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How many meals a day to minimize cannibalism when rearing larvae of the Amazonian catfish *Pseudoplatystoma punctifer*? The cannibal's point of view

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Abstract – Meal frequency is a key parameter in fish larviculture, especially in highly cannibalistic species. Knowledge of the biological bases of cannibalism (growth capacity of cannibals, morphological constraints on cannibalism, prey size preference) can help predicting the risks of cannibalism for different feeding schedules under culture conditions. This study relied on the day-by-day analysis of prey size preference and bioenergetics of individual cannibals of the catfish *Pseudoplatystoma punctifer* (8–65 mm standard length, *SL*, 0.5–400 mg dry mass, *DM*) at 28.5 °C under 12L:12D. The results were equated with the ontogenetic variations of morphological factors (head and mouth width) and feed efficiency of larvae feeding on *Artemia* nauplii, in order to calculate the risks of cannibalism among fish fed 2–7 daily meals. The predation capacities of *P. punctifer* were highest at 8 mm *SL* and decreased in larger fish (largest prey = 86% and 70% *SL* in fish of 8 and >30 mm *SL*, respectively). Cannibals of increasing size preferred increasingly smaller prey relative to their own size, but also to their predation capacities. These morphological and behavioural constraints were largely compensated for by bioenergetics performance. Cannibals consumed high daily food rations (as high as 171 and 29% *DM* in fish <1 and >300 mg *DM*, respectively), exhibited high gross conversion efficiencies (0.50–0.55 and about 0.70, in fish <1 and >30 mg *DM*, respectively), and grew rapidly (90 and 18% *DM* day^{-1} in fish <1 and >300 mg *DM*, respectively). The growth advantage of cannibals over siblings fed *Artemia* nauplii was decisive, except for high meal frequencies (6–7 daily meals). This study supports the view that the risk of cannibalism and adequate feeding strategies can be largely predicted in a particular fish species if the morphological, behavioural and bioenergetics bases of cannibalism are examined altogether in an ontogenetic perspective.

Key words: Aquaculture / Cannibalism / Ontogeny / Growth / Morphology / Behaviour / Siluriformes

1 Introduction

The adoption of adequate feeding strategies is frequently a key to successful larval rearing, as the type of food, mode of distribution, meal size and meal frequency intimately govern fish growth and size heterogeneity (Paller and Lewis 1987; Folkvord and Otterå 1993; Kubitza and Lovshin 1999). Meal size is generally maximised, otherwise there is a differential food intake, heterogeneous growth, greater size dispersal and eventually higher risks of cannibalism (Hecht and Pienaar 1993; Kestemont et al. 2003). By contrast, the number of daily meals, and thus growth is not always maximised, depending on the objectives of the production, operational schedules or technical constraints, which may vary between producers and rearing systems. In species with strong cannibalistic habits, the penalty for not maximising growth can be more severe in terms of survival (Hecht and Pienaar 1993; Folkvord 1997; Baras and Jobling 2002). In general, information on the acceptable numbers of daily meals or meal sizes under culture conditions is gained through experience and essay-errors (e.g. Katavic et al. 1989; Qin and Fast 1996). However, this information can also be predicted, at least in part, from the biological bases of cannibalism and their variations during the ontogeny of fishes.

Most studies aiming at predicting the risk of cannibalism in fishes focused on the morphological factors that govern predation capacities and their ontogenetic variations (Hecht and Appelbaum 1988; Qin and Fast 1996; Parazo et al. 1991;

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Sogard and Olla 1994; Hseu et al. 2003, 2004). In general, during the larval and juvenile stages there is a positive allometric growth of body depth (or width) and a negative allometric growth of mouth dimensions, which altogether force cannibals to select prey that are increasingly smaller relative to their own size (Hecht and Pienaar 1993; Baras and Jobling 2002). This information is indispensable for calculating the largest prey that can be eaten whole by a cannibal of a particular size. However, it is frequent that cannibals do not prefer consuming prey as large as possible, as these prey might not guarantee the highest energy return, because of lower capture success, longer handling time or greater risk of retaliation (synthesis in Baras and Jobling 2002). As for predation capacities, prey size preferences can vary substantially during the ontogeny (Hecht and Appelbaum 1988; Folkvord and Otterå 1993; Baras 1999; Baras et al. 2010a). Any further prediction of the risk of cannibalism requires estimating how many fish are cannibalised per unit of time, and for how long cannibals will continue preying upon the stock. The maximal daily impact of cannibalism can be estimated by multiplying the number of fish that are large enough to exercise cannibalism and the numbers of daily victims *per capita*, which can be obtained by equating the maximal food intake of cannibals and their maximal or preferred prey size. The duration of cannibalism depends on how fast cannibals grow relative to their potential victims, in particular on whether the immediate growth advantage provided by the exercise of cannibalism (Kubitza and Lovshin 1999) suffices to compensate for the increasing morphological constraints upon cannibalism in fish of increasing size (Baras 1999; Baras and Jobling 2002).

This study precisely analysed the ontogenetic variations of the maximal size ratios enabling cannibalism, prey size preference, food intake, conversion efficiency and growth in a species with reputed cannibalistic habits. These performances and constraints are compared with the growth rates of siblings fed *Artemia* nauplii at different meal frequencies to estimate the risks of cannibalism associated to different feeding schedules. The target species is an Amazonian catfish, the surubi *Pseudoplatystoma punctifer* (Castelnau) (Pimelodidae; formerly *P. fasciatum* (L.) for fish of the Amazon River, see Buitrago-Suárez and Burr 2007). This piscivorous catfish is a candidate to the diversification of aquaculture in South America (Kossowski 1996; Nuñez 2009), and its spineless tasty flesh has also raised interest for its culture outside of its original distribution area (e.g. USA, Dabrowski et al. 2008). As in many other piscivorous fish species, cannibalism is most frequent during its larval and juvenile stages, and has largely compromised the development of its aquaculture for a while (Padilla Pérez et al. 2001; Arslan et al. 2008; Nuñez et al. 2008).

2 Methods

2.1 Fish and rearing environment

Fish were half siblings produced from the artificial reproduction of captive broodfish (one female, three males) in the Aquaculture Research Station of the Instituto de Investigaciones de la Amazonia Peruana (IIAP) at Quistococha (Iquitos, Loreto, Peru). Hormonally induced ovulation, egg fertilisation and incubation were performed following Nuñez et al. (2008). Hatching took place 17 h after fertilization. During the hours following hatching, fish were transferred in 30-L square tanks (40 × 40 × 19 [h] cm; stocking densities of about 20 fish L^{-1}) in an indoor recirculating system under a natural photoperiod (12L:12D). Water temperature was maintained at 28.0 ± 0.5 °C with a 2-kW heater connected to a Biotherm 2000 thermostat, and oxygen was near saturation (>90%). From the age of 60 h after hatching (hah) onwards, fish were fed live, freshly hatched brine shrimp (*Artemia* sp.) nauplii. A group of fish was fed in excess five times a day, and four other ones only twice a day, in order to produce rapidly a size differential for the predation experiments (see below). Two other groups of fish, also fed five times a day, were spared for morphological analyses. No food was distributed at night, and uneaten food was removed in the evening with a siphon to ensure that fish had empty guts when predation experiments started the following morning.

