Journal of Tropical Ecology (2003) **19**:301–313. Copyright © 2003 Cambridge University Press
DOI:10.1017/S026646740300333X Printed in the United Kingdom

Growth of young armoured catfish *Megalechis thoracata* in neotropical swamps and a rain-forest creek as revealed by daily micro-increments in otoliths

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(*Accepted 1 June 2002*)

Abstract: The otolith micro-increment technique was applied to assess the growth trajectory of early stages of the neotropical catfish *Megalechis thoracata* in Kaw Swamp, a coastal swamp in French Guiana, and two contrasting habitats in Suriname: the coastal Lelydorp Swamp with standing water and a rain-forest creek with running water, the Maykaboeka Creek. Daily deposition of increments on the lapilli was validated for the first 35 d after hatching and the innermost increments were deposited from hatching onwards. The natural habitats of *M. thoracata* in French Guiana and Suriname showed considerable variation in physico-chemical characteristics of the water, density of food organisms and fish fauna. Instantaneous growth rates and size-at-age differed significantly among two vegetation types in Kaw Swamp (3.5% d^{-1} and 4.1% d^{-1}), Lelydorp Swamp (3.0% d^{-1}) and Maykaboeka Creek (2.5% d^{-1}). Spearman's rank correlation coefficient between instantaneous growth rates and environmental parameters differed significantly from 0 only for water temperature. Hatch date analysis revealed an extended spawning season from January to June in the rain-forest creek.

Key Words: Callichthyidae, French Guiana, growth rate, juvenile fish, otolith microstructures, Siluriformes, size-at-age, South America, Suriname, temperature, tropical freshwater

INTRODUCTION

Although at one time high mortality rates of early life stages of fishes were attributed mainly to starvation, it is now recognized that predation is of equal or greater importance as a cause of mortality (Bailey & Houde 1989). Thus it is often hypothesized that the best way to survive is to grow fast (Sogard 1997): if a young fish can grow quickly past size-specific predators it has a greater chance of survival. Growth is enhanced in habitats where physico-chemical characteristics are optimal and food supply is good. In fishes with an extended spawning season, within-year variations in growth rates of early life stages may be expected owing to variation in biotic and abiotic environmental factors. The discovery of daily deposited micro-increments in fish otoliths (Pannella 1971) has enabled the accurate ageing of individual fish larvae/juveniles and the estimation of the growth of young fishes in their natural habitat (Campana & Jones 1992). Claramunt & Wahl (2000) used the otolith micro-increment technique to evaluate the role of several abiotic and biotic factors in determining the growth rates of larval freshwater fishes. Recently we applied for the first time the otolith micro-increment technique to estimate the growth rate of early life stages of a neotropical freshwater fish *Hoplosternum littorale* (Ponton *et al.* 2001).

Megalechis thoracata (Valenciennes, 1840) (see Appendix 1 for notes on the use of this name) is a medium-sized armoured catfish (100 g, 145 mm standard length, SL) in the family Callichthyidae endemic to neotropical swamps and rain-forest creeks (Mol 1994, Reis 1997). Armoured catfishes are fished extensively in northern South America (Novoa 1982, Ouboter & Mol 1994) and have great promise for aquaculture (Boujard *et al.* 1988, Ramnarine 1994*a*, *b*). Reproduction of *M. thoracata* takes place in the rainy season and in Surinamese swamps the spawning season extends from late December to July (Mol 1996*a*). Males construct and guard a simple floating bubble nest with 1000–8000 eggs (Mol 1993). Incubation of the eggs takes about 3 d (Mol 1993). In both the swamp and creek habitat, larvae and juveniles feed mainly on rotifers, microcrustacea, insect larvae and probably Oligochaeta (Mérigoux & Ponton 1998, Mol 1995). Hatchling *M. thoracata* use branchial respiration, and within approximately 2 wk the juveniles start surfacing for air (Mol *et al.* 1999); adult *M. thoracata* are facultative air-breathers

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(Gee & Graham 1978, Huebner & Chee 1978). In coastal swamps of Suriname, predation pressure on young *M. thoracata* from a broad group of invertebrate and vertebrate predators decreases sharply from hatching to the end of their first 2 mo of life (Mol 1996*b*). Thus, faster-growing fishes that spend less time in the more vulnerable size classes should gain a survival advantage over smaller conspecifics via decreased susceptibility to predation. Juveniles of the closely related catfish *Hoplosternum littorale* showed very different growth rates in two rice fields located within 2 km of each other (Ponton *et al*. 2001). In the Guianas, *H. littorale* is restricted to coastal swamps with standing water, but *M. thoracata* occurs in a wide range of habitats including coastal swamps, black-water streams and rain-forest creeks in the interior (Mol 1994). This variation in the habitat of *M. thoracata* may be expected to result in habitat-related differences in growth rate of young catfish (Claramunt & Wahl 2000).

In the present study we verify that micro-increments are deposited daily in the otoliths of young *M. thoracata* and that these increments are deposited from hatching onwards, and then apply the otolith increment technique to assess growth performance in different habitats in two different swamps and a rain-forest creek.

STUDY SITES

Differences in the growth rate of young *M. thoracata* among habitats within a coastal swamp were studied in Kaw Swamp in north-east French Guiana (Figure 1). The herbaceous Kaw Swamp is a nature reserve situated in a valley bordered by hilly outcrops of the Precambrian Guiana Shield. The Kaw River drains the grass swamps in the valley (water depth > 2 m), but the river and the swamp also receive considerable quantities of water from small creeks draining the *terra firme* rain forest of the Guiana Shield. Human activities in the swamp include fishing and breeding of zebu cattle by the inhabitants of the small village of Kaw (situated at K09 in Figure 1 and only accessible by small boat) and ecotourism. Downstream of Kaw village is the flat coastal plain with extensive swamp forests and, towards the estuary, mangrove forests. We analysed the vegetation at 10 sampling stations (Figure 1) following the method of Braun-Blanquet (1983). Vegetation records of 10×10-m^2 plots were grouped in three vegetation types using Principal Components Analysis (ter Braak 1987). Vegetation type I (sampling stations K02, K03, K08, K09 and K10) was dominated by *Cydista aequinoctialis*, *Utricularia guianensis*, *Polygonum* cf. *acuminatum*, *Montrichardia arborescens*, *Cyperus haspan*, *Oxycaryum cubense*, *Echinochloa polystachya*, *Hymenachne amplexicaulis*, *Leersia hexandra*, *Eichhornia crassipes* and *Salvinia auriculata* (nomenclature according to Boggan *et al*. 1997). Vegetation type II (sampling stations K01, K06 and K07) was dominated by *Cyperus haspan*, *Oxycaryum cubense*, *Eichhornia crassipes* and *Salvinia auriculata*. Vegetation type III (stations K04 and K05) was dominated by *Utricularia guianensis*, *Polygonum* cf. *acuminatum*, *Echinochloa polystachya*, *Hymenachne amplexicaulis*, *Leersia hexandra* and *Salvinia auriculata*. Although a bubble nest of *M. thoracata* was observed at sampling station K04, we did not collect young *M. thoracata* in vegetation type III.

