THE GROWTH OF *MYLEUS RHOMBOIDALIS* (CUVIER, 1817)  
(CHARACIFORME, SERRASALMIDAE)  
IN TWO RIVERS OF FRENCH GUIANA

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The potential for aquaculture of native fish species has been studied during the last few years in various Latin American countries (Benedetti, 1977; Novoa, 1982; Cervignon, 1983; Chavez-Lomeli et al., 1984; Espinosa, 1984; Saint-Paul, 1984, 1985a, b, 1986a, b). The farming of such fishes was attempted to meet the needs of local populations, natural stocks being over-exploited, and the traditional fishery systems becoming uneconomical.

Up to now, the coastal and estuarine small-scale fisheries of French Guiana were able to meet the demand of the local fish market. Consequently, the potentialities of the freshwater species remained untapped. However, a total of 332 freshwater species are presently known in the country (Le Bail et al., 1984a, b, c; Rojas-Beltran, 1984; Boujard et al., 1990a, b; Géry et al., 1991), and some of them appear to be of potential value for aquaculture; such is the case for *Myeleus rhomboidalis*, the Coumarou (Boujard et al., 1988).

One of the most important criteria to be taken into account before attempting to rear a fish is a proper knowledge of its growth rate. However, studying the growth rate of a fish whose biology is little known in its natural environment requires information on its growth history. This can be achieved by means of skeletochronological methods (Castanet et al., 1977; Bourlière, 1980; Casselman, 1987; Meunier, 1988).

The presence of repetitive structures, or growth marks, in the skeleton (scales included) or the otoliths of tropical fishes, has been reported by several authors (Daget, 1952; Fagade, 1974; Hureau and Ozouf, 1977; Meunier et al., 1979; Compean-Jiménez and Bard, 1980). According to the above mentioned studies, these species exhibit either one or two yearly growth cycles. In some cases the structures can be interpreted as growth checks or rest lines (lines of arrested

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growth = L.A.G.) whereas in other cases they are annuli of reduced growth (Meunier, 1988; Castanet et al., 1992, 1993). The occurrence of two growth checks per year has been observed in various fish species of the Great African Lakes (Garrod, 1959; Okedi, 1969; Bruton and Allanson, 1974; Blake and Blake, 1978; Robben and Thys Van den Audenaerde, 1984), in marine Sciaenidae off the West-African coast (Poinsard and Troadec, 1966), as well as in marine catfishes (Warburton, 1978).

Growth studies of some fish species of French Guiana (Arius proops, A. couma, Leporinus friderici) also show two periods of active growth and two periods of reduced growth per year (Lecomte et al., 1985, 1986, 1989; Meunier et al., 1985; Boujard et al., 1991). These periods are synchronous with the two annual rainy and dry seasons respectively, the dry seasons probably playing the role of a « physiological winter » (Lowe-McConnell, 1964), thus generating this bimodal annual cycle (Boujard, 1992).

In order to study the growth of the Coumarou in its natural environment, we will first assess the seasonal character of its growth by skeletochronology, and then examine the growth characteristics of the species, using back calculations and modelling.

**MATERIAL AND METHODS**

The choice of organs for skeletochronological investigations is of major importance for any growth studies in a natural environment. In Characoids the use of otoliths, which are very small, is not warranted, and otoliths were therefore not removed from the specimens captured during our sampling sessions. Although scales are currently used for age determination in Characoids (Daget, 1952; Cordiviola, 1966; Durand and Loubens, 1969; Balon and Coche, 1974; Werder, 1983; Werder and Soares, 1984; Lecomte et al., 1986; Loubens and Panfili, 1992), they were not used in this case either, because of their small size, brittleness and frequent evidence of regeneration. In Leporinus friderici living in the same rivers, the dorsal and anal fin-rays in one hand, and the opercular bone in the other, show definite growth marks that can be used for ageing this fish (Lecomte et al., 1986; Lecomte, 1990; Boujard et al., 1991). However, the use of fin-rays proved to be very difficult in the Coumarou because of the inconstancy and lack of conspicuousness of the L.A.G. whereas growth marks were obvious on the opercular bones. Consequently, this last bony structure was used in the present study.