2.2 Morphology

Fish were sampled every 12 h until 96 h after hatching (hah), at daily intervals until the age of 7 days after hatching (dah) and less frequently afterwards, until they attained 60–70 mm in standard body length (*SL*). At every sampling time, fish were anaesthetised (2-phenoxy-ethanol, 0.4 ml L^{-1}) and photographed under the stereomicroscope by reference to a graduated mark. The study focused on mouth width (*MW*) and head width (*HW*), which are the key morphological factors for cannibalism in this species, and on head length (*HL*), which varies substantially during the larval and juvenile stages of *P. punctifer*. All dimensions were measured from digital photographs (nearest pixel), expressed in proportion of *SL* then equated to *SL*, using simple or polynomial regression models. The largest prey (SL_{Pmax}) that could be ingested by a cannibal of particular size was deduced from the comparison between modelled values of *MW* (for cannibals) and *HW* (for prey).

Additional samples were collected to document the relationships between *SL*, wet body mass (*WM*) and dry body mass (*DM*) in fish with empty guts. Following the measure of *WM* (nearest 0.1 mg), fish were euthanized (2-phenoxy-ethanol, 2.0 ml L^{-1}), placed at 105 °C for 12 h then weighed again for the measure of *DM* (AOAC 1995). *WM* was individually measured in fish >10 mg and in groups of 5–20 individuals of homogenous size for smaller specimens. For *DM*, the measurements were done on groups of fish producing at least 30 mg of *DM* (tens of fish for larvae, at least three fish for large juveniles).

2.3 Predation experiments

Design

The design of predation experiments in this study was almost replicated from Baras et al. (2010a). All predation experiments took place in cages immersed at 90% in an independent water recirculating system where temperature was maintained at 28.5 ± 0.2 °C (mean ± SD) under natural day length.

Two sizes of predation cages were used: 0.5 L (12.5 × 8.0 × 5.0 [h] cm) and 2.5 L (17 × 17 × 11 [h] cm), for cannibals < and >21 mm *SL*, respectively. In each cage, a single large fish (i.e. the future cannibal) was placed together with smaller siblings (potential prey) of known dimensions. No other food was provided. The amount of prey fish per cage (n = 15–20, depending on fish size) was in large excess of the presumed cannibal's food intake (see reasons in Baras et al. 2010a), except on some occasions (n = 0–5 prey) so as to document the relationships between growth and food intake over a broader range. The latter situations were not retained in the analyses of prey size preference. Prey fish were selected on the basis of two criteria: (1) all prey had to be small enough to be eaten whole by the cannibal (based on the results of the morphological study), and (2) their size distribution had to be broad enough to give the cannibal the opportunity of selecting between prey of different sizes, but not excessively broad otherwise prey fish could eat each other. To test whether the latter situation could happen, a control group, consisting of prey fish with a similar size distribution as in the predation cages, but without any large cannibal, was installed in an additional cage and offered no food. The operation was repeated every day.

Every 24 h, fish were collected and cages were cleaned to remove faeces. The cannibal was anaesthetised, weighed (nearest mg), revived and returned rapidly to the same cage as on the previous day, together with a new set of prey fish. Surviving prey fish were anaesthetised and measured again. The method for identifying the victims of cannibalism depended on whether *SL* or *WM* was measured. *SL* was measured preferentially in fish <14 mm *SL* (<30 mg *WM*), and *WM* in larger fish, because of size-dependent accuracy and risk of injuring fish upon weighing. The identification of missing prey was straightforward when *SL* was measured, as this dimension did not vary in fish deprived of food over 24 h. By contrast, *WM* decreased during this interval, thereby requiring a two-step back-calculation protocol for the identification of eaten prey: (1) the *WM* of prey fish after 24 h of food deprivation was estimated by subtracting from the initial *WM* the weight loss that was measured in the control group; (2) missing cases in the actual final distribution of *WM* were moved by successive iterations, in order to determine (with simple linear regression tests) the best fit (i.e. the combination with the highest r^2 and a slope of 1.00; further details in Baras et al. 2010a).

No more than seven predation cages were studied per day, in order to reduce the monitoring period to 30 min. Cannibals were studied over a maximum of five consecutive days. Surviving prey fish were never used again in any subsequent experiment.

Data analysis

All bioenergetics data were expressed in terms of *DM*. For cannibals, which were studied several days in a row, *DM* was deduced from the *WM-DM* models that were determined during the morphological study of well-fed fish (Table 1). These models were not used for prey fish, which had been fed less frequently, as feeding restrictions result in lower *DM*:*WM* ratios. Hence, on each day of experiment, the *DM*:*WM* ratio was measured (1) at the start of each period of 24 h, in an additional group of prey fish of similar size as in the predation cages, and (2) in the control group after 24 h of food deprivation, so as to determine the loss of *DM* over 24 h. The precise timing of cannibalistic bouts was unknown. For the sake of simplicity, it was assumed that prey fish were on average eaten at mid of each 24-h period and therefore that they lost weight over 12 h. The daily food ration of the cannibal (R, mg *DM*) was thus calculated as $R = \sum 0.01(1{-}0.5WC_f - 0.5WC_i)(0.5\,WM_f + 0.5WM_i)$, where WC is the water content (% *WM*), WM is the wet mass (mg) of eaten prey fish, and suffixes f and i stand for final and initial, respectively. WM_f was calculated as $WM_f = WM_i(1 - WML)$, where WML is the proportion of *WM* lost during 24 h of starvation, as measured in the control group. When the *SL* of prey fish was measured, their *WM* at the start of each 24-h period was back-calculated from the *WM-SL* model documented in the morphological study.

The daily relative growth rate of cannibals (G, % DM_ci day^{-1}) was calculated as $G = 100(DM_\mathrm{cf} - DM_\mathrm{ci})\,DM_\mathrm{ci}^{-1}$, where DM_cf and DM_ci are the dry masses of the cannibal at 1-day interval. The gross conversion efficiency (*GCE*, *DM*:*DM*) was calculated as $GCE = GR^{-1}$, where G is the daily growth rate and R is the daily food ration (both in % DM_ci).

Thereafter, the values of R, G and *GCE* were equated to the cannibal's *DM*. Simple (R and G) or polynomial (*GCE*) power regression models were constructed from the highest values in fish of different sizes, with the objective of tracking the top performances of cannibals. In parallel, G was equated with R for calculating the (negative) growth during 24-h starvation (G_s) and the maintenance food ration (R_maint) producing zero growth. The latter calculations were made on a discrete basis, using seven size categories of cannibal (see results).The seven values of G_s and R_maint were equated to the mean *DM* of cannibals in each category.

For each category of cannibals, prey size preference was calculated in two complementary ways. The size of each eaten prey SL_P was expressed as a proportion of the cannibal's size SL_C, and of the largest prey SL_Pmax that could be eaten whole by the cannibal, with the objective of testing whether cannibals of different sizes showed similar prey size preferences in respect to their predation capacities. For both ways of calculations, size ratios were categorized, using 4% intervals. The preference index I_p of cannibals for each class of prey size was calculated as $I_p = N_c N_a^{-1}$, where N_c and N_a are the numbers of eaten and available prey in this size class. Classes with $N_a < 5$ were not taken into account for the calculation of I_p. In order to enable direct comparisons between cannibals of different sizes, I_p values were normalized (i.e., the highest value was set at 1.00).