The Lelydorp Swamp (water depth <1 m) is situated in a shallow gully between Pleistocene ridges of the old coastal plain of Suriname, *c*. 20 km south of Paramaribo. The coastal plain is much better developed in Suriname than in French Guiana and, unlike Kaw Swamp, the Lelydorp Swamp is located *c*. 40 km to the north of the *terra firme* rain forest of the Guiana Shield. The drainage network of creeks is poorly developed in the flat and low coastal plain and the water of the Lelydorp Swamp is drained only slowly into the Suriname River by a long series of small ditches and canals. Human activities in the swamp include cattle breeding and some fishing. The swamp vegetation was characterized by extensive stands of *Eleocharis interstincta* (dominant), *Montrichardia arborescens*, *Scleria microcarpa*, some scattered trees (*Triplaris weigeltiana*, *Pterocarpus officinalis*, *Virola surinamensis*, *Vochysia tetraphylla*), and the aquatics *Nymphaea rudgeana*, *Eichhornia crassipes*, *Salvinia auriculata* and *Utricularia* spp.

The Maykaboeka Creek (length 13 km, catchment area 45.8 km^2) is an intermittent, second-order tributary of the Mindrineti River (Saramacca River System) in the *terra firme* rain forest of the Gros Rosebel Area, *c*. 85 km south of Paramaribo. The width of the Maykaboeka Creek was 3–5 m and bank-full water depth was approximately 2 m at the study site. The bottom substrate of the main channel was sand, but most young *M. thoracata* were caught in three shallow tributaries with a mixed sand-clay bottom. During the long dry season of September–November the Maykaboeka Creek breaks up into little pools and the three tributaries dry up completely. Maximum flows of 2–6 m^3 s^{-1} and current velocities of 1–2 m s^{-1} regularly occurred in the rainy seasons of January–February and April–July. The closed canopy of the rain forest effectively prevented the growth of aquatic vegetation in the creek, but fallen trees, logs, woody debris and leaf banks were abundant.

MATERIALS AND METHODS

Water analysis and sampling procedures

Analyses of water at the study sites followed standard methods (Greenberg *et al*. 1995) and preceded the sampling of fish. Water temperature, dissolved oxygen, specific conductance and pH were determined *in situ* with YSI Model 50B and WTW model LF197-S meters. Cur-

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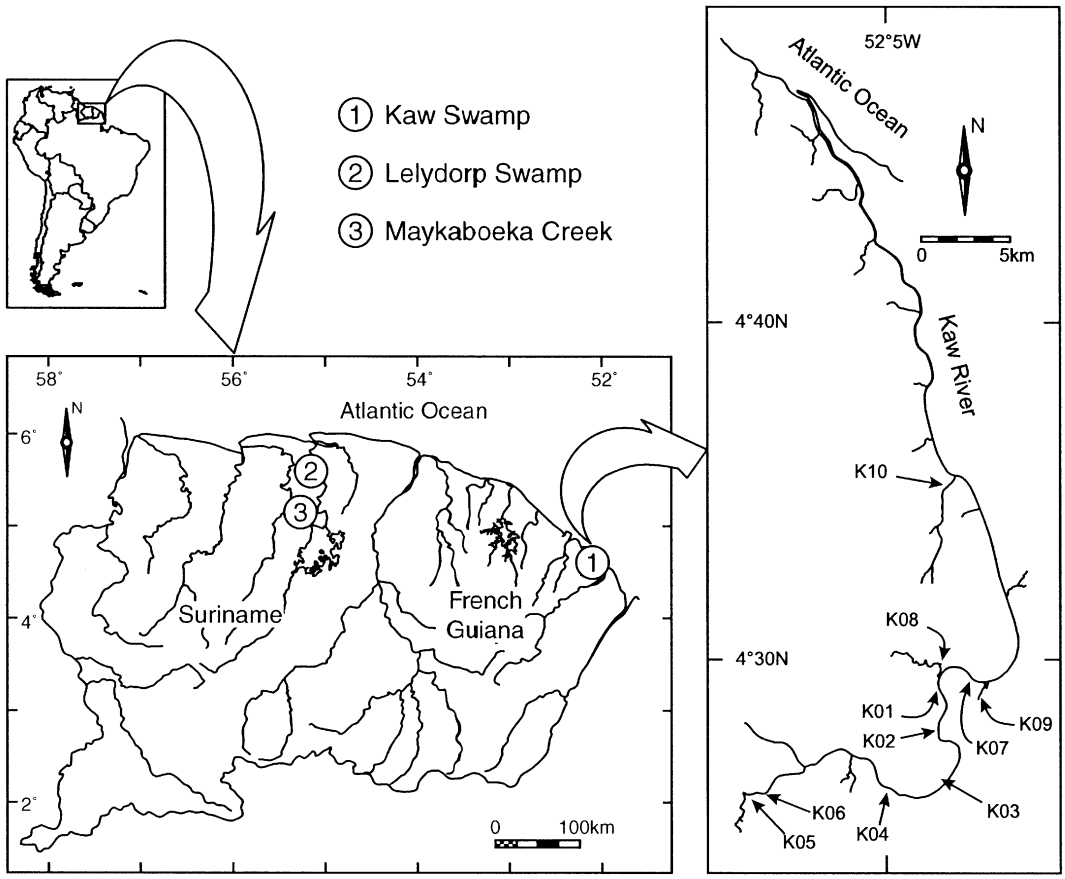

Figure 1. Study sites in French Guiana and Suriname: (1) the Kaw Swamp in north-east French Guiana with 10 sampling stations K01–K10, (2) the Lelydorp Swamp in the old coastal plain of Suriname and (3) the Maykaboeka Creek in the *terra firme* rain forest of the Guiana Shield in Suriname.

rent velocity was measured with a Seba Model F1 current meter. A water sample of 1 litre was collected for the determination of turbidity using a field test kit (Suriname) or a LaMotte Model 2008 digital turbidity meter (French Guiana).

Samples of potential food organisms of *M. thoracata* were collected by pouring 100 litres of water from the study site through a nylon plankton net (mesh size 100 μm). Samples were fixed and preserved in 4% formalin. After the organisms had sunk to the bottom the volume of the samples was adjusted to 50 ml by pouring off water. Two subsamples of 5 ml were taken after thorough shaking of the sample. Each subsample was then spread out on a 5 × 5-cm glass slide with the bottom divided into longitudinal strips and examined systematically under a light microscope (×100). Food organisms were grouped and counted as Rotifera, microcrustacea (Cladocera, Conchostraca, Copepoda, Ostracoda), hydracarina, Oligochaeta, aquatic insect larvae and aquatic insects.

Early life stages of *M. thoracata* were collected with a small seine (2 × 1.5 m; mesh size 1 mm) on one occasion from 11–16 March 1999 in Kaw Swamp, on two occasions, 24 March and 2 April 1999, in Lelydorp Swamp, and on seven occasions between 18 February and 6 July 1999 in Maykaboeka Creek. All specimens were preserved in 95% ethanol in the field and then transferred to fresh 90% ethanol in the laboratory where they were later processed.

