

$$\text{Surface} = 2 \cdot \pi \cdot b^2 \cdot \tau + \delta$$

where a and b equals egg radius for spherical eggs, or a equals major and b equals minor semi axis for elliptical eggs and $\tau = 2$ and $\delta = 0$ for spherical eggs or $\tau = 1$ and

$\delta = 2 \cdot \pi \cdot a \cdot b \cdot \arcsin(1-(b \cdot a^{-1})^2) \cdot (1-(b \cdot a^{-1})^2)^{-1}$ for elliptical eggs.

All measurements were done to the nearest 0.01 mm on ten to 20 fresh specimens, unless otherwise stated. The effect of preservation on the measurements was checked.

Ageing. The age of embryos and larvae was estimated in hours from the activation of the egg, i.e. the moment when water was added to the eggs prior to placing them in the incubators. The difference between activation time and fertilization time is probably negligible in the time scale used throughout this study.

Activation time was back-calculated from hatching for *H. littorale*, *H. malabaricus*, *C. monoculus*, *A. ocellatus* and

Heros sp based in published data at compatible temperatures (Moreira, 1919; Fontenele, 1950, 1951; Jesus *et al.* 1984; Machado, 1987).

3.2.3 Measurements of calorific content of eggs

Calorific content of the eggs (with chorion) were measured with a microcalorimeter (Scott and Marlow, 1981), calibrated with benzoic acid, to the nearest 0.1 calories (Table 4). Most measurements were done with fresh samples dried in an oven at 50 °C for 48 h, but samples preserved in formalin 4% were also used.

Table 4 Parameters for least-square regression of microcalorimeter readings on calories of benzoic acid.

PARAMETER	ESTIMATE	STANDARD ERROR	T VALUE	PROB. LEVEL
Intercept	7.2771	4.2168	1.7258	0.10639
Slope	44.3526	1493.3800	29.6994	<0.00001
r^2	0.9844			
N= 16				

3.2.4 Test of the effect of preservation

Dry weight. The effect of 4% formalin on the dry weight of eggs and larvae was measured by comparing fresh sub-samples weighed in Manaus against sub-samples preserved and weighed after three and up to seven months later at Oban. The balances were intercalibrated. The sample treatment at Manaus was the same

described above, but 20 to 30 pooled whole individuals were weighed with an accuracy of 0.1 mg. Ten and eight species were used for the egg and larval test, respectively.

Egg volume. The effect of 4% formalin on the egg volume was measured by comparing fresh subsamples against subsamples preserved up to seven months. The effect was checked in 11 and 12 subsamples and in six and eight different species for larval length and egg volume, respectively. Each subsample was composed of ten to 20 individuals measured as described above.

Egg calorific content. The effect of preservation on the measurements of the calorific content of the eggs was tested by comparing subsamples of fresh and 4% formalin-preserved egg samples. The test was involved with four species and five subsamples per species and treatment.

3.2.5 Experimental observations

The main characteristics observed are listed below. The number of samples used for each species is shown in Appendix A.

(1) Hatching. When 50% of eggs have hatched. Measured with three subsamples of 20 eggs per species.

(2) Functional status of cement glands. Whether the glands of 50% of the larvae had any adhesive quality when touched by a seeker.

(3) Onset of swimming. All larvae observed had a very heavy yolk sac that constrained swimming. As the yolk was absorbed and the swim bladder became functional, the larvae started to swim. The

onset of swimming was defined as when 50% of the larvae was able to maintain a vertical position by swimming in the water column. The intermittent "swim up" to the surface common in certain species was not considered as swimming.

(4) First feeding. After the larvae were found with functionaljaw, live food was presented at a density of ~10 organisms·ml^{-1}. First feeding was defined as when food was first found in the stomachs of 50% of the larvae. In three cases the estimate of 50% feeding were in the night time (dark period). They were corrected to the time the light was switched on.

(5) Phototaxis. This was tested daily for most spawning batches. The test was done with a known number of individuals (15-20) in a 8 mm diameter petri dish, which was half transparent and half opaque. The dish was placed on a 8 mm light diffuser and the number of larvae in the illuminated section of the dish was counted after 1 min period. Each experiment consisted of a minimum of 11 and a maximum of 20 trials. Before each trial, the petri dish was turned around so exposing the previously shaded side to light. The experiments were conducted in a dark room.

A second type of experiment was carried out with newly hatched *Potamorhina latior*. Approximately 200 larvae were placed in a plastic rectangular container (35x55 cm) divided into eight equal rectangular areas. The container was filled with a 6 cm deep layer of Solimoes river water. A beam of light of diameter equal to half the size of one of the areas was directed on one of the rectangular areas. After five minutes each area was sampled with a small handnet (2x2 cm) and the number of individuals

counted. The experiment was repeated five times changing the illuminated area randomly.

Phototaxis was not measured for *A. ocellatus* and *M. insignis*.

(6) 50% Mortality due to starvation. This was defined as the size and the age when 50% of the larvae died, when deprived of external food. It was tested with batches of 15-20 larvae for ten species and for half of these at least twice. The experiments were done in triplicate - two experimental batches plus a control. The batches were kept in a 500 ml plastic tray floating in the aquaria. The water inside the beakers was changed every 12 h with new filtered water. Control batches were fed twice a day. If mortality in the control was above 20% the experiment was discarded. The results were tested using probit analysis.

Table 5 Experimental design for testing dissolved oxygen tolerance.

	NUMBER OF REPLICATES					
	C.monoculus					
STAGE	NON-SWIMMING			SWIMMING		
OXYGEN LEVEL (% SATURATION)	5%	10%	C	5%	10%	C
BATCH 1	2	2	1	2	2	1
BATCH 2	2	2	-	1	1	-
	P. latior					
STAGE	NON-SWIMMING			SWIMMING		
OXYGEN LEVEL (% SATURATION)	5%	10%	C	5%	10%	C
BATCH 1	2	2	1	2	2	1
BATCH 2	1	1	-	1	-	-

5% SATURATION= 0.4 mg D.O. l^{-1}; 10% SATURATION= 0.8 mg D.O. l^{-1}; C= control; each replicate contained 10 larvae.

(7) Dissolved oxygen tolerance. A series of experiments (static bioassay) were conducted to test whether the developmental stage of larvae of two species that have different spawning grounds (*Potamorhina latior* and *Cichla monoculus*) differed in their tolerance to low concentrations of oxygen. 25 bioassays with four controls were performed in two species, two oxygen concentrations and two developmental stages (non-swimming and swimming larvae) from two different spawning batches as shown in Table 5. Each bioassay consisted of incubating groups of ten larvae in ~2 l of water. Each incubation lasted 1 h. No mortality was found in the control samples.

The preparation of experimental water took place in 20 l glass jars, where the oxygen concentration was regulated by bubbling nitrogen. The dissolved oxygen was measured with an YSI 57 monitor, using membranes with a sensitivity of 0.025 $mg \cdot l^{-1}$ of dissolved oxygen. When the desired concentration was reached samples of water were transferred to the experimental volumetric flasks (~2 l) very gently, and allowed to overflow for at least one flask volume. Dissolved oxygen was constantly monitored during the transfer process. The concentrations of oxygen in the bottles were checked in the preliminary phase and no contamination with atmospheric oxygen was found.

After the flasks were full the larvae were transferred, the flasks were sealed and held for one hour at 29.5 ±0.5 °C. During this time the oxygen concentration fell as the larvae respired. The experimental and control flasks were kept immersed in the 1000 l reservoir, where the temperature was monitored. The contamination of the experimental flasks due to adding the larvae

was below the sensitivity of the monitor. The number of dead larvae at the end of incubation were analyzed using two way ANOVA, using the samples as replicates after arcsin transformation (Snedecor and Cochran, 1980).

Table 6 Spawning time for 17 species of fish of the Central Amazon.

SPECIES	SPAWNING MONTHS												REF.
	J	F	M	A	M	J	J	A	S	O	N	D	
C. macropomum	x	x	x	x							x	x	1
S. insignis	x	x	x									x	2, 3
P. latior	x	x	x	x							x	x	3
P. amazonica	x	x	x	x							x	x	3
B. erytropterum	x											x	4
M. duriventre	x	x	x								x	x	3, 5
E. melanopogon	x	x	x									x	3
P. nigricans	x	x	x									x	3, 7
O. bicirrhosum	x	x	x									x	6
P. multiradiatus	x	x										x	7
H. littorale	x	x									x	x	7
A. ocellatus	x	x	x	x								x	7
C. monoculus	x	x	x	x	x	x						x	7
P. altamazonica	x	x	x	x	x	x						x	7
M. insignis	x	x	x	x	x	x	x	x	x	x	x	x	7
Heros sp	x	x	x	x	x	x	x	x	x	x	x	x	7
H. malabaricus	x	x	x	x	x	x	x	x	x	x	x	x	7

1: Sudepe, 1981; 2: Vazzoler *et al.*,1989; 3: Fernandes, 1989; 4: Zaniboni Filho, 1985; 5: Paixao, 1981; 6: Aragao, 1981; 7: This study.

4 RESULTS

4.1 Reproduction

4.1.1 Timing

The timing of the reproduction of Amazonian fishes has been described to some extent in the literature. Here the data are summarized from the literature with new data for *Hoplosternum littorale, Hoplias malabaricus, Cichla monoculus, Astronotus ocellatus, Heros* sp, *Potamorhina altamazonica* and

Pterigoplichthys multiradiatus. The individual analysis for each of those species is given in Appendix B.

The periods in which the species were at or near spawning are shown in Table 6. Two patterns can be seen, with one group spawning from November/December to June and another spawning throughout the year.

The spawning season of those species can be related to the annual flooding cycle. The water level in the study area starts to rise in November or December and the flood continues until June or July (Figure 2). The first group of species starts to spawn at the onset of the flood. The second group spawns independently of the flooding regime.

With the exception of the siluriforms, which spawn very early in the season, no clear related pattern to taxa appears in Table 6. For example, there are characiforms and cichlids in both groups.

Table 7 Spawning type for 17 of the species of Central Amazon.

SPECIES	SPAWNS/SEASON		METHOD	REFERENCE
	1	>1		
C. macropomum	X		Cohort	Sudepe, 1981
S. insignis	X		Histology	Chaves e Vazzoler, 1984
S. taeniurus	X		Histology	Chaves e Vazzoler, 1984
P. latior	X		Egg diameter	This study
P. amazonica	X		Egg diameter	This study
B. erytropterum	X		Histology	Zaniboni Filho, 1985
M. duriventre	X		Histology	Paixao, 1981
E. melanopogon	X		Histology	This study
P. nigricans	X		Histology	Chaves, 1985
O. bicirrhosum	X		Egg diameter	Aragao, 1981
P. multiradiatus	X		Egg diameter	This study
H. littorale	X		Egg diameter	Machado y Zaret, 1984
P. altamazonica	X		Egg diameter	This study
C. monoculus		X	Histology	Chaves, 1985
A. ocellatus		X	Histology	Chaves, 1985
Heros sp		X	Egg diameter	This study
H. malabaricus		X	-	This study

It was not possible to collect data on *Piaractus brachypomus*, and *Crenicichla* sp, but some observations in addition of those of Goulding and Carvalho (1982) suggest that *P. brachypomus* spawns for a short period, starting very early in the season and should therefore be ranked in the first group. *Crenicichla* sp appears to have a pattern of spawning similar to *Cichla monoculus* and *Astronotus ocellatus*, but this has not yet been confirmed.

4.1.2 Spawning type

Two types of spawning were identified among the species studied. The first comprised the species with only one spawning per year and the second group consists of batch spawners (Table 7). Excluding *H. malabaricus* all the batch spawners are cichlids.

Detailed results of analyses of type of spawning are shown in Appendix B.

4.1.3 Spawning site and style

The information about the spawning sites is very scattered, comprising data on ripe and brooding fishes, sampled for this project, and data from the literature and from fishermen.

Osteoglossum bicirrhosum. Ripe females and brooding males were captured in Lago do Rei (one sample) and Lago do Janauaca (two samples). In general, they have only been sampled successfully inside the lakes (this study; Aragao, 1981; Goulding, 1980) and spawning probably occurs in the lakes. The male has

been reported to carry the fertilized eggs and larvae in its mouth throughout the larval period. The species can therefore be classified as a bearer (mouth brooder).

Pterigoplichthys multiradiatus. Egg clutches were found inside long tubular nests at Lago do Catalao (two samples), channel of Janauaca (one sample), Lago do Rei (one sample) and Lago do Careiro (six samples). The nests examined were more than 1m long, ~10 cm diameter and slightly tilted, penetrating almost horizontally into the muddy-clay banks of lakes and channels at 1-2 m depth. The males were captured in the outermost part of the nests while the egg masses were laid at the closed end. Several nests were found with hatched larvae inside, suggesting that they kept their position after hatching. This species was classified as a nest spawner (hole nester) and its spawning habitats are the margins of rivers, channels and lakes.

Astronotus ocellatus, *Cichla monoculus*, *Crenicichla* sp, *Heros* sp and *Mesonauta insignis*. The egg clusters of those cichlids were sampled in the lakes. They were found attached to woody substrata such as root branches or tree trunks of inundated forests, in general at very shallow depths (<1 m) at Lago do Rei (20 samples), Lago do Catalao (two samples) and Lago Janauaca (two samples). The eggs were 1-2 mm apart in all species. Both male and female guarded the eggs, constantly fanning them with their fins. Parental protection against predation seemed to be quite effective, since in five cases when the parents were removed during the night, the eggs had completely disappeared 6 h later. Protection extends throughout the larval period, when schools of young larvae are commonly seen swimming around their parents.

These observations agreed well with those of Fontenele (1950, 1951) and Machado (1987). The four species seem to spawn on the margins of river, channels and lakes, provided the proper substratum is available. However, they need an area with a weak water current, which would enable them to release the eggs in a dense clutch, therefore increasing the effectiveness of guarding. All five species can be classified as nest spawners (plant nesters).

Hoplosternum littorale. Floating nests were found at the margins of Lago Catalao (five samples), Lago do Rei (six samples), Lago do Careiro (two samples), Lago do Camaleão (two samples) and channel of Careiro (two samples). The nests were shaped like an inverted saucer, made of mucous bubbles and plant debris. The egg masses were retained inside the nest having no direct contact with the water. The nests were found attached to plant branches or hidden in wood holes, sometimes exposed to direct sunlight, but usually protected from below, either by vegetation or by being localized in a very shallow area. The parents guard the nests, attacking intruders with their spines. The hatched larvae stay for a short period close to the nests and then disperse. The species seems to spawn in the lake margins, generally in still areas. It can be classified as a nest spawner (froth nesters).

Hoplias malabaricus. One nest was observed in the margin of Lago Catalao. It consisted of a shallow saucer located on the bottom in a very shallow (5 cm deep) marginal area. The egg clutch was laid in the middle of the nest and protected by one of the parents. These observations agree well with those of Moreira (1919) and Machado (1987). This species appears to spawn in the

margins of lakes and channels (Machado, 1987; Lowe-McConnell, 1987) and it can be classified as nest spawner (gravel nesters).

Semaprochilodus insignis, S. taeniurus, Psectrogaster rutiloides, P. amazonica, Prochilodus nigricans, Potamorhina latior, P. altamazonica, Eigenmannina melanopogon and *Mylossoma duriventre*. Ripe females were captured at Rio Solimoes (11 samples) and Rio Amazonas (four samples). Mature, but not ripe, females were captured in the lakes. *Colossoma macropomum* (Goulding and Carvalho, 1982; Machado, 1987) has been reported as spawning in the main river. Very young larvae of these species are found in high densities drifting in the Rio Solimões/Amazonas, but are not found in the lakes. However, high concentrations of eggs have never been found in the channels (Araujo-Lima, 1984). The eggs are slightly heavier than the water and just float with water turbulence. Although the exact spawning sites have not been confirmed, their reproductive style can be classified as open substratum spawners. Similar conclusions were presented by Ribeiro (1983), Machado, (1987) and Fernandes, (1989). All the above species migrate to spawn from the lakes to the river or from the tributaries to the main river. No exact information is available for *Piaractus brachypomus*, but observations of fishermen suggest that the same holds true for this species.

4.1.4 Fecundity and reproductive expenditure

Fecundity results are presented in Table 8, with more detailed accounts in Appendix C. Fecundity was very variable

between and within species. Differences up to five orders of magnitude were found between the species with the smallest and with the largest fecundity.

Table 8 Total body weight, fecundity and standardized fecundity by weight for 19 species of fishes of Central Amazon.

SPECIES	SIZE RANGE(g)	FECUNDITY(eggs.10^3) RANGE	FECUNDITY(eggs.10^3) AVERAGE	REL.FECUNDITY AVERAGE	REL.FECUNDITY s.d.
O. bicirrhosum[1]	551-1750	0.10-0.25	0.16	0.1	0.05
Heros sp	73-167	0.85-1.60	1.23	10.9	3.5
A. ocellatus[2]	100-915	2.15-3.45	2.72	1.6	10.4
P. multiradiatus	372-650	1.88-10.34	5.23	34.1	14.0
C. monoculus[4]	388-630	5.22-5.59	5.44	1.8	0.7
H. littorale[3]	41-153	3.55-10.16	5.97	148.3	31.2
H. malabaricus	213-651	4.79-14.13	8.21	26.5	7.6
E. melanopogon	60-147	17.62-60.58	36.53	534.4	177.2
M. duriventre[5]	178-436	25.49-100.00	54.29	314.4	79.2
P. latior	120-180	29.07-70.95	50.95	690.6	96.9
S. insignis	273-	-	62.79	260.8	-
P. rutiloides	43-115	26.99-115.30	67.35	1588.9	213.5
S. taeniurus	353-405	63.49-85.05	74.27	200.0	-
P. nigricans	291-877	64.19-331.35	136.07	573.6	93.6
P. altamazonica	173-384	37.81-401.75	185.10	2337.4	795.7
P. amazonica	131-184	115.96-269.48	199.60	4665.1	459.7
P. brachypomus	4500-	-	1436.50	381.8	-
P. brachypomus[7]	-	-	400.00	-	-
C. macropomum[7]	-	-	500.00	-	-
B. erytropterum[6]	579-	36.70-309.29	-	95.9	-

Obs: Size range= Total weight; REL. FECUNDITY= Relative fecundity in standard deviation of fecundity / standard deviation of weight; s.d.= Standard deviation; 1= Aragao, 1981; 2= Fontenele, 1950; 3= Machado y Zaret, 1984; 4= Fontenele, 1951; 5= Paixao, 1980; 6= Zaniboni, 1985 called the species B. cephalus; Others: this study

The variation within species was smaller, but reached ten fold in some cases. Part of this variability can be explained by the size of the female (Appendix C). The relationship between fecundity and body weight, after logarithmic transformation, was tested for three species, in which size of the data set allowed a more detailed analysis (Appendix C). Reduced major axis analysis (Ricker, 1973) used to calculate regressions parameters showed that fecundity increased with weight at slightly higher than one for *P. rutiloides* and *P. nigricans* and smaller than one for

O. bicirrhosum. Correlation between fecundity and body weight was significant for 11 of the 14 species tested.

To compare the fecundity of the different species, size effect had to be excluded. This could be done in two ways: comparing fecundity in fishes of the same size or comparing relative fecundity. The first approach was not possible, since the size ranges of the species were rather diverse; consequently the second approach was used. Normalizing fecundity by fish weight (relative fecundity) is dependent on a linear relationship of fecundity on weight, hence the relative fecundity had to be approximated. The relative fecundity was considered the slope of Ricker's regression with untransformed variables. The error introduced was not very large, since the exponents were close to 1. Approximation by logging both variables (log fecundity/ log fish weight) for each species, was not applicable, since it was strongly biassed.

Fecundity could be related to the extent of the parental care. The lowest absolute and relative values were found for a mouth-brooder species, *Osteoglossum bicirrhosum*, increasing with nest-builder species that have parental care extended throughout the larval period, such as the cichlids, *Hoplias malabaricus*, *Pterigoplichthys multiradiatus*. The higher values were found in species whose parental care was restricted to egg mass protection (*H. littorale*) and in species were no parental care existed (Figure 6).

Fecundity could also be classified by spawning site. The species reported to spawn in the river had fecundities above 17000 eggs or ~90 eggs.g^{-1} and the species known to be less river-

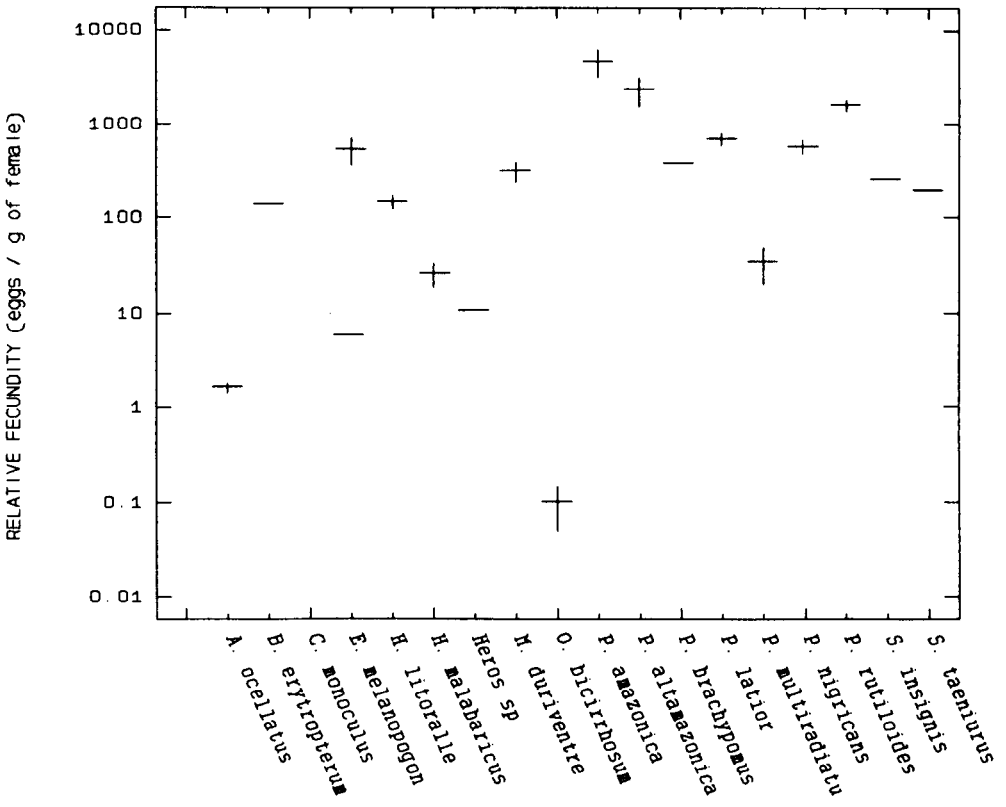


Figure 6 Relative fecundity with standard errors for 18 species of Central Amazon.

dependent have less than 17 000 eggs or than ~40 eggs.g^{-1}. Data for *Hoplosternum littorale* did not fit in this classification, since this species has a relative fecundity up to 148 eggs·g^{-1}.

Fecundity per season can be several times higher than fecundity for batch spawners. Its estimation is especially problematical for species that spawn throughout the year, since is difficult to establish the season (Bagenal, 1978) and the number of spawns. A rough approximation of fecundity per season was considered to be four times the fecundity for *H. malabaricus*, three times the fecundity for *Heros* sp (Appendix B) and twice the fecundity for *C. monoculus* and *A. ocellatus* (Fontenele, 1950, 1951).

A measure of the relative female expenditure on each spawn can be obtained multiplying the relative fecundity by the average amount of calories in each egg (Figure 7). The results were different from those found for relative fecundity. It was minimum among the cichlids and maximum in *P. amazonica* and *P. altamazonica*.

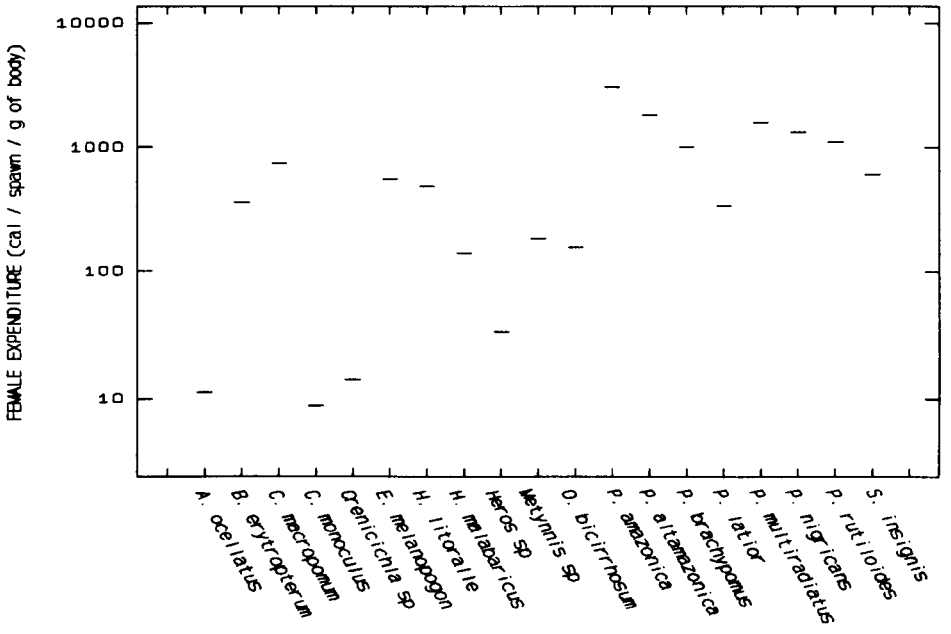


Figure 7 Reproductive expenditure (calories·spawning^{-1}·wet body weight of female^{-1}) for 19 species of Central Amazon.

The correlation with parental care and spawning site was less clear due to the overlapping of values. However, the species that spawn in lotic habitats showed values significantly higher ($t=4.5$; D.F.= 17; $p=0.007$) than the species that spawn in the littoral areas. The latter group is not homogeneous and the cichlids split apart from the other species. The expenditure per season would be higher for species with multiple spawning, but

even so the expenditure of the cichlids still would be lower than the other species.

Table 9 Weights (eigenvectors) for principal component analysis of the reproductive traits of 19 species of Central Amazon fishes.

	PC1	PC2	PC3
Percentage of variance contributed (%)	54.2	23.8	11.6
VARIABLES	**PC1**	**PC2**	**PC3**
Fecundity	0.41	0.18	0.38
Reproductive expenditure	0.43	0.09	-0.19
Calories per egg	-0.29	0.49	-0.20
Number of spawns	-0.39	-0.31	0.30
Relative fecundity	0.44	-0.25	0.02
Parental care	-0.43	0.13	-0.18
Length of season	-0.17	-0.54	0.35
Maximum female weight	-0.05	0.50	0.73

4.1.5 Reproductive strategies

The reproductive traits of the 19 species were analyzed using principal component analysis. The variables were transformed to logarithm scale aiming at reducing the variance and to approach a normal distribution. The analysis only considered the component correlations greater than 0.25 (Chatfield and Collins, 1980). The variables were: absolute fecundity (eggs), relative fecundity (eggs·g^{-1} of female), reproductive expenditure (cal·$spawn^{-1}$), number of spawnings per season (events per year), parental care (1= no parental care; 2= parental care of the eggs; 3= parental care of the eggs and larvae), length of the spawning season (number of spawning months), calorific content of eggs

(calories·egg^{-1}). Female maximum weight based on literature data and in the samples collected were used as the eighth variable.

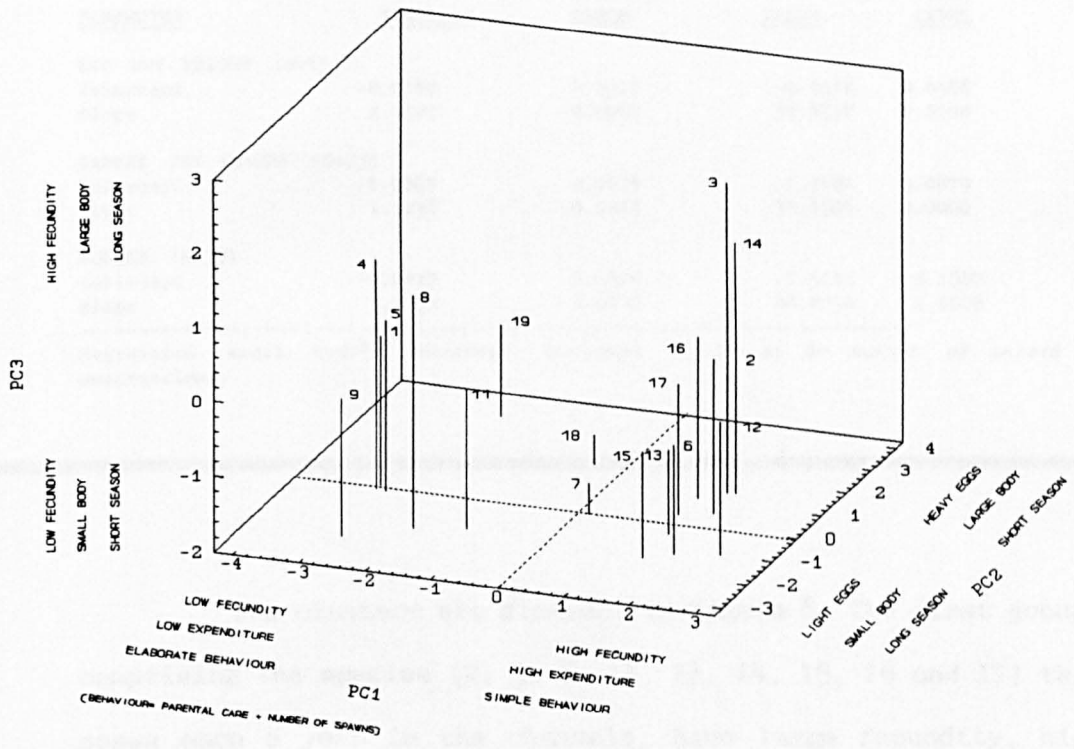


Figure 8 Principal component analysis of reproductive strategies of 19 species of Central Amazon. Data code in Table 11.

The first three components explained 90% of the variance of the data set (Table 9). The first component, accounting for 54% of the variance, seems to balance fecundity and reproductive expenditure with parental care and number of spawning per season. The second component accounts for 24% of the variance and comprises caloric content of the eggs, length of spawning period number of spawning per season and female size. The third component accounting for 11% of the variance and balances fecundity, number of spawns per season, length of the season and female size.

Table 10. Parameters of the curvilinear regressions of dry weight of preserved samples on dry weight of fresh samples for eggs (ten species), larvae (eight species) and eggs and larvae pooled.

PARAMETER	ESTIMATE	STANDARD ERROR	T VALUE	PROB. LEVEL
EGG DRY WEIGHT (N=15)				
Intercept	-0.0140	0.0311	-0.4518	0.6588
Slope	1.0587	0.0267	39.8577	0.0000
LARVAE DRY WEIGHT (N=23)				
Intercept	-0.0767	0.0428	-1.7800	0.0879
Slope	1.1258	0.0323	34.8306	0.0000
POOLED (N=38)				
Intercept	-0.0477	0.0315	-1.5141	0.1387
Slope	1.1074	0.0249	44.4754	0.0000

Regression model $Y=aX^b$; Intercept is equal to ln a; N= number of paired observations.

Two clusters are distinct in Figure 8. The first group, comprising the species (2, 3, 6, 12, 13, 14, 15, 16 and 17) that spawn once a year in the channels, have large fecundity, high reproductive expenditure and lack of parental care. The second group (1, 4, 5, 8, 9 and 11), comprising the cichlids and the characiforms that spawn in the littoral, have low fecundity, low reproductive expenditure, spawn several times per year and may or may not exhibit parental care. The other three species (7, 18 and 19) do not fit in any of the previous groups. *H. littorale*, *P. multiradiatus* and *O. bicirrhosum* spawn once a year in the littoral and exhibit parental care. Fecundity, reproductive expenditure and egg size are very variable among them (Figure 8).