2.4 Growth of larvae fed *Artemia* nauplii

For logistic reasons, it was not possible measuring the growth of groups of larvae fed *Artemia* nauplii at all possible meal frequencies throughout the larval stage. Additionally, different frequencies would have resulted in variable rates of cannibalism, which would have skewed growth estimates. Instead, these growth rates were estimated indirectly as follows.

Two-day old larvae of *P. punctifer* (n = 10) were housed in individual enclosures and offered freshly hatched *Artemia* nauplii four times a day, using a maximal meal size, i.e.

Table 1. Morphological relationships in larvae and juveniles of *P. punctifer* (fish of 4–66 mm SL; 0.5–2 560 mg WM). SL = standard body length; HL = head length; HW = head width; MW = mouth width; SL_{Pmax} = largest prey that can be consumed by a cannibal of a particular SL, WM = wet body mass; DM = dry body mass. All masses are expressed in mg and other dimensions in mm, except for SL_{Pmax} (% SL), $p < 0.0001$ for all models, * indicates that this model is calculated from modelled data, using the models between MW and SL, and between HW and SL (see Fig. 1).

Equation	Size range (mm SL)	r^2	F	df
$HW = 0.140 + 0.0275\,SL + 0.0252\,SL^2 - 0.00077\,SL^3$	<20	0.996	2 090	31
$HW = 1.508 + 0.165\,SL$	>20	0.991	1 618	15
$MW = -0.113 + 0.0994\,SL + 0.0104\,SL^2 - 0.00031\,SL^3$	<20	0.993	1 364	31
$MW = 0.970 + 0.134\,SL$	>20	0.984	862	15
$HL = 0.375 - 0.050\,4SL + 0.0386\,SL^2 - 0.00141\,SL^3$	<13	0.994	1 153	25
$HL = 1.693 + 0.363\,SL$	>13	0.999	8 631	21
$SL_{\mathrm{Pmax}} = -254.4 + 1074.7(\log SL) - 1209.2(\log SL)^2 + 571.3(\log SL)^3 - 97.2(\log SL)^4$	4–66 *	0.993	2 651	84
$\log WM = 1.731 - 10.472 \log SL + 14.721(\log SL)^2 - 5.010(\log SL)^3$	<11.5	0.988	2 403	91
$\log WM = -1.823 + 2.875 \log SL$	>11.5	0.992	26 564	211
$\log(DM{:}WM)(\%) = 1.0459 + 0.01492 \log SL + 0.01003(\log SL)^2$	4–66	0.979	459	22

$M_{\max}(\%WM) = 14.14 + 8.07 \log WM - 2.36(\log WM)^2$ (Baras et al., in press). In the evening, about 30 minutes after the last meal, water was renewed and uneaten nauplii were counted. Fish were measured at 4, 8, 12, 16, 20 and 24 dah to determine their G and GCE. In the calculation of GCE, no correction was made for uneaten nauplii, which were always in low amounts (always <10% and on average 3% of the feeding level). In parallel, fish of various sizes (1–110 mg WM, $n = 35$) were held in isolation and deprived of food over 24 h to model the relationship between WM and G_s. For each period in the growth study (2–4, 4–8, … 20–24 dah), the net conversion efficiency (NCE, $WM{:}WM$) was calculated as $NCE = (G_o - G_s)\,R^{-1}$, where G_o is the observed growth, G_s is the negative growth during starvation, and R is the mean daily food ration over the rearing period (all variables in mg WM day^{-1}; mean WM of 0.015 mg for *Artemia* nauplii). Thereafter, NCE was equated to the geometric mean WM of fish over each period so as to describe its ontogenetic variations in *P. punctifer*.

One major advantage of NCE is that it can serve to estimate the theoretical growth of fish fed n daily meals of known volume, provided that the ontogenetic variations of G_s and $M_{\max}$ are known, which is the case for *P. punctifer*. Based on data of gut evacuation rate in young *P. punctifer* (Baras et al., in press), and current practices in the larviculture of this species, growth trajectories were calculated for fish fed ad libitum up to seven times a day.

2.5 Impact of cannibalism

The risk of cannibalism among fish fed different meal frequencies can be estimated by equating the data collected in the different parts of the study, i.e. the growth trajectories of fish fed *Artemia* nauplii (2.4), the growth and food ration of cannibals feeding maximally (2.3) and the morphological constraints upon cannibalism (2.2). These data enable the calculation of the number of daily victims of an individual cannibal at a particular age, and their iteration over time gives an estimate of how fast the stock is depleted by cannibalism. The final information that is needed to estimate the impact of cannibalism is the proportion of fish that exercise cannibalism, which is probably the most variable component of the cannibalistic dynamics, as it depends on a series of complex interactions between biological and environmental variables (Baras and Jobling 2002). Here, an estimate of this proportion was obtained by examining at 13 dah the size distributions of larvae stocked at 4 dah in sixteen 30-L tanks (25 fish L^{-1}) and fed in slight excess four times a day. It was assumed that the "jumpers" had gained their larger size through cannibalism, and in all instances they were large enough to cannibalise siblings in their respective tanks on the day of measurement.

2.6 Statistical analyses

Contingency tables analyses were used to test for random prey selection in each size category of cannibals, and whether cannibals of different sizes exhibited different preferences with respect to predation capacities. Simple (linear, logarithmic, power) and polynomial regression analyses were used to model the relationships between morphological variables and fish size, and between bioenergetics descriptors (see above). Null hypotheses were rejected at $p < 0.05$.

3 Results

3.1 Morphology

At hatching, embryos of *P. punctifer* were 3.2 ± 0.1 mm in total length (TL; mean ± SD). The notochord was bent at 16–18 hah, the mouth was open at 24 hah, and exogenous feeding commenced at 48–60 hah, when larvae were 4.4 ± 0.1 mm SL (5.2 ± 0.2 mm TL). At this stage, head width (HW) and mouth width (MW) averaged 15.3 and 10.5% SL, respectively (Fig. 1; models in Table 1). Both dimensions exhibited a positive allometric growth and attained their longest extension (relative to the fish SL) at 16.5 mm SL for MW (18% SL) and at 18 mm SL for HW (23.5% SL). Thereafter, they exhibited a period of negative allometric growth, followed by isometric growth in fish >50 mm SL. By contrast, head length increased steadily throughout this ontogenetic interval, from 18% SL at the start

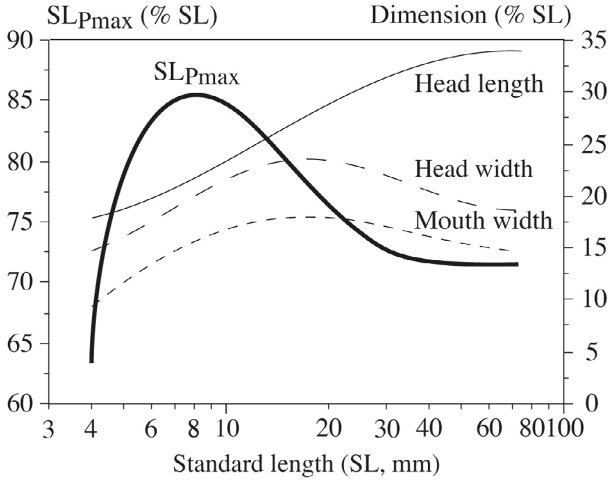

Fig. 1. Variations of mouth width, head width, head length (thin lines, right vertical axis), and the largest prey SL_{Pmax} that can be ingested whole by the cannibal, thick line, left vertical axis) during the ontogeny of *P. punctifer*. All dimensions are expressed in percents of the fish standard body length (*SL*). Curves constructed from the models in Table 1.

of exogenous feeding to about 34% *SL* in fish >50 mm *SL* (Fig. 1).