Validation experiment

Newborn free embryos (yolk-sac larvae) of *M. thoracata* were obtained by collecting a single batch of eggs with wriggling embryos from a nest in the Lelydorp Swamp, and then inducing hatching within 1 h by exposing the eggs to water at 3–5 °C above the temperature of the swamp water. The larvae were transported to the University of Suriname, Paramaribo, in oxygen-inflated polyethylene bags and then carefully transferred to a 50 × 30 × 25-cm cage (mesh size 1 mm) suspended in a 150 × 100 × 50-cm concrete outdoor tank. The cage permitted efficient feeding of the larvae and excluded predators such as Odonata nymphs and *Belostoma* water bugs. Two days after hatching, the yolk sac had been consumed and the larvae started feeding on exogenous food. Larvae and juveniles were fed laboratory-reared *Artemia* nauplii *ad libitum* twice daily at 07h00 and 17h00. After 2 wk, the young fish were gently released from the cage into the

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concrete outdoor tank. Larvae and juveniles were randomly sampled and fixed in 95% ethanol at hatching (n = 40) and then at 2 (n = 45), 5 (n = 46), 7 (n = 15), 10 (n = 12), 14 (n = 15), 21 (n = 16), 28 (n = 14) and 35 (n = 7) d after hatching. Water temperature was not controlled during the 5-wk experiment and ranged from 23 to 29 °C. The natural light period lasted from 06h45 to 18h45. A low hatching percentage of the first batch of *Artemia* cysts resulted in a high mortality of *M. thoracata* larvae in the first week of the experiment, but mortality dropped to < 5% during the rest of the experiment.

Lapilli preparation and examination

The nomenclature of lapillus morphology used here is analogous to the nomenclature employed for the sagitta otolith of non-ostariophysan fishes (e.g. Kalish *et al.* 1995). The core of the otolith was defined as the area surrounding the primordia and bounded by the first prominent discontinuous (D-) zone.

Fish were measured to the nearest 0.1 mm SL with vernier calipers under a binocular microscope before otolith extraction. Only the lapilli of *M. thoracata* (Figure 2a) were used because they are larger than the thin V-shaped sagittae and the discoid and curved asterisci. The lapilli of larvae SL < 7.0 mm were extracted with dissecting needles under a binocular microscope equipped with polarized light. Lapilli were identified by their size and by their lateral position with respect to the sagittae and asterisci. For each individual both lapilli were extracted, cleaned in ethanol, dried and, given their small size, immersed immediately sagitally into a drop of polyester resin (Sody 33 from Escil, Chassieu, France) placed on a microscope glass slide. After polymerization of the resin (24 h at 35 °C), the sagittal preparations of the lapilli were examined without any further polishing (Figure 2b).

For individuals SL ⩾ 7.0 mm, the lapilli were extracted following the right-between-the-eyes method (Secor *et al.* 1992). First the fish head was severed behind the operculum and then cut sagitally. The brain was removed from each half of the head, the labyrinth was located, and the utricular vestibule containing the lapillus was extracted. Each lapillus was cleaned in ethanol and immediately embedded sulcus-side down in polyester resin. In the resin, the longitudinal axis of the lapillus was oriented parallel to the long axis of the mould. After polymerization, each otolith was prepared to obtain a thin transverse section following Secor *et al.* (1992). Briefly, each block was cut transversally with an Isomet® (Buehler, Lakebuff, USA) low-speed saw equipped with a 300-μm diamond blade (ref D100 from Escil, Chassieu, France) to leave 0.8–1.0 mm of material on each side of the core (Figure 2a). The embedded section of the otolith was glued with thermoplastic glue (CrystalBond™ 509, Buehler, Lakebuff, USA) to a 1 × 1-cm piece of glass fixed on a microscope slide (Secor *et al.* 1992). The side of the block containing the sectioned lapillus was ground rapidly with wet sandpaper of 1200 μm grit size and then polished finely up to the otolith core using aluminium oxide slurry of successively 3, 1 and 0.3 μm on polishing cloths. When the core was reached the preparation was cleaned, dried, turned and prepared the same way on the other side. Finished preparations were 20–40 μm thick (Figure 2c).

Lapilli preparations were observed at ×400 and ×600 magnification with an Olympus BX40 light microscope equipped with a Sony 3CCD DXC-930C colour video camera. Measurements of the lapilli and the core were performed with the TNPC (Traitement Numérique des Pièces Calcifiées) module of the Visilog© image analysis software (Noesis SA, Courtaboeuf, France) using calibrated images. Increments were counted manually on a Sony PVM-2950QM Triniton video monitor. For counting the number of increments in transversal preparations, the long axis, corresponding to the interior of the fish (Figure 2c), appeared most appropriate with respect to increment clarity. The same reader performed a minimum of two complete counts: one count starting at the first increment after the core and towards the otolith edge, the second starting from the otolith edge towards the core. Then a selected number of preparations (n = 50) was counted by a second reader, disagreement among readers expressed as the index of average per cent error (Beamish & Fournier 1981) was 5.6% and the number of increments counted did not differ significantly among the two readers (Wilcoxon's two-tailed signed ranks test, P = 0.246).

Otolith examination

For the validation of daily increment deposition we examined the lapilli of 59 individuals 0–35 d old: 11 newly hatched larvae, seven larvae of age 2 d, seven larvae of age 5 d, eight larvae of age 7 d, six fishes of age 10 d, six fishes of age 14 d, seven fishes of age 21 d, four fishes of age 28 d, and three fishes of age 35 d. We further collected 131 young *M. thoracata* from Kaw Swamp (6.7–40.3 mm SL), 41 from Lelydorp Swamp (8.1–26.8 mm SL) and 36 from Maykaboeka Creek (8.9–36.5 mm SL). Randomized stratified subsampling on the basis of 5-mm length categories resulted in a total of 68 *M. thoracata* from Kaw Swamp, 15 from Lelydorp Swamp and 24 from Maykaboeka Creek that were examined for otolith microstructure.

Calculations and statistics

Daily instantaneous growth coefficients (g in mm d^{-1}) were calculated from the log-transformed exponential

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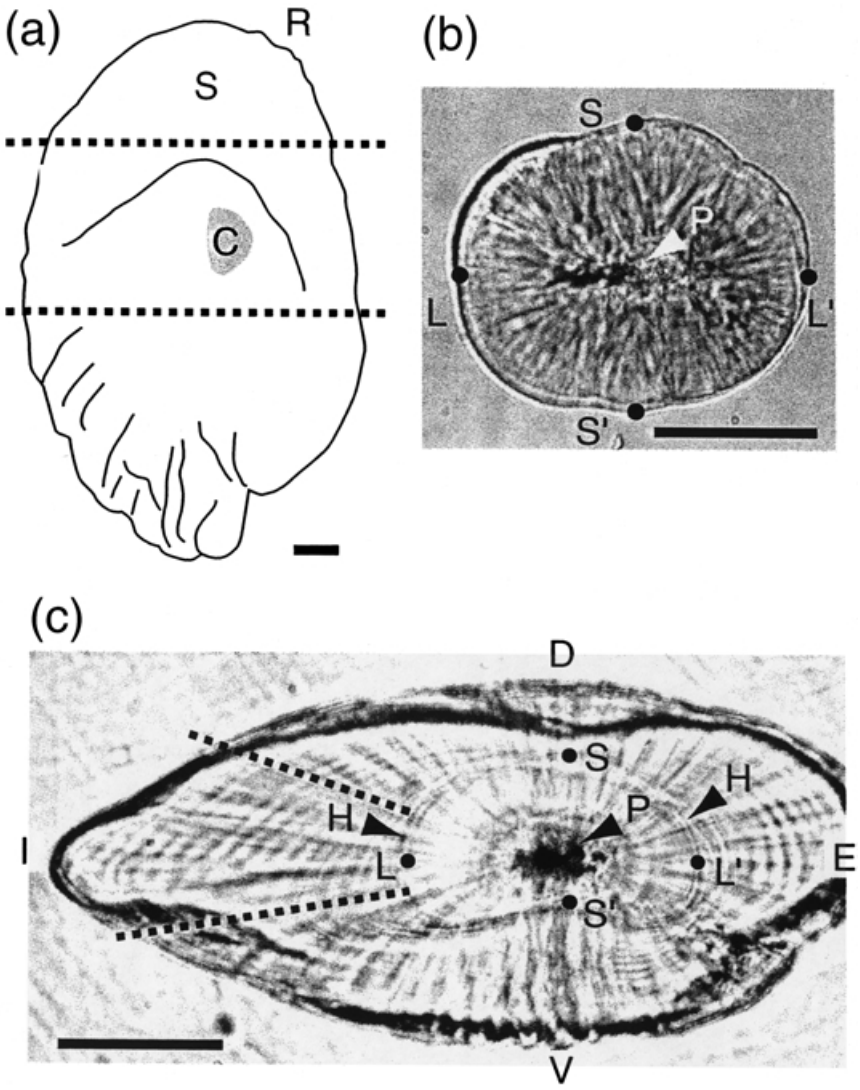