1) **Sampling**

Two sampling sessions were carried out in 1982/83 on the Sinnamary River (5° 05' N; 53° 05' W), and simultaneously on the Sinnamary and Approuague (4° 10' N; 52° 20' W) rivers in 1986/87 (Table I). Each session involved 4 days of fishing using gill nets with 10 to 60 mm bar mesh. Nets totalling 300 m were laid every 24 h, and hauled up every morning and evening, according to the protocol used during other studies in the same environment (Boujard and Rojas-Beltran, 1988a, b). A total of 230 fishes was sampled.
TABLE I

Time schedule of Myleus rhomboidalis catches in the two rivers studied.

<table>
<thead>
<tr>
<th>Month/Year</th>
<th>Sinnamary</th>
<th>Month/Year</th>
<th>Sinnamary</th>
<th>Approuague</th>
</tr>
</thead>
<tbody>
<tr>
<td>7/82</td>
<td>3</td>
<td>8/86</td>
<td>—</td>
<td>12</td>
</tr>
<tr>
<td>10/82</td>
<td>4</td>
<td>9/86</td>
<td>—</td>
<td>14</td>
</tr>
<tr>
<td>12/82</td>
<td>18</td>
<td>11/86</td>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>1/83</td>
<td>4</td>
<td>1/87</td>
<td>—</td>
<td>4</td>
</tr>
<tr>
<td>2/83</td>
<td>4</td>
<td>2/87</td>
<td>—</td>
<td>9</td>
</tr>
<tr>
<td>3/83</td>
<td>5</td>
<td>3/87</td>
<td>—</td>
<td>9</td>
</tr>
<tr>
<td>4/83</td>
<td>36</td>
<td>4/87</td>
<td>14</td>
<td>—</td>
</tr>
<tr>
<td>5/83</td>
<td>12</td>
<td>5/87</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>6/83</td>
<td>12</td>
<td>7/87</td>
<td>—</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8/87</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>98</td>
<td>34</td>
<td>98</td>
<td></td>
</tr>
</tbody>
</table>

The weight and standard length of each specimen were measured, and opercular bones were removed and stored dry.

2) Preparation of skeletal pieces

The opercular bones of the Coumarou are rather thin, almost triangular, their dorso-ventral axis being longer than the antero-posterior one (Fig. 1). They exhibit characteristic growth zones. After cleaning, they were directly observed with a magnifying glass under reflected light on a black background, and later with transmitted light for comparison. In order to improve the optical contrast between growth zones, some opercular bones were observed in a 20% glycerol solution.

3) Counting the growth marks on the opercular bones

Two types of growth marks may be seen on the opercular bones: the large opaque «zones» that appear white in reflected light and the narrow transparent annuli that look dark (see Meunier, 1988; Baglinière et al., 1992; Castanet et al., 1992, 1993). Such growth marks are relatively easy to count. Yet, in the largest fishes the first, and sometimes the second, annuli can be difficult to distinguish because of the thickening of the bone close to the articular fossa. In such a case, the number of invisible annuli of the thick central region of the opercular bone is extrapolated by comparison with transparent opercular bones of similar size.

Following Meunier (1988) and Castanet et al. (1993), the count of annuli on the opercular bones was made in three steps. First, counting was performed separately by two observers. Next, the opercular bones for which the two observers disagreed on the number of annuli were checked again by the same people with extreme caution. Finally, the correspondence between the annuli counts and biological and ecological parameters had to be ascertained.
Figure 1. — Internal view of the left opercular bone (dorsal apex at the top, ventral at the bottom) of *Myileus rhomboidalis*. Reflected light on black background. Specimens of the Sinnamary river, 1982-83.

a) 2 annuli; b) 4 annuli; c) 7 annuli, the first one in the center of the opercular being invisible; d) 8 annuli, the first one being invisible; e) 10 annuli, the first and the second ones being invisible.
If no agreement on the interpretation of the growth marks was reached on such «bones of contention» they were no longer taken into account.

After the first step, the annuli counts of the two observers agreed in 41% of the 230 fishes studied, which is a low figure, but only 9% of the observations were in disagreement for more than one annulus. After the third step only two fishes were discarded in the first sample and two in the third. Nevertheless, our hypothesis on the interpretation of bone growth zones in this species should be further tested by experimental studies (Casselman, 1987; Meunier, 1988).

RESULTS

1) The rhythm of growth

In order to better interpret bone structures and to understand the yearly pattern of growth of our fish, the situation of the last annulus relative to the edge of the opercular bone was determined monthly for 12 successive months. The highest percentage of annuli close to the opercular bone edge (Figs. 2) was found in March-April (1983 and 1987) and August-September (1986-1987), indicating a reduction in growth rate during these months. This rhythm of formation of two annuli per year is similar to that already observed in French Guiana for the Ariidae so far studied, and for another species of Characoid, L. friderici (Lecomte et al., 1985, 1986, 1989; Lecomte, 1990; Meunier et al., 1985). This supports the hypothesis of a bimodal growth cycle in numerous fishes in French Guiana rivers.