Throughout the larval and early juvenile stages, *HW* was the largest cross-sectional body dimension, and the morphological constraints upon cannibalism were governed by the ratio between the *MW* of the cannibal and the *HW* of the prey. At the start of exogenous feeding (4.4 mm *SL*), the largest prey that could be ingested whole by a cannibal (SL_{Pmax}) was about 73% *SL*. It increased rapidly, peaked at 86% at 8 mm *SL*, then decreased and attained a plateau at about 70% *SL* in fish >30 mm *SL* (model in Table 1). Remnants of incomplete cannibalism, in which the victim is ingested tail first and its cephalic region is discarded by the cannibal, were occasionally observed in the rearing tanks spared for the morphological study. This behaviour was no longer observed beyond 8–9 dah (fish >8–9 mm *SL*), supporting the view that complete prey ingestion was the main mode of cannibalism in this species.

3.2 Predation experiments

Cannibals ranging from 8 to 65 mm *SL* (corresponding body masses of 4 to 2 437 mg *WM*, and 0.5 to 397 mg *DM*) were studied over 147 days × fish (Table 2). In total, 2 337 prey (5–32 mm *SL*) were offered, of which 581 (25%) were eaten. This proportion suggests that food availability was always in excess of the cannibals' needs. Only two (out of 300) fish died in the control groups, and none of them had been consumed in part or totality, which suggests that the missing fish in the predation cages had been eaten by the large cannibals exclusively, and that natural mortality was low and did not impact substantially on prey size selectivity.

Prey size selectivity

The hypothesis of random prey selection was rejected at $p < 0.05$ in all size categories (Table 2). Cannibals of increasing sizes preferred eating prey of decreasing sizes relative to their own (Fig. 2a), which was expected as predation capacities decrease in fish >8 mm *SL* (Fig. 1). However, size-dependent differences persisted after prey size was equated to SL_{Pmax} (Fig. 2b), thereby indicating that cannibals of increasing size preferred increasingly smaller prey by reference to their predation capacities. The size-dependent models constructed from this analysis were highly significant ($r^2 > 0.97$, $p < 0.0001$; see caption of Fig. 2). They predict that each time the cannibal *SL* doubles, the relative size of its preferred prey decreases by 20% by reference to its body length, and by 14% by reference to its predation capacities.

Bioenergetics

In every size categories of cannibals, the relationship between growth (*G*) and food ration (*R*) was systematically best described by a simple linear regression model ($p < 0.0001$; Table 3). The weight loss during starvation (G_s) and the maintenance food ration (R_{maint}) were high in larvae <1 mg *DM* (6.5% *DM* day^{-1} and 12.2% *DM*, respectively). The values of both variables decreased rapidly until cannibals were about 30 mg *DM*, and stabilised around 2.8% *DM* day^{-1} (G_s) and 3.9% *DM* (R_{maint}) in larger fish (Table 3). The value of the highest food ration consumed by the cannibal ($R_{\max}$) decreased rapidly with increasing fish size (Fig. 3a), passing from 171% *DM* in fish <1 mg *DM* to 29% *DM* in fish >300 mg *DM*. The value of $G_{\max}$ (i.e. the growth at $R_{\max}$) also decreased in fish of increasing size (90 and 18% *DM* day^{-1} in fish <1 and >300 mg *DM*, respectively; Fig. 3b), but at a slower rate than for $R_{\max}$ (log-log relationships, slopes of –0.265 and –0.292, respectively; Table 3). This difference reflected ontogenetic variations of *GCE*, which passed from 0.50–0.55 in fish <1 mg *DM* to 0.65–0.70 in fish >30 mg *DM* (Fig. 3c). This curvilinear increase of *GCE* paralleled the curvilinear decrease of their R_{maint} and G_s during the ontogeny of *P. punctifer* (Table 3).

3.3 Growth advantage of cannibals and impact of cannibalism

As was the case for measurements on cannibals, the relationship between the weight loss during 24-h starvation (G_s, % *WM* day^{-1}) and *WM* was curvilinear (Fig. 4a). Larvae raised in isolation and fed *Artemia* nauplii four times a day averaged 159 ± 12 mg *WM* (25 ± 1 mm *SL*) at 24 dah. Their *GCE* (*WM*:*WM*) at 2–4 dah (0.8 mg *WM*, 4.8 mm *SL*) averaged 0.24 (Fig. 4b). It increased rapidly in fish of increasing age and size, and attained a plateau at 0.38–0.39 in fish >10 mg *WM* (10 mm *SL*). The value of *NCE* for a particular fish size was calculated from the modelled values of G_s and *GCE*, and served to model the growth of fish fed two to seven daily meals (see Sect. 2.4). The resulting growth trajectories are shown in Figure 5, together with those of cannibals growing maximally, and those of their largest and preferred prey. The proportion

Table 2. Characteristics of the experiments for studying the bioenergetics and prey size preference in larvae and juveniles of *P. punctifer*. *WM* is the fish wet body mass, *DM* is its dry body mass and *SL* is its standard body length. Indices ci and P refer to the initial size of cannibal and prey at the start of each 24-h cycle. Prey size expressed by reference to the cannibal size SL_{ci} or to the largest prey that can be eaten whole by the cannibal (SL_{Pmax}, see Fig. 1). Prey size preference tested by contingency table analyses: Symbols ***, ** and * stand for $p < 0.001$, <0.01 and <0.05, respectively, and NS for $p > 0.05$.

Cannibal size categories			1	2	3	4	5	6	7
Cannibal	WM_{ci} (mg)	mean	6.2	15.7	47.8	147.7	358.2	1145	1967
		range	4.0−8.2	9.5−24.0	26.9−77.2	83.9−212.4	252.1−537.7	687−1572	1611−2437
	DM_{ci} (mg)	mean	0.7	1.9	6.0	19.8	50.7	175.9	314.8
		range	0.5−1.0	1.1−3.0	3.3−9.9	10.9−29.0	34.8−78.0	101.4−246.9	253.4−396.6
	SL_{ci} (mm)	mean	8.9	11.2	16.5	24.5	33.3	49.9	60.2
		range	8.0−9.6	9.9−13	13.5−19.5	20.1−27.8	29.5−38.4	41.8−55.7	56.2−64.9
N observations (day × fish)			16	20	19	21	16	36	19
n prey offered			225	209	210	302	179	503	128
n prey eaten			72	90	69	69	45	179	57
Prey SL_P(mm)		range	5.0−7.8	6.3−8.8	7.3−11.6	9.9−17.6	13.0−19.8	15.6−30.6	18.1−32.6
Preference (4% SL_{ci} class)			***	***	***	***	**	***	**
Prey size (% SL_{Pmax})		range	63−103	64−93	58−89	51−95	51−80	43−82	42−72
Preference (4% SL_{Pmax} class)			***	***	***	***	NS	***	**