Figure 2. (a) Ventral view of a lapillus of a 17.9-mm SL *Megalechis thoracata* showing rostrum (R), sulcus (S), position of core (C) inside the lapillus, and lines where the otolith was cut for transversal preparation. (b) Sagittal preparation of the lapillus of a newly hatched *M. thoracata* larvae (age 0 days, SL = 4.5 mm) from the validation experiment showing the long (LL′) and short axis (SS′) of the core and the primordia (P). (c) Transversal preparation of the lapillus of a 11.5-mm SL *M. thoracata* from Kaw Swamp (station K03) showing the long axis (LL′) and short axis (SS′) of the core, the primordia (P), the hatching check (H), and the sector where micro-increments were counted. With D: dorsal and V: ventral side of the otolith, E: exterior and I: interior of the fish. The horizontal bars represent 0.1 mm.

model $\log(SL_t) = SL_o + gt$ where SL_t = standard length at time t in mm, SL_o = estimated standard length at hatching in mm, and t = age in d. All the resulting linear models provided adequate fits of growth relationships based on residual analysis. Student's t-test was used to test for differences in the shape of the otolith core and, in the analysis of the validation experiment, to test for differences among the number of increments counted and true age. ANCOVA was used to test for differences in daily instantaneous growth coefficients among sampling sites. Kruskal–Wallis tests and Mann–Whitney-U tests were used to test for differences in environmental variables among sampling stations. All these analyses were performed with SYSTAT® 9.0. Correlation between fish growth and environmental parameters was tested with Spearman's correlation coefficient (an equivalent of the Pearson product-moment correlation coefficient but computed from ranks) with StatXact-3®, a statistical software for exact distribution-free inference using the algorithms developed by Mehta & Patel (1995) for performing permutation tests. The P value associated to each test was based on complete enumeration of the original data (Mehta & Patel 1995). Significance was accepted when $P < 0.05$.

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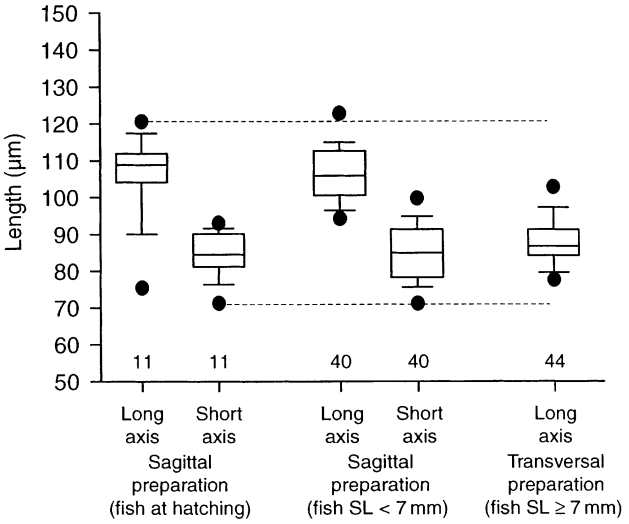

Figure 3. Validation experiment on *Megalechis thoracata*. Size of the core of lapilli delimited by the conspicuous discontinuous zone: the length of the long axis of the core prepared transversally (individuals older than 10 d; n = 44) lies between the lengths of the short axis and the long axis of the core observed in sagittal preparations (fish at hatching; n = 11, and individuals < 7 mm, n = 40). Upper and lower limits of the boxes correspond to the first and third quartiles respectively, horizontal bars indicate the median, whiskers the 10th and 90th percentile, and dots the outliers. See Figure 2 for the location of the short and long axis of the core as measured in sagittal and transversal preparations.

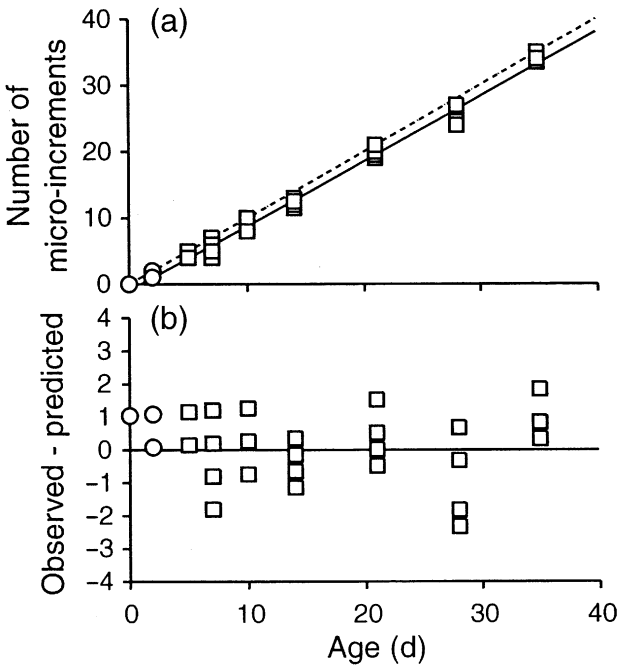

Figure 4. Validation experiment on *Megalechis thoracata*. (a) Number of micro-increments counted in lapilli preparations and (b) difference between observed and predicted number of micro-increments as a function of true age in days. Data points are individual fish. The dotted line indicates the 1:1 relationship between number of micro-increments (n) and true age (A) and the solid line represents the model $n = 0.977 \times A - 1.032$ established for individuals between 5 and 35 d old (squares; n = 41). Data outside the range of the model (circles) are presented for comparison.

RESULTS

Validation of daily increment deposition

Newly hatched larvae of *Megalechis thoracata* had lapilli that averaged 106 µm on their longest longitudinal axis and 85 µm on their shortest transverse axis (Figure 3) and some presented up to three very faint microstructures. The multiple primordia were only loosely fused and the large core was surrounded by a conspicuous discontinuous zone. This discontinuous zone was observed in both sagittal and transversal preparations of lapilli (Figure 2b, c). The length of the long axis of the core in transversal preparations fell between: (1) the lengths of the transverse and longitudinal axis of the lapillus of newly hatched larvae and (2) the lengths of the short and long axis of the core in sagittal preparations (Figure 3). Thus, the discontinuous zone delimiting the core in sagittal and transversal preparations corresponded to the same structure formed at hatching.