Temperature and photoperiod are the two major seasonal growth synchronizers for fishes of temperate waters (Castanet et al., 1977; Bourlière, 1980). However, such parameters do not exhibit striking seasonal variations in tropical regions (Poinsard and Troadec, 1966; Blake and Blake, 1978). This led most authors to think that the growth cycles in these regions are controlled by the alternation of rainy and dry seasons (Lowe-McConnell, 1964, 1987; Blake and Blake, 1978; Warburton, 1978; Robben and Thys Van den Audenaerde, 1984).

In French Guiana, the seasonal variations of the water level, which is directly correlated to rainfall, appears to be the major climatic determinant of growth periodicity. Annuli formation in the Coumarou corresponds to the two periods of the year when the flow rate of the rivers is the lowest (Figs. 2). Alternating rainy and dry seasons could therefore play a major role in determining periodical growth in this species.

Although the growth cycle is controlled through reproduction in some Amazonian species (Schwassmann, 1977), there is little evidence that this is the case for the Coumarou. Indeed, this species probably matures all year round, as does M. ternetzi (Le Bail et al., 1989), which shares the same habitat, though the number of eggs is more variable during its breeding seasons. Furthermore, reproduction cannot be held responsible for the annuli observed in immature individuals (Meunier et al., 1979; Meunier and Pascal, 1981).

On the other hand, M. rhomboidalis shows marked variations throughout the year in its level of gastric repletion (Boujard et al., 1990). The diet of the Coumarou is also seasonally variable, this fish mainly feeding on seeds during the rainy season and on «Coumarou grass» (Podostemonaceae) during the dry season (Boujard et al., 1990). Lowe-McConnell (1964), Knöpfler (1970) and Goulding (1980) all emphasized that herbivorous, and more precisely frugivorous fishes, depend mostly on forest products and enter flooded areas (notably flooded
Figure 2 a. — Percentages of annuli close to the edge of the opercular bone of *M. rhomboidalis* from
the Sinnamary river (dashed line) and seasonal variations of the water level of the river in 1982-83
(thin line).

Figure 2 b. — Percentages of annuli close to the edge of the opercular bone of *M. rhomboidalis* from
the Approuague river (dashed line) and seasonal variations of the river flow in 1986-87 (thin line).
forests) during the rainy seasons. Such seasonal dietary variations could well provide a link between rainfall seasonality and annual growth cycle.

2) Growth characteristics of the Coumarou

Our observations led us to hypothesize the existence of two growth cycles per year in the Coumarou. In order to propose an adequate growth model, an experimental verification of our hypothesis appears essential. Unfortunately this cannot be done for the present time. We have therefore to content ourselves with the material at hand. Nevertheless, if the growth rate of the Coumarou slows down twice a year, resulting in the formation of two annuli, its age could be estimated by halving the number of observed annuli. To simplify the calculations, we can ever consider that the two yearly cycles are both of a six months duration.

A growth study was carried out separately for each population sampled. The average standard-lengths are given in table II. Male and female data were pooled as there was no significant sex difference in length distributions (Student t-test, p. 0.05; confirmed by a nonparametric Mann-Whitney U. test, p. 0.05). However, the maximum size reached by the males slightly exceeded that of the females (380 and 370 mm, respectively). The oldest fishes in our samples were 5 years old.

According to our hypothesis the size reached at 1 year was 110 to 130 mm (Table II). This implies a rather slow growth rate, as compared to other Characoids of similar maximum size (Cordiviola, 1966; Cordiviola de Yuan, 1971; Freire Dourado et al., 1971; Bayley, 1973; Khan and Siddiqui, 1973); for instance, Salminosus maxilosus reaches 480 mm within 2 years (Cordiviola, 1966). During the following years, the growth of the Coumarou averaged 50 mm per year (43-56 mm) in the Approuague River, and ranged from 50 to 90 mm per year in the Sinnamary River (1982-83) (Fig. 3).