Table 3. Bioenergetics of cannibalism in *P. punctifer*. Upper part: relationships between growth *G* and daily food ration *R* (both in DM_{ci} day^{-1}) in the seven size categories of cannibals (see Table 2). DM_{ci} is the dry body mass (mg) of the cannibal at the start of a 24-h period over which growth is measured. Lower part: size-dependent variations of maximum daily food ration ($R_{\max}$), maximum growth ($G_{\max}$), maximum gross conversion efficiency ($GCE_{\max}$, *DM*:*DM*), maintenance food ration (R_{maint}, % DM_{ci}) and negative growth during 24 hours of food deprivation (G_s, % DM_{ci} day^{-1}). The models for R_{maint} and G_s are constructed from the seven models in the upper part of the table. The models for $R_{\max}$, $G_{\max}$ and $GCE_{\max}$ are deduced from the highest scores observed in cannibals of different sizes (Fig. 3). Symbols ***, ** and * stand for $p < 0.001$, <0.01 and <0.05, respectively.

Equation	r^2	*F*	*df*	*p* intercept	*p* slope
Size category 1: $G = -6.458 + 0.531\,R$	0.980	697	15	**	***
2: $G = -5.160 + 0.571\,R$	0.979	852	19	*	***
3: $G = -4.482 + 0.606\,R$	0.990	1 737	18	***	***
4: $G = -3.142 + 0.697\,R$	0.983	1 123	20	**	***
5: $G = -2.692 + 0.715\,R$	0.994	2 303	15	***	***
6: $G = -2.662 + 0.693\,R$	0.964	924	35	***	***
7: $G = -2.799 + 0.688\,R$	0.988	1 431	18	***	***
$\log R_{\max} = 2.190 - 0.292 \log DM_{\text{ci}}$	0.969	1 231	40	***	***
$\log G_{\max} = 1.930 - 0.265 \log DM_{\text{ci}}$	0.943	647	40	***	***
$\log GCE_{\max} = -0.267 + 0.085 \log DM_{\text{ci}} - 0.021(\log DM_{\text{ci}})^2$	0.832	94	40	***	***,***
$\log R_{\text{maint}} = 1.051 - 0.391 \log DM_{\text{ci}} + 0.082(\log DM_{\text{ci}})^2$	0.963	52	6	***	**, *
$\log(-G_s) = 0.784 - 0.281 \log DM_{\text{ci}} + 0.055(\log DM_{\text{ci}})^2$	0.966	56	6	***	**, *

of jumpers at 13 dah among groups of 750 fish fed four meals a day varied very little between experimental tanks and averaged 0.5 ± 0.3% (mean ± SD). Calculations of the impact of cannibalism were done on the basis of this proportion (Fig. 6).

Based on these models, fish fed seven daily meals would always grow fast enough to escape cannibalism (Fig. 5), except possibly during the very first rearing days, when cannibalism consists in the incomplete ingestion of the prey, and does not require any size differential for its exercise. In fish fed six daily meals cannibalism would become virtually impossible after 12 dah and the total losses would be <15%. By contrast, fish fed two or three meals a day would grow at a slower rate than the preferred prey size of cannibals. The number of daily victims would increase rapidly, and 90% of the stock would have succumbed to cannibalism at the ages of 14 or 21 dah, for two or three daily meals, respectively (Fig. 6). Fish fed four or five daily meals would always fall between the maximal and preferred prey size of cannibals (Fig. 5) and for both situations the number of daily victims would decrease rapidly beyond 10–12 dah (Fig. 6). However, the total impact of cannibalism at 21 dah with four daily meals would be almost twice as high as with five daily meals (48 versus 25%).

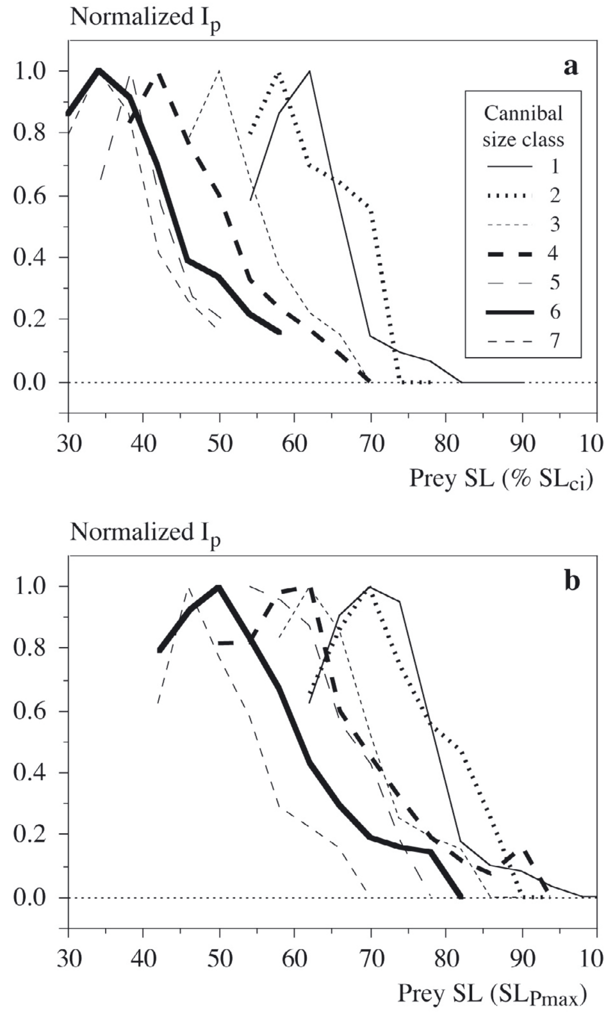

Fig. 2. Prey size preference in cannibalistic *P. punctifer* of different sizes (categories 1–7, Table 2). For each category, the preference index (I_p) is normalized so that the maximum is 1.00. Prey size expressed as a proportion of the cannibal's standard body length (SL_{ci}, a), and of the largest prey that can be ingested whole by the cannibal (SL_{Pmax}, b). The relationships between SL_{ci} and preferred prey size (P_P), using the modes shown in graphs a and b, stand as: log P_P (% SL_{ci}) = 2.107–0.336 log SL_{ci} (r^2 =0.983, F =293, df = 6, $p < 0.0001$ for both intercept and slope), log P_P (% SL_{Pmax}) = 2.065–0.219 log SL_{ci}(r^2 = 0.974, F = 188, df = 6, $p < 0.0001$ for both intercept and slope).