In the concrete outdoor tanks, young *M. thoracata* grew from approximately 4.5 mm SL at hatching to 27.9 mm SL at 35 d (end of the experiment). The lapilli showed broad increments from the date of hatching on, but the increments were counted more easily in transversal preparations. The number of micro-increments did not differ significantly with the direction of counting, core to edge or edge to core (paired t-test, P = 0.134), and so the two different counts were averaged. For fish 5–35 d old, the number of micro-increments (n) as a function of true age (A) of the fish fitted well to a linear model: $n = 0.977 \times A - 1.032$ (n = 41, F = 3980, P < 0.001) (Figure 4). The slope of the model did not differ significantly from 1 (t-test, P > 0.1; 95% confidence interval 0.946–1.008), i.e. increments were deposited daily on the otolith. However, the intercept differed significantly from 0 (t-test, P < 0.001), which means that age was underestimated by increment counts. Adding individuals of age 0 and 2 d did not improve the fit of the model.

Otolith size at hatching

At hatching the size of the lapillus of *M. thoracata*, as measured along the long axis of the core in transversal preparations, varied between 40 and 110 µm. With otolith size at hatching expressed as long axis × short axis of the core (LL′ × SS′ as identified in Figure 2), it was possible to distinguish between young *M. thoracata* from Kaw Swamp with 'large-core' otoliths (n = 44) and individuals with 'small-core' otoliths (n = 24); the otolith size at hatching of the 'small-core' otoliths fell outside the range of observations of the validation experiment (Figure 5). The shape of the large core was dorso-ventrally flattened

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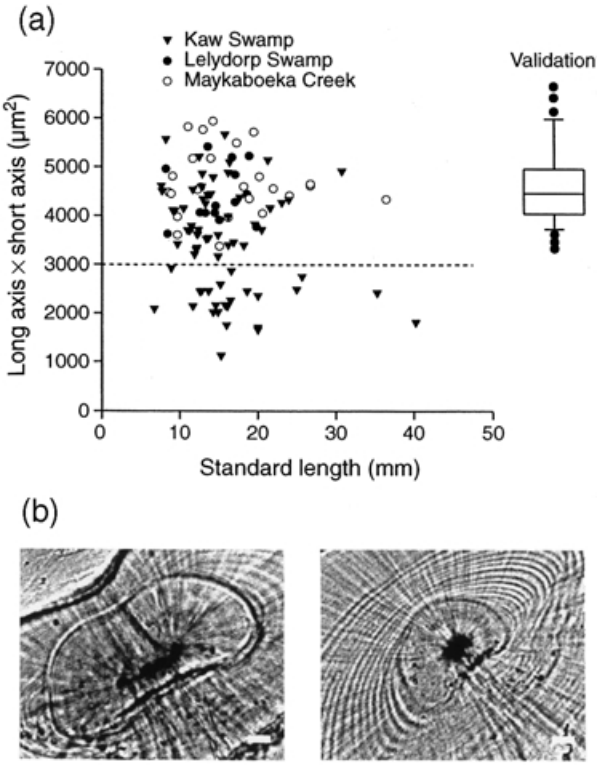

Figure 5. Otolith size at hatching. (a) Core size as measured by long axis × short axis of the core in transversal preparations (LL′ × SS′; see Figure 2c) for *Megalechis thoracata* from natural habitats in French Guiana (Kaw Swamp) and Suriname (Lelydorp Swamp and Maykaboeka Creek) as compared with the range of core-size observations for individuals of the validation experiment (box plot). Data points are individual fish. Upper and lower limits of the box correspond to the first and third quartiles respectively, horizontal bar indicates the median, whiskers the 10th and 90th percentile, and dots the outliers. (b) Core of the lapillus of a fish with a 'large-core' otolith (LL′ × SS′ > 3000 µm²) and a 'small core' otolith (LL′ × SS′ < 3000 µm²); both individuals were caught at sampling station K07 in Kaw Swamp, French Guiana. Note that the large core is dorsoventrally flattened (LL′/SS′ = 1.88) when compared with small core (LL′/SS′ = 1.66). The horizontal white bar represents 10 µm.

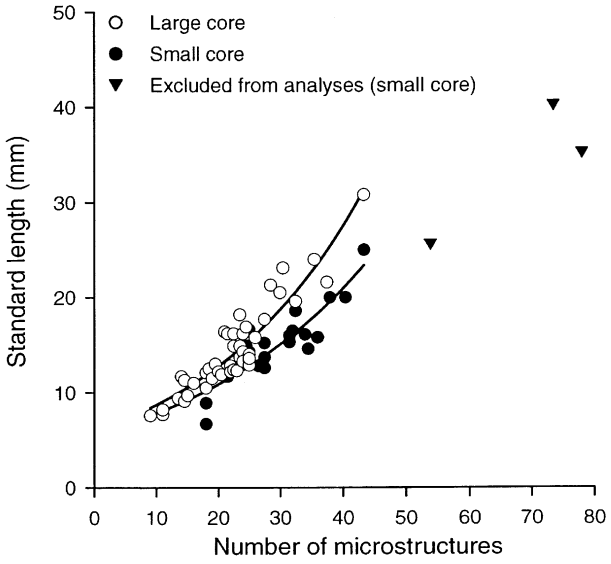

Figure 6. Standard length (SL in mm) vs. number of microstructures (n) on 'large-core' (open circles) and 'small-core' (closed circles) lapilli of young *Megalechis* from Kaw Swamp, French Guiana and fitted growth models $SL = 5.59 \times e^{0.040\,n}$ (n = 44, F = 261.3, P < 0.001) and $SL = 5.11 \times e^{0.036\,n}$ (n = 21, F = 59.6, P < 0.001) respectively. Data points are individual fish. Observations corresponding to $n > 50$ were not included in analyses and are presented for information only.

(LL′/SS′ = 1.88 ± 0.052, mean ± SD) when compared with the shape of the small core (LL′/SS′ = 1.66 ± 0.046) (t-test, P < 0.001) (Figure 5b). Fishes with small-core otoliths were collected only in Kaw Swamp where they occurred syntopically (i.e. at the same sampling station) with large-core individuals. Using the number of micro-increments as an estimator of age in d for otoliths presenting less than 50 microstructures, the instantaneous growth rate of fish with small-core otoliths (3.6% d^{-1}) did not differ significantly from the growth rate of fishes with large-core otoliths (4.0% d^{-1}) (ANCOVA, n = 65, df = 1, F = 1.004, P = 0.320), but the length-at-age of fishes with small-core otoliths was significantly lower than the length at age of individuals with large-core otoliths (ANCOVA, n = 65, df = 1, F = 28.4, P < 0.001; Figure 6). As the 24 small-core individuals may represent a second *Megalechis* species (see Appendix 1), we omitted them in all further analysis.

Comparison of natural habitats of *M. thoracata*

The natural habitats of *M. thoracata* in French Guiana and Suriname showed considerable variation in physico-chemical characteristics of the water (Table 1), density of food organisms (Table 2) and fish fauna (detailed faunistic list available from the authors upon request). The main difference was between the coastal swamps with standing water (Kaw and Lelydorp) and the running-water habitat of the Maykaboeka Creek in the *terra firme* rain forest of the Guiana Shield. Although Kaw Swamp showed many characteristics of a coastal swamp, the swamp was also affected by the relatively large Kaw River and small creeks draining the rain forest on the hills surrounding the swamp (Figure 1).