The differences between the mean lengths of fishes at a given age from the first and third samples are statistically significant (p. 0.05, comparisons of means, factorial plane). For the second sample, the number of fishes was too low to use factorial plane analysis; but a Student t-test for the age classes 1, 2, 3 and 6 also

### Table II

<table>
<thead>
<tr>
<th>Annuli</th>
<th>Years</th>
<th>Sinnamary 1982/83</th>
<th>Sinnamary 1986/87</th>
<th>Approuague 1986/87</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>85.2 (5)</td>
<td>93.4 (9)</td>
<td>100.6 (5)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>130.7 (16)</td>
<td>108.3 (15)</td>
<td>123.1 (22)</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>163.2 (21)</td>
<td>149.1 (7)</td>
<td>155.0 (26)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>201.5 (8)</td>
<td>178.9 (14)</td>
<td>201.4 (11)</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>235.4 (5)</td>
<td>226.3 (3)</td>
<td>227.1 (9)</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>292.8 (5)</td>
<td>223.0 (3)</td>
<td>270.7 (4)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>296.2 (4)</td>
<td>300.0 (1)</td>
<td>352.0 (1)</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>342.7 (15)</td>
<td>300.0 (1)</td>
<td>352.0 (1)</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>370.0 (3)</td>
<td>300.0 (1)</td>
<td>352.0 (1)</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>373.3 (3)</td>
<td>300.0 (1)</td>
<td>352.0 (1)</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>352.0 (1)</td>
<td>352.0 (1)</td>
<td>352.0 (1)</td>
<td></td>
</tr>
</tbody>
</table>
show significant (p 0.05) differences in the rate of growth. We do not know whether such differences are due to inter-annual climatic variations in a given river (as shown for *L. friderici* by Boujard *et al.*, 1991), to between-rivers variations in food resources as for *L. friderici* (Boujard *et al.*, 1990), or to genetic differences between populations (see Renno *et al.*, 1990).

3) *Modeling the growth of the Coumarou?*

Back-calculation supplies additional information on the growth of *M. rhomboïdalis*. This technique implies a close linear relationship between the length of a fish and a linear measurement of a skeletal element displaying annuli (Tesch, 1968). It allows us to figure out the growth of a fish cohort by estimating their mean size at the assumed date of formation of each annulus.

There is a good linear relationship between fish standard length (SL) and opercular bone radius (Op.L.) measured between the articular fossa and its ventral apex (Fig. 4):

- Sinnamary 1982-83, \( SL = 12.0 \text{ Op.L.} - 11.2 \) (\( n = 43, r = 0.99 \)) (Fig. 4b)

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Figure 3. — Growth curve of the Sinnamary river population in 1982-83, and of the Approuague river population in 1986-87.
Figure 4. — Top left : Schematic representation of the opercular bone, left side, internal view (Op.L = opercular bone radius length ; Op.nL = distance between the articular fossa and the first annulus. Below : Linear relationship between the length of fishes (SL) and opercular bone radius (Op.L).


The study of growth by back-calculation is therefore made possible using the method of Frazer (1916) and Lee (1920) (in Tesch, 1968). This method was applied to the two groups of 31 individuals from the Sinnamary River (1982-83) and of 27 individuals from the Approuague River captured at two different months, August 1986 and July 1987 (to have an homogeneous and large enough sample). For these selected fishes, the two observers agreed on their age at the first step. The results are given in table III. A significant difference (factorial plane, p. 0.05) is again found between these two series of back-calculated values (Table IV).

A growth model was then built up for the two groups, i.e. Sinnamary (1982-83) and Approuague (1987). To that end, Von Bertalanffy’s equation (Von Bertalanffy, 1938) was applied to the pooled male and female values :

— Sinnamary : SL = 552.5 (1 – e – 0.105(t + 0.709))
— Approuague : SL = 242.2 (1 – e – 0.357(t + 0.039)).

The theoretical maximum size was much higher than the maximum length actually observed in the Sinnamary sample (380 mm), but the reverse was found in the Approuague sample where a 352 mm long specimen was included. However the maximum length is a theoretical value with restricted explanatory or practical significance (Philippart, 1975). Figure 3 shows that if an exponential model for the
### Table III

*Back-calculated mean standard length (in mm) at each annulus; () number of specimens in each class.*

<table>
<thead>
<tr>
<th>Annuli</th>
<th>Age in years</th>
<th>Sinnamary 1982/83</th>
<th>Approuague 1986/87</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>73,1 (4)</td>
<td>88,6 (6)</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>120,3 (6)</td>
<td>118,8 (6)</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>172,9 (6)</td>
<td>147,4 (5)</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>208,7 (5)</td>
<td>170,5 (4)</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>241,8 (4)</td>
<td>193,2 (3)</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>271,1 (3)</td>
<td>211,3 (2)</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>301,2 (2)</td>
<td>217,1 (1)</td>
</tr>
<tr>
<td>8</td>
<td>4</td>
<td>330,4 (1)</td>
<td>—</td>
</tr>
</tbody>
</table>

Nombre de poissons | 31 | 27 |

### Tableau IV

*Calculated mean standard length (in mm) at each annulus using Von Bertalanffy’s equation.*

( ) extrapolated data due to the lack of fish belonging to the group with only one mark.