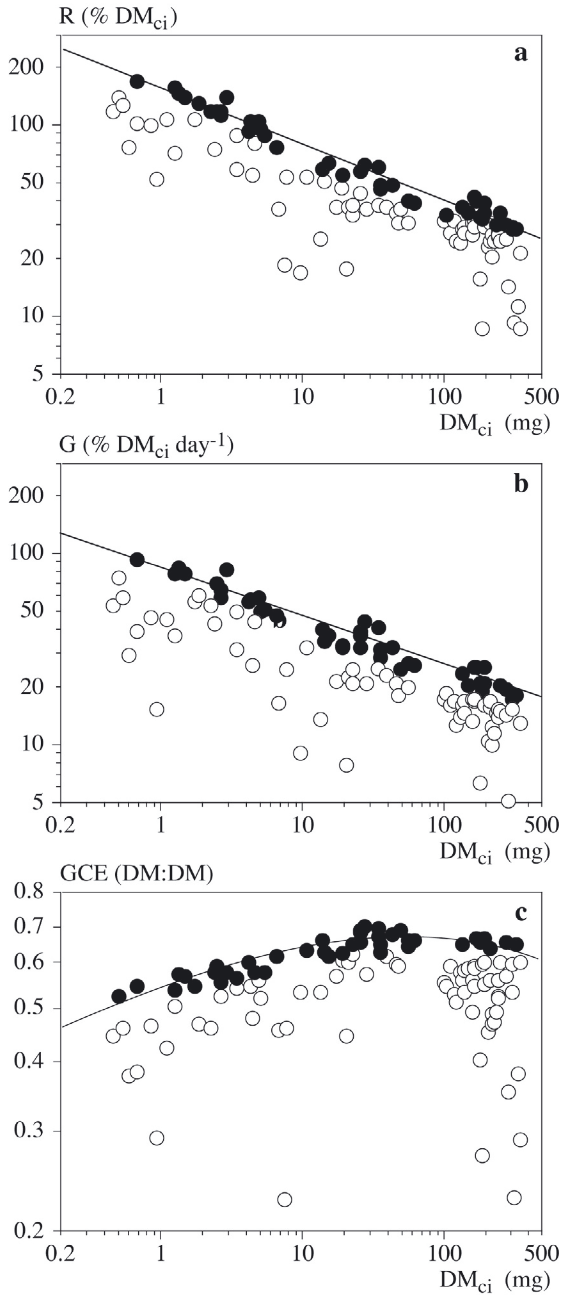

Fig. 3. Size-dependent variation of daily food ration (R), growth (G) and gross conversion efficiency (GCE, DM:DM) in cannibalistic *P. punctifer*. DM_{ci} is the dry body mass (mg) of cannibals at the start of the 24-h cycle over which growth and food intake are measured. Data points refer to individual measurements. Polynomial (GCE) or simple (R and G) power regression models are constructed from the highest points only (dark circles; equations and statistics in Table 3).

4 Discussion

4.1 Morphological constraints on cannibalism and prey size preference

This study highlighted that young *P. punctifer* suffered from little morphological restrictions for cannibalising siblings, although their mouth width never exceeded 17% *SL* (Fig. 1), which is quite low by reference to many piscivorous fish species (Shirota 1970). However, throughout the larval and early juvenile stages, the body shape of *P. punctifer* remained slender, thereby facilitating cannibalism (SL_{Pmax} of 86% at 8 mm *SL*, and around 70% in fish >30 mm *SL*, corresponding *WM* ratios of 57 and 40% respectively). These scores compare to those of highly cannibalistic species such as barramundi *Lates calcarifer* (Parazo et al. 1991), northern pike *Esox lucius* (Bry et al. 1992; Ziliukiene and Ziliukas 2006), tunas (Sawada et al. 2005) and groupers *Epinephelus* spp. (Hseu et al. 2003, 2004, 2007).

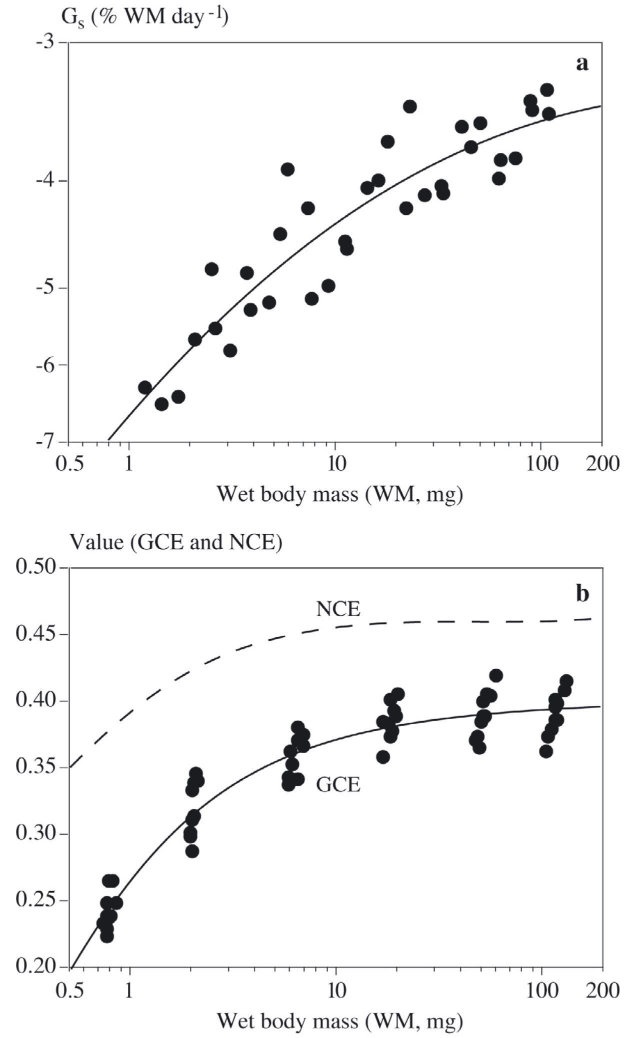

Fig. 4. Size-dependent variation of the negative growth during 24-h starvation (G_s, a) and of the gross (GCE, WM:WM) and net conversion efficiency (NCE, WM:WM) in young *P. punctifer* fed four meals a day (b). The NCE curve is calculated from the values of GCE and G_s in fish of different wet body mass (WM; see methods). The models stand as: $\log(-G_s) = 0.821–0.216 \log WM + 0.040 (\log WM)^2$ ($R^2 = 0.843$, $F = 85$, $df = 34$, $p < 0.0001$, <0.0001 and 0.0410 for intercept, first and second order polynomials). $GCE = 0.266 + 0.189 \log WM - 0.102 (\log WM)^2 + 0.019 (\log WM)^3$ ($R^2 = 0.925$, $F = 230$, $df = 59$, $p < 0.0001$, except for 3rd order polynomial, $p = 0.013$). $NCE = 0.394 + 0.124 \log WM - 0.080 (\log WM)^2 + 0.017 (\log WM)^3$ (calculated from the two models above).

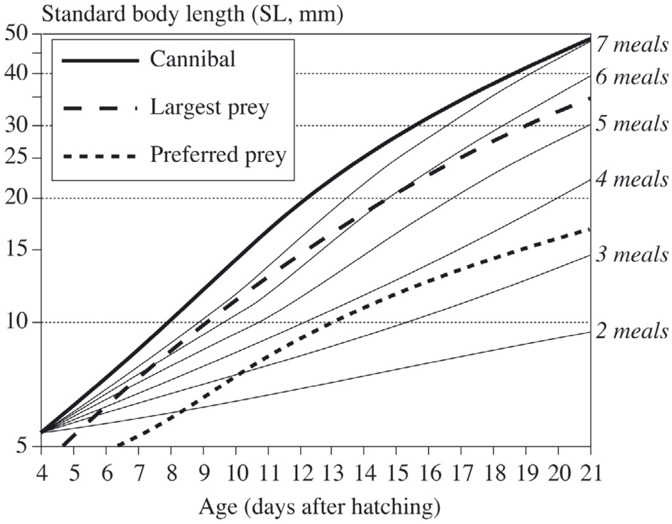

Fig. 5. Growth of young *P. punctifer* fed *Artemia* nauplii two to seven times a day with a maximal meal size (thin plain lines), in comparison to cannibals feeding maximally (thick plain curve), their largest (thick dashed curve) and preferred prey sizes (thick dotted curve).