The shaded Maykaboeka Creek had high current velocities, low water temperatures, high dissolved oxygen levels and a high turbidity when compared with the swamps of Lelydorp and Kaw (Table 1). Kaw Swamp had higher oxygen concentrations than the Lelydorp Swamp. Densities of the most important food organisms of young *M. thoracata* (rotifers, microcrustacea and aquatic insect larvae) were low in the Maykaboeka Creek when compared with the swamps of Lelydorp and Kaw (Table 2). The small Maykaboeka Creek had a rich fish fauna (55 species from 22 h seining effort) when compared with the fish fauna of

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Table 1. Physico-chemical data (n: number of observations, median and range) for collection sites of young *Megalechis thoracata* in two coastal freshwater swamps, Kaw Swamp (French Guiana) with vegetation types I and II and Lelydorp Swamp (Suriname), and a rain-forest creek Maykaboeka Creek (Suriname). Results of Kruskal–Wallis tests (P) are given. For any given water quality parameter, medians with the same superscript are not significantly different (Mann–Whitney U tests).

Parameter		Kaw Swamp Veg. type I	Kaw Swamp Veg. type II	Lelydorp Swamp	Maykaboeka Creek	P
Water	n	4	3	5	19	
temperature	Median	27.4[a]	27.5[a]	25.7[a]	23.8[b]	< 0.001
(°C)	Range	25.1–28.0	25.2–30.0	25.0–25.9	23.5–25.6	
Conductance	n	4	3	6	15	
at 25 °C	Median	20.0[ac]	14.3[a]	47.0[b]	30.0[c]	0.002
(µS cm^{-1})	Range	18.0–54.0	9.0–22.0	35.0–60.0	18.0–42.0	
Dissolved	n	4	3	5	16	
oxygen	Median	3.0[a]	3.2[a]	0.9[b]	7.3[c]	< 0.001
(mg l^{-1})	Range	1.9–3.6	1.3–4.7	0.6–1.0	2.8–9.4	
Turbidity	n	3	3	3	6	
(NTU)	Median	1.5[a]	4.5[a]	7.8[ab]	30.0[b]	0.014
	Range	1.0–11.0	3.0–7.0	5.0–17.0	16.0–70.0	
pH	n			8	7	
	Median			5.7	5.7	0.728
	Range			5.1–6.5	5.1–6.4	
Maximum	n	4	3	8	21	
velocity	Median	0.0[a]	0.0[a]	0.0[a]	23.8[b]	< 0.001
(cm s^{-1})	Range	0.0–0.0	0.0–0.0	0.0–0.0	0.0–110.8	

Table 2. Densities of aquatic food organisms (individuals l^{-1}) of young *Megalechis thoracata* in two coastal freshwater swamps, Kaw Swamp (French Guiana) with vegetation types I and II and Lelydorp Swamp (Suriname), and a rain-forest creek Maykaboeka Creek (Suriname). Densities of food organisms are presented as median with number and range of observations. Results of Kruskal–Wallis tests (P) are given. Medians with the same superscript within a food organism category are not significantly different (Mann–Whitney U-tests).

Food organism		Kaw Swamp Veg. type I	Kaw Swamp Veg. type II	Lelydorp Swamp	Maykaboeka Creek	P
Rotifera	n	4	3	3	3	
	Median	3.80[a]	3.20[ab]	11.20[ab]	0.00[b]	0.040
	Range	3.00–8.80	2.40–32.80	9.60–13.60	0.00–0.00	
Micro-	n	4	3	3	3	
crustacea	Median	15.39[a]	40.81[b]	47.16[c]	1.00[d]	0.112
	Range	9.15–16.90	1.15–205.00	7.60–67.20	0.20–1.60	
Hydracarina	n	4	3	3	3	
	Median	0.18[b]	0.10[ab]	0.24[ab]	0.00[a]	0.077
	Range	0.05–1.40	0.10–4.00	0.24–0.40	0.00–0.00	
Oligochaeta	n	4	3	3	3	
	Median	0.35[b]	0.05[a]	2.64[ab]	0.40[ab]	0.040
	Range	0.20–4.80	0.05–0.10	0.90–3.95	0.20–0.40	
Aquatic	n	4	3	3	3	
insect	Median	1.23[a]	1.10[b]	0.80[c]	0.20[d]	0.177
larvae	Range	0.92–1.38	0.00–5.00	0.24–1.68	0.00–0.20	
Aquatic	n	4	3	3	3	
insects	Median	0.05[a]	0.46[b]	0.24[c]	0.20[d]	0.503
	Range	0.01–0.35	0.05–4.05	0.00–0.48	0.00–0.20	

the Lelydorp Swamp (31 species from 17 h). With sampling efforts restricted to the shallow parts of the swamp and not including the Kaw River, Kaw Swamp still showed a rich fish fauna (50 species from 18 h) clearly affected by rain-forest creeks draining into the swamp.

Hatch date and growth in different natural habitats

The number of micro-increments in the otolith preparations of wild-caught *M. thoracata* did not differ significantly with the direction of counting, core to edge or edge to core (paired t-test, P = 0.390), and so the two different counts were averaged. When the hatch date was back-calculated by subtracting the number of micro-increments (as an estimator of age) from the date of capture, all *M. thoracata* from Kaw Swamp and Lelydorp Swamp were born in the short rainy season January–March while *M. thoracata* from Maykaboeka Creek were born in both the short rainy season and the long rainy season of April–July (Figure 7).

Instantaneous growth rates differed significantly among Kaw Swamp vegetation type I (3.5% d^{-1}), Kaw

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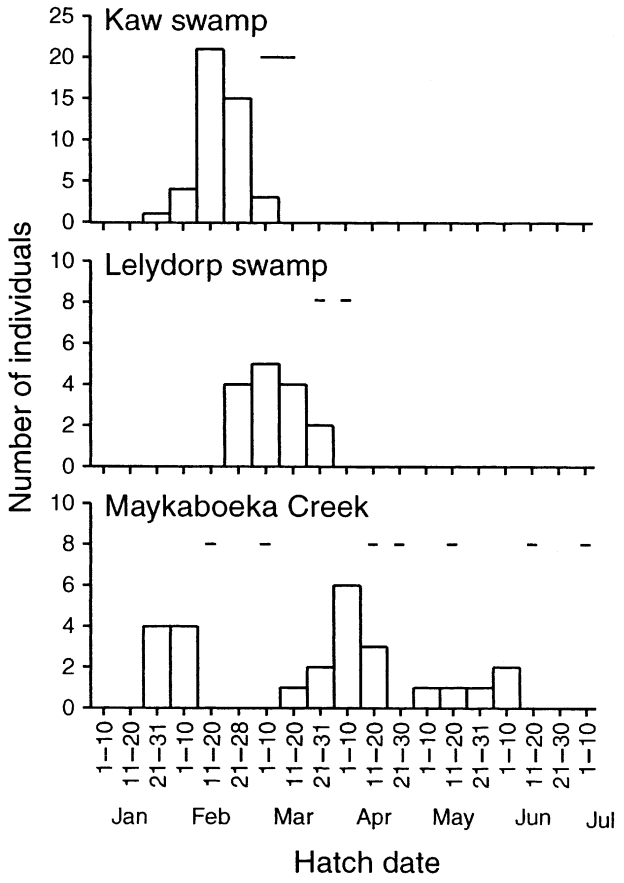

Figure 7. Hatch date frequency distribution for young *M. thoracata* from Kaw Swamp (French Guiana; large-core individuals only), Lelydorp Swamp (Suriname) and Maykaboeka Creek (Suriname). The horizontal black lines correspond to the sampling periods.