Despite their common features the groups have specific differences as shown mainly by the second and third components. The high fecundity group is variable in the calorific load of the eggs, body weight, length of spawning season and total fecundity

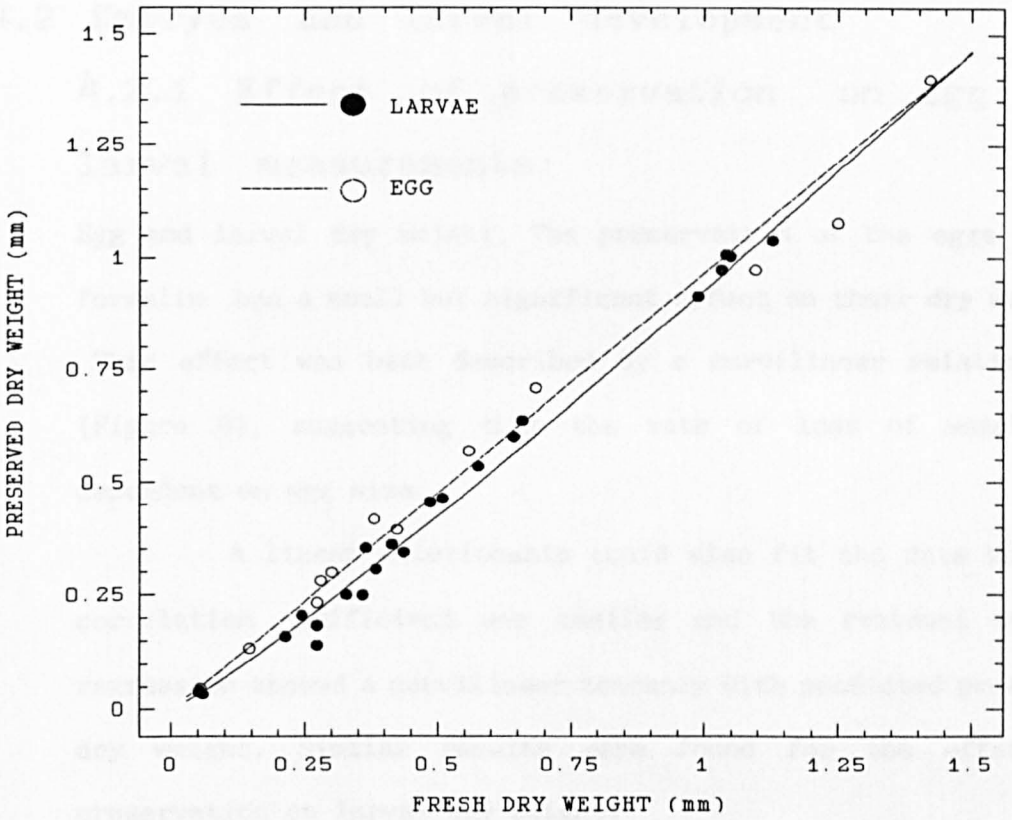


Figure 9 Scatterplots and regression lines of preserved dry weight on fresh dry weight for eggs and larvae. Data points refer to 10 species for eggs and 8 species for larvae.

(Figure 8). The low fecundity group is very variable in body size and length of spawning season, but is more homogeneous in relation to total fecundity.

The clusters were formed mainly by the first and second component. They seem to describe at least two convergent reproductive strategies.

4.2 Embryos and larval development

4.2.1 Effect of preservation on egg and larval measurements:

Egg and larval dry weight. The preservation of the eggs in 4% formalin had a small but significant effect on their dry weight. This effect was best described by a curvilinear relationship (Figure 9), suggesting that the rate of loss of weight is dependent on egg size.

A linear relationship could also fit the data but the correlation coefficient was smaller and the residual of the regression showed a curvilinear tendency with predicted preserved dry weight. Similar results were found for the effect of preservation on larval dry weight.

The dry weight of fresh samples explained 99.2% and 98.3% of the variability of preserved samples of egg and larvae, respectively (Table 10). The residuals of both regressions had no correlation with the duration of preservation period, with egg surface area or with the amount of yolk of the larvae.

Further analysis showed that neither regression was statistically different ($t=1.457$; D.F.= 34; $p<0.05$) and a pooled model (Table 10) would efficiently predict ($r^2= 0.9821$) both egg and larval fresh dry weight from their preserved dry weight.

Egg volume. A significant interaction was found between species and preservation effect on egg volume (ANOVA; $F=2.95$; N= 386; D.F.=11; $p<0.0009$). Species with larger eggs showed a small

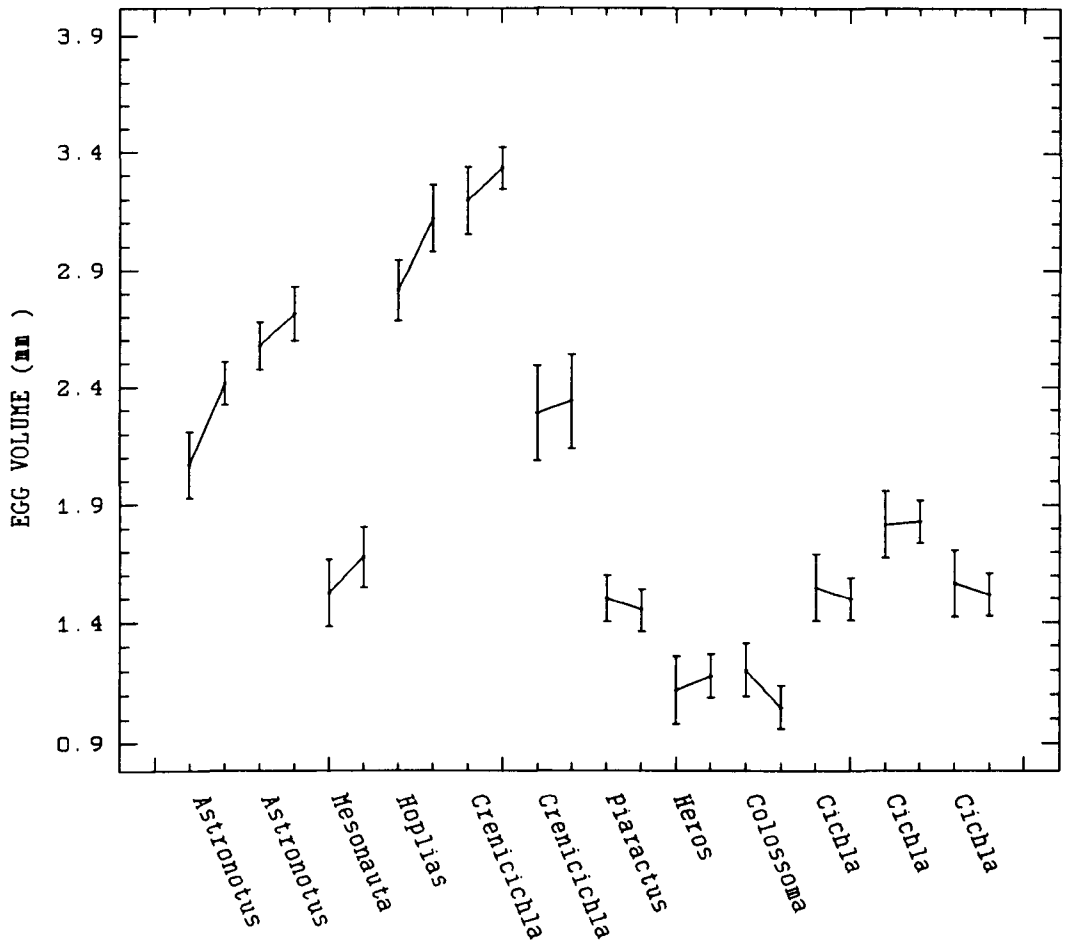


Figure 10 Averages and 95% confidence limits of fresh (left bar) and preserved (right bar) egg volumes for eight species.

increase in egg volume, but little effect, if any, were observed in the species with smaller eggs (Figure 10). Splitting the data set into egg volumes larger and smaller than ~2 mm^3, showed two different tendencies. The group with smaller eggs showed no significant effect of preservation, whereas the group with larger eggs had a significant increase of 7.81% in egg volume after preservation (ANOVA; F=17.36; N= 136; D.F.=1; $p<0.0001$).

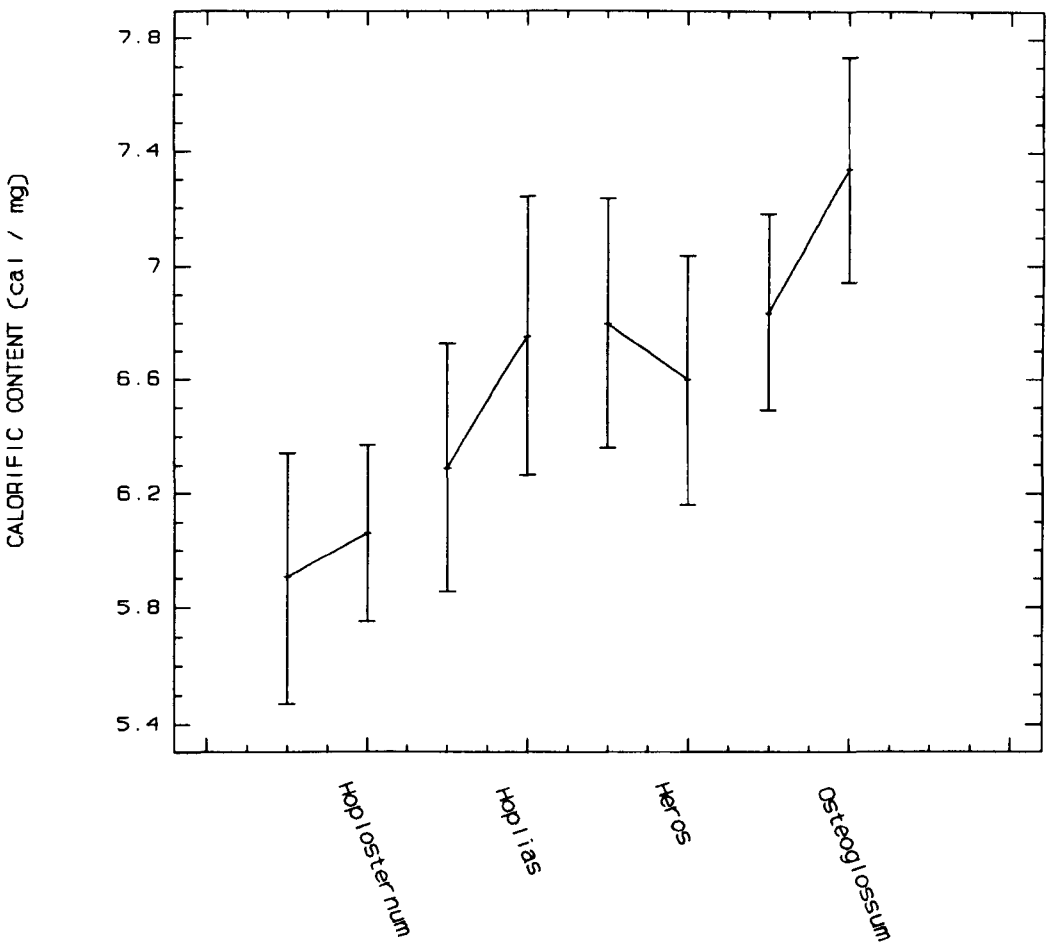


Figure 11 Averages and 95% confidence limits of calorific content of fresh (left bar) and preserved (right bar) eggs of four species.

Egg caloric content. No significant differences in the calorific content was found between fresh and preserved eggs (ANOVA; F=2.896; N=47; D.F.=1; p=0.0966) (Figure 11). The result supports the use of preserved samples for determination of calorific content on eggs.

4.2.2 Activated eggs: shape, size, calorific value and other features.

The activated eggs were very variable in shape, volume, surface area, dry weight and calorific value. The shape and some characteristics of the eggs are shown in Table 11.

Table 11 Main characteristics of the activated eggs of 19 species of Central Amazon.

SPECIES	SHAPE	P.V. SPACE % EGG VOL.	CHORION ADHESIVE.	EGG MASSES	INCUBATION SITES	CODE
S. insignis	Spher.	>70%	Weak	No	Lotic	17
S. taeniurus	Spher.	>70%	Weak	No	Lotic	20
P. nigricans	Spher.	>70%	Weak or null	No	Lotic	16
E. melanopogon	Spher.	>90%	Weak	No	Lotic	6
P. altamazonica	Spher.	>90%	Weak	No	Lotic	12
P. latior	Spher.	>90%	Weak	No	Lotic	15
P. rutiloides	Spher.	Unknown	Unknown	No	Lotic	21
P. amazonica	Spher.	>80%	Weak	No	Lotic	13
B. erytropterum	Spher.	>80%	Weak or null	No	Lotic	2
C. macropomum	Spher.	>90%	Weak or null	No	Lotic	3
M. duriventre	Spher.	>50%[1]	Weak or null	No	Lotic	22
Metynnis sp	Spher.	<40%[2]	Weak or null	No	Littoral	11
P. brachypomus	Spher.	>80%	Weak or null	No	Lotic	14
H. malabaricus	Spher.	<50%	Strong	Yes	Littoral	8
H.littorale	Spher.	<40%	Strong	Yes	Littoral	7
P. multiradiatus	Spher.	<40%	Strong	Yes	Littoral	18
A. ocellatus	Ellip.	<30%	Strong	No	Littoral	1
C. monoculus	Ellip.	<30%	Strong	No	Littoral	4
Crenicichla sp	Ellip.	<30%	Strong	No	Littoral	5
Heros sp	Ellip.	<30%	Strong	No	Littoral	9
M. insignis	Ellip.	<30%	Strong	No	Littoral	10
O. bicirrhosum	Spher.	<50%	Weak or null	No	Mouth	19

Spher.= Spherical; Ellip.=Elliptical; P.V.SPACE= perivitelline space; VOL.= volume; ADHESIVE.= Adhesiveness; [1]= from Kossoski, 1980; [2]= from Franke, 1967.

Spherical eggs were dominant among the species studied and elliptical eggs were found only in cichlids. A perivitelline space smaller than 50% of total egg volume were found for all eggs of all species, except for those incubated in the channels. Chorion adhesiveness had not a clear relation with incubation site, nor has the formation of egg masses.

Egg volumes were measured in fresh samples for all batches, except *Metynnis* sp and *M. duriventre*. Correction of the volume to fresh dry weight was applied only for the former species. This varied from 1.25 mm^3 in *Heros sp* to 1149.76 mm^3 in *Osteoglossum bicirrhosum*. The coefficient of variation of egg volumes within the species ranged from 9 to 20%. The egg volumes (Figure 12) were significantly different between species (ANOVA; $F=893.348$; $D.F.=343$; $p<0.0001$), but the variations could not be satisfactorily explained by phylogenetic relationships, since differences in egg volume within families were, in some cases, larger than differences between species of distinct groups, for example: *Metynnis sp*, *C. macropomum* and *P. brachypomus* or *Heros sp* and *Crenicichla sp*.

Incubation site also had no clear relationship with egg volume. The average volumes of eggs incubated on the littoral were not statistically different from those incubated in the channels. Egg volume of *O. bicirrhosum* was much larger than the other species. Ecological reproductive guilds (Balon, 1985) also had no sharp relationship with egg volume. Open substratum spawners like *P. latior* or *Metynnis* sp had egg volume similar to nest spawners. Similar results were found for the surface area of the eggs.

Egg dry weight immediately after activation for batches sampled in the field was calculated summing chorion and yolk weight at activation and assuming embryo weight as negligible. Details of the estimation of yolk weight are shown in the Appendix D.

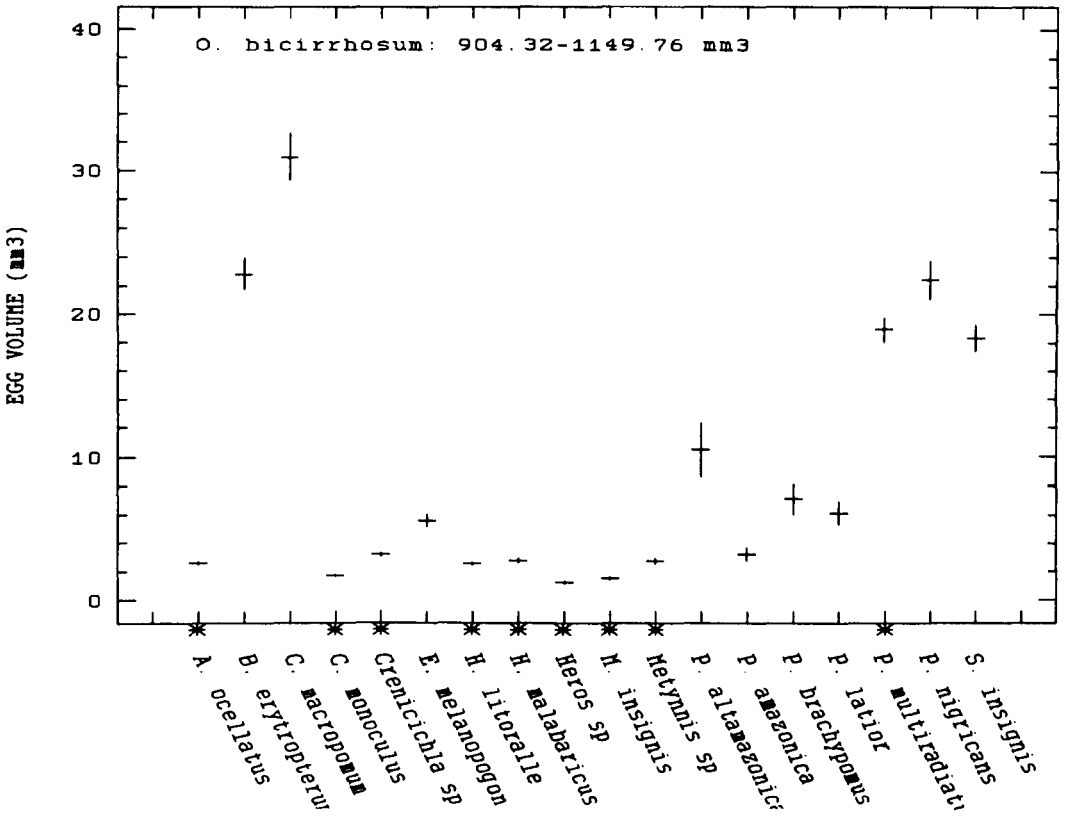


Figure 12 Average and 95% confidence limits for the volume of activated eggs of 19 species of Central Amazon. Asterisks indicate eggs incubated on the littoral.

Egg dry weight varied from 0.079 mg in *P. latior* to 394.825 mg in *O. bicirrhosum*. The coefficient of variation within species ranged from 2 to 20%. Differences between species were large and egg dry weight was found to be statistically different (ANOVA; F=225.195; D.F.= 85; p<0.0001). *O. bicirrhosum* and *P. multiradiatus* were excluded of the analysis, since they had egg dry weight much heavier than the other species and would bias the analysis.

Ranking the species by egg dry weight showed some patterns (Figure 13). The lightest eggs belonged to characiforms species of the family Curimatidae and a close relative, *E. melanopogon*. The remaining values of egg dry weight appeared

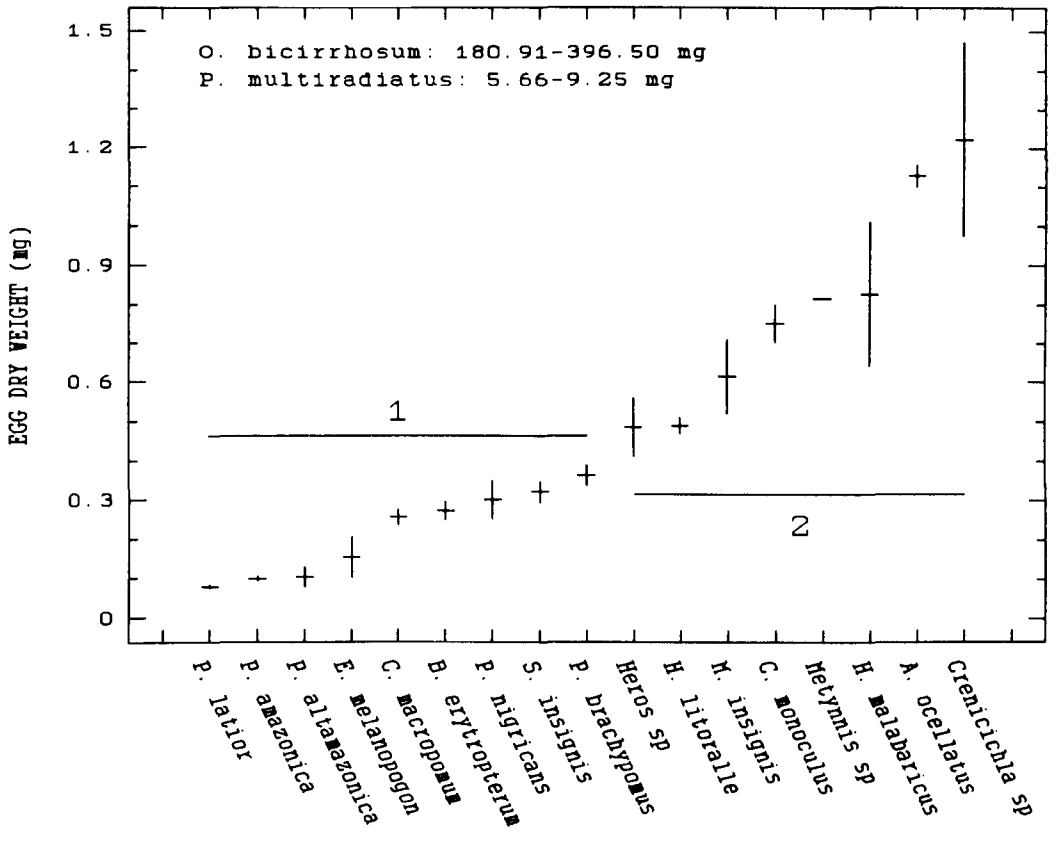


Figure 13 Averages and 95% confidence limits for dry weight of activated eggs of 19 species of Central Amazon. 1= Eggs incubated in the channels; 2= Eggs incubated on the littoral.

quite independent of phylogeny.

The species could also be ranked by the incubation site (Figure 13), with eggs incubated in the channels being lighter than eggs incubated on the littoral of river and lakes. Ecological reproductive guilds (Balon, 1985) had no sharp relationship with egg dry weight. Open substratum spawners like *Metynnis* sp, for instance, had egg dry weights not significantly different from nest spawners species.

The dry weight of the chorion of the eggs was very variable among the species, since it is related to the size of the eggs. The square root of egg dry weight explained 83% of this

variability, while egg volume explained only 1.9% and egg surface nil. The chorion of the eggs of *O. bicirrhosum* was very heavy and had be excluded or it would bias the analysis. No correlation of egg incubation site was observed with the remaining variability. However, one species, *P. multiradiatus*, was found to have a chorion dry weight:egg dry weight ratio significantly higher ($p<0.05$) than the others. Chorion dry weight can be approximated from $c= 0.05 \cdot m^{0.5}$, where c equals chorion dry weight (mg) and m equals egg dry weight (mg).

The ratio between surface area and egg dry weight varied from 2.366 in *O. bicirrhosum* to 223.194 $mm^2 \cdot mg^{-1}$ in *P. altamazonica*.

There were not enough data for all the species to allow a general analysis between species and an estimation of the coefficient of variation within species; nevertheless some patterns can be seen. The eggs incubated on the littoral had an average ratio 13 times higher (95% confidence limits: 9-17), than the eggs incubated at channels ($t=7.195$; D.F.= 8.1; $p<.0001$). However, those groups were not homogeneous. A comparison between the eggs incubated on the littoral showed that two species, *H. littorale* and *P. multiradiatus*, had eggs with a surface:dry weight ratio, respectively, higher and lower than the cichlids (Tukey, Unplanned multiple comparison; $p<0.05$).

The average calorific content of the eggs per species varied from 5.732 in *H. littorale* to 7.731 $cal \cdot mg^{-1}$ in *P. nigricans*. The coefficient of variation within the species was very variable ranging from 0.1 to 15 %. Differences between species were significant (ANOVA; $F= 7.730$; D.F.= 133; $p<0.0001$),

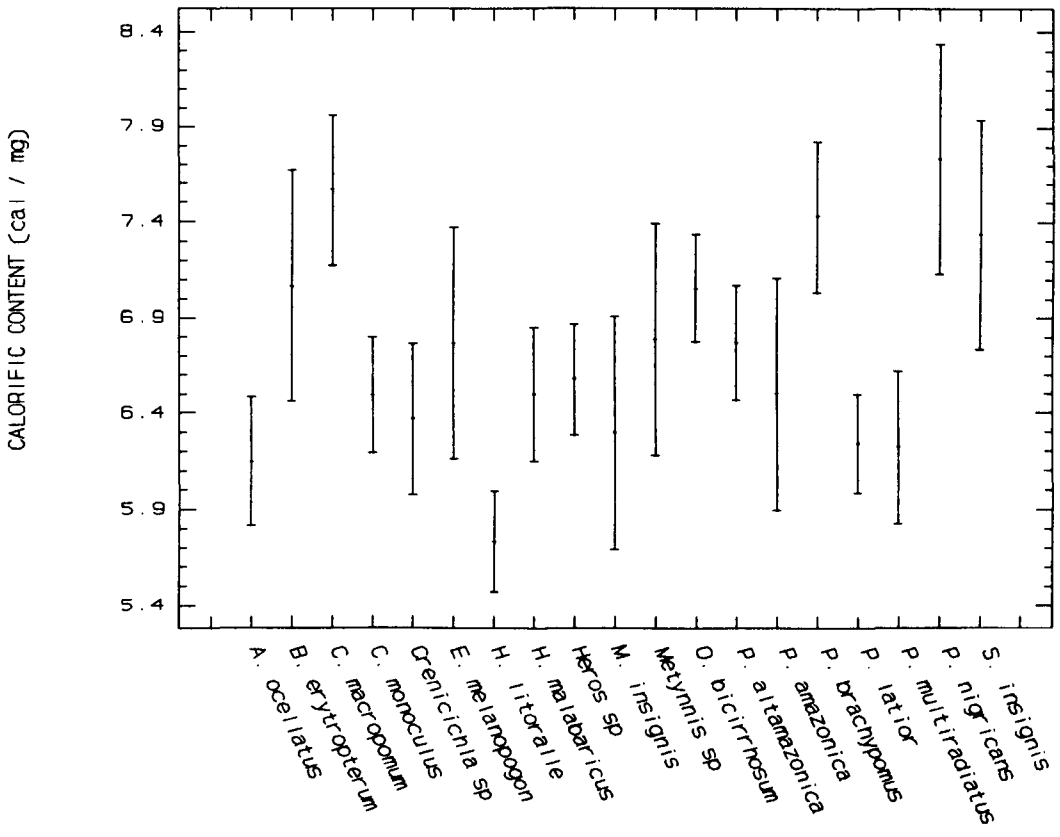


Figure 14 Averages and 95% confidence limits for caloric content of activated eggs of 19 species of Central Amazon.

but this variation could not be satisfactorily explained by any phylogenetic relationships alone (Figure 14). The average for eggs incubated on the littoral was 0.62 calories per mg (~10%; 95% confidence limits: 0.2-1.0) smaller than eggs incubated in channels ($t=3.12$; D.F.= 17; $p=0.006$), but a lot of overlapping occurred among the two distributions. Ecological reproductive guilds (Balon, 1985) also had no clear relationship with calorific content of the eggs, since open substratum spawners had egg with calorific values similar to mouth brooders.

The amount of calories per egg were heavily dependent on egg size and its variability. Therefore, the results followed

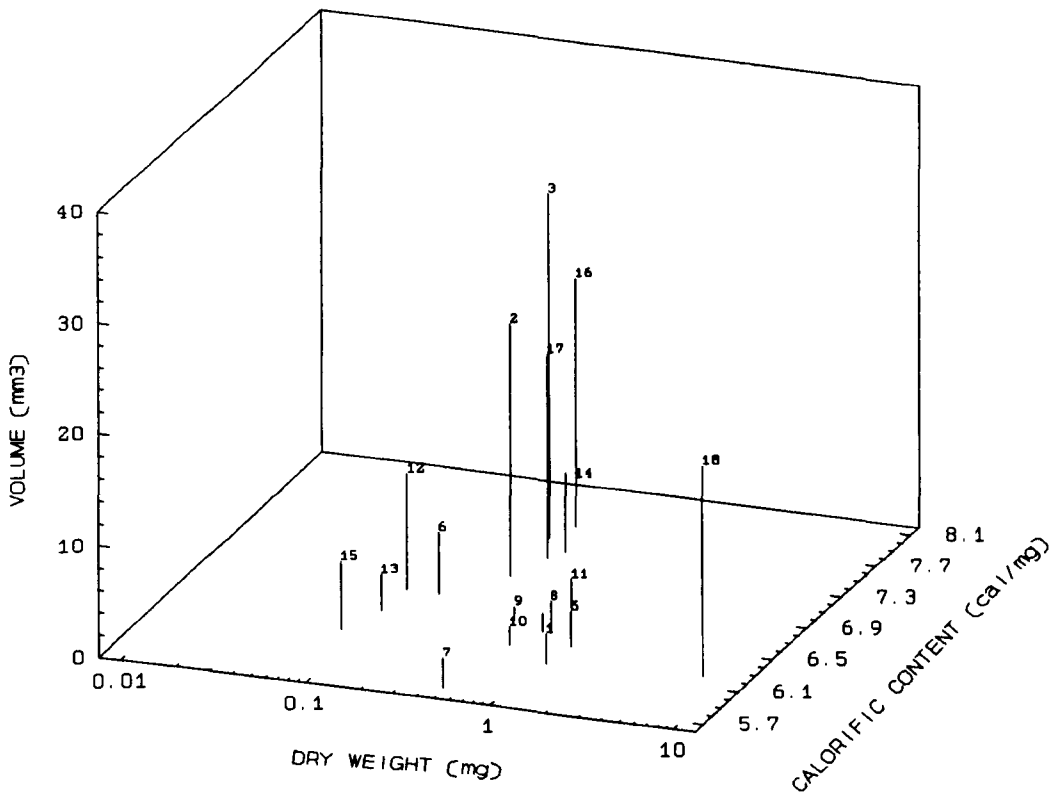


Figure 15 Plot of egg main characteristics of 18 species of Central Amazon. Data codes in the Table 11.

roughly the same patterns found for dry weight of the eggs. The average of amount of calories per egg was 2 times higher (95% confidence limits: 1.1-3) in eggs incubated in lakes than in eggs incubated in the channels ($t = 5.155$; $D.F. = 9.9$; $p < 0.0001$).

Figure 15 shows how the three main quantitative features of the eggs are linked together. Surface area is highly correlated with volume; therefore it will show the same pattern. Two main groups are clearly visible in this figure, i.e. eggs spawned in the channels and eggs spawned in the margins. The eggs spawned in the channels (the left group in the figure) have lighter eggs and a large variation on egg volume and calorific content. Possibly, this group can be split into eggs with high (numbers 2-17 in

Figure 15) and median calorific content (numbers 6-15). The eggs spawned in the littoral are heavier and have a relatively lower calorific content. Three species (numbers 7-18 and *O. bicirrhosum*) diverge from the main clusters. The plot also show that egg dry weight and calorific content are correlated for riverine eggs (r= 0.91; D.F.= 10; r=0.006), but are not for littoral eggs.

4.2.3 Larval development

Larval sampling was done on a daily basis, but several events in larval development occurred between sampling times. Interpolation, therefore, had to be used to estimate the size at these events.It was not possible to find a model to fit the relation between larval weight and age properly. Most models that were tried underestimated the maximum weight or were too complex for the proposed goal. So interpolation was used by averaging two sequential points, assuming an exponential growth. Since interpolation was based on two points, it included variations of those two points

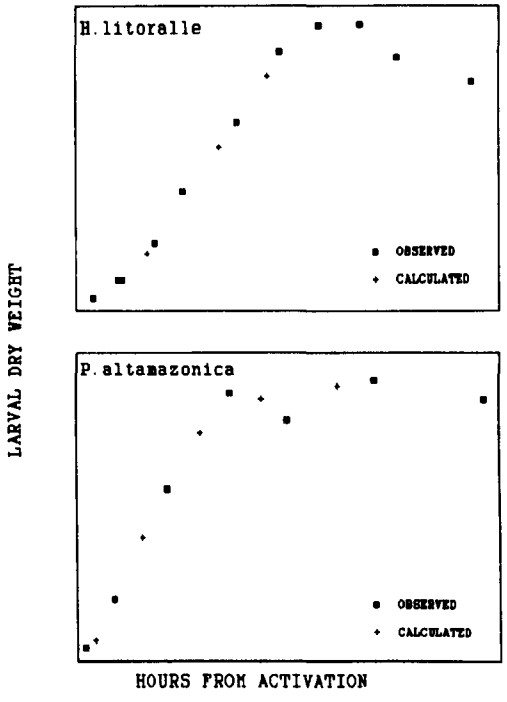


Figure 16 Observed and estimated larval body weight as a function of age for two species.

(Figure 16). However, observed data points were averages of averages (pooled larvae) and consequently had their variations minimized.

Table 12 Parameters of functional regression of larval weight at developmental events on yolk weight at activation for 9-14 species of Central Amazon.