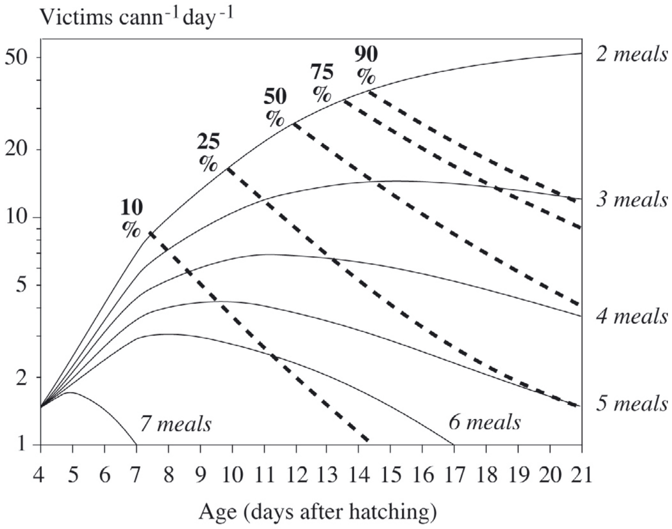

Fig. 6. Theoretical variation in the numbers of victims of cannibalism in *P. punctifer*, depending on fish age and number of daily meals (plain thin curves). The intersection with a dotted thick curve indicates the age of fish when cannibalism has eliminated a given proportion (10, 25, 50, 75 or 90%) of the initial stock, considering that 0.5% of stocked larvae become cannibals (see results).

Cannibals of *P. punctifer* in the present study never consumed prey as large as allowed by their mouth dimensions, possibly because stomach capacity was limiting. This factor is rarely invoked for large-sized piscivores, the stomach of which is several times as large as their maximum daily food ration (e.g. Essington et al. 2000 for largemouth bass *Micropterus salmoides*), but it can apply to larvae or small juveniles that consume much larger amounts of food relative to their size. Here, the largest prey fish ingested whole by cannibalistic *P. punctifer* were about 85, 75 and 70% SL_C, in fish of 10, 25 and >40 mm SL, respectively (Fig. 2). The corresponding WM ratios are 31, 22 and 16–17%, respectively, in good concordance with the maximal stomach capacities of young *P. punctifer* (i.e. 20–21% WM in fish <16 mm SL, and slightly less in larger fish; Baras et al., in press).

The preferred prey size of *P. punctifer* was always well below their predation capacities. It is not frequent that cannibals or piscivores prefer prey as large as possible, because suffocation is frequent when the prey is slightly too large, especially in species with spiny fin rays that prevent regurgitation (Eurasian perch *Perca fluviatilis*, Brabrand 1995; brown-marbled grouper *Epinephelus fuscoguttatus*, Hseu et al. 2007).

In the vast majority of fish species, the size preference curve is dome-shaped and its mode well below the maximal ingestion capacities of cannibals (review in Baras and Jobling 2002). This general pattern is thought to reflect the conflicting influences of different factors within the context of optimal foraging theory (Stephens and Krebs 1986): the energy return is proportional to prey size, but capture success decreases and risks of retaliation increase with increasing prey size (e.g. Lundvall et al. 1999). In *P. punctifer*, capture (or ingestion) success might refer to the increasing difficulty of swallowing large prey growing long bony pectoral spines, in addition to the genuine difficulty of capturing fish with faster swimming speeds. It is also possible that prey size preference in cannibalistic *P. punctifer* was influenced by their degree of satiation (Turesson et al. 2006). The exact moment of cannibalistic bouts was unknown in the present study, so was the degree of satiation of cannibals by then. If the cannibal's stomach was not empty upon a new cannibalistic attempt, this might have been another incitation for selecting a smaller prey, especially if the prey ingested formerly was large.

It cannot be excluded that the patterns of prey size preference documented here were strongly contextual, as predation cages were small, prey were abundant and could not escape. In these circumstances, cannibals might trade off immediate energy return against capture success and risk of retaliation, thereby giving preference to relatively small prey. Similar preferences for small prey size have been observed in cannibalistic *Pangasius djambal* in similar experimental conditions (Baras et al. 2010a). Hence, the curves in Figure 2 can probably not be used to predict prey size preference of young *P. punctifer* in the wild. This is no major shortcoming, as the present study aimed at estimating the risk of cannibalism under culture conditions, where potential prey are numerous and cannot escape, as was the case here.

4.2 Food ration, conversion efficiency and growth performance

Young cannibals of *P. punctifer* consumed large daily food rations (155 and 40% *DM* at 1 and 100 mg *DM*, respectively), they had a high food conversion efficiency (0.50–0.70), and grew at a fast rate (85% and 25% *DM* day^{-1}, at 1 and 100 mg *DM*, respectively). Similar or higher food consumption rates have been reported in other fish species, although generally at a much smaller size (daily rations of 120% *DM* at 0.15 mg *DM* in spotted seatrout *Cynoscion nebulosus* at 28 °C, Wuenschel and Werner 2004; 170% *DM* at 0.10 mg *DM* in Senegal sole *Solea senegalensis*, and 242% *DM* at 0.23 mg *DM* in gilthead seabream *Sparus aurata*, Parra and Yúfera 2001; over 300% *DM* in *Anchoa mitchilli* <0.05 mg *DM*, Houde and Schekter 1981). When taking into account the effect of body mass, *P. punctifer* consumes higher food rations, and nevertheless exhibits better *GCE* (>0.50) than larvae of most fishes (Houde 1994). High *GCE* values were observed in other fishes, but generally for low daily ration or meal size, as large meals have shorter gut residence time and are generally associated with lower assimilation (syntheses in Houde 1994; Keckeis et al. 2001). Parra and Yúfera (2001) suggested that fish species have evolved towards diametrically opposed strategies, consisting in maximising either food intake or *GCE*. The present results on *P. punctifer* suggests that the antagonism between food ration and *GCE* does not apply to all fish species or situations, at least when the diet is highly digestible, as is normally the case when preying on fish larvae.