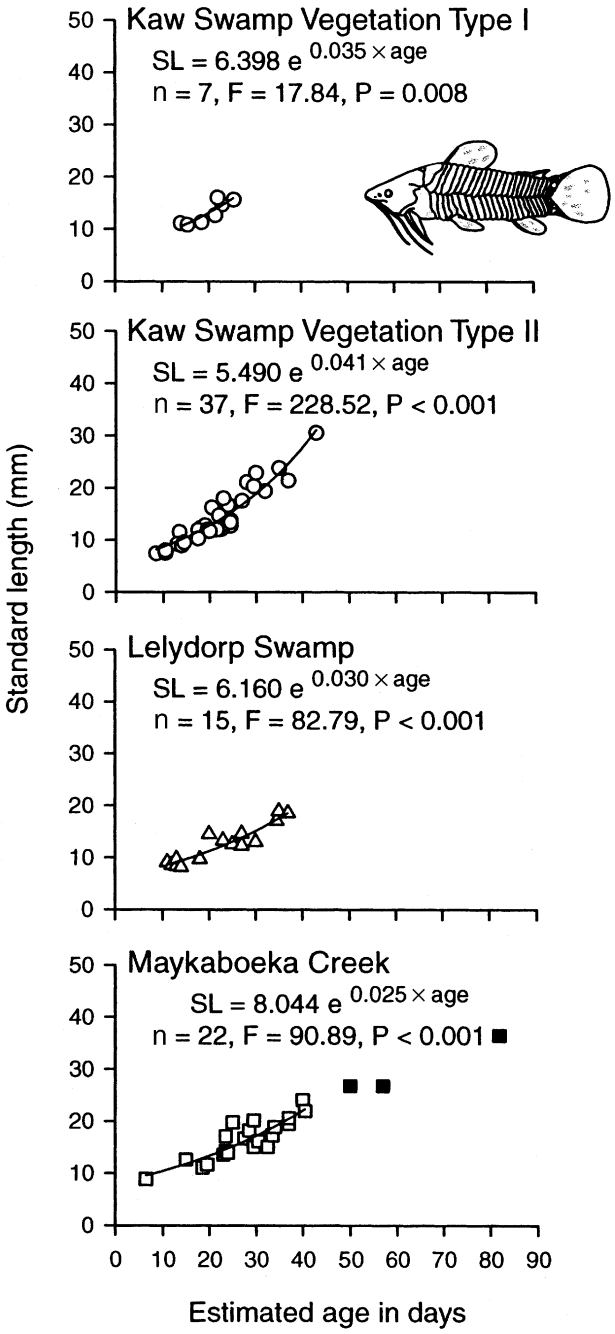

Figure 8. Standard length vs. number of microstructures used as an estimator of age for young *Megalechis thoracata* in Kaw Swamp vegetation types I and II, French Guiana, and in Lelydorp Swamp and Maykaboeka Creek in Suriname. Data points are individual fish. Closed symbols corresponding to individuals estimated age > 50 d are presented for information only.

Swamp vegetation type II (4.1% d^{-1}), Lelydorp Swamp (3.0% d^{-1}) and Maykaboeka Creek (2.5% d^{-1}, ANCOVA, n = 81, df = 3, F = 3.473, P = 0.001, Figure 8) as did size at age (ANCOVA, n = 81, df = 3, F = 7.104, P < 0.001). Highest values of Spearman's coefficient of rank correlation between instantaneous growth rates and environmental parameters were observed for water temperature (R = 1.000), conductance (R = –0.800), turbidity (R = –0.800), densities of Oligochaeta (R = –0.800) and densities of aquatic insect larvae (R = 0.800) although these last four coefficients did not differ significantly from 0 (Table 3).

DISCUSSION

Annual growth marks in otoliths have proved useful in estimating the age and growth rate of large Neotropical freshwater fishes (Jepsen *et al.* 1999, Loubens & Panfili 1995, 1997, 2000). However, most Neotropical freshwater fishes are small, with a short life span and most of their growth occurring in the first year of their life (Weitzman & Vari 1988). Daily increments lend themselves much better than annual marks in ageing both small, short-lived species and early stages of large fishes. Recently we applied the otolith micro-increment technique for the first time to study the growth of early stages of a Neotropical freshwater fish in its natural habitat

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Table 3. Spearman's rank-order correlation coefficient (R) between instantaneous growth rates of young *Megalechis thoracata* and environmental parameters of their habitat in two coastal freshwater swamps, Kaw Swamp (French Guiana) with vegetation types I and II and Lelydorp Swamp (Suriname), and a rain-forest creek Maykaboeka Creek (Suriname). With P = associated one-sided probability based on complete enumeration of the possible outcomes (exact probability following Mehta & Patel 1997).

	R	95% confidence interval	P
Water temperature	1.000	1.000–1.000	0.042
Conductance	–0.800	–1.000– –0.212	0.167
Dissolved oxygen	–0.200	–1.000–1.000	0.458
Turbidity	–0.800	–1.000– –0.212	0.167
Rotifera	0.200	–1.000–1.000	0.458
Microcrustacea	0.400	–0.726–1.000	0.375
Hydracarina	0.200	–1.000–1.000	0.458
Oligochaeta	–0.800	–1.000– –0.212	0.167
Aquatic insect larvae	0.800	0.212–1.000	0.167

(Ponton *et al*. 2001) and the present work is thus the second of this kind.

In order to use increment number to estimate the age of young fish, it is necessary to validate the increment formation rate (Geffen 1992). One of the most rigorous and reliable procedures of validation is the examination of otoliths from individuals of known age, reared in outdoor enclosures where photoperiod and temperature cycles reflect natural conditions (Geffen 1992). In the outdoor tanks of the validation experiment, the instantaneous growth rate of young *Megalechis thoracata* (5.3% d^{-1}) was higher than the growth rate observed in natural habitats (ranging from 2.5 % d^{-1} in Maykaboeka Creek to 4.1 % d^{-1} in Kaw Swamp). Thus, the outdoor tanks were considered an optimal environment for validation during the first 35 d after hatching. The high mortality of the larvae after consumption of the yolk sac (day 3–6) was probably caused by starvation as a result of the low hatching percentage of the first batch of *Artemia* cysts. Increments deposited over periods of food shortage are generally narrow (Mugiya & Oka 1990, Neilson & Geen 1985, Paperno *et al*. 1997), thus explaining why we systematically counted one or two increments short of the known age in days. However, the regression slope of increment number vs. age was not significantly different from 1 and we conclude that increments were deposited daily on the lapilli of young *M. thoracata* and that the innermost microstructures were deposited from hatching onwards.