	SLOPE (b)	S.E.	INTERCEPT (a)	D.F.	r^2
Hatching	0.5445	0.0486	0.0682	12	0.9100
Pectoral bud	0.3615	0.0650	0.0827	12	0.6115
Eye pigmentation	0.4648	0.0667	0.1593	11	0.7734
Jaw formation	0.5802	0.1070	0.1778	10	0.6572
Swim bladder	0.7512	0.0122	0.3050	09	0.8484
Swimming	0.7606	0.0477	0.3536	09	0.9551
First feeding	0.7445	0.0667	0.3806	07	0.9437
Maximum size	0.8096	0.0397	0.4676	10	0.9760

Regression model: $y = a \cdot x^b$; S.E.= standard error of b; D.F.= degrees of freedom; r^2= coefficient of determination; maximum size= maximum weight gained in endogenous feeding.

Larval dry weight (yolk excluded) at hatching varied from 0.014 mg in *P. latior* to 0.263 mg in *P. multiradiatus*, with coefficients of variation within species ranging from 16% to 23%. Hatching age varied from 12.5 h in *P. latior* to 67.0 h in *M. insignis* (no data were available for *P. multiradiatus*), with coefficients of variation within species ranging from 3% to 9%.

Correlation analysis using data averaged per species showed significant results for larval dry weight at hatching, hatching age and yolk weight at activation (Appendix D), but partial correlation analysis showed that only hatching dry weight and yolk weight at activation were linked (Appendix E). Yolk

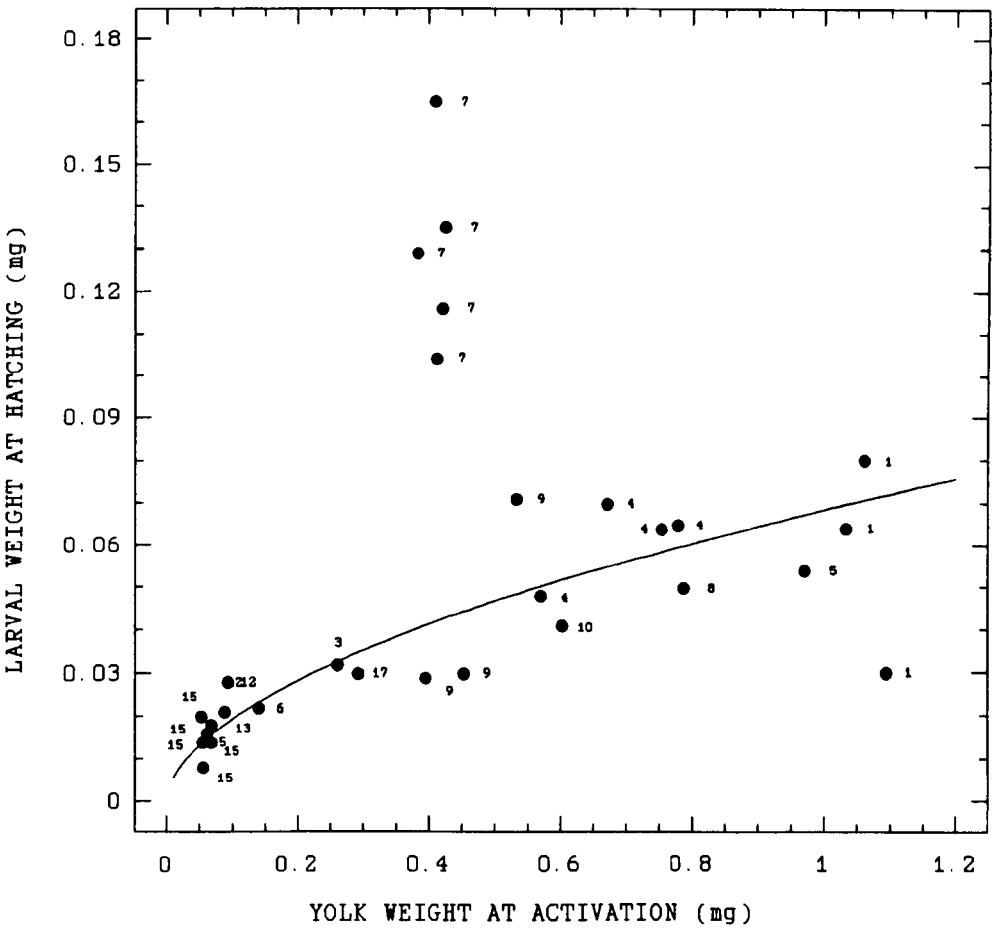


Figure 17 Scatterplot and functional regression fit of larval weight at hatching on the yolk weight at activation for 14 species of Central Amazon. Data codes in Table 11.

weight at activation was therefore considered the best predictor of larvae weight at hatching.

Functional regression (reduced major axis regression) was used to fit a curve to the scatterplot, since both variables were random and subject to experimental error (Figure 17). The regression was calculated averaging data per species to avoid bias due to unequal number of batches between species. This relationship explained 90.9% of the variability of hatching weight for the 14 species studied (Table 12). *H. littorale* was excluded from the analysis, since the species, a froth nester, was a clear

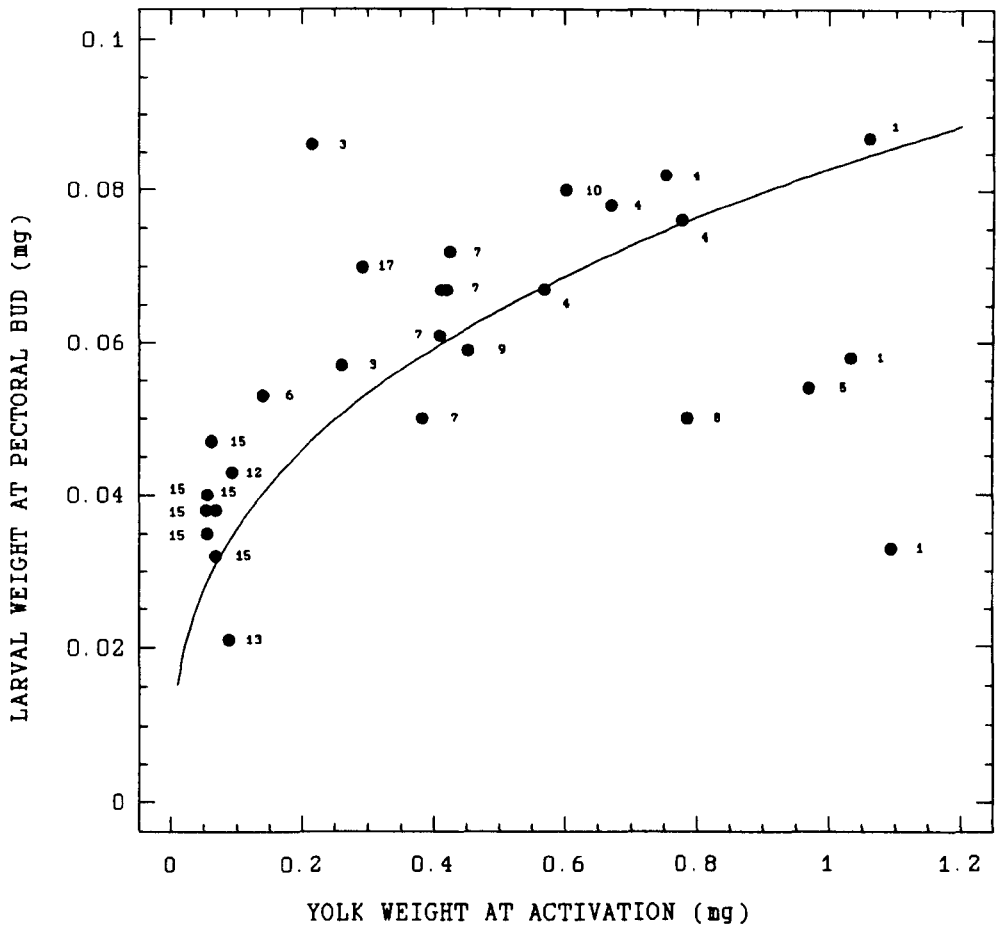


Figure 18 Scatterplot and functional regression fit of larval weight at formation of pectoral bud on yolk weight at activation for 13 species of Central Amazon. Data codes in Table 11.

outlier (Figure 17; number 7) and seemed to hatch at a relatively larger weight than the remaining species.

Larval dry weight at the formation of the pectoral fin bud varied from 0.021 mg in *P. amazonica* to 0.162 mg in *P. multiradiatus*, with the coefficients of variation within species ranging from 8% to 45%. The age at formation of the pectoral fin bud varied from 18 h in *H. littorale* to 85 h from activation in *C. monoculus* (no data were available to *P. multiradiatus*), with the coefficients of variation within species ranging from 10% to 23%.

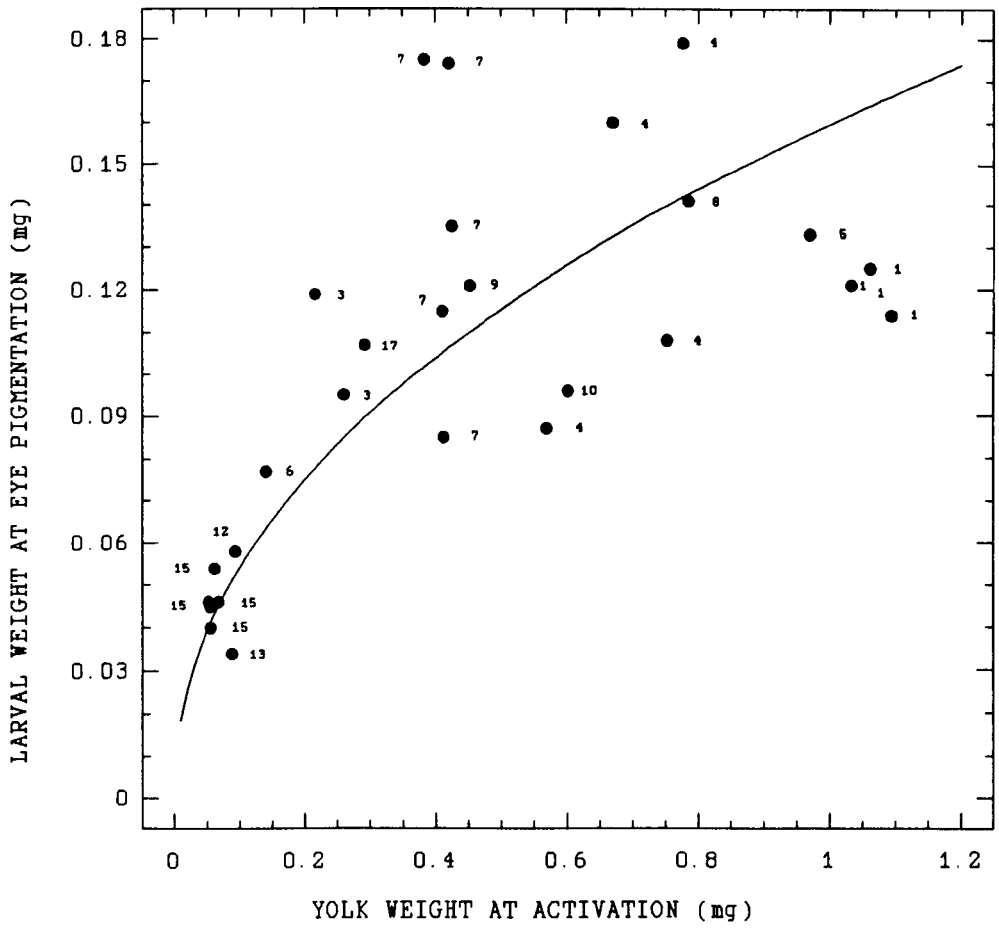


Figure 19 Scatterplot and functional regression fit of larval weight at pigmentation of the eye on yolk weight at activation for 13 species of Central Amazon. Data codes in Table 11.

The correlation analysis showed similar results to the analysis done for hatching, but partial correlation gave no significant result (Appendix E).

Taken into account the limitations, yolk weight was used as a first explanatory variable for regression analysis. Functional regression (Figure 18) was used as above . This relationship explained 61.3% of the variability of larval weight at pectoral fin bud formation for the 14 species studied (Table 12).

Larval weight at pigmentation of the eye varied from 0.034 mg in *P. amazonica* to 0.179 mg in *C. monoculus*, with the coefficients of variation within species ranging from 5% to 32%. Larval age at pigmentation of the eye varied from 40.0 h in *H. littorale* to 123.0 h in *C. monoculus*, with the coefficients of variation within species ranging from 11% to 30%.

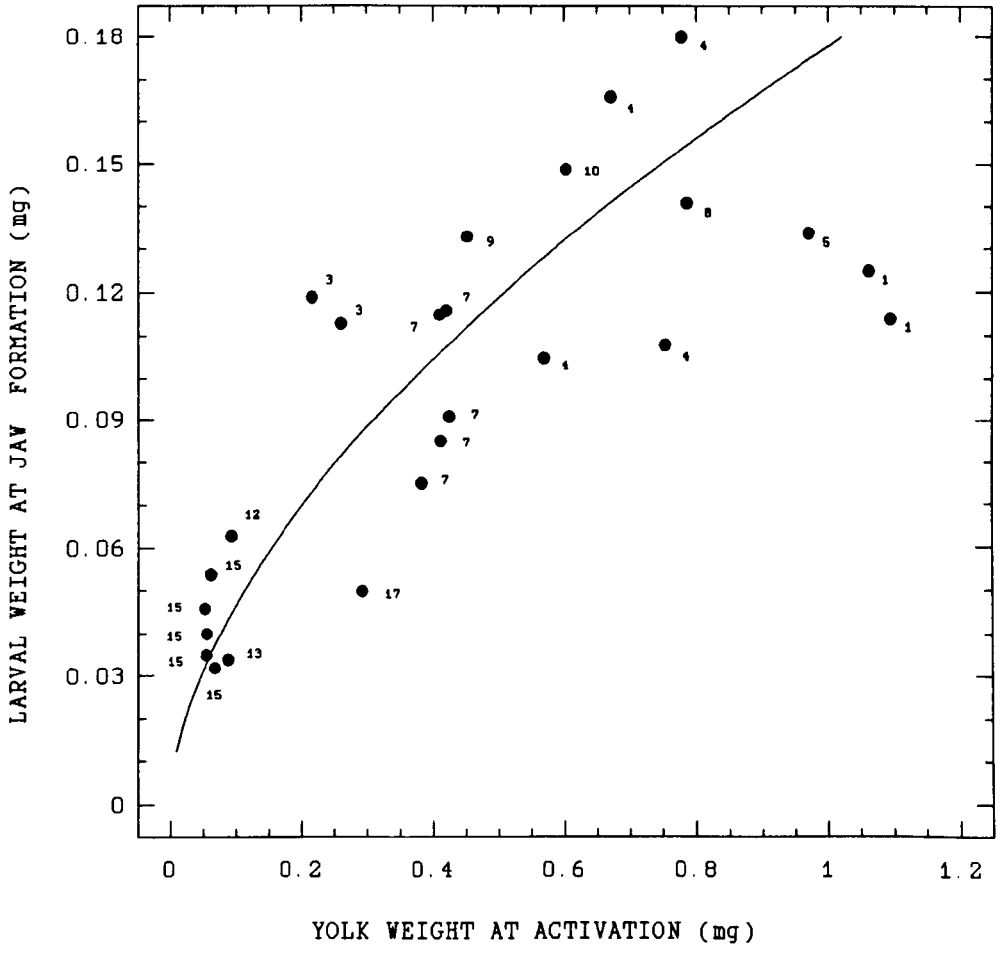


Figure 20 Scatterplot and functional regression fit of larval weight at formation of the jaw and yolk weight at activation for 12 species of Central Amazon. Data codes in Table 11.

Correlation and partial correlation analysis showed similar results for all following events, except the formation of the caudal rays. The correlations between larval weight at events

and yolk weight at activation were maintained in the partial correlation analysis (Appendix E). Consequently, yolk weight at activation was used as explanatory variable in all the following regression analyses. Data for *P. multiradiatus* was lacking for several events, otherwise stated.

Functional regression was used as above (Figure 19). This relationship explained 77.5% of the variability of larval weight at pigmentation of the eye for the 12 species studied (Table 12).

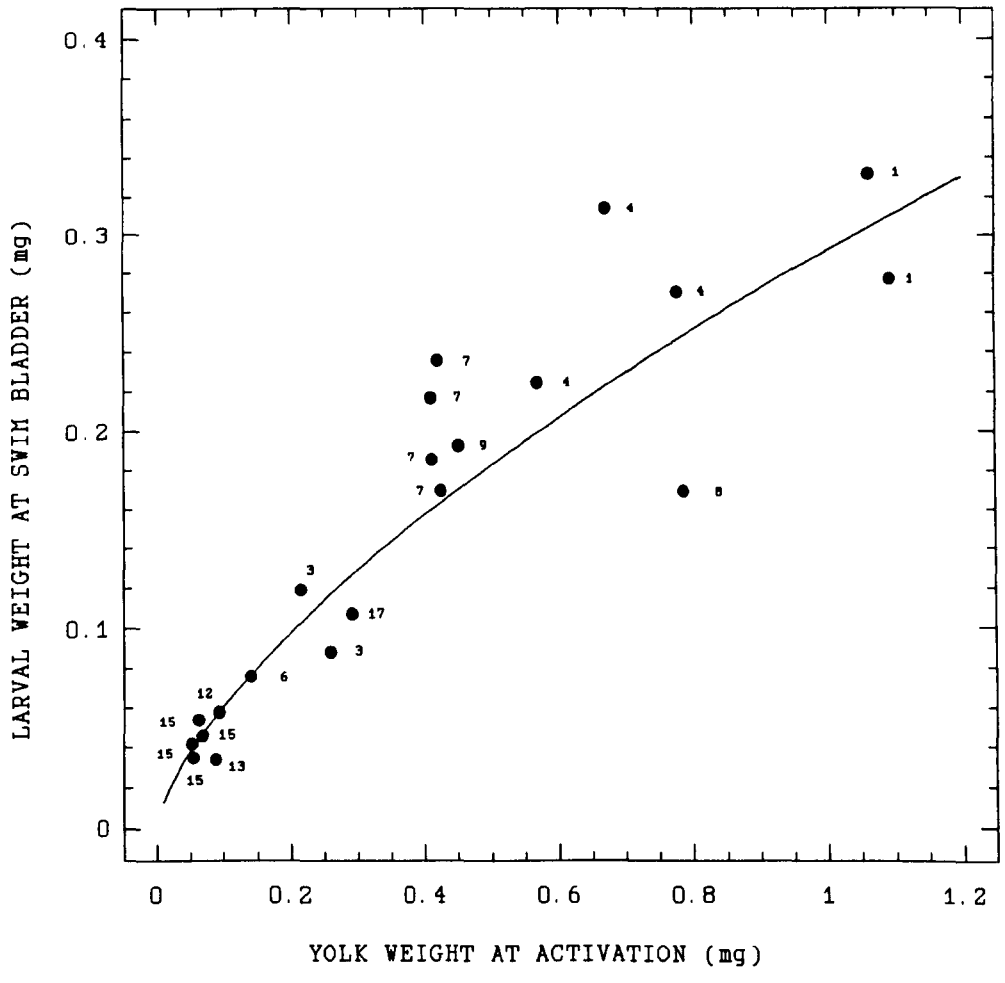


Figure 21 Scatterplot and functional regression fit of larval weight at inflation of swim bladder and yolk at activation for 11 species of Central Amazon. Data codes in Table 11.

Larval dry weight at formation of the jaw varied from 0.032 mg in *P. latior* to 0.224 mg in *P. multiradiatus*, with the coefficients of variation within species ranging from 12% to 30%. Age at formation of the jaw varied from 40.0 h in *H. littorale* to 123.0 h in *C. monoculus*, with the coefficients of variation within species ranging from 9% to 25%.

Functional regression was used as above (Figure 20), the relationship explaining 65.7% of the variability of larval weight at formation of the jaw for the 12 species studied (Table 12). No outlier was observed.

Larval weight at the inflation of swim bladder varied from 0.034 mg in *P. amazonica* to 0.332 mg in *A. ocellatus*, with the coefficients of variation within the species ranging from 15% to 18%. Age at inflation of swim bladder varied from 45.1 h in *P. latior* to 180.0 h *C. monoculus*, with the coefficient of variation within the species ranging from 5% to 25%.

Functional regression was used as above (Figure 21). This relationship explained 92.9% of the variability of larval weight at inflation of swim bladder for the 11 species studied (Table 12).

Larval weight at onset of swimming varied from 0.032 mg in *P. latior* to 0.421 mg in *Crenicichla* sp, with the coefficients of variation ranging from 13% to 16%. Age at onset of swimming varied from 41.0 h in *H. littorale* to 192.0 h in *C. monoculus*, with the coefficients of variation ranging from 11% to 40%.

Functional regression applied to the scatterplot (Table 12) explained 97.3% of the variability in larval weight at onset of swimming for the 11 species studied (Figure 22).

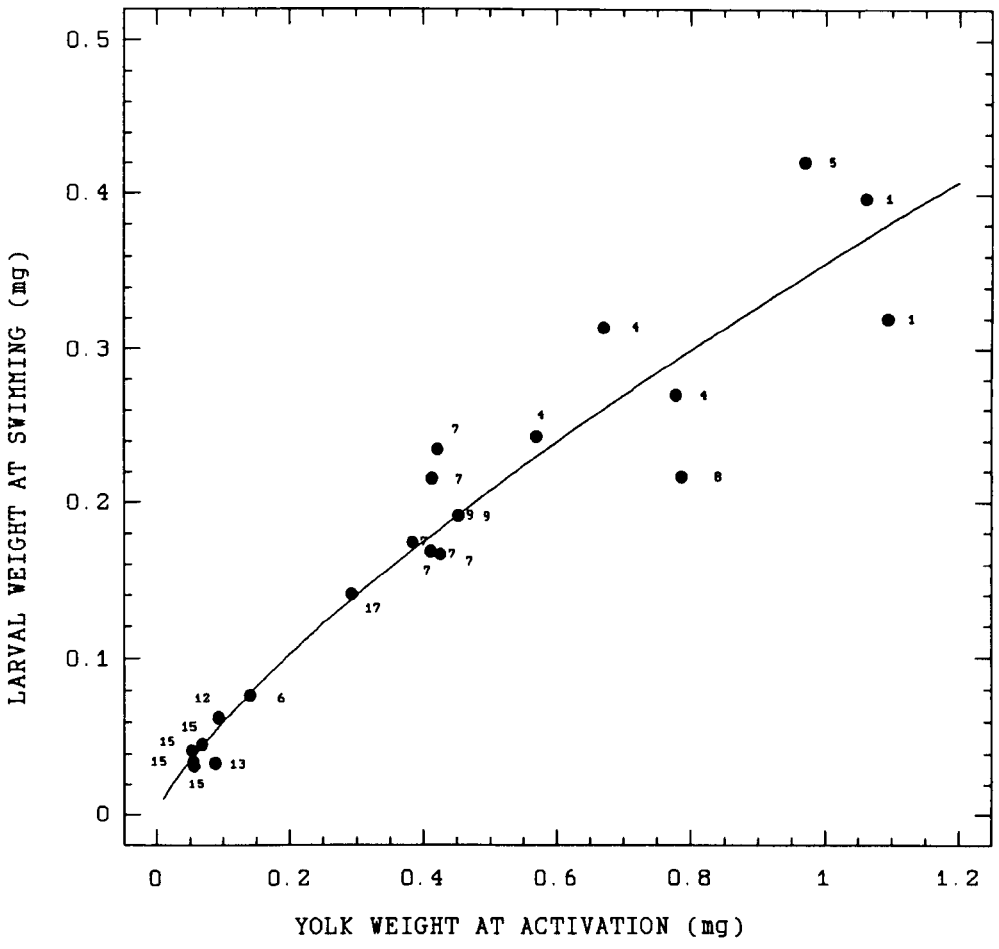


Figure 22 Scatterplot and functional regression fit of larval weight at onset of swimming on yolk weight at activation for 11 species of Central Amazon. Data codes in Table 11.

Larval weight at first feeding varied from 0.032 mg in *P. latior* to 0.398 mg in *C. monoculus*, with the coefficients of variation within species ranging from 16% to 24%. Larval age at first feeding varied from 89.0 h in *P. amazonica* to 214.0 h in *C. monoculus*, with the coefficients of variation within species ranging from 8% to 12%.

Functional regression applied to the scatterplot (Table 12) explained 94.8% of the variability in larval weight at first feeding of 9 the species studied (Figure 23). No outlier was

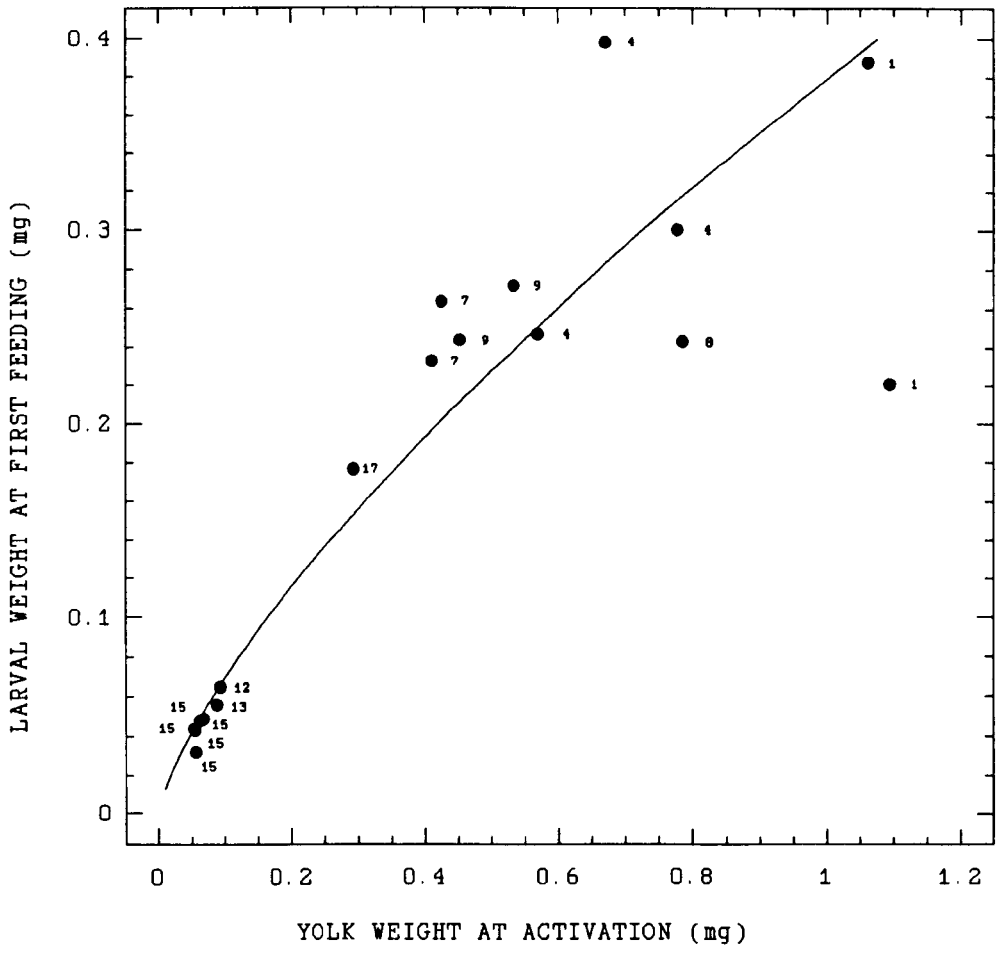


Figure 23 Scatterplot and functional regression fit of larval weight at first feeding on yolk weight at activation for 9 species of Central Amazon. Data codes in Table 11.

observed.

The maximum larval weight attained, with exclusively endogenous feeding, varied from 0.040 mg in *P. latior* to 0.515 mg in *Crenicichla* sp, with the coefficients of variation ranging from 9% to 13%. The age at maximum weight varied from 86.0 h in *P. latior* to 241.0 h in *A. ocellatus*, with the coefficients of variation within species ranging from 9% to 25%.

Functional regression applied to the scatterplot (Table 12) explained 97.7% of the variability in maximum larval

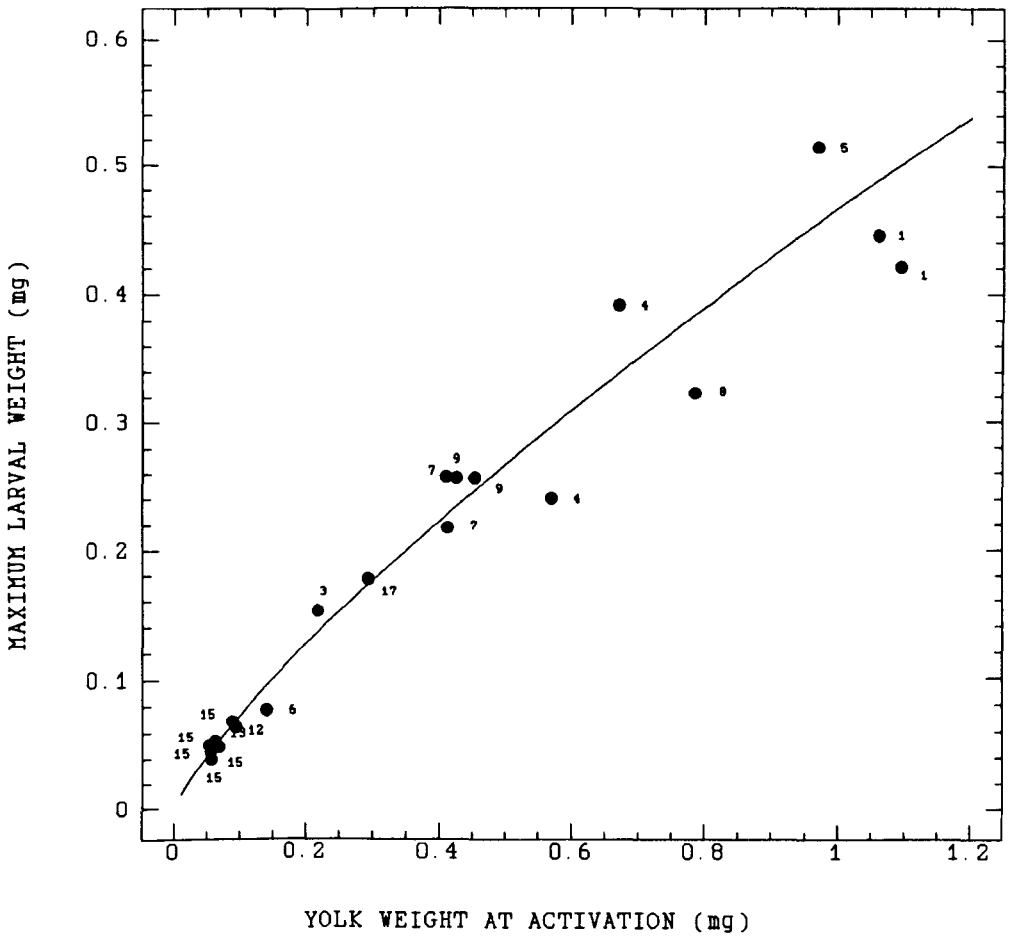


Figure 24 Scatterplot and functional regression fit of maximum larval weight on yolk weight at activation for 12 species of Central Amazon. Data codes in Table 11.

weight of 12 species studied (Figure 24).

The residuals of the regressions were plotted against the values predicted by the model to check the fitness of the regression line on the scatterplot. Negligible tendencies were observed on most plots, but those for hatching, pectoral bud formation and eye pigmentation were slightly unbalanced (Appendix E). Assuming yolk weight at activation as a explanatory variable (x axis), the component of the residuals to larval weight at developmental events was tested against age at developmental

events and calorific content of the eggs, but no relationship was found (Appendix E). The temperatures varied ±1 °C between different batches. To check their effect on weight and age at developmental events the regressions were recalculated using batch values instead of species average. The residuals of these regressions were correlated against temperatures. Again no significant effect was found.