<table>
<thead>
<tr>
<th>Annuli</th>
<th>Age in years</th>
<th>Sinnamary 1982/83</th>
<th>Approuague 1986/87</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>90,8</td>
<td>(75,1)</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>136,8</td>
<td>125,2</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>178,2</td>
<td>160,3</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>215,5</td>
<td>184,9</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>249,1</td>
<td>202,1</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>279,4</td>
<td>214,1</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>306,6</td>
<td>222,6</td>
</tr>
<tr>
<td>8</td>
<td>4</td>
<td>331,1</td>
<td>—</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>353,2</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>5</td>
<td>373,0</td>
<td>—</td>
</tr>
</tbody>
</table>

The growth rate of *M. rhomboidalis* is accepted, our sample is only made of fish in their fast growth period; the specimens with an « asymptotic length » are not represented and this can explain the difficulty to fix a realistic L. On the other hand, as the mean lengths estimated by this method were close to those observed, it suggests that this model, despite the unrealistic maximum length, could be used to describe the growth of this species.

**Conclusion**

The growth rate of *M. rhomboidalis* during its first year of life is rather slow. Its longevity seems to be short (5 years). The maximum size in all our samples was
380 mm. These results show that the Coumarou has an interesting growth potential without, however, reaching the very high values of Characoid species such as *Prochilodus scrofa*, *Labeo rohita*, *Colossoma maxillosus* or *Salminus maxillosus* (De Godoy, 1959; Cordiviola, 1966; Khan and Siddiqui, 1973; Petrere, 1983). However, our preliminary results must be confirmed by those of capture-recapture studies and/or by vital bone labelling *in natura*, in order to test the present hypothesis of a bimodal cycle of yearly growth in the Coumarou.

Furthermore, this study shows that there are marked differences in growth rate between the *M. rhomboidalis* living in the two rivers investigated. However, because of the short life-span of this species and the large time interval between our two sampling sessions, it is not possible to reach a definite conclusion on the respective roles of the climatic and genetic factors involved in the control of growth rate in this species.

Further studies of *M. rhomboidalis* growth in its natural environment, coupled with investigations on the genetic structure of these populations, are therefore required for a better understanding of the respective role of these parameters. Likewise, rearing trials in a controlled environment may contribute to assess possible differences in growth potential between various populations. This would allow to select the population showing the best growth potential.

**SUMMARY**

*Myleus rhomboidalis* is a freshwater fish from French Guiana which seems to have a large potential for aquaculture. The pattern of growth of this fish was investigated in its natural environment with the aim of using the data obtained as a reference for fish farming trials. In the first part of the paper it is shown that this species exhibits two growth cycles per year, as fishes from French Guiana often do. These bimodal cycles are synchronous with the alternating dry and rainy seasons, the two growth periods corresponding to the two rainy seasons of the year. In the second part, the growth pattern of *M. rhomboidalis* is described, first on the basis of uncorrected data on size and skeletochronological ages, and then by back-calculation and growth-curve modelling, according to Von Bertalanffy’s model.

**RÉSUMÉ**

*Myleus rhomboidalis* est un poisson d’eau douce qui semble présenter un important potentiel aquacole. La croissance de cette espèce est étudiée dans son milieu naturel dans le but d’obtenir des données de référence pour des essais d’élevage en bassins. Dans la première partie du travail nous montrons que cette espèce présente deux cycles de croissance annuels comme d’autres espèces guyanaises. Ces cycles sont synchronisés avec l’alternance des saisons. Les deux périodes de croissance active correspondent aux deux saisons des pluies de l’année et les deux ralentissements ou arrêts de croissance aux deux saisons sèches. Dans la deuxième partie du travail, la croissance de *M. rhomboidalis* est décrite grâce à la squelettocronologie sur la base de données non corrigées. Un modèle de croissance est ensuite proposé après rétrocalcul et selon l’équation de Von Bertalanffy.
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