At hatching the size of the lapillus of *M. thoracata*, as measured along the long axis of the core in transversal preparations, varied between 70 and 110 μm. With the small-core individuals from Kaw Swamp included, the range of otolith size at hatching increased to 40–110 μm. This variation in otolith size at hatching may reflect temperature-dependent differences in incubation time (Hostache *et al*. 1992), especially where the eggs of *M. thoracata* are deposited above the water surface in bubble nests (Mol 1993). However, the variation in otolith size at hatching in the closely related bubble nester *H. littorale* (45–60 μm) (Ponton *et al*. 2001) was much smaller than in *M. thoracata*. *Megalechis thoracata* embryos probably encounter a larger range of temperatures during their development than *H. littorale* embryos because nests of *M. thoracata* are built in a larger range of habitats, from open swamp (warm) to shaded rain-forest creek (cool), than *H. littorale* nests that are always built in the open swamp habitat (Mol 1993, 1996*a*). In addition, we have evidence (J. H. Mol, unpublished results) that in the Maykaboeka Creek, *M. thoracata* probably deposits its eggs under the water surface for the greater part of the reproductive season; bubble nests were observed only in dry-season pools after the first rains in December/January.

We identified 24 *Megalechis* fishes from Kaw Swamp with (1) the otolith size at hatching well below the range of observations of core size of *M. thoracata* from the validation experiment (Figure 5a); (2) a dorso-ventrally expanded core (Figure 5b); and (3) a low length-at-age (Figure 6). Early stages of *Megalechis* are easily distinguished from two other syntopic callichthyinids *H. littorale* and *C. callichthys* by their pigmentation pattern and form of the caudal fin (Mol 1996*a*). However, a second *Megalechis* species is present in Guyana (Reis 1997) and this second *Megalechis* species could also be present in Kaw Swamp due to the Amazonian influence in the fish fauna of eastern French Guiana (Jégu & Keith 1999). Early stages of the two *Megalechis* species are probably not easily distinguished from each other (Reis 1997). We thus decided to remove the 24 small-core individuals from our analyses as they may represent a second *Megalechis* species. We have examined only three adult specimens of *Megalechis* from Kaw Swamp and additional sampling is required to confirm the presence of the second *Megalechis* species in the swamp.

We detected intra- and inter-site differences in instantaneous growth rates of early stages of *M. thoracata*, the highest growth rate being observed in exposed swamp vegetation, and the lowest in the shaded Maykaboeka Creek with cool, running water. Spearman's rank correlation coefficient between instantaneous growth rates and environmental parameters differed significantly from 0 only for water temperature. The effect of temperature on the somatic growth of young temperate fishes has been

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extensively studied, but we are not aware of examples concerning the neotropics. Temperature-induced differences in incubation time may also explain differences in the estimated size at hatching and size at age that we observed within and among natural habitats.

The small difference in the instantaneous growth rate of early stages of *M. thoracata* between two contrasting habitats in Suriname, the Maykaboeka Creek (2.5% d^{-1}) and the Lelydorp Swamp (3.0% d^{-1}), was unexpected because in 1999 we found instantaneous growth rates of early stages of the closely related catfish *Hoplosternum littorale* to be significantly different, by a factor of 1.8, in two nearby rice fields in the district of Coronie, Suriname (Ponton *et al*. 2001). Recently obtained information from interviews with rice farmers in Coronie (Ponton & Mol, unpubl. data) revealed that the rice field with fast-growing *H. littorale* was not used for growing rice in 1999. The occurrence of a conspicuous check in the otoliths of *H. littorale* with a low growth coincided with the timing of a tillage practice ('puddling') in the rice field. Thus the difference in growth performance of young *H. littorale* in the two Coronie rice fields can be attributed to human-induced habitat degradation.

Inter-cohort variation in growth rates may be expected in species with an extended spawning season (Szedlmayer & Conti 1998). In coastal swamps of Suriname, *M. thoracata* has an extended spawning season from January to July (Mol 1996*b*), and this extended reproductive season was also evident in the Maykaboeka Creek (Figure 7). However, hatch-date analyses showed that most young *M. thoracata* we analysed were born in January–March, i.e. the short rainy season. Future studies should address the question of whether growth rates differ between *M. thoracata* hatched in the first rains immediately after the long dry season of September–November and fishes hatched later in the year in the long rainy season of April–July.

The instantaneous growth rates described in the present study were obtained from population (cohort) averages. However, growth rate variability among individuals is likely to affect cohort survival and age structure (Rice *et al*. 1993), especially in species like *M. thoracata* for which mortality sources of early stages are highly selective towards the smallest individuals (Mol 1996*b*). Thus, the differences in instantaneous growth rate we observed within and among habitats may be even more pronounced if the slowest-growing individuals (and thus the smallest individuals for their age) disappear rapidly under negative selective pressure. Such negative selective pressure exerted upon slow-growing individuals would be detected only by regularly sampling individuals of a given cohort and determining whether the distribution of the individual growth rates (as indicated by increment width) shifts towards a higher value with time.

ACKNOWLEDGEMENTS

We thank P. Deixonne, J. P. Lamoureux and S. Ramanand for help with sampling, T. Girard for taking vegetation records at the sampling stations in Kaw Swamp and M. Hoff, IRD-Muséum National d'Histoire Naturelle de Paris, for checking vegetation analyses. This investigation was funded by the Fonds Interministériel de Coopération Régionale Caraïbes-Guyanes contract # 42-10-67 and IRD (Institut de Recherche pour le Développement).

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Appendix 1. Study species.

Reis (1997) recognized that *Hoplosternum thoracatum* (Valenciennes, 1840) has been confounded with a second species and described a new genus to accommodate the two species: *Megalechis personata* (Ranzani, 1841) and *M. thoracata* (Valenciennes, 1840). Although Reis (1997) held that both species occur in the Guianas, he found only one species present in his specimens from Suriname and he failed to examine material from French Guiana, including the holotype of *H. thoracatum* from the Mana region (MNHN 4266). Recently, P. Y. Le Bail (INRA, Rennes, France) studied the holotype of *H. thoracatum* following the diagnostic morphometrics and meristics of Reis (1997). Based on the measurements and counts of the holotype, especially the number of unbranched anal rays (6) and the length of the dorsal spine (0.39% of the dorsal-fin base), Le Bail concluded that: '*Megalechis personata sensu* Reis is *Megalechis* (*Hoplosternum*) *thoracata sensu* Valenciennes' (letter of 16 April 1999 to J. H. Mol, including measurements and a photograph of the holotype). Thus, *M. personata* (Ranzani, 1841) is a junior synonym for *Megalechis thoracata* (Valenciennes, 1840) and consequently we follow Le Bail *et al*. (2000) in using the latter name for the species *M. personata* of Reis (1997). When adult *Megalechis* from the collection sites in French Guiana (three fishes from Kaw Swamp) and Suriname (14 fishes from Lelydorp Swamp and 13 fishes from Maykaboeka Creek) were examined using the criteria of Reis (1997), all specimens could be identified as *M. thoracata*. In Guyana, however, two *Megalechis* species are present (Reis 1997; Mol, pers. obs.): *M. thoracata* seems restricted to the coastal plain, while the second *Megalechis* species was found only in the interior (Mol, *pers. obs.*). Although we cannot confirm the occurrence of the second *Megalechis* species in Suriname and French Guiana, this species could be present in eastern French Guiana (e.g. Kaw Swamp) because the Oyapock River is the northern distribution limit of several Amazonian fish species reported for the wetlands of Amapá, Brazil (Jégu & Keith 1999). The early life stages (< 25 mm SL) of the two *Megalechis* species show a similar pigmentation pattern of four to five dark transverse bands (Reis 1997) and they are probably not easily distinguished from each other.

https://doi.org/10.1017/S026646740300333X Published online by Cambridge University Press