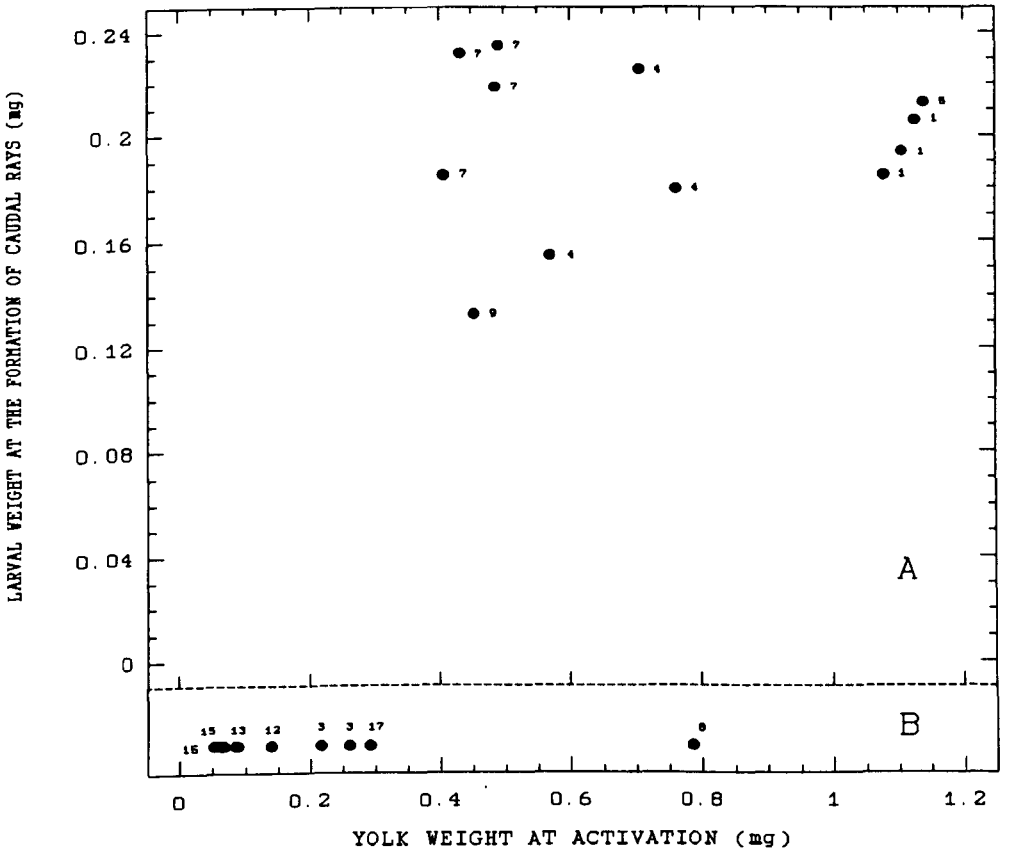


Figure 25 Scatterplot of larval weight at caudal rays formation against yolk weight at activation for 5 species (A). Yolk weight at activation is shown for 6 species that did not form caudal rays (B). Data codes in Table 11.

The larval weight at formation of the rays of the caudal fin showed no relation with yolk weight at activation (Figure 25A) or age. None of characiforms studied had rays before death by starvation (Figure 25B), whereas siluriforms, osteoglossids and

cichlids formed rays prior to or at first feeding. Data obtained for larvae of *P. multiradiatus* (one batch) with yolk weight at activation of 6.4 mg, showed caudal rays at 0.224mg.

Other features of larval development were also noted. All species studied (11 spp), except *P. multiradiatus*, had a type of cement gland. Cichlids had very distinctive cement glands on the top of the head and on their snout. The glands were large and extremely active, judged by touch with a seeker, anchoring the larvae to any available substratum and to each other. The activity started immediately after hatching and lasted until first feeding.

The characiforms had small and weak cement glands on the head and on the posterior extremity of the fin fold. The glands were not very noticeable, and at certain times it was difficult to ascertain their activity using a seeker. The larvae did not attached themselves to any underwater substratum or to each other. The glands became active when the larvae developed pectoral buds and lasted to the onset of swimming.

H. littorale had weak cement glands on the extremities of the fin fold and on the barbels. However, individuals of this species were observed hanging vertically on the aquarium walls. The duration of activity was similar to the cichlids, but its intensity was less.

The characiforms and *H. littorale* exhibited a common behaviour. They were able to fix themselves to surface film (usually sideways) of the water, using the terminal extremities of the fin fold.

4.2.4 Phototaxis

Several species studied showed a significant tendency to swim towards the light (Wilcoxon signed rank test; $p<0.05$). Negative phototaxis was found only in three species *P. altamazonica*, *P. latior* and *P. amazonica*. The actual size when positive phototaxis appeared was very variable (Table 13). Two species of cichlids (*C. monoculus* and *Heros* sp) showed it at the onset of swimming, or just prior to first feeding and *Crenicichla* sp showed at jaw formation size and the three species kept it throughout the experiment.

Table 13 Averages and coefficients of variation (in parenthesis) of larval weight and age at start and end of positive phototaxis behaviour.

	BATCHES	WEIGHT (mg)		AGE (h)	
		START	END	START	END
P. latior	3	0.017(27%)	0.020(32%)[1,2]	21.8(17%)	30.0(20%)[1,2]
P. amazonica	1	0.021	0.025[2]	23.0	31.0[2]
P. altamazonica	1	0.032	0.038[2]	23.0	28.0[2]
H. malabaricus	1	n	n	n	n
H. littorale	2	n	n	n	n
C. monoculus	3	0.287(17%)	>	165.0(12%)	>
Heros sp	2	0.251(23%)	>	156.0(15%)	>
Crenicichla sp	1	0.133	>	-	-

[1]= phototaxis was present again in larger or older larvae; [2]= negative phototaxis was present in larger or older larvae; n= phototaxis not found; >= found until the end of experiment.

P. latior, *P. altamazonica* and *P. amazonica* showed strong phototaxis at an intermediate weight between hatching and formation of the pectoral fin bud or ~24 hours after fertilization, but it lasted for a short time. This behaviour was confirmed for *P. latior* (ANOVA; $F= 9.917$; $D.F.= 28$; $p<0.0001$) in

a large container (second type of experiment), when the larvae were easily concentrated in a small illuminated area. The larvae at this stage did not have their eyes pigmenting or pigmented. At onset of swimming size *P. amazonica*, *P. latior* and *P. altamazonica* showed significantly negative phototaxis (Wilcoxon sign rank test; $p < 0.005$) for a brief period (~24h), and then no phototactic behaviour at all. Positive phototaxis was observed again after first feeding for *P. latior*, but not for *P. altamazonica*. No data were available for *P. amazonica* at this stage.

H. malabaricus and *H. littorale* did not shown any type of phototaxis and no conclusive results were obtained for the remaining species.

The general variation of phototaxis could not be explained by spawning site differences. Species that spawn in the channels had similar tendencies at young stages, but those that spawn on the margins did not always show positive phototaxis. The cichlids showed the behaviour approximately at the same relative size suggesting that it is a pattern of the group, but it was not so clear in the characiforms larvae even when they live in the same habitat.

4.2.5 Age at starvation

Larval age at starvation showed no significant general relationship with yolk weight at activation, calorific value per egg or temperature. However, if the data set was split by spawning site the larval age at starvation of the species that spawn in

the channels were positively correlated (r= 0.84; D.F.= 5; p< 0.05) with yolk weight. The species that spawn in the littoral areas showed no relationship (Figure 26). It is interesting to note that riverine larvae last longer under starvation than some floodplain larvae from much larger egg, such as *H. littorale*. Furthermore, proportionally to egg size riverine larvae survived longer to starvation.

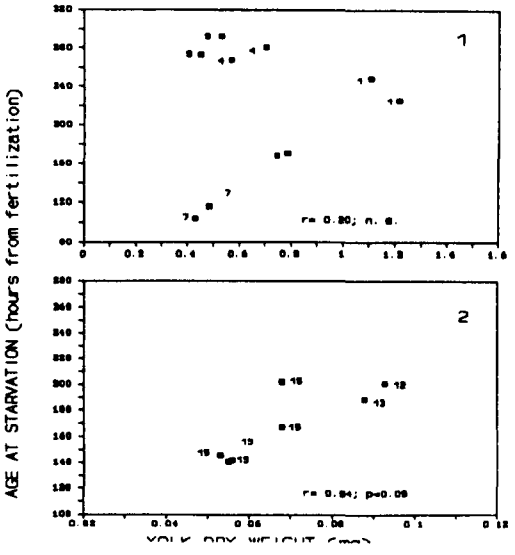
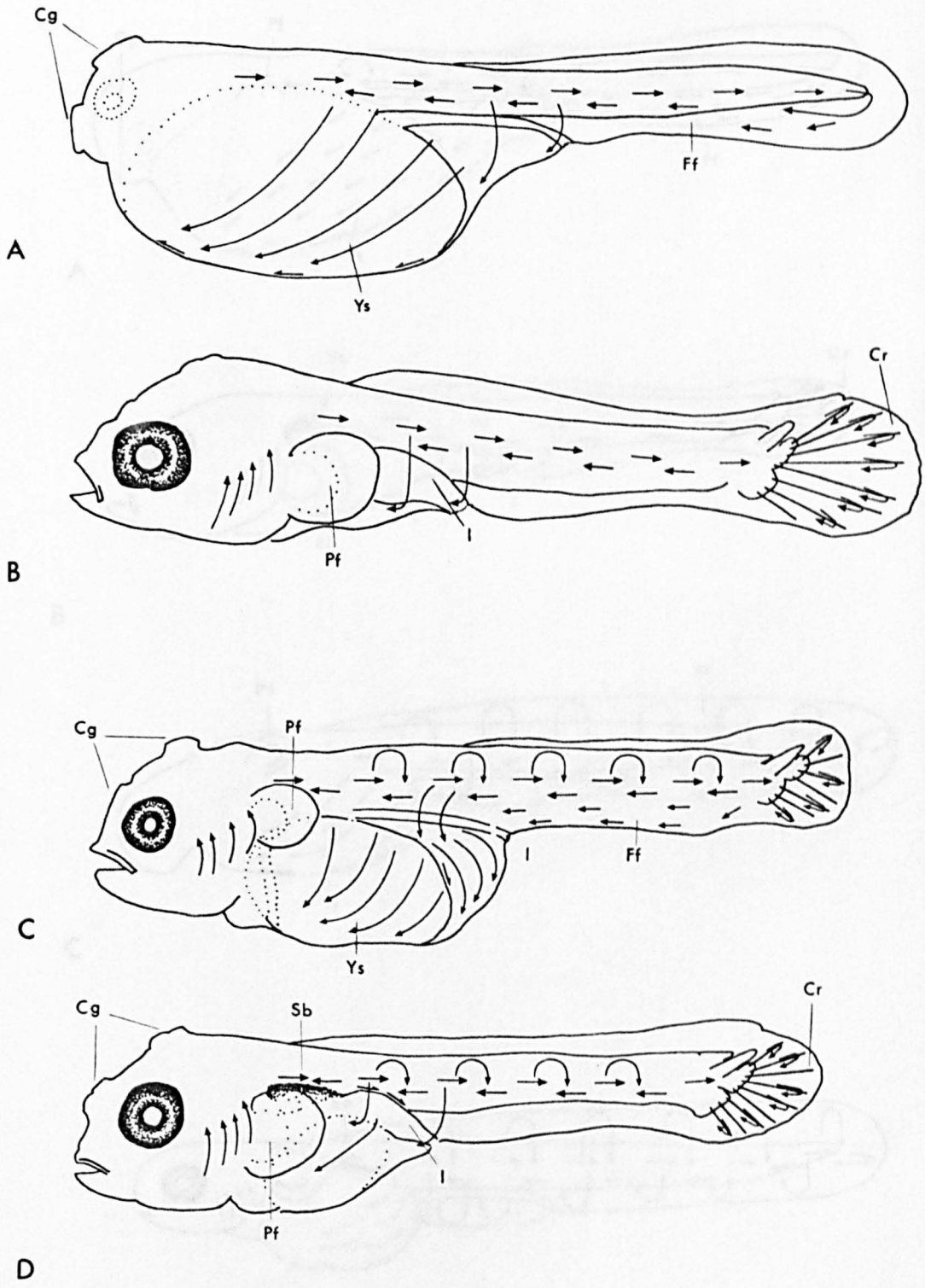


Figure 26 Relationship between larval age at starvation and yolk weight for species spawning in littoral areas (1) and in the channels (2). Data codes in Table 11.

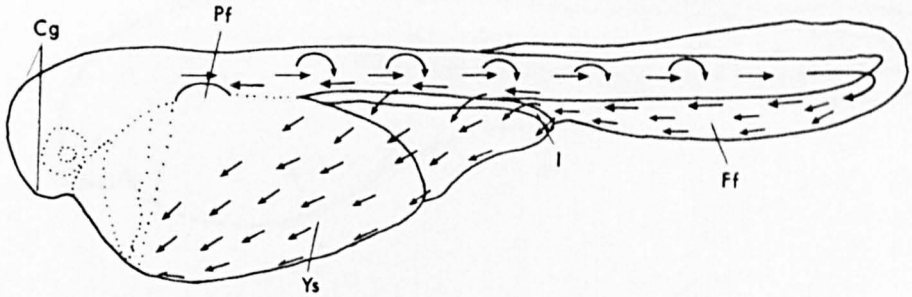
4.2.6 Patterns on the distribution of blood vessels.

Diagrams of blood circulation are shown for three species of cichlids (Figure 27 and Figure 28), three species of characiforms (Figure 28 and Figure 29) and two species of siluriforms (Figure 30). The blood circulation observed for *A. ocellatus* and *M. insignis* and *P. amazonica* and *P. altamazonica* were similar to those illustrated for *C. monoculus* and for *P. latior*, respectively.

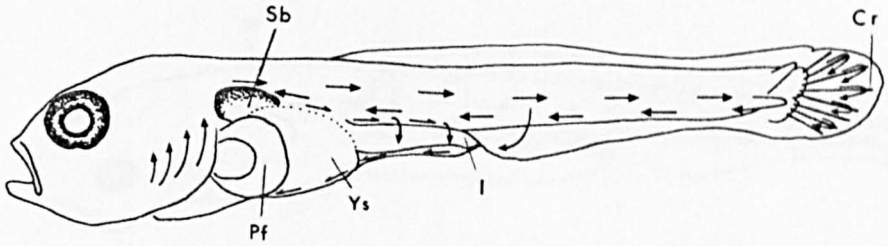


KEY
Cg: Cement glands
Cr: Caudal rays
Pf: Fin fold
I: Pectoral fin bud
Sb: Swim bladder
Ys: Yolk sac

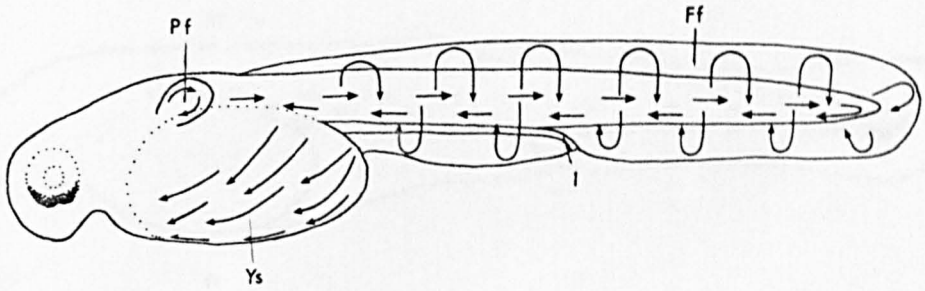
Figure 27 Diagram of blood circulation on newly hatched stage (3.5 mm) (A) and at first feeding stage (4.9mm) (B) for Heros sp and eye pigmentation stage (4.8mm) (C) first feeding stage (7.0mm) (D) for Crenicichla sp larvae.



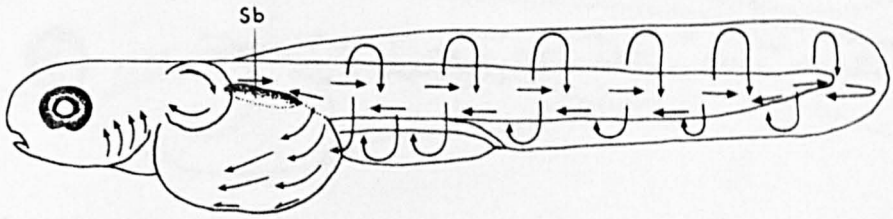
A



B



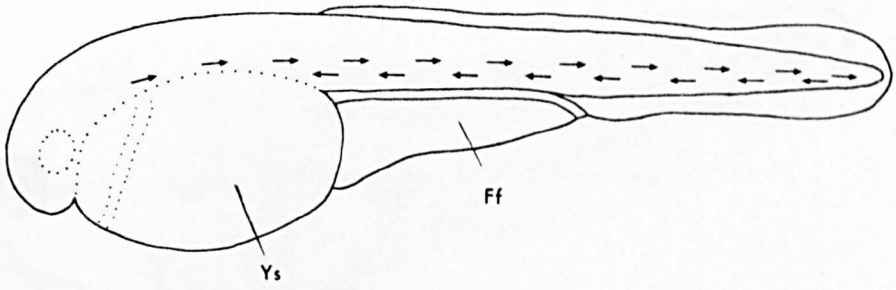
C



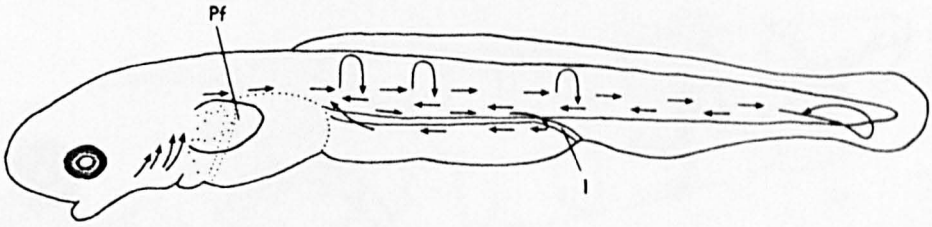
D

KEY
Cg: Cement glands
Cr: Caudal rays
Pf: Fin fold
I: Pectoral fin bud
Sb: Swim bladder
Ys: Yolk sac

Figure 28 Diagram of blood circulation on newly hatched stage (4.6 mm) (A) and at first feeding stage (6.2mm) (B) for C. monoculus and on pectoral bud stage (5.2mm) (C) and swim bladder stage (6.2mm) (D) for H. malabaricus larvae.



A



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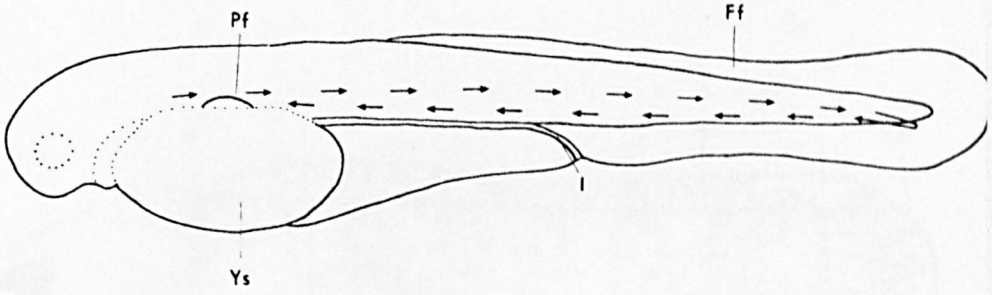

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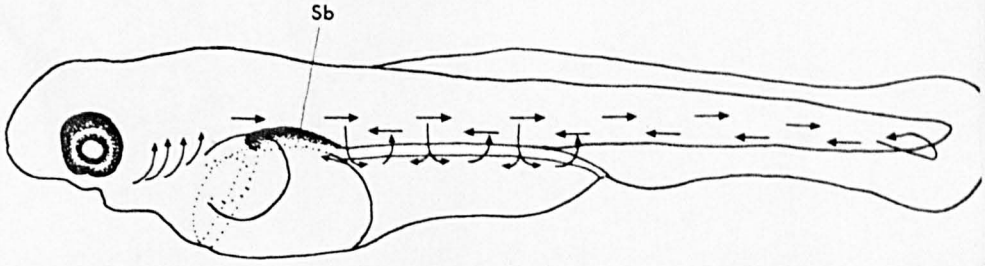
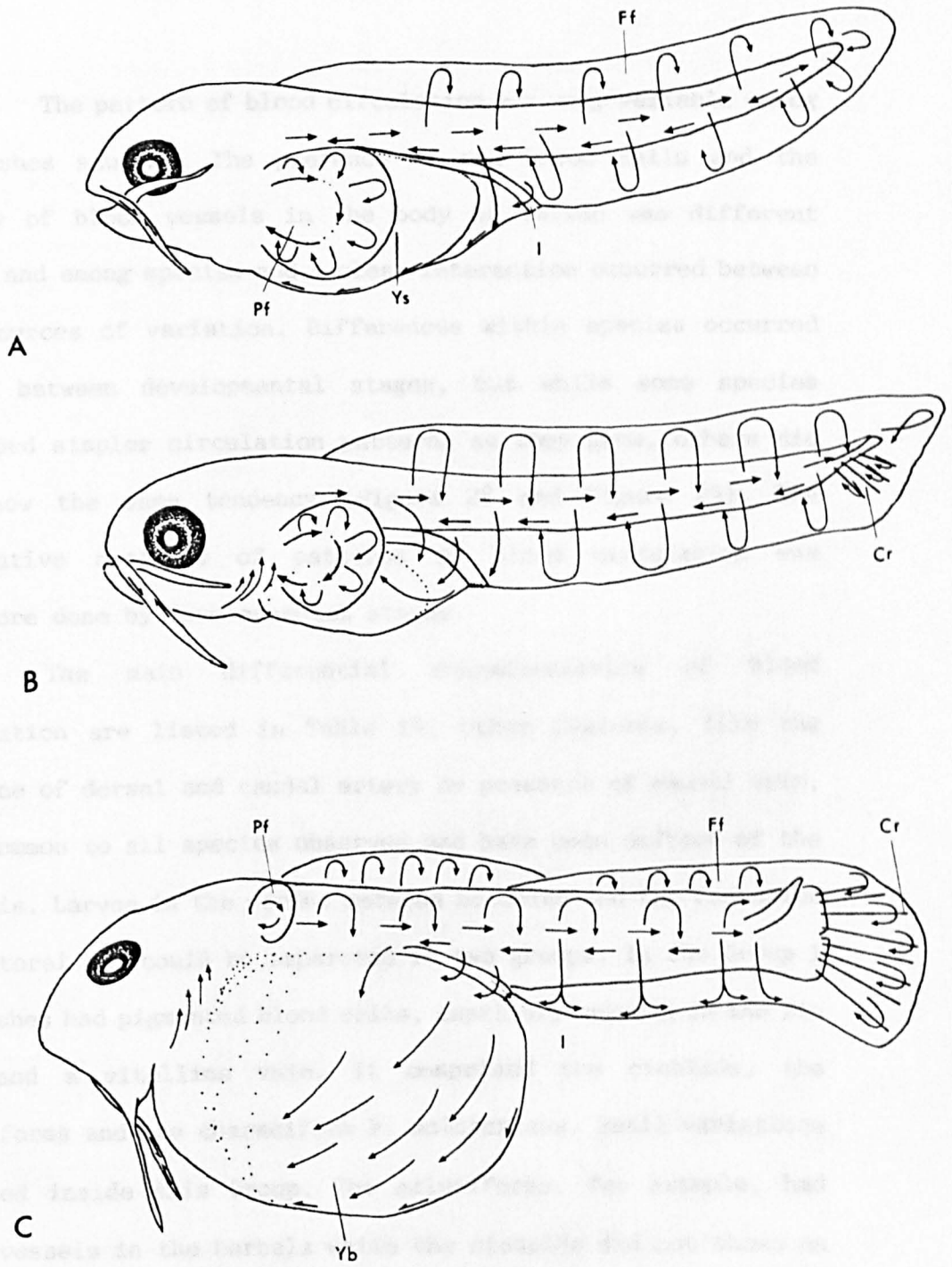


D

KEY
Cg: Cement glands
Cr: Caudal rays
Ff: Fin fold
I: Pectoral fin bud
Sb: Swim bladder
Ys: Yolk sac

Figure 29 Diagram of blood circulation on newly hatched stage (4.0 mm) (A) and at swim bladder stage (4.6mm) (B) for P. latior and pectoral bud stage (5.0mm)(C) and swim bladder stage (5.5mm) (D) for C. macropomum larvae.



KEY
Cg: Cement glands
Cr: Caudal rays
Ff: Fin fold
I: Pectoral fin bud
Sb: Swim bladder
Ys: Yolk sac

Figure 30 Diagram of blood circulation on newly hatched stage (4.4 mm) (A) and at first feeding stage (5.8mm) (B) for H. litoralle and newly hatched stage (6.0mm) (C) for P. multiradiatus larvae.

The pattern of blood circulation was very variable among the fishes studied. The presence of red blood cells and the density of blood vessels in the body of larvae was different within and among species and a clear interaction occurred between both sources of variation. Differences within species occurred mainly between developmental stages, but while some species developed simpler circulation patterns as they grew, others did not show the same tendency (Figure 28 and Figure 29). The comparative analysis of patterns of blood circulation was therefore done by developmental stages.

The main differential characteristics of blood circulation are listed in Table 14. Other features, like the presence of dorsal and caudal artery or presence of caudal vein, were common to all species observed and have been omitted of the analysis. Larvae in the period between hatching and the formation of pectoral bud could be separated in two groups. In the Group 1 all fishes had pigmented blood cells, capillary network in the fin fold and a vitelline vein. It comprised the cichlids, the siluriforms and the characiform *H. malabaricus*. Small variations occurred inside this Group. The siluriforms, for example, had blood vessels in the barbels while the cichlids did not shown an intense vascularization of the pectoral fin buds. These variations seemed to be characteristics of the taxonomic groups. The capillary network on the yolk was presented in all species of the Group, except for *H. littorale*. The second Group comprised species that had none of the above features, and consisted only of characiforms.

Table 14 Differential blood circulation features among 12 species of Central Amazon.

DIFFERENTIAL FEATURES

1. Red blood cells
2. Capillary network in fin fold
3. Capillary network in pectoral bud
4. Capillary network in yolk sac.
5. Branchial arteries
6. Blood circulation in barbels
7. Subintestinal vein
8. Vitelline vein

PERIOD: NEWLY HATCHED LARVAE/PECTORAL BUD LARVAE

SPECIES	PRESENCE OF THE FEATURES							
	1	2	3	4	5	6	7	8
A. ocellatus	X	X		X				X
C. monoculus	X	X		X				X
Crenicichla sp	X	X		X				X
Heros sp	X	X		X				X
M. insignis	X	X		X				X
P. multiradiatus	X	X	X	X		X		X
H. littorale	X	X	X			X		X
H. malabaricus	X	X	X	X				X
P. latior								
P. altamazonica								
P. amazonica								
C. macropomum								

PERIOD: SWIMMING LARVAE/FIRST FEEDING LARVAE

SPECIES	PRESENCE OF THE FEATURES							
	1	2	3	4	5	6	7	8
C. monoculus	X				X		X	
Crenicichla sp	X				X		X	
Heros sp	X				X		X	
H. littorale	X	X	X		X	X	X	
P. latior	X				X		X	
P. altamazonica	X				X		X	
P. amazonica	X				X		X	
C. macropomum	X				X		X	

The differences between the two patterns of blood circulation in newly hatched/pectoral bud larvae can not be explained by phylogenetical relations alone, since characiform larvae are present in both groups. In the other hand, spawning site seems to be well correlated with the patterns of blood

circulation. All species of Group 1 spawn on the littoral whereas those of Group 2 spawn in the channels.

Swimming stage and first feeding stage larvae showed less variation in the blood circulation pattern between species. Most features were common to all species: i.e. red blood cells, branchial arteries and a subintestinal vein.

Table 1 Results of two-factor analysis of variance for oxygen tolerance of two larval stages of P. latior and C. monoculus.

Potamorhina latior

SOURCE OF VARIATION	S.S.	D.F.	M.S.	F-RATIO	SIG.
MAIN EFFECTS	9383.3	2	4691.6	114.0	<0.0001
OXYGEN	2227.8	1	2227.8	54.1	0.0002
STAGE	7900.8	1	7900.8	191.9	<0.0001
INTERACTIONS	2784.7	1	2784.7	67.6	0.0001
RESIDUAL	288.1	7	41.2		
TOTAL	12456.1	10			

Cichla monoculus

SOURCE OF VARIATION	S.S.	D.F.	M.S.	F-RATIO	SIG.
MAIN EFFECTS	10717.1	2	5358.5	94.5	<0.0001
OXYGEN	5942.7	1	5942.7	104.9	<0.0001
STAGE	4774.4	1	4774.4	84.2	<0.0001
INTERACTIONS	4774.4	1	4774.4	84.2	<0.0001
RESIDUAL	566.7	10	56.7		
TOTAL	16058.2	13			

S.S= Sum of squares; D.F.= degrees of freedom; M.S.= Mean square; SIG.= Significance level; OXYGEN= Dissolved oxygen concentration (5% and 10%); STAGE= Developmental stage (non-swimming and swimming)

4.2.7 Dissolved oxygen tolerance

The mortality of *P. latior* larvae showed a significant interaction between developmental stage and initial dissolved

oxygen concentration (Table 15). Mortalities of non- swimming larvae were very high at 5% and 10% saturation, but swimming larvae was significantly less sensitive to both concentrations at swimming stage (Figure 31).

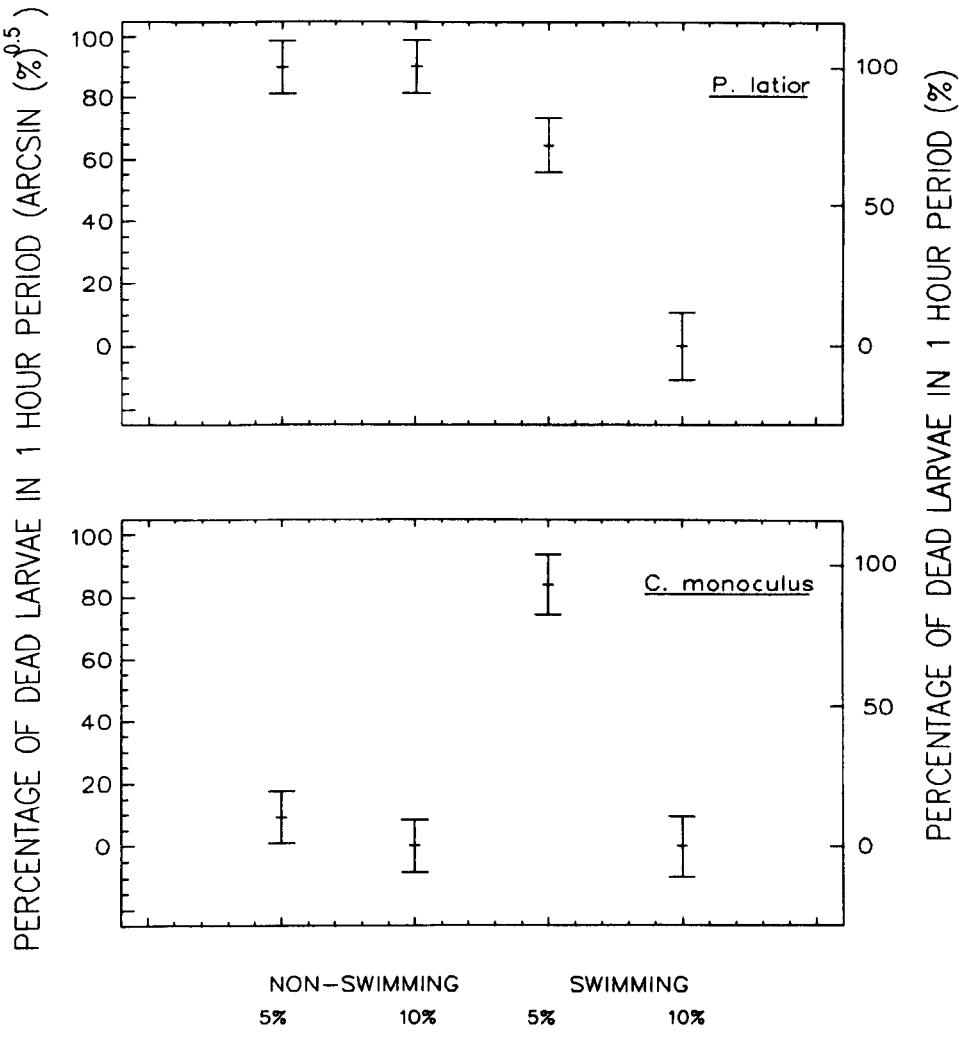


Figure 31 Average and 95 % confidence limits bars for larval mortality for two species at two larval stage when exposed to two concentrations of dissolved oxygen during one hour period.

Significant interaction was also found for *C. monoculus* (Table 15). Non-swimming larvae showed low mortality at both concentrations of dissolved oxygen, but swimming larvae showed a

significantly higher mortality when exposed to 5% D.O saturation than to 10% D.O. saturation (Figure 31). Mortality of swimming larvae at 10% D.O. saturation was not different from the 5% saturation.

5 DISCUSSION

5.1 General results and their validation

Reproduction

Results found for timing of spawning were straightforward, since they were based on two years sampling. The spawning season of *C. macropomum* should be shorter than reported by Sudepe (1981). The values reported are for the whole basin and it is known that the populations upriver start to spawn before those of the middle river (Araujo-Lima, 1984).