The *GCE* values in larger cannibals of *P. punctifer* feeding maximally (about 0.70 in fish >30 mg *DM*) were also much higher than in most species documented to date (e.g. 0.42 in nase *Chondrostoma nasus* of 60–80 mg *DM*, Keckeis et al. 2001; $\leqslant$0.46 in 50-mg *DM* gray snapper *Lutjanus griseus* fed live fish prey, Wuenschel et al. 2004). Such high *GCE* values typically compare with those in juveniles of top piscivores or other reputedly efficient species, such as the tambaqui *Colossoma macropomum* (van der Meer et al. 1997). There might be at least three reasons for why cannibalistic *P. punctifer* had a high *GCE* from the early larval stage onwards. (1) By analogy with other species, it is likely that digestion and assimilation are more efficient after gut coiling. In *P. punctifer*, the stomach pouch is formed and a pyloric sphincter is conspicuous at 48 hah (<4.5 mm *SL*), before the start of exogenous feeding (Baras et al., in press). (2) Except possibly during the early larval stage, *P. punctifer* behave as ambush predators, which generally have higher *GCE* than active swimming foragers (Adams and Breck 1990; Houde and Zastrow 1993). (3) During the ontogeny of *P. punctifer*, head length passes from 20% *SL* at 8 mm *SL* to about 34% *SL* in fish >50 mm *SL* (Fig. 1). In general, a long snout facilitates the capture and handling of large prey (see a parallel in the family Lepisosteidae, which comprises species with different dynamics of snout elongation during the ontogeny; Echelle and Riggs 1972; Aguilera et al. 2002). The observation that R_{maint} decreased rapidly as the head of *P. punctifer* elongated, and came to a plateau thereafter, supports the latter interpretation.

The combination of high food rations and high *GCE* in *P. punctifer* produced a fast growth, similar to the performances of tunas exercising piscivory ad libitum (e.g. Pacific bluefin tuna *Thunnus orientalis*, Sawada et al. 2005) or fast growing catfishes (sharptooth catfish *Clarias gariepinus*, Verreth and Den Bieman 1987; vundu catfish *Heterobranchus longifilis*, Legendre 1992; Indonesian catfish *Pangasius djambal*, Legendre et al. 2000; striped catfish *Pangasianodon hypophthalmus*, Baras et al. 2011). Based on the slope of the (log-log) relationship between growth and body mass (–0.265), the decline of growth capacity with increasing body size in *P. punctifer* is less dramatic than in many fish species (slopes from –0.30 to –0.45; Jobling 1994), but not exceptionally shallow either (slope of –0.28 in *C. gariepinus*, Conceição et al. 1998; –0.25 in *P. djambal*, Baras et al. 2010a).

There might be several reasons why the slope of the (log-log) *G-M* relationship in *P. punctifer* was not as steep as in most other studies on fishes. (1) Most data on bioenergetics come from studies of large juvenile fish, which also invest some energy into the construction of gonads. (2) In contrast to juveniles, larvae do not systematically incur a regular decrease of their exchange surfaces (gills and intestine) relative to their body mass, thereby resulting in lower constraints of increasing body mass on metabolism and growth (synthesis in Kamler 1992). (3) There is increasing evidence that the cost of growth in young larvae is lower than in juvenile fish, possibly because the cost of protein synthesis decreases with increasing growth rate (Smith and Houlihan 1995; review in Pedersen 1997). (4) The present study was conducted at a constant temperature of 28.5 °C. By analogy with other tropical species (blue tilapia *Oreochromis aureus*, Baras et al. 2002; *P. hypophthalmus*, Baras et al. 2011), it is likely that the thermal optimum for growth (T°_{opt}) in young larvae of *P. punctifer* is warmer than 28.5 °C and decreases in larger fish. If it were the case, then *P. punctifer* of increasing size would have been raised at temperatures closer to their T°_{opt}, and could have expressed their growth capacities to a greater degree than did small fish. Hence, rearing fish at constant temperature in the present study presumably produced a *G-M* relationship with a shallower slope than if fish of different sizes had been raised at their respective T°_{opt}. Information on the thermal biology of *P. punctifer* is currently too scarce to speculate any further. Anyhow, cannibals of *P. punctifer* can grow at very fast rates, and this accounts for why their growth advantage can be substantial or decisive wherever feeding strategies are inadequate under culture conditions.

4.3 Impact of cannibals and selection of adequate meal frequencies

The models produced here suggest that cannibalism be very low in *P. punctifer* fed maximally at least six times a day, but increase almost exponentially for any missing meal. This accounts for why massive losses to cannibalism were observed in early studies where the food ration and growth of *P. punctifer* were strongly underestimated (Padilla-Pérez et al. 2001).

There are several reasons for why the impact of cannibalism under culture conditions could differ from our predictions. (1) The proportion of jumpers that was used for calculations was estimated at 0.5%, based on experimental evidence. However, this proportion can vary, as it depends on food availability, temperature, initial size heterogeneity, proportion of deformed hatchlings or other family effects (syntheses in Baras 1998; Baras and Jobling 2002; for *P. punctifer*, see Nuñez et al. 2011). (2) The proportion of cannibals was estimated from the occurrence of jumpers, which is a minimalist view, as other fish having exercised cannibalism infrequently, and gained a lower growth advantage would not have been identified as cannibals/jumpers on the day of measurement. (3) The growth of potential victims of cannibalism was calculated here for isolated fish, which is sound from the viewpoint of bioenergetics (see methods), but overlooks the issue of dominance hierarchies that can depress growth, enhance size dispersal and thus increase the number of daily victims of cannibals. (4) In the present study, cannibals could select ad libitum between prey that were all small enough to be eaten, whereas under culture situations, not all siblings might have the adequate size, thereby resulting in greater difficulties for exercising cannibalism, fewer daily victims, slower growth of cannibals and eventually lower overall losses to cannibalism.

Based on factors 2 and 3, the predicted risk of cannibalism is underestimated, whereas it is exaggerated on the basis of factor 4. Factor 1 could produce either situation. There is some evidence however that our predictions are not unrealistic. In a recent study, the mortality at 11 dah of larvae fed seven times a day was 20%, with about half of the fish dying from cannibalism (R. Dugué, unpublished data), which compares well with our predictions (Fig. 6). Likewise, when larvae were offered five daily meals, losses to cannibalism amounted to 21% at 24 dah and were negligible among older fish (E. Baras, unpublished data), also in good concordance with the prediction for this feeding schedule.

Finally, it is worth remembering that during the larviculture of *P. punctifer*, fish die from causes other than cannibalism, in particular from bites associated with unsuccessful cannibalistic attempts or aggressive behaviours. The severity of bites depends on the relative size of oral teeth, which is maximal during the early larval stage and decreases rapidly in fish >9–10 mm *SL* (authors' unpublished observations). This is a further encouragement to feed young larvae of *P. punctifer* maximally and grow them rapidly through this developmental interval, in addition to growing beyond the reach of cannibals. Similar recommendations were proposed for the Asian catfish *P. hypophthalmus*, which also grows long oral spines and is subjected to a major risk period during its early ontogeny (Baras et al. 2010b, 2011).

4.4 Synthesis, conclusions, perspectives

This study highlighted the morphological, bioenergetics and behavioural bases of cannibalism during the ontogeny of *P. punctifer*, and indicated how this information could be used to mitigate cannibalism with adequate feeding strategies. This implies feeding fish outside of normal working hours and thus higher overall production costs, but eventually lower costs per fish produced. In a broader context, there is one particular question that was not addressed in the present study, i.e. whether the fish that become cannibals under culture conditions have genuine advantages over others, in terms of growth potential, conversion efficiency or possibly aggressiveness. Here, the fish used as cannibals were selected at random, but nevertheless grew faster than ever reported for this species. This suggests that most siblings of *P. punctifer*, except for those suffering from deformities, enjoy similar high growth potentials and can become cannibals if given the opportunity. Nevertheless, this "lottery-winner" hypothesis (Baras and Lucas 2010), remains to be tested experimentally in *P. punctifer*.

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