The timing of spawning was found to be very similar to that reported for other systems near the Amazon (Venezuela and Guiana). In these systems the species also spawn during the flood. The timing of spawning, however, seems more variable for species like *H. malabaricus*, *Heros* sp (syn. *Cichlasoma severum*) and *M. insignis* (syn. *Cichlasoma festivum*) that spawn throughout the year. These species showed maximum of frequency of ripe females in the beginning of the flood and minimum frequency at the low water period. In Venezuela *H. malabaricus* and *M. insignis* spawn only during the rainy season (Machado, 1987), but in Guiana (Lowe-McConnell, 1964, 1969) they were found with ripening eggs throughout the year. *Heros* sp was found spawning only in the rainy season in both systems. Lowe-McConnell (1964) reported that species with extended spawning seasons have peaks of spawning during the flood

period. Since neither author gave details about the methods they used for their analyses it is difficult to be precise about the extent of those differences. Yet it is possible that they may result from distinct reproductive tactics (Leggett and Carscadden, 1978; Wootton, 1984; Mann *et al.*, 1984) used by the species.

There are some methodological problems in measuring spawning frequency by analysis of the gonads. The presence of more than one modal group of oocytes in the gonads does not show conclusively that multiple spawning is occurring, but can be regarded as a potential basis for multiple spawns. Lowe-McConnell (1964) suggested that a second spawn might occur if, for any environmental circumstances, the first one fails to survive. Similar to the Amazon system, cichlids and *H. malabaricus* are also batch spawners in Guiana (Lowe-McConnell, 1964, 1969).

Very similar descriptions of the spawning style found for Central Amazon species are available for populations of Rio Madeira floodplains (Goulding, 1980), upper Solimões (Eckman, 1984), Central Brazil (Von Ihering e Azevedo, 1934), Guiana (Lowe-McConnell, 1964, 1969) and Venezuela (Machado, 1987), but spawning sites do not always agree. *Osteoglossum bicirrhosum* was cited by Lowe-McConnell (1964) to spawn in the river, but this seems improbable, since this species is a mouth-brooder.

The values found for fecundity are of the same order of magnitude as results described for matching species in Peru (Eckman, 1984), Venezuela (Machado, 1987) and elsewhere (Lowe-McConnell, 1987). The differences found were expected, since food supply and others specific attributes of riverine systems effect fecundity (Nikolsky, 1963; Bagenal, 1973; Mann *et al*, 1984; Zaniboni, 1985).

Curvilinear relationships between fecundity and weight are rather common in fishes (Bowering, 1978; Zaniboni, 1985; Wright and Shoesmith, 1988). It implies that fecundity changes as a power function of weight, so that relative fecundity changes with fish weight. This prevents a precise estimation of the relative fecundity. However, the exponents were close to 1. Furthermore, the confidence intervals of the relative fecundity calculated linearly (Table 8) were close the maximum and minimum values estimated using the power model . This model estimated for the smallest and largest females of *P. nigricans* a relative fecundity equal to 378 and 683 egg·g^{-1}, respectively. The smallest and the largest females of *P. rutiloides* have a relative fecundity equal to 1247 and 1814 eggs·g^{-1}, respectively. These values approximate the standard deviations of relative fecundity presented (Table 8). The results found for *O. bicirrhosum* are higher than those predicted by the power model (0.55 and 0.35 eggs·g^{-1}) and interpretations should be cautious. Clearly, the approximations were not strongly biassed, and even in the latter case the exponential and linear estimations were of the same order of magnitude. Similar problems have been experienced by other authors and the advantage of using this parameter to compare species and populations seems to overcome its limitations (Albaret, 1982).

Species that do not exhibit parental care and that lay their eggs in open water or on plants usually have higher fecundity than nest-builder and mouth-brooder species (Nikolsky, 1963). This rule also applied in the present study, but exceptions occurred such as *H. littorale*. However, the data for the latter species refer to populations of Rio Orinoco (Machado y Zaret, 1984) and may reflect geographical differences.

The same limitations cited for relative fecundity can be extended to reproductive expenditure, since its calculation is heavily dependent on the relative fecundity. The relative fecundity of *O. bicirrhosum* is expected to be slightly smaller than the estimated value and conclusions for *H. littorale*, *C. monoculus* and *A. ocellatus* should consider the possibility of a geographical bias. These drawbacks may effect also the analysis of reproductive traits.

Reproductive expenditure was higher in the lotic spawners and lower in the cichlids. However, females of species with parental care, such as *P. multiradiatus* and *H. littorale*, have an expenditure as high as lotic spawners, such as *P. latior*, *B. erytropterum* and others. The differences between the species might be even smaller. The relative fecundity of *O. bicirrhosum* was slightly underestimated and its expenditure might be higher. The relative fecundity per season of *H. malabaricus*, *Metynnis* sp and the cichlids might be three to five times higher. Results calculated for other species such as *S. gairdneri* (Kamler and Kato, 1983; Bromage and Cumaranatunga, 1988) and several gadoids (Hislop, 1984; Hislop and Bell, 1987) showed values ranging between 200 and 800 cal·g^{-1}of female·spawn^{-1}. These results are very similar to those found for Amazonian fishes, suggesting the female expenditure per year is much less variable than egg size or fecundity. It appears that the reproductive effort is independent of egg size, fecundity and also spawning style. Nevertheless the combination of very low fecundity, as found in the cichlids, and multiple spawns seems to reduce the annual reproductive expenditure. However, this is very hard to show, since is not possible to obtain a good estimation of seasonal fecundity of batch spawners.

Two main reproductive strategies are evident: species with low fecundity, low reproductive expenditure and multiple spawning per season and species with high fecundity, high reproductive expenditure and one spawning per season. The two main patterns correlate with spawning site. Species with high fecundity spawn in the channels and species with low fecundity spawn in the floodplain. Three species, however, have characteristics of fecundity, reproductive expenditure and egg size that split them from the two main groups.

The reproductive strategies found do not match with those described by Lowe-McConnell (1987) for tropical freshwater fishes. Similar to the present study, her grouping was based on fecundity, spawning season and type of spawning. Therefore it is not clear how she gathered into the same group the cichlids, *Osteoglossum* and *Hoplosternum*, all species that show distinct traits.

Effect of preservation on egg and larval dry weight

The loss of weight of eggs and larvae due to preservation was small and dependent on the original weight. Both slopes (egg and larvae) were significantly different from one (Table 10). The distribution of the residuals supports the conclusion that a curvilinear was a better fit than linear model. The x axis (fresh dry weight) was not error-free, but the very high correlation coefficient (>0.99) between both variables implies that the bias caused by the failure of this assumption of the least-square regression model would be trivial. Considering all such details it is acceptable that the model used to estimate the fresh dry weight of eggs and larvae used was satisfactory.

The eggs and larvae of the Amazon species lost 0% to 24% of their weight, in large (~1 mg) and small (~0.06mg) samples, respectively. There is a lack of information for freshwater species, but this range of loss is compatible with results published for marine eggs and larvae of 0% to 33% (Hempel and Blaxter, 1967; Bailey, 1982; Hay, 1984; Hislop and Bell, 1987). No effect of preservation was found on the measurements of calorific content, agreeing with the report of Hislop and Bell (1987).

Egg size, shape and calorific value

When analyzing the morphometry and gravimetry of activated eggs it was assumed that egg dimensions could be reasonably estimated from dimensions of up to one-day-old eggs. External morphometry was assumed to remain unchanged after the water hardening of the egg, but yolk dry weight had to be back-calculated to the time of activation. Predictions of values beyond the range of the data set can add gross errors to the estimations. However, the Gompertz function fitted the data well, with the coefficient of determination usually better than 95%. The activation times were usually only a few hours before the first data sampled and the consumption rates of yolk at this initial time were very low, so it is unlikely that the estimations are strongly biassed.

Results found for egg size showed that is not possible to categorize egg volumes of Central Amazon species based on phylogenetic relationship, spawning site or reproductive guild (Balon, 1985). Egg volume can be considered a bad index of egg size. Species spawning in similar environments and presenting similar guilds show remarkable differences in the volume of their eggs. Eggs of the characiforms

Inpaichthys kerri, *Chilodus punctatus* and *Piabucina pleurotaenia*, that spawn on the littoral on submerged vegetation, with demersal eggs and no parental care, have average volumes of 0.52 mm^3, 8.2 mm^3 and 10.3 mm^3, respectively (Franke, 1963, 1979; Machado, 1974). The characiform *Mylossoma duriventre* spawns in open water, has no parental care and has an average egg volume 1.43 mm^3 (Kossowski, 1980). Yet this species spawns in the same habitat as *Prochilodus nigricans* and *Potamorhina altamazonica* (Fernandes, 1989), species with egg volumes equal to 22.3 mm^3 and 10.5 mm^3, respectively.

The results for egg dry weight and calorific content showed a different perspective. Based on these parameters the eggs could be categorized by spawning site. Species that spawn on the littoral had eggs which were heavier, had a smaller calorific content and no relationship between egg weight and calorific content was visible (Figure 15). Conversely, species that spawn in the channels had lighter eggs with higher calorific content and the calorific content of the eggs increased with egg weight (Figure 15).

The calorific content of the eggs studied can be considered to be high compared with marine fishes, but are in the range of freshwater fishes (Miller, 1979; Heming and Buddington, 1988). Calorific values of dry weight are related to the amount of organic matter. The percentage of ash in eggs varied from 3 to 9 % (Heming and Buddington, 1988), therefore it does not explain the 25 - 35% variation in the calorific content of the eggs. Variations in calorific values of dry organic matter are also connected with varying proportions of proteins, carbohydrates and lipids (Prus, 1970). A mass balance using the calorific values reported by Heming and Buddington (1988) for lipids (9.7 $cal \cdot mg^{-1}$), proteins (5.5 $cal \cdot mg^{-1}$) and chorion

(3.61 cal·mg^{-1}) shows that the yolk of most species was composed of 70-90% of protein and 30-10% of lipids. However, exceptions occurred. The eggs of *H littorale* were almost lipid-free and the eggs of *B. erytropterum*, *C. macropomum*, *P. brachypomus*, *P. nigricans*, *S. insignis* and *O. bicirrhosum* have 35-45% of lipids. Calorific content of animals is usually associated with life history of feeding habits (Thayer *et al.*, 1973). However, feeding habits alone cannot explain the difference of lipids found between *P. nigricans* and *S. insignis* and the Curimatidae, since they have similar diets (Araujo-Lima *et al.*, 1986). High lipid content can be expected to improve the buoyancy of the eggs, which would be beneficial for those spawned in lotic habitats. Based on this assumption heavy eggs should have high lipid content. There is a positive correlation between lipids and egg dry weight ($r= 0.95$; $n= 9$; $p=0.0005$) for the species that spawn in the channels, suggesting that this might be the case. This may also explain the correlation found between calorific content and surface area. The benefit for the other two species is different. Dabrowski *et al.*, (1987) found that lipid content influences positively the percent of normal hatchlings.

Larval development

Larval weight at various developmental events was better described by the yolk weight at activation. Age at each developmental event was correlated with larval weight, but this correlation seemed spurious.

Similar results can be found in the literature. The relationships between yolk weight at activation and larval size at hatching, first feeding and maximum size have been found for several

species, such as *Clupea harengus* (Blaxter and Hempel, 1963), *Salmo gairdneri* (Kamler and Kato, 1983), *Sarotherodon mossambicus* (Rana, 1985) and *Etheostoma spectabile* (Marsh, 1986). On the other hand, correlation between larval size and age at hatching (incubation time) is not always clear (Blaxter, 1988).

The relationship between larval weight at developmental events and yolk weight at activation was clearly curvilinear, as shown by the scatterplots and exponents always smaller than one (Table 12). Most fits were good, with yolk weight explaining over 85% of the variance in larval weight. However, for pectoral bud formation and jaw formation, the proportion of the variance explained was below 65%. In eye pigmentation the quality of the fit, checked by the distributions of residuals, was poor. These errors could be caused by the subjectiveness in determining a fully pigmented eye, but in the cases of pectoral bud and jaw formation this subjectiveness was similar to those involved in the assessment of the others developmental events. Another possibility is that the error was introduced by one species and since the data set was small (9-14 species), the effect of one outlier on the calculation of the parameters was strong. This seems the case, since exclusion of *P. multiradiatus* for hatching weight and pectoral bud weight stabilizes the distribution of the residuals. The yolk weight of this species was over five times higher than the others species.

The relationships between larval developmental and yolk size used data for over 12 species. This number is small if compared with the number of species of fish of Central Amazon. The range of species comprised, however, three of the most important taxonomical groups and several different spawning strategies. The data set also comprised a

large range of egg size (≈0.05-6.5 mg). Therefore, despite the small sample size, the data set can be considered representative.

The fact that larval weight increases as a power law of the yolk weight has some implications. First, larvae that come from small eggs reach each developmental stage at a relatively larger size than larvae that come from large eggs. In terms of the maximum larval weight attained, this means that small larvae are more efficient than large larvae in using their yolk. This agrees with Heming and Buddington (1988) who attributed this to maintenance costs of tissue weight. Furthermore, since the exponent of the relationship for first feeding is smaller than that for maximum size, the larger the larvae the larger is the difference between the size at first feeding and the maximum size that larvae can grow on yolk reserves. Consequently, when larvae from larger eggs start to feed they have a better "buffer" to failure than those from small eggs. In nature this effect should be further extended, since the yolk consumption should drop after the beginning of exogenous feeding.

Secondly, if weight at each developmental stage could be described as a function of original yolk size, a chronological sequence of these stages should occur related to yolk weight. For example, a larvae originated from an egg weighing 1 mg, for example, would chronologically: (1) hatch with its pectoral fin formed or forming; (2) have its jaw and the eyes pigmented approximately at the same size; (3) inflate its swim bladder; (4) start to swim and to feed and; (5) attain its maximum size. This is roughly the same order of stages that can be observed in the batches of larvae presented in Figure 17 to Figure 24. Figure 32 shows that an inversion in this sequence occurs only between eye pigmentation and jaw formation for larvae coming from an egg weighing

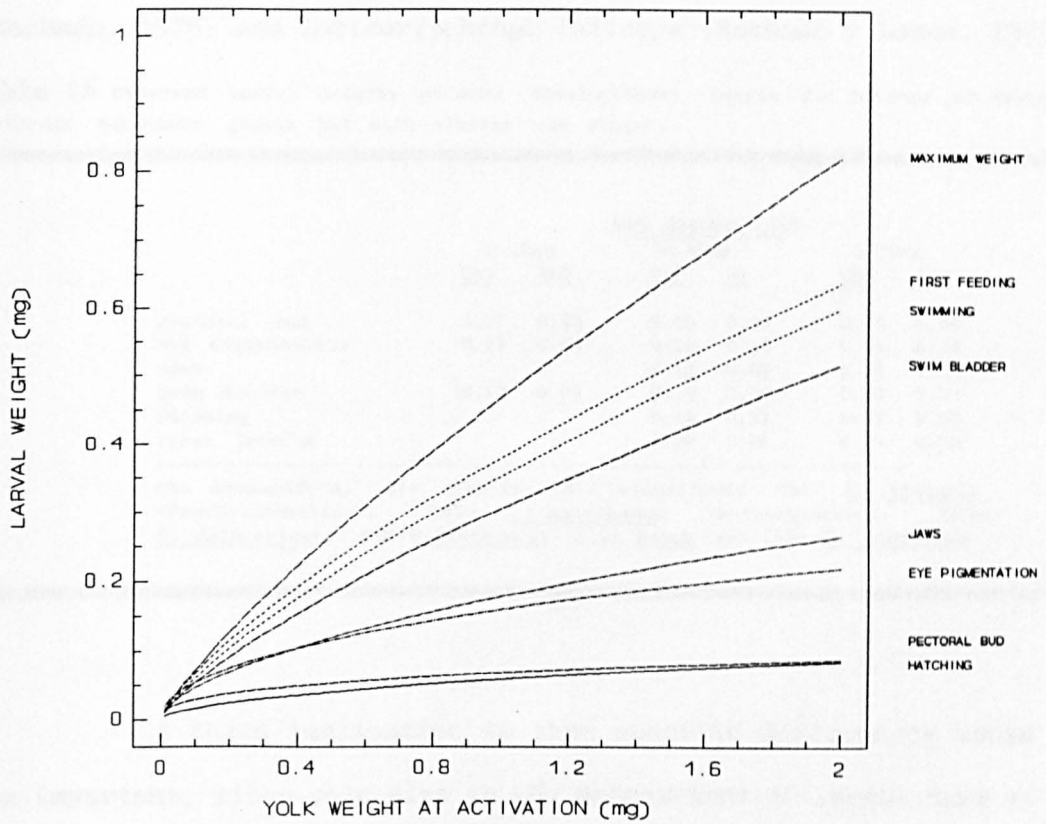


Figure 32 Predictive lines for larval weight at developmental events from yolk weight at activation for 13 species of Central Amazon.

less than 0.4 mg, and between hatching and pectoral buds formation for larvae coming from a yolk heavier than 2.0 mg. Since the intercepts of both functions (jaw and eye pigmentation) are very close and the slope of the function for jaw formation has a relatively high standard error, the former is unlikely to be real; a more reasonable interpretation is that both stages are approximately concurrent for yolk size smaller than 0.4mg. The inversion of the lines for hatching and pectoral bud formation predicts that larvae from yolks weighing over 2 mg should have pectoral buds before hatching. This happens with larvae of *O. bicirrhosum* and *P. multiradiatus*. It also occurs in other floodplain larvae that have eggs equal or larger than *P. multiradiatus*, such as

Symbranchus marmoratus (Taylor, 1913), *Loricaria laticeps* (Lopez y Machado, 1975) and *Loricarichthys laticeps* (Machado y Lopez, 1975).

Table 16 Observed larval weights at some developmental events for batches of larvae of different taxonomic groups but with similar egg weight.

	EGG WEIGHT (mg)					
	~0.28mg		~0.47mg		~0.77mg	
	Ch1	Ch2	Ci1	Si	Ch3	Ci2
Pectoral bud	0.07	0.09	0.06	0.07	0.05	0.08
Eye pigmentation	0.11	0.09	0.12	0.14	0.14	0.18
Jaws			0.13	0.09	0.14	0.18
Swim bladder	0.10	0.09	0.19	0.17	0.20	0.27
Swimming			0.19	0.17	0.17	0.27
First feeding			0.24	0.26	0.25	0.30

Ch= Characiform; Ci= cichlid; Si= siluriform; Ch1= S. insignis (Prochilodontidae); Ch2= C. macropomum (Serrasalmidae); Ch3= H. malabaricus; Si= H littorale; Ci1= Heros sp; Ci2= C. monoculus.

A third implication is that specific differences would not be important, since yolk size is the determinant of larval size at any particular stage. Therefore, different species with eggs of the same size should attain developmental stages at the same larval size. The data for Amazon larvae support this hypothesis (Table 16). The average difference equals 22%, ranging from 8 to 35%, which is similar to within-species coefficients of variation reported for the size at developmental stages.

This sequence of stages seems to happen to several species, if hatching and caudal rays formation are excluded, independently of egg size or habitat. It can be found in *O. niloticus* (Rana, 1988), *Anarhichas lupus marisalbi* (Pavlov, 1986), *Roccus americanus* (Mansueti, 1964), *G. aculeatus* (Wootton, 1976), *Labeotropheus* sp (Balon, 1985), *Etheostoma caeruleum* (Paine and Balon, 1984), *Stizostedion vitreum* (Balon, 1985), *Catostomus commersoni* (Balon, 1985), *Hucho hucho* (Witkowski and Kokurewicz, 1981), *Thymallus thymallus* (Witkowski and

Kokurewicz, 1978), *Parophrys vetulus* (Orsi, 1968) and others. However, exceptions can also be listed such as *Clupea harengus* (Russell, 1976) or *Microgadus tomcod* (Peterson *et al.*, 1980) that inflate the swim bladder after first feeding size or before eye pigmentation, respectively. Therefore, it seems that this chronology is a characteristic of Amazonian species, suggesting a strong convergence in the development. If the development of these features could occur at any stage of the larval period, why do they occur as a function of egg size?

The adaptive meaning of this chronology in development is unclear. The timing of some of the stages are more meaningful than others. The development of the swim bladder and swimming behaviour seem to be basic steps towards first feeding and occur just before this stage. However, why do not larvae from larger eggs start feed at a smaller size, further optimizing the period between first feeding and the maximum size?

Rosenthal and Fonds (1970) suggest that the early development of the pectoral bud improves embryo respiration. The perivitelline fluid is the main constraint to embryo respiration (Rombough, 1988). Early formation of the pectoral fins might be useful in circulating the perivitelline fluid so improving the gaseous exchange of the egg. Several species with demersal eggs and large embryos have pectoral fins before hatching (Rosenthal and Fonds, 1970; Machado, 1975; Wootton, 1976; Witkowski and Kokurewicz, 1978; Balon, 1985; Pavlov, 1986; Rana, 1988). However, if the presence of the pectoral fin increases the efficiency of the respiration of the embryo, why do only few Amazon larvae, that live in poorly oxygenated waters, have the bud before hatching?

The pigmentation of the eye suggests that it is functional (Blaxter *et al.*, 1983). Vision is an important sense, influencing feeding and predator avoidance (Miller *et al.* 1988). Jaw formation is essential to first feeding; it is essential also to inflate the swim bladder and to start branchial respiration. Several species fill the swim bladder first by gulping air at the water surface (Hunter and Sanchez, 1976; Doroshev *et al*, 1981). Furthermore, feeding without the swim bladder being formed might be detrimental to the larvae because of being negatively buoyant. Larvae from small eggs (<0.2 mg) pigment the eye and develop the jaw at a larval size close to first feeding. At this size they are probably in the lakes where light penetration in the water enables vision and where branchial respiration seems to be important. The advantage is similar to larvae from large eggs, even if they form the jaw and pigment the eyes at a relatively small size. Although some of the species are gathered in nests when the eyes and jaw are formed, branchial respiration is starting (Figure 27C). Functional eyes may offer further protection against predators, specially to species without parental care.

All the above stages can be considered as a step-by-step development to attain the complexity for first-feeding, i.e. shaping the pectoral fin, the opening of the mouth, the developing of vision (eye), the improving of buoyancy (swim bladder). Pectoral fins have been found important for the swimming of some species (Batty, 1981). A developed swim bladder may be crucial to swimming in Amazon waters, which have a low specific gravity due to the lack of inorganic salts, compared with other freshwater systems (Welcomme, 1985). When the larvae can maintain their buoyancy and hence manoeuvre better they are ready to start feeding. This seems a quite distinct stage, since during

the experiments to measure first feeding size, food was available from the moment of opening the mouth. Therefore, a minimum size of egg may exist that is adaptive in these environments. An embryo of a very small egg might not have enough energy to develop the eyes and mouth before first feeding, so survival may be compromised independently of food availability. Larvae of *Sardinops caerulea*, for example, have been reported to resorb the yolk before eye and jaw formation (Lasker, 1962). Other species with small eggs develop these organs concurrently with first feeding (Heming and Buddington, 1988). These species may thus be extremely sensitivity to factors that affect the efficiency of yolk utilization.

Hatching was an early stage in most species. It occurred at 30% and 18 % of first-feeding size for larvae from small eggs (~0.1 mg) and large eggs (~1 mg), respectively. Its relation with yolk size is flattened (Figure 32) indicating that earlier hatching is optimized. The effect of oxygen concentration on incubation time and size have been described by several authors (Oseid and Smith, 1971; Rombough, 1988). Usually, in low availability of oxygen the embryos hatch smaller or younger. Most of the large eggs found are demersal and early hatching may be an effect of oxygen deficiency of the embryo. The larvae of species with less oxygen limitation, such as *H. littorale*, hatch relatively larger. However, there are other advantages in being a larva instead of an embryo. Eggs are often adhesive and grouped in these species, so demanding parental protection to escape predation. They are more exposed to water level fluctuations, since they cannot be moved by the parents in such a situation. Furthermore, larvae have more a greater surface area than embryos, so cutaneous respiration is also optimized.

Other developmental stages, such as the formation of fin rays, the development of phototaxis or the cutaneous circulatory system, do not show correlation with egg size. The development of these features certainly requires a part of the energy allocated to growth and the small eggs may not be able to "afford" it.

The formation of the rays of the caudal fin was not related to yolk weight. All species that showed this stage before yolk resorption had approximately the same larval weight (~0.20 mg), including the unhatched embryo of *P. multiradiatus* with a yolk weight of 6 mg. The characiforms did not show this feature within the range of sizes studied, but it is known that *S. insignis*, *P. latior* and *E. melanopogon* develop rays in caudal fin rays after they start exogenous feeding (Araujo-Lima, 1985; 1987), as do some other species of this group (Machado, 1975).

Cement glands and their activity are well know for the cichlids (Fontenele, 1950, 1951, 1952). They enable the newly hatched larvae to attach to the spawning substratum until the moment when they transfer to the nest. In the nests the glands keep the larvae connected in small groups often together with a large piece of detritus. The advantage of having powerful cement glands is obvious, since they keep the larvae in a restricted area, but let them move their body. To restrict the larval distibution might be important to the efficiency of parental care. Movement of the body might be important to improve cutaneous respiration by reducing the boundary layer around larval body.

The same rationale does not apply to the characiforms and *H. littorale*, even if parental care is operating during the larval period. Species such as *H. malabaricus*. *H. littorale* and *H. malabaricus*

use their cement glands to attach themselves vertically to underwater objects and the surface film. This behaviour allows the larvae to escape from the anoxic water near the bottom and perhaps to remain close to the oxygen-rich water surface. Here, the larvae are camouflaged in the vegetation so avoiding predators and surprising prey. Both species have a very dense dorsal pigmentation when they start to swim, which doubtless helps in the camouflage. An anchorage point to the substratum may also let the larvae swing the body more efficiently and, therefore improve cutaneous respiration. The weak activity of the glands probably gives them better control and use of the glands, allowing them to release and reattach.

The advantage of cement glands for the larvae of riverine characiforms is not clear. The larvae have not been observed attached on any substrata in the aquaria, except underneath the surface film. The activity of these cement glands has not been noticed by other workers (Kossoski, 1980; Machado, 1987). It seems likely that their major advantage is to let the larvae use the oxygen-rich microboundary layer more effectively. A strong cement gland could have a disadvantageous effect on the larvae since it could agglutinate sediments particles, so increasing larval weight and reducing its buoyancy.

The lack of intensively used cement glands seems a characteristic of the Amazonian species that spawn in lotic habitats, since hanging behaviour on plants was described for other species of characiforms with similar spawning habits in the south and northeast of Brazil (Azevedo *et al*, 1938; Moraes Filho e Schubart, 1955).

Phototaxis

The results found for phototaxis were not correlated with the general trends in spawning sites or habits and are probably related to the specific strategies of the larvae. Positive phototaxis was strongly evident in the cichlids. *C. monoculus* and *Heros* sp showed this behaviour from the onset of swimming. Phototaxis in the former species co-occurs with the loss of the cement glands and may be an adaptation to keep the larvae together. In the aquarium the larvae were often shoaling in the direction of the light. Observations on both species in their natural habitat showed that they usually rear their young in marginal areas of the floodplain and flooded forest and it is common to see the parents swimming around with shoal of young (Fontenelle, 1950; Lowe-McConnell, 1964, 1969; Zaret, 1980). In the natural habitat positive phototaxis would have at least two consequences: (1) to attract the larvae to the upper part of the water column; (2) to attract the fish to the open areas of the lake where there is less shade. Shoals of larvae are commonly seen in the upper part of water column, but seldom in open waters of lakes. This suggests that, despite positive phototaxis, the range of larval movement is restricted by the parents. Observations on the behaviour of *Mesonauta insignis* and reports from Lowe-McConnell (1969) suggest that the larvae follow the parents. There is, therefore, a paradox: how can the larvae follow the parents if they are strongly attracted towards light? One possible explanation is that there is a hierarchy in these conflicting behaviours and the larvae would follow the parents as a first priority. A second possibility is that the parents reflect light to the larvae so attracting them. The commonly reported bright colours of breeding cichlids (Lowe-McConnell, 1969, Zaret, 1977) suggest that the last explanation is feasible. Furthermore, depending on the maximal

absorption of the cone pigments of the larval eye, the colours of the parents might appear very bright to the larvae (Ali *et al*, 1977)

The data for *Crenicichla* sp showed that the larvae of this species had positive phototaxis at jaw formation. At this size they were still attached by the cement glands and the swimming capabilities had not yet developed. The guarding behaviour for this species is less known, but in one occasion a nest was taken containing one of the parents and several non-swimming larvae. The advantage of having this early positive phototaxis is not clear and more samples are necessary to confirm the extent of this behaviour. However, it can be assumed that when *Crenicichla* sp larvae start to swim they already exhibit the positive phototaxis and would be shoaling with their parents.

Positive phototaxis was also found in the characiforms *P. lattor*, *P. altamazonica* and *P. amazonica* in a strong and transient form, lasting less than 12 h. It occurs very early in the development, before the formation of pectoral fin bud for most species. Response to light stimuli independent of functional eyes has been shown for *C. harengus* and *P. platessa* (Wales, 1975), but those species respond negatively, swimming up at a low intensity light (Blaxter, 1975). The advantage of such adaptations in the larvae of the Curimatidae is not clear. It might, however, have a useful application for sorting newly hatched larvae in aquaculture rearing tanks.

Similar behaviour has not been detected for others characiforms that spawn in the same habitat e.g. *C. macropomum* (Silva *et al.* 1977; Malca, 1989; Bello *et al*, 1989; Valencia y Puentes, 1989) or *M. duriventre* (Kossoski, 1980), *S. insignis* (Araujo-Lima, 1985) or *B. erytropterum* (Eckman, 1984). However, this could be biassed by the conditions in which the larvae were incubated in the above studies and

by transient characteristics of the phototaxis that make it hard to detect.

The transient negatively phototactic behaviour found for the larvae of the three species of Curimatidae at the onset of swimming was the only behaviour of this nature observed throughout this study. It occurred only during a brief period at onset of swimming. This behaviour may be advantageous for the larvae once in the lakes, enabling them to avoid the open waters where they are more susceptible to predators.

Age at Starvation

The lack of a general correlation between yolk weight and age at death by starvation suggests that other factors different from initial egg size may improve the survival time of starving larvae. Larvae from riverine eggs survive to starvation almost as long as some of floodplain larvae, despite coming from a much smaller egg. The lack of effect could be caused by differences in temperature during larval rearing, but no such effect was found on the residuals. Age at starvation is, however, positively correlated within a group of related species (fam. Curimatidae) that spawn in the channels.

Published results are confusing. Egg size affects survival time of starving larvae in *Clupea harengus* (Blaxter and Hempel, 1963), *Etheostoma spectabile* (Marsh, 1986) and *Oreochromis* spp (Rana, 1985, 1988). No real effect was describe for *Leuciscus leuciscus* (Mann and Mills, 1985) or *Stizostedium vitreum* (Moodie *et al.*, 1989). Evidence that starvation time is more dependent on other specific differences than on egg size is noticed if egg size is constant. Larvae of *C. harengus* (Blaxter and Hempel, 1963) and of *E. spectabili* (Marsh,

1986) from eggs of same size and reared at similar temperature range (8-12 °C) have a resistance to starvation of 27 and 57 days, respectively. Larvae of *O. mossambicus* and *O. niloticus* from similar eggs and rearing temperature have a resistance to starvation of 20 and 13 days, respectively (Rana, 1985, 1988). Larvae of *A. ocellatus* and larvae of *O. mossambicus* from similar egg size and rearing temperature have a resistance to starvation of 8 and 14 days, respectively. These discrepancies might be related to differences in specific growth rates. If so, larvae of the floodplain grow much faster than riverine larvae. Whether this result is taxonomically biassed or can be generalized to all species that spawn in the channels cannot be decided here, but for riverine larvae of Curimatidae larger eggs mean a longer existence on the yolk. The same is not true for littoral larvae.

Patterns on the distribution of blood vessels

The patterns found in blood circulation of newly hatched larvae correlated well with the oxygen conditions of their spawning sites. Availability of oxygen is very different between the lentic and the lotic habitats (Table 1). The river and the channels have oxygen concentrations that are relatively stable compared to the littoral, which shows strong diel and seasonal variations. The larvae of all studied species that spawn in the margins (cichlids, siluriformes and *H. malabaricus)* have a dense vascularization on the body surface and red blood cells, whereas species spawning in the river have none of these features. Such a correlation implies that the newly hatched larvae live in a habitat similar to the eggs (which is the case for most species, except *H. littorale)* and that respiration in the early larval stages is mainly cutaneous (Blaxter, 1986, 1988; Rombough,

1988). The presence of haemoglobin and the extended pathways for the circulation of the erythrocytes are features that probably enhance the efficiency of cutaneous respiration. The lack of capillary network on the yolk sac of *H. littorale*, unique among the species that spawn in the littoral, can be explained in the same way. The yolk surface comprises a large fraction of the total surface of the embryo (the perivitelline space of the egg is very small, allowing only one side of the embryo to face the outside); consequently, to optimize respiration, the yolk surface must be well vascularized. However, *H. littorale* incubates the eggs in floating nests, where there is plenty of oxygen.

A possible caveat to the above hypothesis is a sampling bias. All species studied from the littoral areas were 2 to 10 times heavier than the riverine larvae. Littoral larvae have a smaller surface area: weight ratio and need to improve the efficiency of their cutaneous respiration. The pattern of cutaneous circulation (cutaneous respiration) could then be a size effect instead of an adaptation to environmental anoxia.

Larvae hatching from littoral and lotic eggs do not show many different features in the blood circulation patterns at swimming to first-feeding stage. They all have red blood cells, circulation in branchial arches and a well developed subintestinal vein. This similarity is to be expected, since both groups will be exploring the same habitat i.e., the marginal areas of the lakes (Bayley, 1983; Goulding e Carvalho, 1983; Araujo-Lima, 1985). For the species that were hatched in the littoral areas the reduction of the circulation on the yolk sac and primordial fin might be related to the change from the demersal habitat to shoaling, and to the development of branchial respiration. The increase in body surface area is smaller than the

increase in oxygen demand with growth, so that the increase of respiratory area can only be achieved by the development of branchial respiration (de Silva, 1974; Blaxter, 1986). Blood circulation to the digestive tract is also increased to prepare the system for digestion of exogenous food. The species hatched in the lotic habitats feed in the lake, where oxygen concentrations are more variable than in the channels. Therefore they also need a better developed respiratory system.

Although it is poorly studied in the Amazon, correlations between adaptations to improve cutaneous respiration and the oxygen availability in the larval habitat are well known in other systems (Taylor, 1913; Sawaya, 1942; Pasteels, 1958; Lagler *et al*, 1962; Nikolsky, 1966). Such adaptations are yolk and fin fold vascularization (Lanzing, 1976; Liem, 1981; Balon, 1985). Patterns similar to the littorally-hatched Amazonian larvae have been found for the bream *Abramis* spp (Nikolsky, 1966; Balon, 1985; Pliszka, 1953), zahrte *Vimba vimba* (Pliszka, 1953), white sucker *Catostomus commersoni* (Balon, 1985), *Labeotropheus* sp (Balon, 1985) and *Tilapia mossambica* (Lanzing, 1976), all species that spawn adherent eggs on submerged vegetation, on coarse gravel of river beds or mouth-brood the eggs. The larvae hatched in lotic habitats are simpler than the ones described for the riverine species cited above, resembling the larvae of *Stizostedium vitreum*, a pelagic freshwater larvae (Balon, 1985).

This study comprised only 12 species, which can be considered to be a very small sample compared with the size of fish fauna of the Central Amazon. It included, however, different families of the three main fish groups of the area and five different spawning strategies (Appendix A). Considering that correlations between dissolved oxygen

availability and patterns of cutaneous blood circulation are quite established in other systems the results seem conclusive, since all the patterns found fit perfectly well with the expectations.

Dissolved oxygen tolerance

The tolerance tests performed with larvae of two species, one a littoral spawner and other a lotic spawner, showed that they has responded differently to low concentrations of oxygen. The nested (non-swimming) larvae of the cichlid *C. monoculus* resist very low concentrations of oxygen (5% dissolved oxygen saturation) better than swimming larvae. Conversely, non-swimming larvae of the characiform *P. lattor* were very sensitive to low concentrations of oxygen (below 10% oxygen saturation), but their resistance improved at the swimming stage.

The resistance of non-swimming larvae of *C. monoculus* to low concentrations of dissolved oxygen is probably related to its enhanced cutaneous respiratory plexus (Figure 28A) compared with the swimming form (Figure 28B). The lower sensitivity of swimming larvae of *P. lattor* to low concentration of oxygen is presumably due to the development of branchial respiration at this stage (Figure 29). These changes in sensitivity are correlated with changes of habitat of the larvae. Oxygen concentration at the bottom of the floodplain, and therefore in the nests of cichlids, is always lower than in the water column. Oxygen concentration in the floodplain often reaches low values compared with the concentrations in the channels (Table 1). Therefore, when the larvae of *P. lattor* reach the floodplain they should be better prepared to resist such fluctuations.

Changes in the affinity of haemoglobin could also have an effect on the sensitivity of the larvae to low concentrations of oxygen. Larval haemoglobin displays a higher oxygen affinity than juvenile and adult haemoglobin (Iuchi, 1973; Rombough, 1988). However, it is unlikely that the larval haemoglobin affinity explains the variation in the sensitivity found in Amazon larvae. The change in sensitivity was opposite in the larvae of *P. latior*. Furthermore, haemoglobin affinity increasing with size has not been reported yet (Rombough, 1988). A second possibility is that the interference of respiration during the experiments affected the general results. Considering that the oxygen consumption of the larvae increases with body weight and that the lighter larval stage (non-swimming) of *P. latior* were more sensitive than the heavier one (swimming) it is improbable that respiration during the experiments altered the overall conclusion for this species. The effect on *C. monoculus* is more dubious, since oxygen consumption and the experimental results are correlated. An estimation of the effect of respiration on the results can be tried using published observations for other tropical species. Based on a consumption rate of *S. mossambicus* (Rombough, 1988) at 30 °C, the non-swimming stage of *C. monoculus* should consume 0.07 mg $O_2 \cdot h^{-1}$ and the swimming larval stage 0.08 mg $O_2 \cdot h^{-1}$, 8% and 10% of the oxygen available (at 0.4 $mg \cdot l^{-1}$) respectively. It is unlikely that the 2% difference in the experimental concentration could have affected the overall result.

Eggs of *Colossoma macropomum* have been reported to be very sensitive to concentrations of oxygen of 40% saturation, but with the concentration above 50% egg mortality is negligible (Valencia y Puentes, 1989). This is approximately the range of concentrations found

in the floodplains and channels respectively (Table 1). This supports the conclusion that embryo and newly hatched larvae of channel spawners may not survive in the lakes before they reach certain developmental stages.

Similar correlations between larval habitat and tolerance to dissolved oxygen have been found by De Silva and Tytler (1973). Planktonic larvae of plaice are less tolerant to low concentrations of dissolved oxygen than the demersal metamorphosed larvae. Conversely newly hatched herring, from demersal eggs, are less sensitive than the metamorphosed larvae.

Main conclusions related to larval development age at starvation and patterns of blood circulation.

1. The larval size at developmental stages/events such as hatching, pectoral fin bud, jaw formation, eye pigmentation, swim bladder inflation, onset of swimming, first feeding and the maximum size attained with exclusively endogenous nutrition is highly correlated with egg size.
2. The larval size at formation of caudal fin rays is independent of egg size.
3. Larvae from larger eggs continue to grow for a longer time, if they fail to feed, in comparison with larvae from small eggs. The extent of this growth also increases with egg size. As a result the larvae from large eggs may withstand fluctuations in food availability better than larvae from small eggs.
4. Time to death by starvation is not always related to egg size. Larvae from a small egg may starve at the same age as larvae from a large egg.

5. Larvae from small eggs are more efficient at yolk utilization. They reach the same developmental stages at a relatively larger size, in relation to the amount of energy available.
6. Newly hatched larvae of lentic spawners, that experience high fluctuations in dissolved oxygen availability, have complex networks of cutaneous circulation. Conversely, newly hatched larvae of lotic spawners, that live in a habitat rich in dissolved oxygen, do not shown such features.

There are considerations related to the above conclusions that should be mentioned. Large larvae also have: a large mouth (Shirota, 1970) and consequently a large spectrum of food (Werner and Gillian, 1985); a higher cruising and burst swimming speed (Blaxter, 1966; Theilacker and Lasker, 1974; Miller *et al.*, 1988) which is advantageous for catching prey and to avoid predators (Ware, 1975). However, there also seems to be a "trade-off" between size and predator avoidance. This effect is described for zooplankters (Werner and Gillian, 1985). Recently Fuiman and Gamble (1989) showed that, regardless of having a better escape response, large larvae experience higher instantaneous mortality rate than small larvae, probably through their conspicuousness. Additionally, large eggs have less tolerance to low oxygen concentrations (Beacham and Murray, 1985).

Some authors have shown that, despite the initial advantages offered by egg size, such as high growth rate, these are soon lost after first feeding (Thorpe *et al.*, 1984; Springate and Bromage, 1985). However for most species, the greatest potential for regulation of year-class size lies in the larval period. Houde (1987) suggests that larval mortality rates in species with large egg size, such as *Morone*

saxatilis, are less sensitive to prey density then species with small eggs such as *Anchoa mitchilli*. In this context egg size offers a benefit at the recruitment level.

A few ecological remarks must be made here. Considering that there is no food for the larvae in the channels (Araujo-Lima, 1984) and all species share the littoral areas of the floodplain for feeding and growing, it can be established that there is only one nursery ground for the whole community. As a result the larval community can be divided into those larvae which are hatched in the nursery grounds and those which are not and need to be transported to the nursery grounds. The larvae hatched on the nursery ground are adapted to the fluctuations in oxygen concentration in this habitat from the embryonic period. Parental care is present in most species and fanning behaviour of the eggs by the parents is common in some of species. Most species have large conspicuous eggs which may attract predators, so that parental care can be considered a response to this threat.

The larvae hatched in the channels experience a habitat with favourable physico-chemical conditions for embryonic development. However, they are sensitive to low concentrations of oxygen in the young stages and their survival in the lakes is compromised during this period. When the larvae reach the stage of first feeding, they attain the morpho-physiological requirements of this habitat. Those adaptations consist mainly of the presence of red blood cells and branchial respiration and the anatomical apparatus to feed.

5.2 Reproductive strategies and larval development of Central Amazonian fishes.

According to Wootton (1984), reproductive strategy of a species is a complex of reproductive traits that is manifested in an attempt to leave offspring. The adaptation of a reproductive strategy is a consequence of natural selection. When interpreting patterns of reproductive traits it is sometimes difficult to know what is the consequence of and what is the cause of a particular strategy (Fenchel, 1987). Establishing some assumptions might help this discussion. The first one is that natural selection should tend to produce animals that maximize their reproductive value at each age (Stearns, 1976; Ware, 1980; Partridge and Harvey, 1988). By reproductive value is meant the total number of young a female can expect to have during her life span discounted back to the present. The second assumption is that each species is tuned to the present environment and its fluctuations. This may seem simplistic, since species, like the environment, are in a dynamic state. The reproductive parameters measured are the phenotypic expression of the genome. If the phenotype has some plasticity, adapting it to the environmental conditions (Stearns, 1980; Mann *et al.*, 1984), then it is possible to accept that it is constantly tuned to the environmental characteristics. The third assumption is that natural selection acts on the individuals and not on the population. Population selection is still a controversial theme (Stearns, 1976; Maynard-Smith, 1982; Caswell, 1989) and it will not be considered here.

The implication of these assumptions is that the fish species reproducing in the Central Amazon evolved specific strategies that permit them to optimize the production of offspring in the present

Table 17 Characteristics of the main reproductive strategies found for Central Amazon species.

TRAITS	GROUP 1	GROUP 2	OTHERS
Spawning season (months)	5-12	2-6	3-4
Spawns/season	>1	1	1
Spawning style[1]	os ns	os	ns eb
Parental care	yes/no	no	yes
Abs. fecundity (10^3 eggs)	0.85-16	17-1000	0.1-10
Rel. fecundity ($eggs \cdot g^{-1}$)	2-26	90-4000	0.1-150
Expenditure ($cal \cdot spawn^{-1} \cdot g^{-1}$)	10-160	210-3172	163-1680
Egg dry weight (mg)	0.4-1.2	0.06-0.3	0.4-225
Egg calorific cont. ($cal \cdot mg^{-1}$)	6.1-6.8	6.2-7.7	5.7-7.1
Egg surface:dry weight ($mm^2 \cdot mg^{-1}$)	8-12	50-229	2-18
Newly hatched larvae with cutaneous blood vessels	yes	no	yes

[1] following Balon (1985) ecological reproductive guilds; os= open substratum spawner; ns= nest spawner; eb= external bearer spawner.

Group 1= A. ocellatus, C. monoculus, Crenicichla sp, Heros sp, M. insignis, H. malabaricus and Metynnis sp.

Group 2= B. erytropterum, C. macropomum, E. melanopogon, P. amazonica, P. altamazonica, P. brachypomus, P. latior, P. nigricans, P. rutiloides and S. insignis.

Others= O. bicirrhosum, H. littorale and P. multiradiatus.

environmental conditions of the basin.

The 19 species studied have reproductive strategies that converge into two groups (Table 17). Three species that did no fit this scheme are considered separately. The first immediate link between the reproductive strategies of adults and larval development depends on egg size, since larval size at most developmental stages is strongly dependent on the yolk size. A second link is the spawning and nursery sites, since the differentiation of the larval circulatory system is

sites, since the differentiation of the larval circulatory system is highly correlated with the variations of oxygen concentration in these sites.

GROUP 1

The species of the Group 1 spawn in the nursery grounds of the floodplain and the larvae show adaptations to overcome the fluctuations of dissolved oxygen. The larvae are sensitive to starvation if compared with riverine larvae. The eggs are relatively heavy, with the largest weighing three times the smallest. Egg size could have evolved from several selective pressures:

(1) Egg size was selected to optimize the respiration of the embryo in the environmental conditions of the incubation site. Diffusion of oxygen into the eggs is a function of the boundary layer and the perivitelline space. The driving force required to overcome the diffusional resistance of the boundary layer is directly proportional to the rate of oxygen consumption and the thickness of the boundary layer and inversely proportional to egg surface area. Heavy eggs demand higher pressures differences, since they (generally) have larger metabolic rates and thicker boundary layers (Rombough, 1988). On the other hand the specific oxygen requirement decreases as egg mass increases. If, the resistance of the boundary layer increases proportionally to egg mass to the power of 0.25 (Appendix F), and the specific oxygen requirement decreases proportionally to egg mass to the power of - 0.20 (Blaxter, 1988), then the opposite forces more-or-less match. This suggests that reducing egg size might not be a very effective way for reducing the consequences of the thickness of the boundary layer on egg respiration. A more productive way is probably

increasing water speed around the egg which will reduce the thickness of the boundary layer. The fanning behaviour of the cichlids can be regard as an adaptation to reduce the boundary layer of their heavy eggs.

(2) Egg size was selected to optimize the development of the larval circulatory system. The embryos and larvae living in the littoral areas have mostly evolved networks of blood vessels. Due to their presence in all the species examined from these areas, they seem essential to survival in this habitat. The energy required for differentiation must be increased to develop the circulatory systems. No species with small eggs were found in this group, perhaps because energy reserves in the yolk are inadequate to meet the requirements of developing the circulatory systems.

(3) Egg size was selected to avoid overcrowding and intraspecific competition. Aquatic species use the egg and larval period as a dispersal phase. Spawning in the floodplain lakes, a system where the eggs do not disperse very much, may result in a overcrowding that may increase the intensity of intraspecific competition, hence favouring the evolution of larger (and more competitive) larvae (Pianka, 1970; Parker and Begon, 1986). Although this hypothesis is hard to test, the lack of density-dependent effects in small and large juveniles of the floodplain community (Bayley, 1988) suggests that it is unlikely that egg size was selected to avoid intraspecific or interspecific competition.

(4) Large egg size was selected because they experience lower mortality rates than would experience larvae of same size. Large eggs are likely to evolve whenever the survival rate of the embryos is significantly higher than that of larvae of similar body sizes (Shine, 1978, 1989).

Unless the egg period is safer than the larval period a female should make her eggs as small as possible. This model implies that increasing egg size proportionally increases the length of the embryonic period. Egg mortality might be lower than larval mortality only in the presence of hidden eggs or parental care. Although parental care occurs in several species it does not occur in all. Furthermore, increasing egg size in this group does not mean longer periods of parental protection and hatching size increases at a much lower rate than the maximum size. Therefore, for some species increasing egg size means that the larval period will be longer than the embryonic period. A larva from a 1 mg egg hatches with 7% of yolk consumed, whereas a larva from 0.5 mg egg hatches with 10% of yolk consumed. Therefore this hypothesis seems unlikely.

(5) Since large eggs reduce the danger of starvation, natural selection should favour very large eggs. From the results it is clear that large eggs produce larvae that start to feed with larger reserves of yolk, but there was no relationship between survival time and egg size. Therefore, the larvae are "buffered" against failures in feeding at the first-feeding stage, but they are relatively sensitive to starvation once the yolk is gone.

(6) Egg size was selected to optimize fecundity. If the female has a finite amount of energy to devote to egg yolk, natural selection favours a female that allocates her energetic investment in each egg to maximize the number of her offspring that survive to reproduce (Hempel and Blaxter, 1967; Smith and Fretwell, 1974). So, a "trade-off" between egg size and fecundity should exist. No correlation was found between egg size and batch fecundity or relative fecundity, but this might be caused by poor estimation of fecundity for batch spawners.

GROUP 2

The species of this group (characiforms) have relatively small eggs that are spawned in the channels. At first feeding the larvae have to be transported to the nursery grounds. The channels are physico-chemically stable habitats, but can be considered hydrologically variable (or patchy) when one considers the variation in the changes of water level ($cm \cdot d^{-1}$) during the flood (Figure 2). The transport of the larvae into the floodplain depends on the difference of water level between floodplain lakes and the river. Small scale variation is poorly studied in the Amazon, but on a few occasions reverse flow was observed in the lateral channels. These situations occurred when the river level was dropping or when the level was not changing, but rainfall was high in the catchment area of the lakes. This effect may explain why most species have only one spawning per season concentrated at the beginning of the flood. During this period the hydrological regime seems less variable (Figure 3). The potential predators are not well known, but are likely to be few. Light penetration is very poor in the channels and would make predation difficult. Turbulence and sediment load are extremely high in the system, what limits filter-feeder predators. However, cannibalism was observed in certain larval clusters formed by the water currents. The extremely low concentration of larvae larger than the first-feeding stage compared with the yolk sac stages suggests heavy mortality in the channels (Araujo-Lima, 1984). Starvation seems to be the main source of mortality in this habitat.

Egg size is small, but very variable. There is a five-fold range in egg weight. The pattern in egg size found could be explained in a number of ways:

(1) Egg size was selected to optimize the dispersion of the larvae into the lakes. The success of the transport of eggs and larvae into lakes would increase with the number of eggs laid by the parents. So as guarantee maximum drift into the floodplain, fecundity should be maximized. Consequently egg size should be as small as possible, although a minimum egg size should be allowed to let the larvae reach the lakes before starvation. This hypothesis does not explain egg size variability and, therefore, can be rejected. A further support for the rejection is the fact that spawning occurs mostly in the main channel where the dispersion distance to the floodplain is minimized.

(2) Egg size was selected to optimize larval survival in the channels. To optimize larval survival the species should increase the energetic content of the egg size, reducing the possibility of starvation. Egg size in the species of the group is not maximized, therefore, this hypothesis can be rejected.

(3) Egg size was selected to optimize the success and the distance for the dispersal of the larvae. If successful dispersal is dependent mainly on fecundity, increasing egg size would not improve the chances of larvae reaching the lakes. Increasing egg size would, however, increase the potential range of the drift and the probability of a larger number of lakes being colonized. To guarantee dispersal egg size should be minimized and fecundity maximized. However, to optimize larval

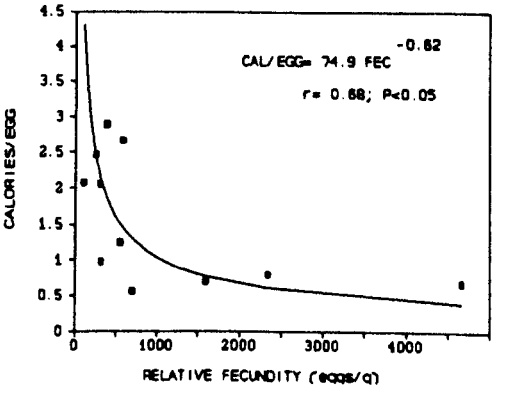


Figure 33 Relationship between calories in the egg and relative fecundity for 11 species of Central Amazon.

survival in the channels, egg size had to be optimized. A balance between egg size and high fecundity seems to have been reached. Species with smaller egg size and lower absolute fecundity would have to "trade-off" larval survival against successful dispersal. As a result a negative correlation should be expected between egg size and relative fecundity and a positive relationship should be expected between egg size and resistance to starvation. These assumptions seem to be fulfilled. There is, indeed, a relationship between relative fecundity and egg size (Figure 33) and a correlation was found between egg size and starvation time for some species of the community (Figure 26).

(4) Egg size was selected to optimize larval transport into the lakes and optimize resistance to starvation on the nursery grounds. Again balance between fecundity and egg size would be expected and a positive relationship should be found between egg size and starvation. Nevertheless, to optimize transport into the lakes spawning should be in the channels leading to the lakes. Consequently, larval density in those channels should be very high and larval density in the main river low. The available evidence on larval distribution in the channels shows equal densities of larvae in both the channels and the river (Araujo-Lima, 1984), suggesting that this hypothesis is not valid.

Others species

Pterigoplichthys multiradiatus has large eggs. They are deposited in nests dug deep into the banks. The embryos and the larvae have a well developed respiratory plexus. The nests are dug always below 1m depth. The eggs and larvae are, therefore, relatively safe from large and small predators and possible extremes of fluctuations in water level.

Osteoglossum bicirrhosum has also fairly large eggs and it carries the embryos and larvae for extended periods; mouth-brooded larvae can be 60 mm long. The parent, being a relatively large fish, is also less susceptible to predation, so enhancing the protection for the young.

Hoplosternum littorale has median size eggs that are laid in floating nests outside water. The larvae have well developed respiratory structures. Parental protection is, however, limited to the embryonic period. However, this species seems to be an exceptional case due to its high fecundity.

These three species have many differences between them and from the others littoral species, such as fecundity and egg size, but they share a common difference from the species of Group 1. They have a higher reproductive expenditure per spawn compared with other species that are littoral spawners.

From the above discussion it seems that the egg size of the species of Group 1 is potentially influenced by biological pressures such as predation and/or starvation of embryos and larvae. However, probability of catastrophic mortality cannot be completely discarded. The common reproductive strategy for those species is low fecundity, low reproductive expenditure, several spawns per season and large eggs. This strategy correlates with larvae large at first feeding and resistant to the anoxic conditions of the floodplain bottom. The large size of the embryos overexposes them to potential predators, an effect that parental care may counteract. Egg clutches are subject to death due to desiccation caused by extreme water level fluctuations. Batch spawning may have evolved in the group as a response to the possibility

of this catastrophic mortality due to environmental fluctuations. The short embryonic period may also be an adaptation to avoid such problems. The eggs, when in the nest, cannot be moved in an event of danger, since they are stuck on the substratum. However, the larvae can be moved from one nest to other when there is danger of desiccation.

Further protection against predation and environmental threats are present in *O. bicirrhosum*, *P. multiradiatus* and *H. littorale*. They all have nests safe from deleterious water level fluctuations. The smaller probability of heavy loss of the eggs may explain the reduced number of spawnings showed. The high fecundity shown by *H. littorale* may reflect its size limitation and the consequent short life span, a characteristic of small fishes (Miller, 1979)

Conversely, the pressures on the species of Group 2 seem to be related to random environmental effects. The reproductive strategy of the group relies on three traits: high fecundity, one spawn per season and small egg size. This strategy correlates with small larvae, sensitive to low concentrations of oxygen when newly hatched, and with small yolk reserves. However the larvae show a relatively high resistance to starvation, which is advantageous in the channels.

The spawning strategies of the species are highly correlated with their larval development. The species of Group 1 cannot spawn successfully in the channel, since the water currents would scatter the eggs during oviposition and parental care would not be feasible. Furthermore, the fecundity of the group is very limited to support the heavy mortality, that may be linked to dispersion. Conversely, the eggs of the species in Group 2 may not survive the anoxic conditions of the sediments, and cannot, therefore, spawn successfully in the lakes.

However, the larvae are able to tolerate better the variation of oxygen availability when they start to feed.

Among the general theories to explain the bionomics of the species, *r* and *K* selection is one of the best known. The concept was developed by MacArthur and Wilson (MacArthur, 1972) based on the components of the rate of population growth.

$$dN/dt = r \cdot N \cdot (1 - N/K)$$

where N is population density, *K* is maximum equilibrium density and *r* is the intrinsic rate of natural increase. Some environmental situations, such as low population density and high food supply, favour populations, that have a higher *r*, which MacArthur (1972) called "*r*-selection". Other environmental situations, such as high population density and low food supply, favours populations with higher *K* or "*K*-selection". Therefore, in density-dependent situations, *K* can replace *r* as a fitness measure (Stearns, 1976). The model has been used to describe density-dependent and density-independent selection. Despite criticism of its misinterpretations (Boyce, 1984), several reproductive traits have been correlated with this concept (Stearns, 1976). Stearns and Boyce have compilated some. "*r* selection" correlates with higher allocation of energy to reproduction, larger fecundity, smaller eggs, less parental care and few breeding periods per season. "*K* selection" correlates with smaller amount of energy allocated to reproduction, smaller fecundity, larger eggs, more parental care, more breeding periods per season and large organism size.

The species that spawn in the littoral areas fit into the predictions of *K*-selection. The floodplain areas can be considered to vary in an almost predictable way. Conversely, the species that spawn in the channels show overall features of *r*-selection. The environment

can be considered relatively unpredictable, if one considers the strong dependence of the success of reproduction on current directions into the floodplain, and how it varies during the flooding period.

A second theoretical line aims to link environmental features of the habitats with the life strategies of the species. The models are based in the idea that organisms that live in particular environment are likely to have certain common adaptations. Therefore, a relationship between the features of the habitat (templet) and the optimal life history strategy may exist (Southwood, 1988). Southwood, analyzing the main models that used this approach concluded that they are related and have similar predictions. The templet is defined by three axes: the disturbance axis, the adversity axis and the biotic interaction axis. Following Souza (1984) disturbance is "a discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly creates opportunity for new individuals to become established. The adversity axis describes the severity of the environment, such as abiotic stress (oxygen deprivation and temperature), resources level (food availability) (Southwood, 1988). The biotic interaction axis describes the impact of biotic agents such as predation, parasitism and competition. The templet model predicts that conditions of low adversity and high disturbance favours migration, low tolerance and many small offspring. Conditions of low disturbance and high adversity favour low migration, high tolerance and low fecundity with large offspring. The main problem in using the templet system is characterizing what is low and what is high adversity. The Amazon, for example, has extremely low productivity, but has good conditions of oxygen and temperature, and therefore high and low adversity, respectively. If the Amazon is considered a habitat

with high disturbance (random fluctuation in flooding rate) and low adversity the strategy correlates with the predictions. However, the larvae migrate from the river to the floodplain "because" river production is low (no food), e.g. because the habitat becomes adverse. Therefore, there is a switch in the degree of adversity of the habitat as a function of the organism scale. Consequently, the predictions of the model for number and size of offspring should change with the degree of adversity.

This study focused on 19 species of a community with over 250 species. No very small species (weight< 10g), or very large ones (weight> 100kg) were studied. The reason for this omission was mainly operational, since large fishes are hard to sample at their spawning sites. Small fishes are hard to identify taxonomically and nothing is known about their reproduction and the ecology of their eggs and larvae.

Among the species omitted there are a few, whose spawning sites and egg characteristics (Sterba, 1973; Araujo-Lima, 1987) would allow some inference about their reproductive strategies. These are:
Strategy of Group 1: *Serrasalmus nattereri*, *Anostomus* spp, *Chalceus macrolepidotus* and *Loricaria* spp.
Strategy of Group 2: *Anodus elongatus*, *Hemiodus* spp, *Mylossoma aureum*, *Raphyodon vulpinus*, *Triportheus elongatus*, *Triportheus angulatus*, *Raphyodon* sp, *Curimata* spp and *Rhytiodus microlepis*.

Several others pattern of reproduction may exist in the community. The small characiforms certainly have a different pattern. Preliminary information revealed that *Moenkhausia dichroura*, a batch spawner, has relative fecundity equal to 800 eggs$\cdot g^{-1}$ and small eggs. The spawning site of the species is unknown, but due its size and

absolute fecundity it is unlikely to be in the channels. Small characiforms are very numerous in the Amazon, but their ecology is almost unknown. It would be interesting to know whether these larvae have the adaptations to exist in low concentrations of dissolved oxygen, as do the larvae hatched in the lakes.

5.3 Comparison with other systems

Tropical freshwater systems

Several tropical river systems share some of the features described for the Amazon. The water level fluctuates seasonally. Flooding areas occur in most of them, whether laterally or at the lower reaches (Goulding, 1980; Welcomme, 1985). Oxygen concentration is generally high in the lotic areas, but anoxic conditions alternate with oxygenated ones in the floodplains. Specially critical conditions are found under the floating mats of vegetation and the input of flooding water is reported to increase dissolved oxygen concentrations in several systems (Beadle, 1974; Welcomme, 1985). However, some exceptions have been reported. In floodplains lakes of the Rio Orinoco, well oxygenated conditions are found year-round (Hamilton and Lewis Jr, 1987).

Spawnings in the main channel, such those found for the Amazon, have been described in South America (Machado, 1987; Lowe-McConnell, 1964; Azevedo *et al.*, 1938; Rosa Junior and Schubart, 1945; Moraes Filho and Schubart, 1955) or Africa (Durand and Loubens, 1970; Albaret, 1982; Welcomme, 1985; Lowe-McConnell, 1987). This strategy is usually found with migratory species with high fecundity. The larvae in those habitats might experience constraints similar to those

described for the Amazon, since zooplankton is also rare as well (Welcomme, 1985). Published data about larval development are mainly related to larval length and age, so limiting comparisons. However, the size and pattern of larval development suggest that they are similar to riverine larvae of the Amazon (Rosa Junior and Schubart, 1945; Moraes Filho and Schubart, 1955; Durand et Loubens, 1971; Machado, 1987). Observations on the pattern of cutaneous blood circulation have not been reported.

Littoral spawners such as those found for the Amazon are also common in other tropical riverine systems. In the Orinoco and Rupununi systems several species of cichlids, characiforms and siluriforms spawn at the banks of the rivers or in the floodplain (Machado, 1987; Lowe-McConnell, 1964). They usually have low fecundity and large eggs, but species with small eggs have also been reported (Machado, 1987). Parental care is common in these communities (Welcomme, 1985). Fryer and Iles (1972) studied the reproductive behaviour of African guarder cichlids. They described nest formats, pattern of the spawn and parental care, cement glands and larval development remarkably similar to those described for the Amazon. Cutaneous circulatory plexuses are described for a few species (Sawaya, 1942; Fryer and Iles, 1972). Low fecundity and small eggs seems related to small sized fishes (Machado, 1987), but their larval ecology is poorly studied and most information come from the aquarium literature. Machado suggests that they spawn in the vegetation close to the river banks, where dissolved oxygen conditions are expected to be good.

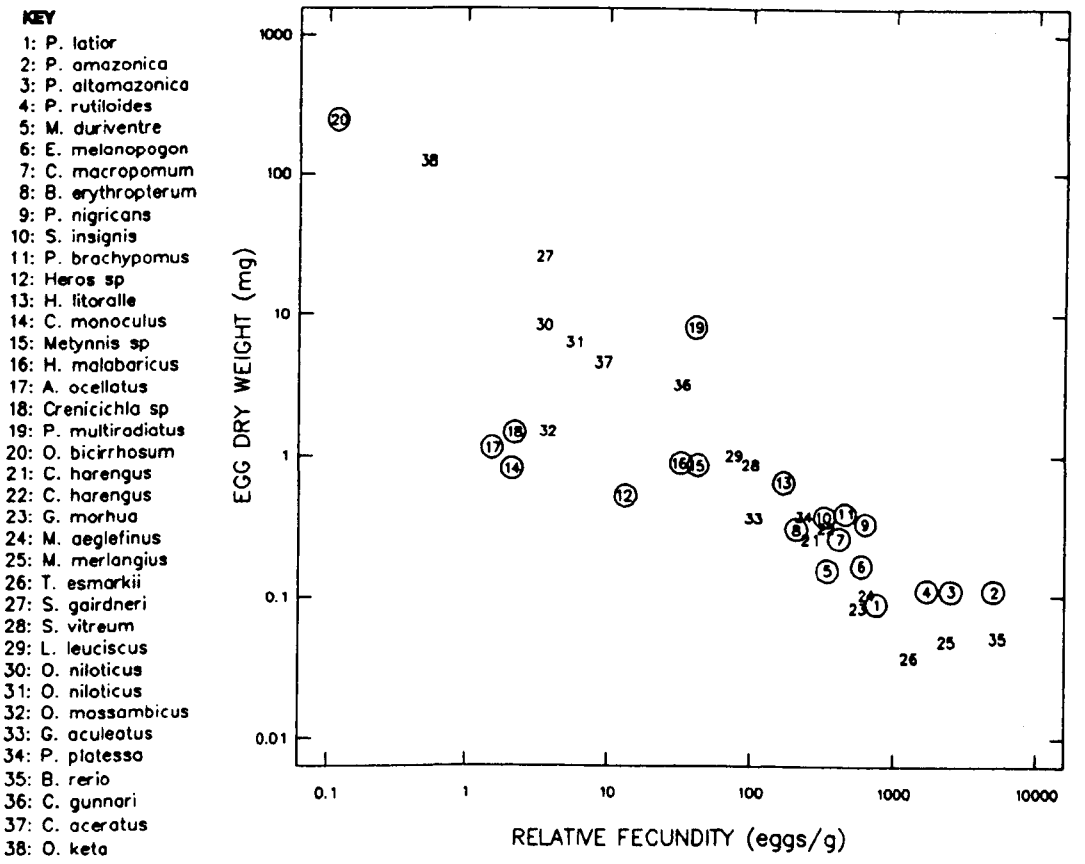


Figure 34 Scatterplot of egg dry weight on relative fecundity for 36 species of fish. Amazonian species (circles) are 1-20, others 21-38. Data sources listed in footnote 1.

Other systems[1]

Among the components of reproductive strategy directed toward survival of offspring, egg size, fecundity and spawning season can be considered the most important. Relative fecundity plotted against egg dry weight gives a good idea of how both traits co-vary (trade-off). The trend in the scatterplot can be considered an approximation to the inverse of the ratio reproductive expenditure:calorific content of the egg. So Figure 34 permits a rough comparison of the three traits.

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[1] 21-22: Blaxter and Hempel, 1963 and Baxter, 1959; 23 - 26: Hyslop, 1984 and Kjesbu, 1989; 27: Kamler and Kato, 1983 and Bromage and Cumaranatunga, 1988; 28: Moodie et al., 1989 and Craig, 1987; 29: Mann, 1974 and Mann and Mills, 1985; 30-32: Rana, 1988; 33: Wootton, 1976; 34: Bagenal, 1973 and obs. pess.; 35: Miller, 1979; 36-37: Everson, 1984 and Kock, 1979; 38: Bakala, 1970.

Relative to the egg size of other habitats the Amazonian riverine spawners are among the most fecund and with smallest egg size. Egg size:fecundity ratio showed a variation very much like the species of temperate marine habitats, such as *P. platessa*, *C. harengus* and the gadoids or small cyprinids, such as *Brachydanio rerio*. This convergence is expected, since both groups of species have a tendency to maximize fecundity in order to disperse their eggs and larvae towards the nursery grounds. In small fishes, such as *B. rerio* the aim is to attain a minimum total fecundity necessary to leave offspring. However, in relation to the energetics of the female, Amazonian species expend more calories per spawn than do temperate species (Hislop, 1984; Hislop and Bell, 1987; Bagenal, 1973). The difference seems linked mainly to the higher calorific content of the Amazonian eggs and their higher lipid content. This difference might be extended to other freshwater species, since the calorific values of their eggs are on average higher than marine fishes (Wootton, 1979; Heming and Buddington, 1988). Increasing lipid content is a more efficient way of "packing" energy, but can also be considered a form of reducing yolk burden for larvae in waters with low specific gravity.

The species that spawn in the floodplain are in the intermediate range. Their fecundity per season has been underestimated, since they are batch spawners and only mature oocytes have been counted. However, their egg size:fecundity ratios are comparable with the species that spawn adhesive eggs in temperate lakes and rivers. Both groups are characterized by spawning in the nursery area (Pliszka, 1953; Mills, 1980; Craig, 1987).

The species with small fecundity and large eggs found in the Amazon showed a similar egg size:fecundity ratio to African mouth

brooders, temperate brood hiders and Antarctic species. The reproductive expenditure seems to be also similar. The female expenditure of *S. gairdneri*, for example, is ~400 cal·g of female·spawn (Kamler and Kato, 1983; Bromage and Cumaranatunga, 1988), a value closer to the one found for *O. bicirrhosum*. This convergence suggests that salmoniforms and Antarctic fishes may experience rates of egg and/or larval mortality comparable with species with complex parental care behaviour. The strategy used by the salmoniforms is of hiding the eggs and spawning in the winter. Not much is known about the incubation of the eggs of the Antarctic species, but they are laid in the winter and hatch in the summer (Everson, 1984). Perhaps the cold and dark conditions, where they develop, limit the number of potential predators.

From the above discussion it seems that fecundity:egg size ratios vary independently of habitats. Large eggs have evolved wherever they are relatively safe, independent of parental care. Small eggs have evolved in response to dispersion or in small sized species. Interpretation of intermediate ratios are more difficult, but they seem to balance larval mortality due to predation and availability of food for the larvae.

Spawning season and larval feeding

Spawning timing is seasonal in most fish communities. In temperate seas it is closely linked with the spring bloom (Cushing, 1975). Gobioids (Miller, 1984) of temperate climates time the spawning season and larval development according to the production cycles. Some lacustrine species of freshwater, such as *Esox lucius* have larvae that prey upon other larvae (Pliszka, 1953). Their spawning season matches the spawning season of the species they prey upon. Wootton (1984), in

a preliminary analysis of the reproductive traits of Canadian freshwater species, found that spawning was largely confined to late spring, summer or autumn months. One of the strategies comprises only salmonids species that are characterized by large eggs and spawning during autumn or winter. However, salmonids embryos can take four months to hatch at winter temperatures (Beacham and Murray, 1986). Antarctic species have their spawning cycles synchronized to summer and early winter (Everson, 1984). Everson suggests that the spawning season is tied to the higher abundance of zooplankton for the feeding larvae.

In tropical habitats, where the production cycle is less clear, and therefore the environment is less predictable, the gobioids show another strategy (Miller, 1984). Breeding occurs during most of the year. This seems the most common strategy for most species of coral reefs (Barlow, 1981; Munro, 1983). Some freshwater species of tropical lakes show ripe females year-round, but with peaks of spawning related to larval food (Lowe-McConnell, 1979, 1987). The cichlids and other species with parental care also spawn throughout the year (Fryer and Iles, 1972; Lowe-McConnell, 1979, 1987). Seasonality in breeding, however, was found among species whose broods are dependent on planktonic food (Lowe-McConnell, 1979).

Although it may seem an oversimplification (Bye, 1984), it appears that the timing of annual spawning in seasonal environments has evolved to ensure that the young start feeding at the season most convenient for their survival. In less predictable environments, such as tropical lakes and coral reefs, the time of the spawning seems to vary between species. This has been explained by the stability in food offered to the larvae.

This aspect has been discussed by Lowe-McConnell (1979) for floodplain rivers. In these systems the seasonality is geared by the flood cycle. The flood increases the environment by up to 50% annually and also brings nutrients, which stimulate the growth of micro-organisms, invertebrates and plants. Production cycles are, therefore, correlated with the seasonal flood (Welcomme, 1985). The flood brings water and nutrients into the system and stimulates the photosynthetic production as a whole (Welcomme, 1985; Forsberg *et al.* 1988). However, a clear relationship between the planktonic production cycle and larval season is not apparent. Phytoplankton production and zooplankton biomass in the Amazon reach their maximum between high and low water seasons. The density of zooplankton is generally low when the water level is rising, being diluted by the flood, except for the rotifera (Marlier, 1968; Junk, 1973; Robertson and Hardy, 1984). This is probably true for other tropical floodplains (Welcomme, 1985; Hamilton and Lewis Jr, 1987).

Several Amazonian species spawn during the flooding season and those with continuous breeding have peaks during this season. However, spawning is concentrated at the beginning of the flood. Therefore, planktonic production and spawning cycles do not appear to match. Larval food is, however, poorly studied in the Amazon. The limited information suggests that young larvae prey upon zooplankton, but switching to other items occurs before juvenile stage (Aragao, 1981; Araujo-Lima *et al.*, 1986; Araujo-Lima and Hardy, 1987). Zooplankton might, therefore, be considered a primary resource for larvae only at the very early stages.

There are three possible explanations for the mismatch between planktonic primary production and larval season:

(1) Spawning at the beginning of the flood is an adaptation to utilize the biomass accumulated during the previous dry season. There are two drawbacks in this hypothesis. Since primary production is low at the beginning of the flood the larvae would rapidly deplete the accumulated biomass of zooplankton. Furthermore, access to this zooplankton would be denied to the riverine larvae, since they come into the floodplain with the diluting medium. The inflow of river water is negatively correlated with the zooplankton density (Fisher and Pairsley, 1979).

(2) The spawning cycle may be related to other production cycles. The production of the macrophytes is high during this season, but it is unlikely to influence zooplankton production. Periphyton biomass is reported to be high (Sioli, 1984), but its production cycle and its relationship with zooplankton are unknown. Following the flood, there is a high input of biomass of terrestrial plants at the fringes of the floodplain. These plants rot fast when submerged and support a fauna of invertebrates, which is poorly studied. It is, therefore, possible that larval production is linked to other cycles instead of the planktonic production.

(3) The density of zooplankton in the littoral areas is high enough to support larval production but other factors are determining the seasonality of larval production. The only study on the invertebrate fauna of the Amazonian littoral was limited to organisms larger than 200µm (Junk, 1973). It, therefore, underestimates the potential food for the larvae, since it does not include small zooplankters. Junk reports an average density of 50 ind·l^{-1} of these large organisms. Similar concentrations of prey have been show to guarantee high survival and growth temperate larvae (Gamble *et al.*, 1981; Houde, 1987). Although these results cannot be translated to tropical larvae,

they suggest that its is possible that the density of zooplankton of the floodplain may not compromise the larval production.

Possible advantages of spawning at the beginning of the flood are the better water quality and the reduction of predation pressure. Dissolved oxygen availability is reported to be better during the beginning of the flood (Welcomme, 1985). The littoral habitat is expanding and so predation pressure is being reduced. Furthermore, the larvae and juveniles would have longer periods to grow before the probability of being advected to the river increases after the peak of the flood.

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APPENDIX A Number of samples (spawning batches) used for the analysis of embryonic and larval development.

SPECIES	FAMILY	SPAWNING SITE	GUILD[1]	MORPHOLOGICAL AND EXPERIMENTAL OBSERVATIONS												
				HA	PE	JA	EY	SB	SW	FE	CR	MS	ST	PH	CE	CI
S. insignis	Prochilodontidae	river	open substratum	1	1	1	1	1	1	1	1	1				
E. melanopogon[2]	Curimatidae	river	open substratum	1	1		1	1	1			1				
P. altamazonica	Curimatidae	river	open substratum	1	1	1	1	1	1	1	1	1	1*	1	1	1
P. latior	Curimatidae	river	open substratum	6	6	5	5	4	4	5	5	5	5*	3	5	4
P. amazonica	Curimatidae	river	open substratum	1	1	1	1	1	1	1	1	1	1*	1	1	1
C. macropomum	Serrasalmidae	river	open substratum	1	2	2	2	2	1*		2	1			1	1
H. malabaricus	Erythrinidae	littoral	gravel nester	1	1	1	1	1	1	1	1	1	1*	1	1	1
H. litoralle	Callichthydae	littoral	froth nester	5	5	5	5	4	5	2	4	3	2*	2	4	4
P. multiradiatus	Loricariidae	littoral	hole nester	1	1	1					1				1	1
A. ocellatus	Cichlidae	littoral	plant nester	3	3	2	3	2	2	2	3	2	2*		2	3
C. monoculus	Cichlidae	littoral	plant nester	4	4	4	4	3	3	3	3	2	2*	3	2	3
Crenicichla sp	Cichlidae	littoral	plant nester	1	1	1	1		1**		1**	1**		1	1	1
Heros sp	Cichlidae	littoral	plant nester	3	1	1	1	1	1	2	1	2	2*	2	2	2
M. insignis	Cichlidae	littoral	plant nester	1**	1**	1**	1**									1
Number of samples per species per stage/event				14	14	13	13	11	12	9	12	12	8	8	11	12
Total number of samples per stage/event				30	29	26	27	21	22	18	24	21	16	14	21	23
Number of samples per riverine species per stage/event				6	6	5	6	6	6	4	5	6	3	3	4	5
Number of samples per littoral species per stage/event				8	8	8	7	5	5	5	7	6	5	5	7	7

[1]= following Balon, 1985; [2]= sometimes considered in the family Hemiodontidae; HA= hatching; PE= Pectoral fin bud; JA= Presence of functional jaw; EY= Eye pigmentation; SB= Presence of swim bladder; SW= Onset of swimming; FE= First feeding; CR= Presence of caudal rays; MS= Maximum size attained with exclusively endogenous feeding; ST= 50% mortality due to starvation; PH= Phototaxis; CE= Functional status of cement glands; CI= Pattern of blood circulation; *= just age was sampled; **= just body and yolk weight were sampled.

Appendix B

Time of spawning

The total numbers of females and mature plus ripe females of *Astronotus ocellatus*, *Cichla monoculus*, *Heros sp*, *Pterigoplichthys multiradiatus*, *Potamorhina altamazonica* and *Hoplias malabaricus* sampled during 1987 and 1988 in the Lago do Rei are shown in Table A18.

The percentage of mature and ripe females captured every two

Table A18 Total number of females and number of mature plus ripe females captured in Lago do Rei during 1987-1988 period.

SPECIES	NUMBER OF FEMALES CAPTURED	
	TOTAL	RIPE+MATURE
Astronotus ocellatus	30	5
Cichla monoculus	70	10
Heros sp	77	30
Hoplias malabaricus	99	34
Potamorhina altamazonica	193	67
Pterigoplichthys multiradiatus	130	20

months (years pooled) are shown in the Figure A35.

Type of spawning

Examination of the slides of gonad tissue of *Eigenmannina melanopogon* and *P. altamazonica* revealed three types of oocyte. The first type was very small, strongly basophilic and clearly nucleated; the second type was medium sized in which the presence of cytoplasmic vesicles indicated lipid vitellogenesis. The last group consisted of larger size oocytes with contracted nuclei and with the cytoplasm totally occupied by acidophilic yolk granules. The number of oocytes of the

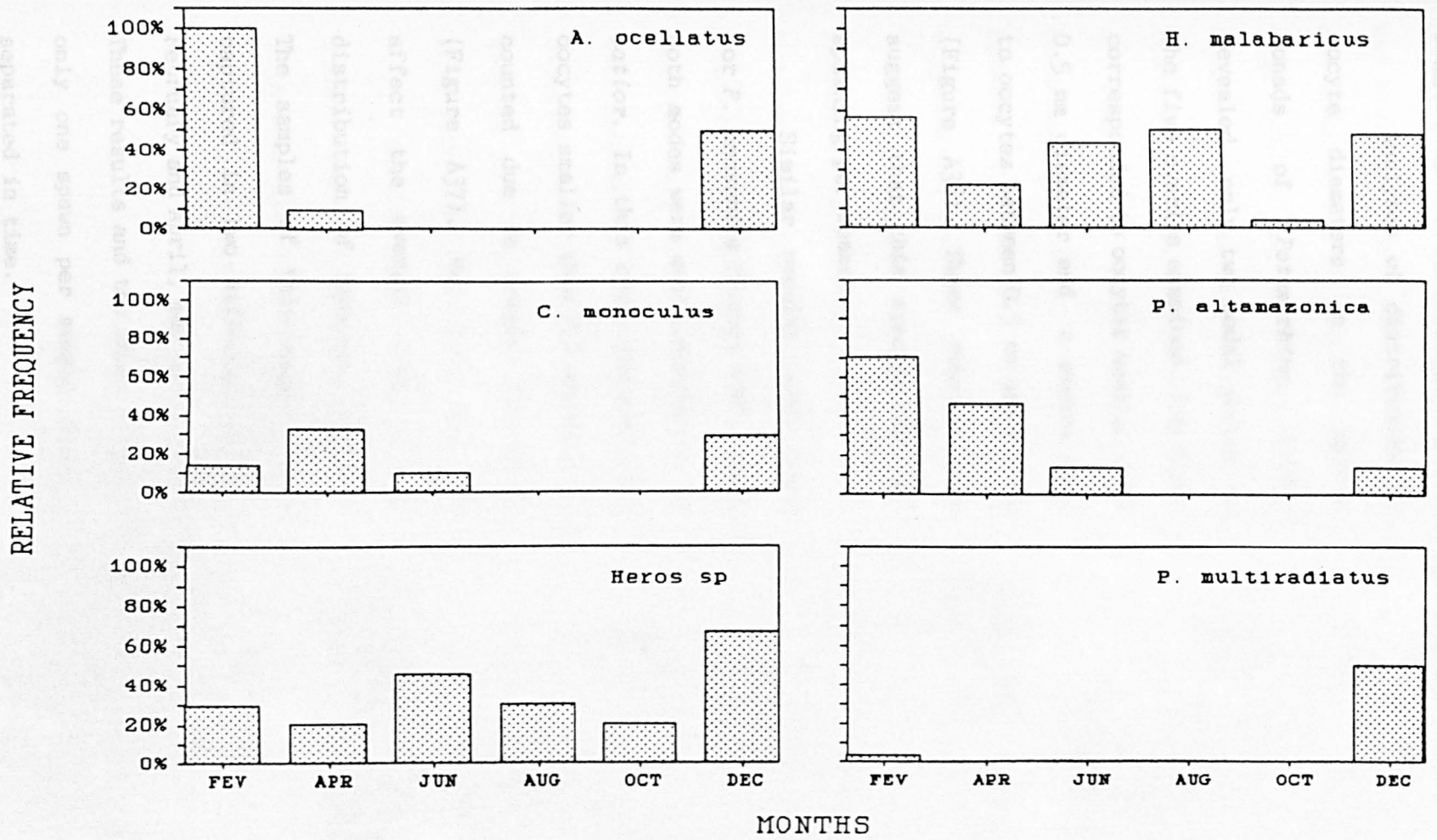

Figure A35 Bimonthly percentage of mature plus ripe females captured in Lago do Rei.

second type was very small compared with the two others groups, suggesting that both species have one spawning per season.

Analyses of distribution of oocyte diameters in the mature gonads of *Potamorhina latior* revealed only two modal groups in the five ovaries examined. The first corresponded to oocytes smaller than 0.5 mm diameter and a second mode to oocytes between 0.5 mm and 0.9 mm (Figure A36). These results also suggest that this species has one spawning per season.

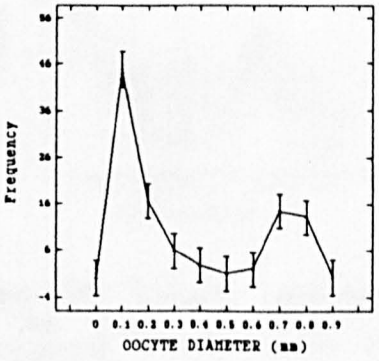

Figure A36 . Frequency distribution and 95% conf. intervals of oocyte diameter for P.latior. i=1,2,...5; N_i=100.

Similar results were found for *P. amazonica* (Figure A37), where both modes were quite similar to *P. latior*. In this case, however, the oocytes smaller than 0.2 mm were not counted due to sample processing (Figure A37), but this did not affect the overall form of the distribution of maturing oocytes. The samples of this species were captured in two different months, February and April, and in both the form of the distribution was similar. These results and the short spawning period of the species suggests that only one spawn per season occurs, but different schools might spawn separated in time.

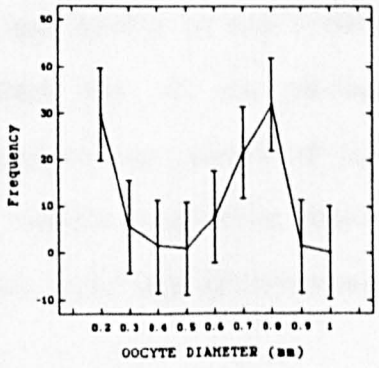

Figure A37. Frequency distribution and 95% conf. intervals of oocyte diameter for P.amazonica. i=1,2,...5; n_i=100.

The frequency distribution of oocyte diameter for *P.multiradiatus* was bimodal (Figure A38). There was one modal group of oocytes smaller than 0.6 mm and a second group formed by oocytes larger than 2.6 mm (mature oocytes). Very small numbers of oocytes of intermediate size occurred, but they were variable between individuals. The result suggests one spawning per season.

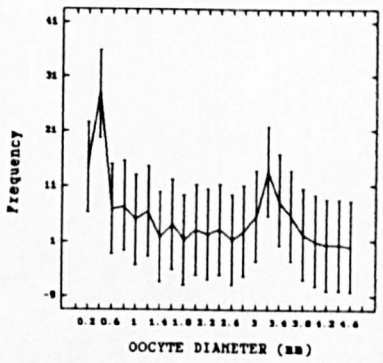

Figure A38. Frequency distribution and 95% conf. intervals for P.multiradiatus. i=1,2,...5; N_i= 150.

Six samples were collected in 1987 for *Hoplias malabaricus*: two samples in January and October and three sample in February, April and October. They all showed a composite distribution of oocyte diameter, which could be split, by MIX in five (January and April) or six (February and October) normal distributions. The good fit of the estimated distribution on the observed distribution support the number of normal distributions selected (Figure A39). This result indicates that the species is a batch spawner, which agrees well with the observations of Lowe-McConnell (1987).

Similar results were found for *Heros sp.* All four samples analyzed showed composite distributions of oocyte diameter, which could be split into four (October, 1987 and 1988 and April 1988) and five (January, 1988) normal distributions (Figure A40).

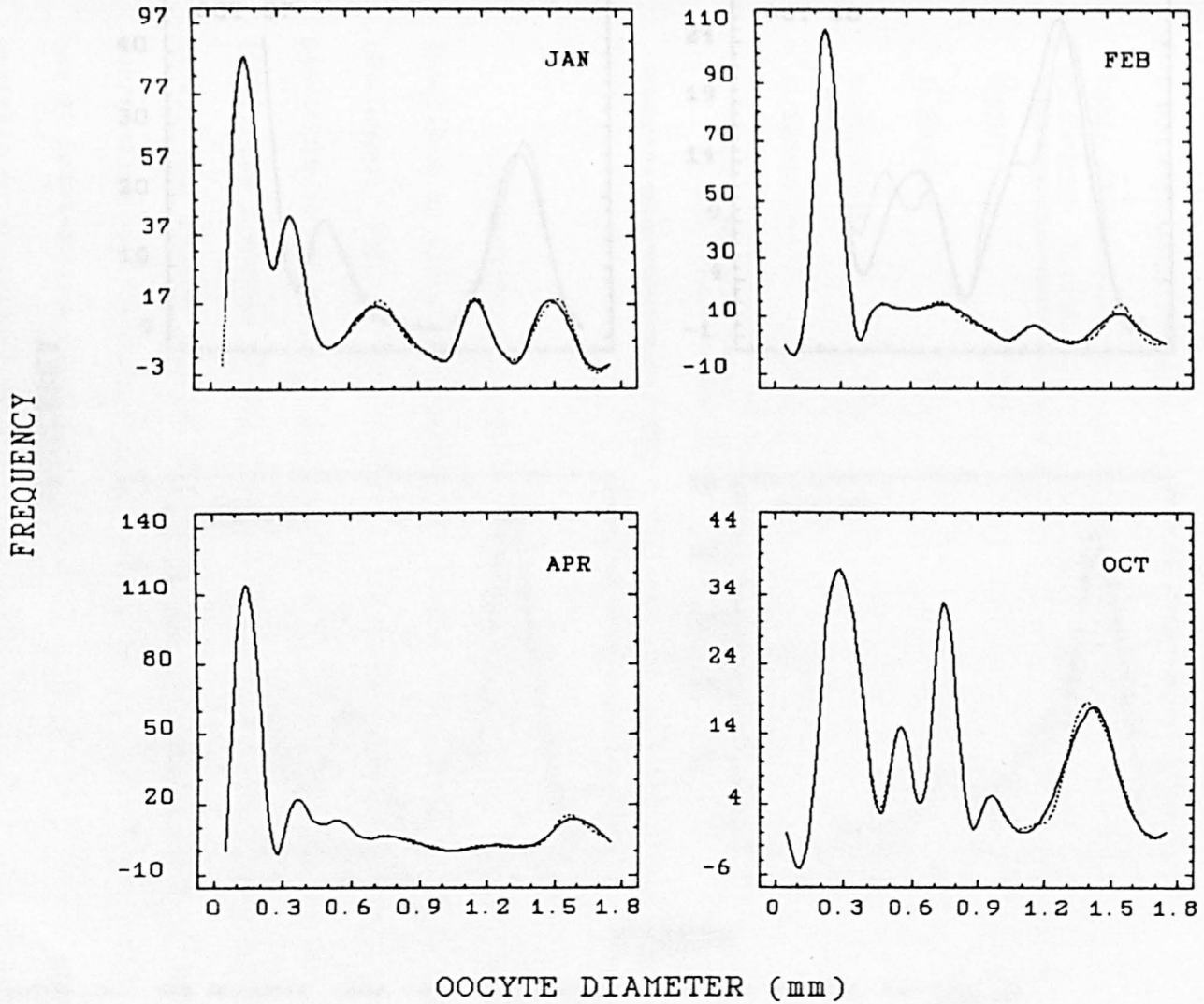

Figure A39 Observed (solid line) and estimated (dash line) distributions of oocyte diameter for H. malabaricus.

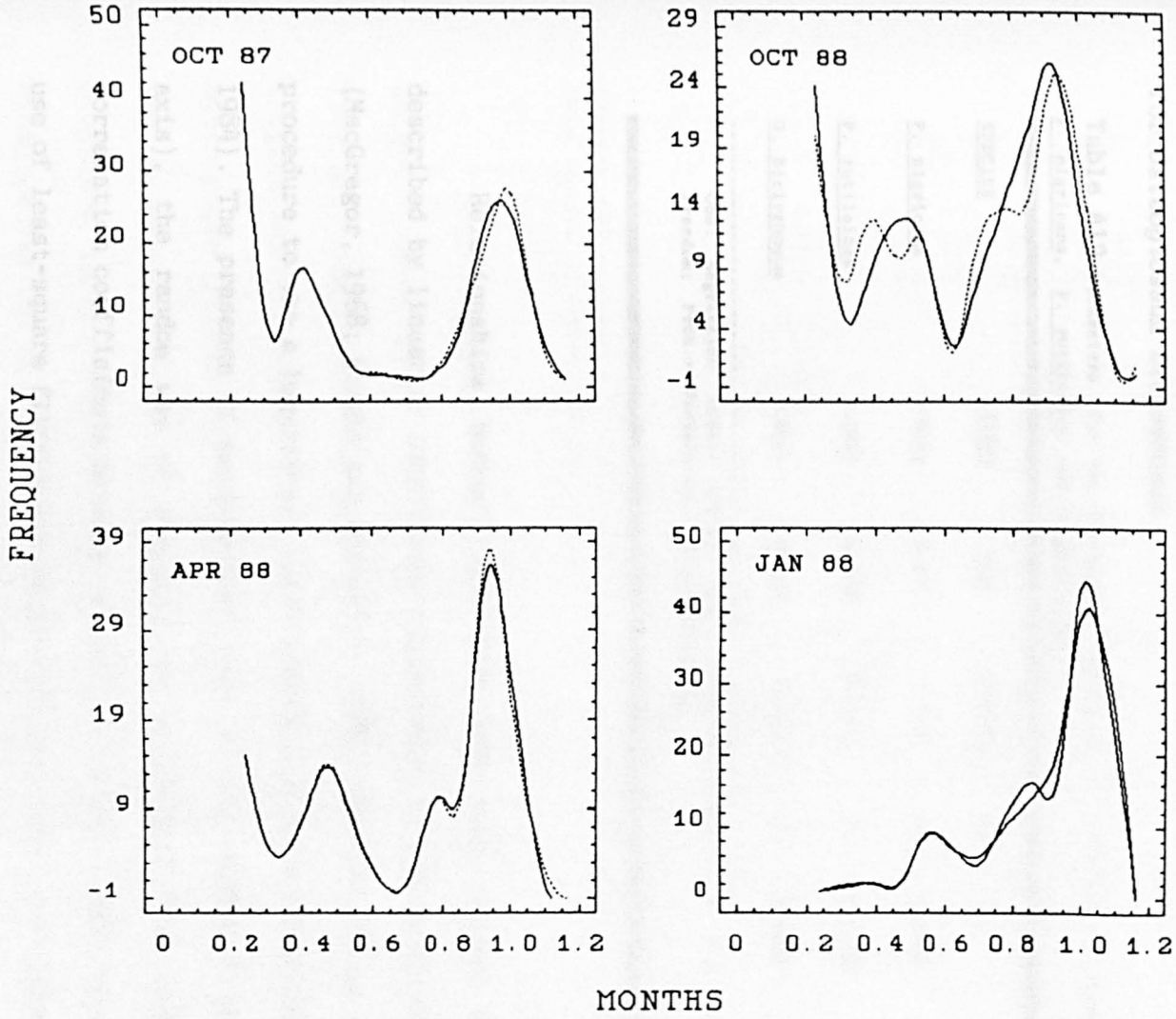

Figure A40. Observed (solid line) and estimated (dash line) distributions of oocyte diameter for Heros sp.

Appendix C

Fecundity

Fecundity of *Prochilodus nigricans* and *Psectrogaster rutiloides* was estimated by counting the oocytes with diameter larger than 0.4 and 0.9 mm, respectively. Aragao (1981) used diameters larger than 5.93 mm for *Osteoglossum bicirrhosum*.

Table A19 Parameters for the functional regression of fecundity on body weight (g) P. nigricans, P. rutiloides and O. bicirrhosum.

SPECIES	SLOPE	S.E.	INTERCEPT	D.F.	r^2	PROB.
P. nigricans	1.6163	0.2711	7.6084	19	0.6820	<0.002
P. rutiloides	1.3813	0.1738	233.2500	25	0.7775	<0.001
O. bicirrhosum	0.6511	0.1054	0.5831	29	0.4907	<0.01

Obs: Regression model= $y=a \cdot x^b$; S.E.= Standard Error of b; D.F.= Degrees of Freedom; Prob.= Probability of accepting H_0

Relationships between fecundity and body weight have been described by linear or curvilinear regressions depending on the species (MacGregor, 1968; Wright and Shoesmith, 1988). However, it is a standard procedure to use a logarithmic transformation on both variables (Calder, 1984). The presence of experimental error in the weight of the fish (x axis), the random way of sampling the individual fish and the low correlation coefficients between fecundity and fish weight prevented the use of least-square fitting and an alternative model, reduced major axis analysis or functional regression (Ricker, 1973), was used (Table A19). The fit of the curves on the scatterplots are shown in Figure A41. The slopes for the three species (Table A19) were different of one ($p<0.05$).

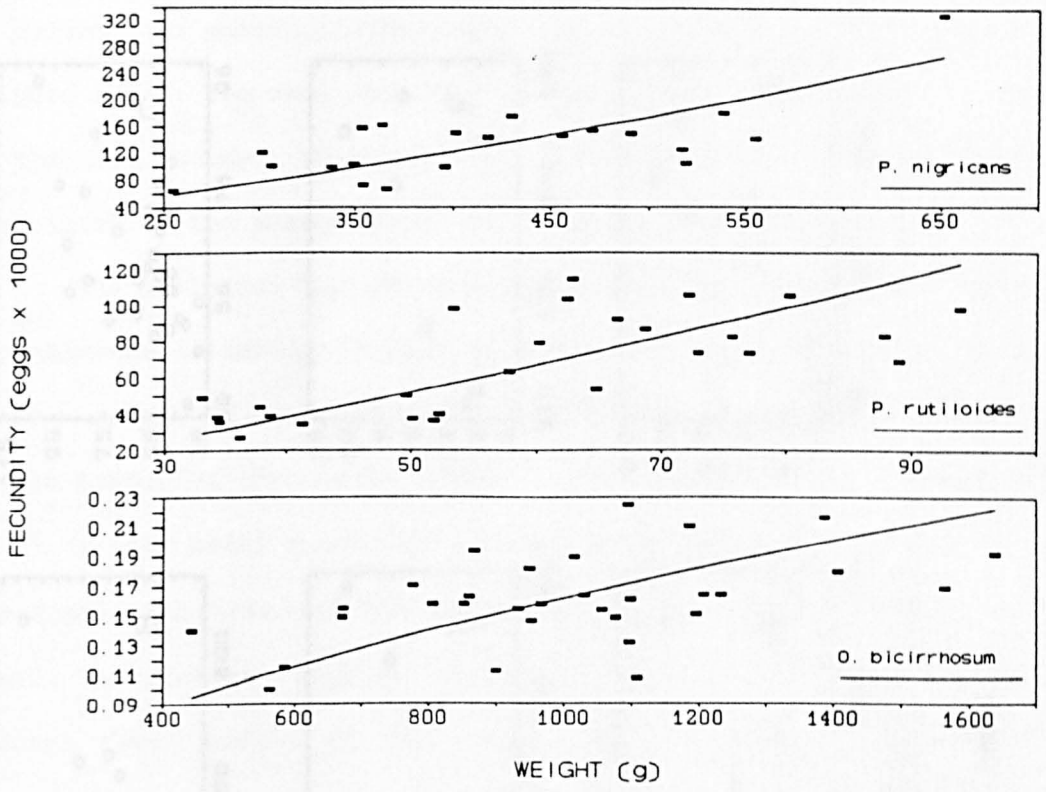

Figure A41 Scatterplots with functional regressions fit of fecundity on body weight for three species of Central Amazon.

Significant correlations ($p<0.05$) between fecundity and body weight were also found for *Potamorhina latior* (Figure A42E), *Pterigoplichthys multiradiatus* (Figure A42F), *Psectrogaster amazonica* (Figure A42G), *Potamorhina altamazonica* (Figure A42H) and *Eigenmannina melanopogon* (Figure A42I), all fishes with only one spawning per season. For *P. multiradiatus* fecundity estimation was based on oocytes with diameters larger than 2mm; for the remaining species the critical diameter was 0.4 mm.

The fecundity estimation for the batch spawners *Hoplias malabaricus* and *Heros sp* followed a different procedure. Only the proportions of oocytes in the ripening modal group, estimated by the

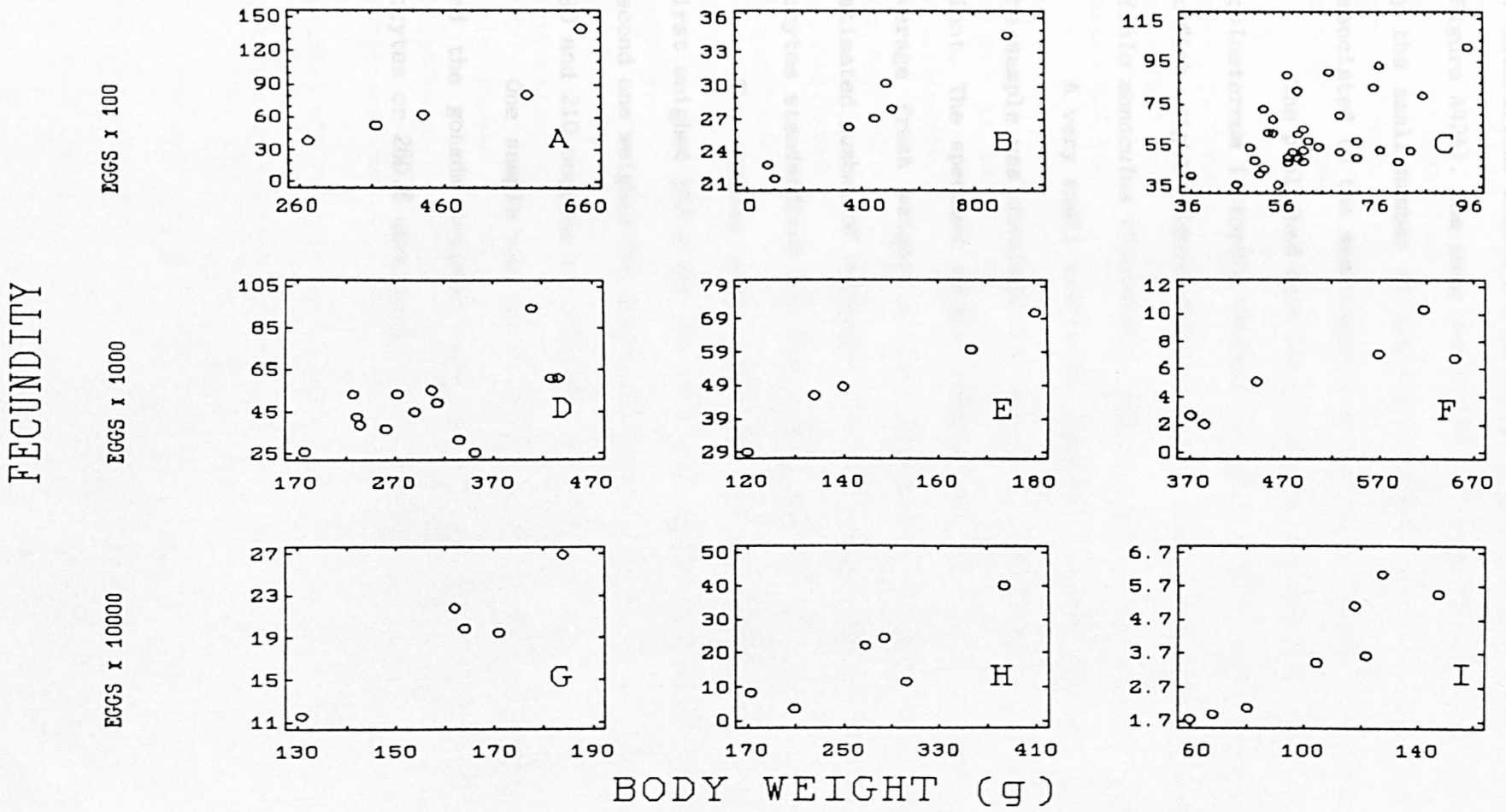

Figure A42 Scatterplot of fecundity on total weight for 9 species of Central Amazon.

program MIX, were used for the calculation. The fecundity of *H. malabaricus* showed a significant ($p<0.05$) correlation with body weight (Figure A42A). The same was not true for *Heros sp*, what might be caused by the small number of samples available and also to the difficulties associated to the measurements of fecundity in batch spawners.

The published data for *Astronotus ocellatus* (Fontenele, 1950) and *Hoplosternum littorale* (Machado y Zaret, 1984) showed similar relations to fish weight (Figure A42B and C), but not enough data were obtained for *Cichla monoculus* (Fontenele, 1950) to show a significant relationship.

A very small number of samples was collected for three species. One sample was obtained for *Piaractus brachypomus* from an aquaculture plant. The specimen weighed 4500 g and had 1300 g of ovary. Since the average fresh weight of each oocyte was 0.905 g (s.d.= 0.047) the estimated number of oocytes in the gonad was $1.436.10^6$ and the number of oocytes standardized per fish body weight was 381.7.

Two samples were collected for *Semaprochilodus taeniurus*. The first weighed 352 g and had 32.6 g of gonads and 63488 oocytes and the second one weighed 405 g and had 43.7 g of gonads and 85051 oocytes,i.e. 190 and 210 oocytes$\cdot g^{-1}$ of fish, respectively.

One sample was obtained for *Semaprochilodus insignis*. The fish and the gonads weighed 273 g and 32.3g, respectively and had 62792 oocytes or 260.8 oocytes$\cdot g^{-1}$ of fish body.

Appendix D

Calculation of yolk weight at activation

The eggs of most characiforms were extruded from the mother, so it was possible to have a good estimation of egg weight and yolk weight (egg minus chorion weight) at the moment of activation. However, the eggs of cichlids, siluriforms, and *H. malabaricus*, were collected in the field, usually, at the gastrulation stage. Therefore, the egg and yolk weight at the time of activation had to be back-calculated from the weight at later stages. The relationship between yolk weight and time was an estimated fit of the scatterplot by the growth model. A type of the Gompertz function (Ricker, 1979) was chosen, since it has a known application for larval growth studies and had a good fit to the scatterplot of yolk weight on time from activation. The form was

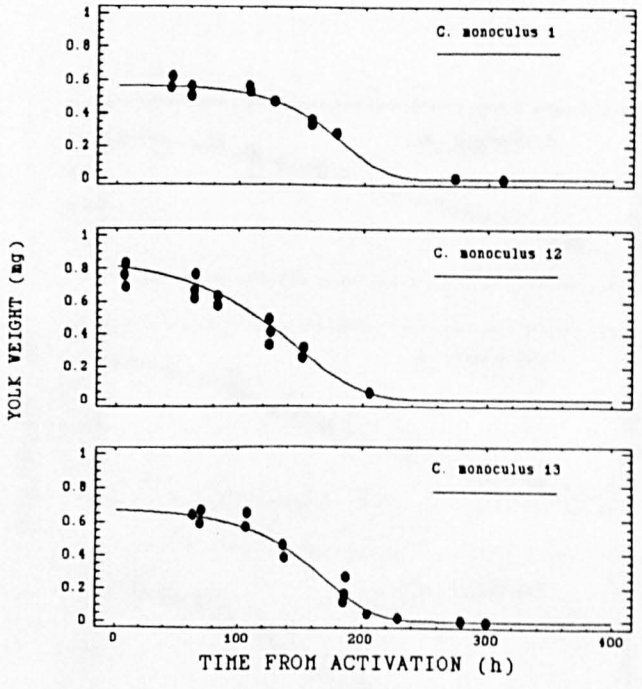

Figure A43 Scatterplot and least-square nonlinear fit of yolk weight on time from activation for three batches of C. monoculus.

$$W = W_0 \cdot e^{-e^{-g(t-t0)}}$$

where W_t is the dry weight at any time t; W_0, the asymptotic dry weight; g, the instantaneous rate of growth; to, the inflection point of the curve. A least-square fit of the model was obtained using MARQUARDT algorithm.

The fit was reasonable (Figure A43; Figure A44; Figure A45) explaining at least 95% of the variability in yolk weight for all batches tested (Table A20), except for batch Number 8 of *H. littorale*. In the latter case the poor fit might have been caused by the small number of samples, concentrated in the beginning of the plot. However, the pattern seemed similar to the one obtained for the remaining four batches for this species so assuring the validity of the result. The residuals of the regression were tested against the cumulative temperature at each time, but no significant trend was observed.

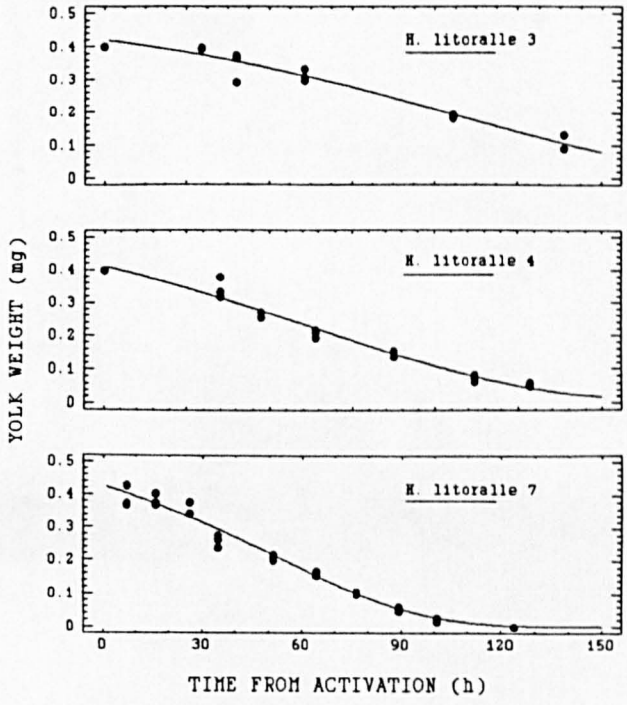

Figure A44 Scatterplot and least-square nonlinear fit of yolk weight on time from activation for three batches of H. littorale.

In the remaining batches (*M. insignis*, *P. multiradiatus* and batch number one of *Heros* sp and others), there were not enough replicates to ensure a proper fit. Yolk weight at activation was then estimated, calculating the rate of loss of yolk weight at the first three

earliest samples and back calculating yolk weight to the time of activation.

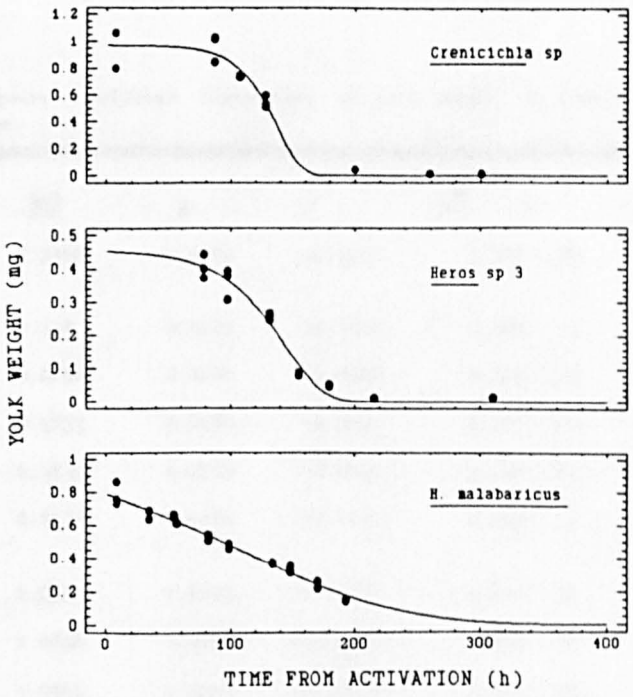

Figure A45 Scatterplot and least-square nonlinear fit of yolk weight on time from activation for three fishes of Central Amazon.

Table A20 Parameters for least-square nonlinear regression of yolk weight on time from activation for 15 batches of larvae.

SPECIES	BATCH	WO	g	tO	r^2	N
H. malabaricus	1	1.2480	0.0075	104.3120	0.974	29
H. littorale	3	0.518	0.0183	85.7831	0.945	15
	4	0.6156	0.0146	62.5994	0.975	19
	7	0.5733	0.0232	52.5719	0.977	29
	8	0.3835	0.2582	78.8823	0.722	12
	10	0.4794	0.0235	79.1795	0.970	19
A. ocellatus	2	1.0330	0.1003	120.6532	0.850	12
	4	1.0836	0.0228	169.3241	0.981	26
	5	1.0945	0.0218	167.6737	0.971	29
C. monoculus	1	0.5696	0.0294	184.5679	0.987	19
	2					
	12	0.8263	0.0192	147.1261	0.966	17
	13	0.6800	0.0251	171.5648	0.980	26
Crenicichla sp	1	0.9712	0.0516	137.6181	0.966	16
Heros sp	3	0.4563	0.0323	144.4013	0.967	18
	5	0.5752	0.0183	140.9490	0.980	21

WO= asymptotic weight; g= instantaneous growth rate; tO= inflection point of the curve; r^2= coefficient of determination; N= number of paired samples.

Appendix E

Correlation and residual analyses between yolk weight at activation, age, larval weight at different developmental stages and calorific content of the eggs.

Species average of larval dry weight, age and yolk weight at activation were correlated for most developmental stages studied, when data were logarithmically scaled . To check whether those correlations applied and to eliminate the influence of other, known and unknown, variables, partial correlations were carried out on the same data (Table A21; Table A22).

Partial correlation coefficients between age and larval weight at developmental stage dropped dramatically, in comparison with correlation coefficients, for most stages analyzed. Such results suggest that age had a very weak, if any, effect on larval weight. On the other hand partial correlation coefficients between larval weight at stages and yolk weight at activation were maintained or improved in comparison with the correlation coefficients for all developmental stages, suggesting that these two variables are strongly correlated.

Using calories per egg instead of yolk weight did not improve the coefficients significantly.

The residuals of the functional regressions were estimated by multiplying the deviations relative to both axis (Imbrie, 1956; Harvey and Mace, 1982), yolk weight at activation and larval weight at developmental stages. Plotting the residuals against the predicted values does not show any tendency for most developmental stages, suggesting that the model used was the best fit. In three cases, weight

at hatching, pectoral fin bud formation and eye pigmentation the distribution residuals where curved and/or unbalanced, suggesting that the model was not fitting the scatterplot perfectly (Figure A46). This was probably caused by the inclusion of the data for *P. multiradiatus*. Excluding this species did not change the regression parameters markedly, but stabilized the residuals. In the latter case *P. multiradiatus* was not included in the analysis. However, the number of data points were not large enough to allow a better conclusion, and the fit was still considered as the better description of the scatterplot.

The residuals of the functional regressions relative to deviations on the *y* axis (larval weight at developmental stages) were plotted against age at developmental stages (log transformed) to check whether the variability not explained by the independent variable (yolk weight at activation) had any relationship with age. In all cases the residuals were evenly distributed and no tendencies were clear (Figure A47).

The same type of test were conducted between the residuals (deviations of the *y* axis) of the functional regressions and the calorific content of the eggs. For most of developmental stages the distributions of residuals were evenly dispersed around the zero line, but in two cases, pectoral bud formation and jaw formation, they seemed positively related to the calorific content. However, neither showed a significant correlation (Figure A48).

Table A21 Correlation and partial correlation (in parenthesis) coefficients between yolk weight at activation (mg), larval weight (mg) and age at events (h) for 12 fishes of Central Amazon.

	YOLK AT ACTIVATION	LARVAL WEIGHT	AGE
YOLK AT ACTIVATION	1.000 (-1.000)	**0.941** (0.785)	**0.843** (0.185)
LARVAL WEIGHT AT HATCHING	**0.941** (0.785)	1.000 (-1.000)	**0.863** (0.380)
AGE AT HATCHING	**0.843** (0.185)	**0.863** (0.380)	1.000 (-1.000)
YOLK AT ACTIVATION	1.000 (-1.000)	**0.612** (0.516)	0.393 (0.094)
LARVAL WEIGHT AT PECTORAL BUD	**0.612** (0.516)	1.000 (-1.000)	0.540 (0.411)
AGE AT PECTORAL BUD	0.393 (0.094)	0.540 (0.411)	1.000 (-1.000)
YOLK AT ACTIVATION	1.000 (-1.000)	**0.841** (0.850)	0.274 (-0.350)
LARVAL WEIGHT AT JAW	**0.841** (0.850)	1.000 (-1.000)	0.518 (0.553)
AGE AT JAW	0.274 (-0.350)	0.518 (0.553)	1.000 (-1.000)
YOLK AT EYES PIGMENTATION	1.000 (-1.000)	**0.822** (0.803)	0.453 (0.420)
LARVAL WEIGHT AT EYES	**0.822** (0.803)	1.000 (-1.000)	0.248 (-0.148)
LARVAL AGE AT EYES	0.453 (0.420)	0.248 (-0.148)	1.000 (-1.000)

Coefficients in bold are significant at 5% level.

Table A22 Correlation and partial correlation (in parenthesis) coefficients between yolk weight at activation (mg), larval weight (mg) and age at events (h) for 12 fishes of Central Amazon.

	YOLK AT ACTIVATION	LARVAL WEIGHT	AGE
YOLK AT ACTIVATION	1.000 (-1.000)	**0.957** (0.915)	**0.710** (-0.214)
LARVAL WEIGHT AT SWIM BLADDER	**0.957** (0.915)	1.000 (-1.000)	**0.707** (0.503)
AGE AT SWIM BLADDER	**0.707** (-0.214)	**0.780** (0.503)	1.000 (-1.000)
YOLK AT ACTIVATION	1.000 (-1.000)	**0.975** (0.931)	**0.789** (-0.036)
LARVAL WEIGHT AT SWIMMING	**0.975** (0.931)	1.000 (-1.000)	**0.815** (0.330)
AGE AT SWIMMING	**0.789** (-0.036)	**0.815** (0.330)	1.000 (-1.000)
YOLK AT ACTIVATION	1.000 (-1.000)	**0.974** (0.960)	0.619 (0.194)
LARVAL WEIGHT AT FIRST FEEDING	**0.974** (0.960)	1.000 (-1.000)	0.598 (-0.020)
AGE AT FIRST FEEDING	0.618 (0.194)	0.598 (-0.020)	1.000 (-1.000)
YOLK AT ACTIVATION	1.000 (-1.000)	**0.988** (0.981)	**0.651** (-0.246)
LARVAL WEIGHT AT MAXIMUM SIZE	**0.988** (0.980)	1.000 (-1.000)	**0.686** (0.370)
AGE AT MAXIMUM SIZE	**0.654** (-0.246)	**0.686** (0.370)	1.000 (-1.000)

Coefficients in bold are significant at 5% level.

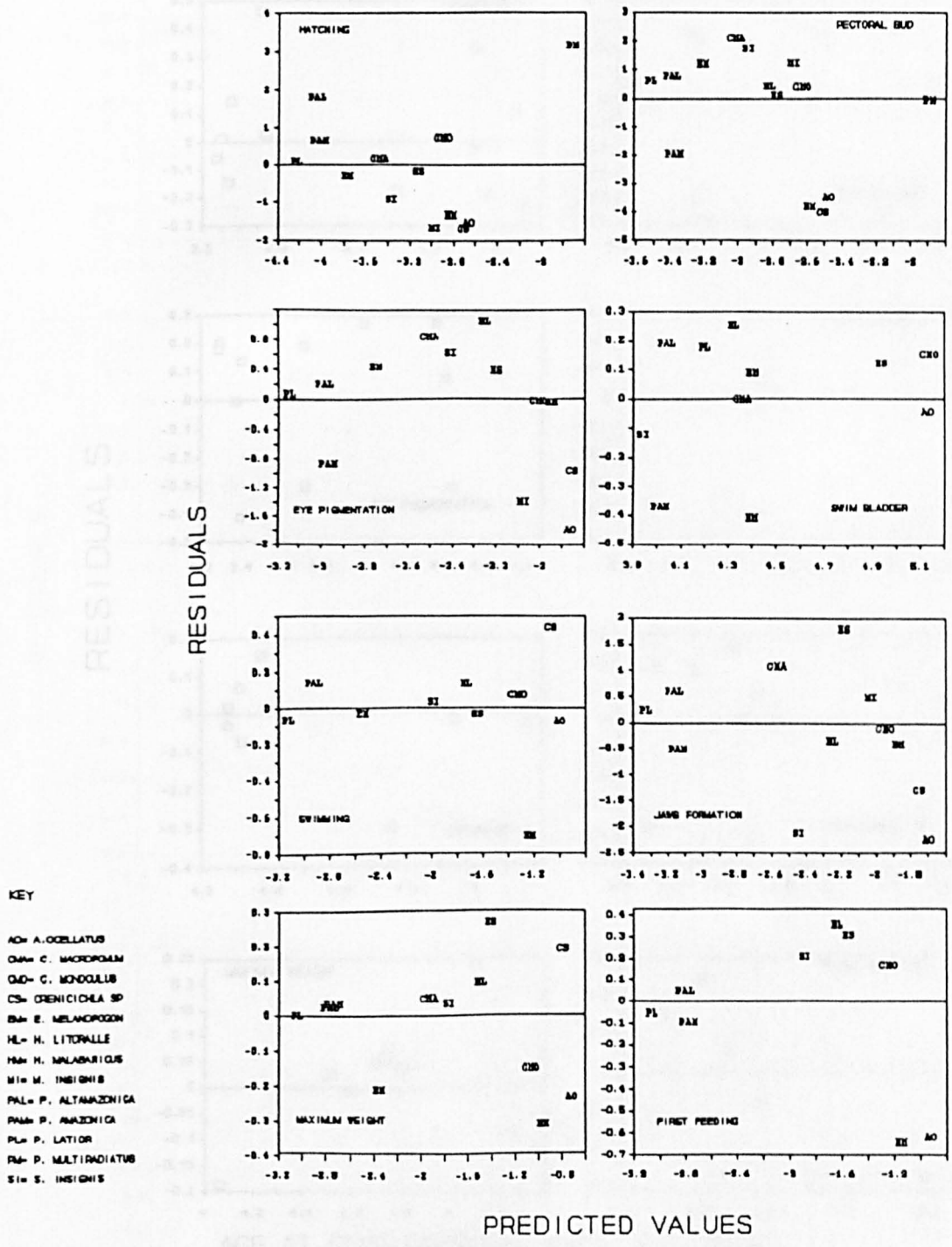

Figure A46 Plot of residuals (deviations of x and y axis) against predicted values of the functional regressions of larval weight at developmental events on yolk weight at activation for 13 species of Central Amazon.

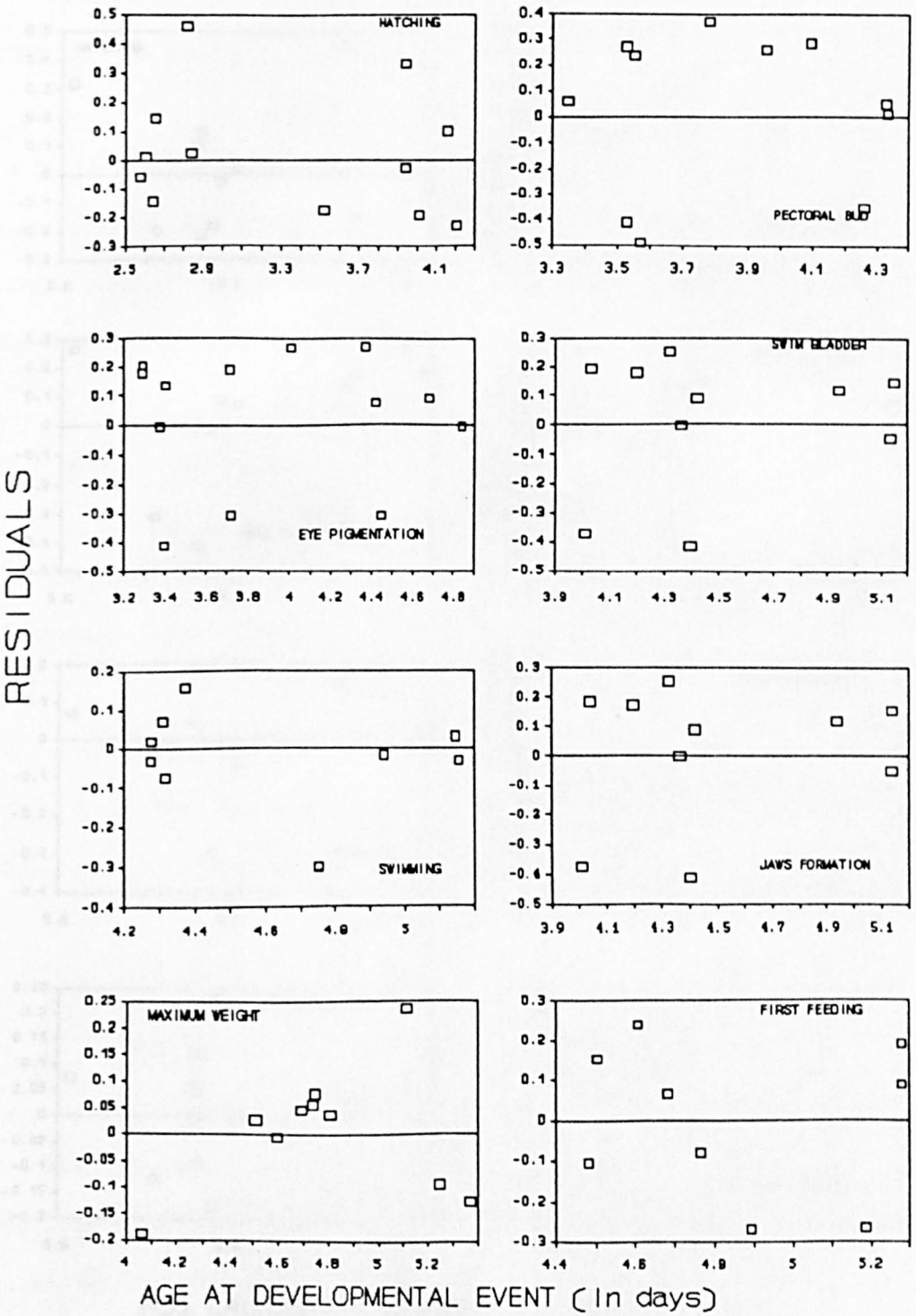

Figure A47 Plot of the residuals (deviations on y axis) of functional regressions against age at developmental events for 13 species of Central Amazon.

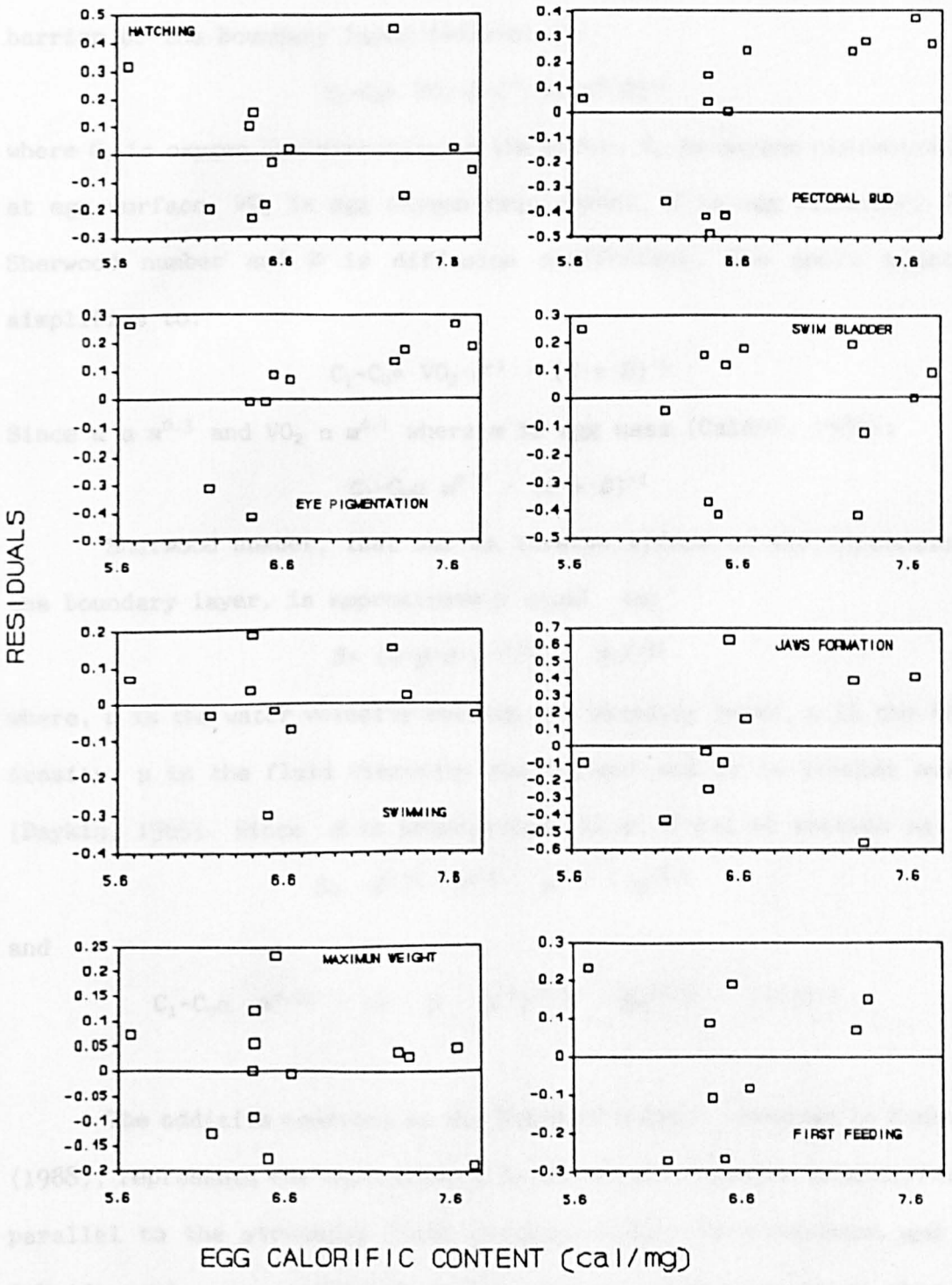

Figure A48 Plot of residuals (deviations of y axis) of functional regressions against calorific content of the eggs ($cal \cdot mg^{-1}$) for 9-14 species of Central Amazon.

Appendix F

Effect of egg mass on egg boundary layer

Assuming that the driving force required to overcome the diffusion barrier of the boundary layer (solute) is:

$$C_1-C_0= VO_2 \cdot d \cdot S^{-1} \cdot (\pi \cdot d^2 \cdot D)^{-1}$$

where C_1 is oxygen concentration in the water, C_0 is oxygen concentration at egg surface, VO_2 is egg oxygen requirement, d is egg diameter, S is Sherwood number and D is diffusion coefficient. The above equation simplifies to:

$$C_1-C_0= VO_2 \cdot d^{-1} \cdot (S \cdot \pi \cdot D)^{-1}$$

Since $d \alpha m^{0.3}$ and $VO_2 \alpha m^{0.7}$ where m is egg mass (Calder, 1984):

$$C_1-C_0 \alpha m^{0.4} \cdot (S \cdot \pi \cdot D)^{-1}$$

Sherwood number, that has an inverse effect on the thickness of the boundary layer, is approximately equal to:

$$S \approx (v \cdot p \cdot d \cdot \mu^{-1})^{0.5} \cdot Sc^{0.33}$$

where, v is the water velocity outside the boundary layer, p is the fluid density, μ is the fluid viscosity coefficient and Sc is Schmidt number (Daykin, 1965). Since d is proportional to m, S can be written as:

$$S \alpha m^{0.15} \cdot v^{0.5} \cdot p^{0.5} \cdot \mu^{-0.5}$$

and

$$C_1-C_0 \alpha m^{0.25} \cdot (v \cdot p \cdot \mu^{-1})^{-0.5} \cdot Sc^{-0.33} \cdot (\pi \cdot D)^{-1}$$

The additive constant to the Sherwood number, observed in Rombough (1988), represents the contribution to the solute transfer from diffusion parallel to the streaming fluid (Daykin, 1965). This constant and the Schmidt number are neglected in the present discussion since they are independent of mass.