

Feeding in darkness alleviates density-dependent growth of juvenile vundu catfish *Heterobranchus longifilis* (Clariidae)

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Abstract – Sibling juvenile vundu *Heterobranchus longifilis* reared at 27 ± 1 °C under 12L:12D were fed during the day, at night or over the entire 24-h cycle, for periods of 14–15 d. Nighttime feeding gave the highest growth rates, best feed conversion, lowest mortality, fewest losses due to cannibalism and least growth heterogeneity. The trends were seen in fish of all ages and weights (31–101 d and 0.3–30.0 g), but differences were significant only for the smallest fish that were reared at the lowest stocking biomass (< 3.5 g·L⁻¹). The effects of daytime and nighttime feeding were examined in 151-d old (85 g) juveniles stocked at different biomasses (3.4 and 13.6 g·L⁻¹). The growth of vundu was density-dependent, being impaired at low stocking density, but this was substantially mitigated under nighttime feeding. Rearing at high stocking density, feeding at night or in darkness, may act through similar mechanisms that involve changes in the level of aggressive behaviour. It is suggested that nighttime feeding in intensive catfish culture could be replaced by 24-h feeding under conditions of permanent darkness. © Ifremer/Elsevier, Paris

Feeding / growth / stocking density / meal timing / cannibalism / Siluroidei / *Heterobranchus longifilis*

Résumé – Effet de l'horaire des repas et de la densité d'élevage sur la croissance des juvéniles du poisson-chat *Heterobranchus longifilis* (Clariidae). Des juvéniles du poisson-chat *Heterobranchus longifilis* élevés à 27 ± 1 °C en régime d'éclairage 12L–12N sont nourris soit de jour, soit de nuit ou bien en continu par périodes de 14 à 15 jours. L'alimentation nocturne induit la plus forte croissance, les meilleurs indices de conversion, les plus faibles taux de mortalité et de cannibalisme, et, en définitive, la plus faible hétérogénéité de croissance. Ces tendances sont perceptibles chez les poissons-chats de tous âges et tailles (31–101 jours et 0,3–30,0 g), mais ne sont significatives que chez les poissons les plus jeunes, qui sont stockés à faible biomasse ($< 3,5$ g·L⁻¹). L'adéquation des distributions diurnes et nocturnes d'aliment est évaluée chez des juvéniles plus âgés (151 jours, 85 g) à différentes biomasses (3,4 et 13,6 g·L⁻¹). La croissance des poissons-chats est toujours plus réduite à faible qu'à forte densité, mais l'effet de densité-dépendance est significativement réduit lorsque l'aliment est distribué dans l'obscurité. Ces éléments indiquent que la densité d'élevage et la distribution d'aliment en conditions d'obscurité agissent probablement via des mécanismes comparables impliquant une réduction du niveau d'agression. Ils suggèrent que l'alimentation nocturne présenterait peu d'avantages dans un élevage intensif de poissons-chats, et pourrait être remplacée par une alimentation continue en obscurité permanente. © Ifremer/Elsevier, Paris

Nutrition / croissance / densité de population / horaire des repas / cannibalisme / Siluroidei / *Heterobranchus longifilis*

1. INTRODUCTION

The vundu catfish, *Heterobranchus longifilis* (Siluroidei, Clariidae), is a promising candidate for aquaculture [18, 29], its growth performance exceeding that of the most widely cultured catfish, the sharp-tooth catfish *Clarias gariepinus*, and of the reciprocal hybrids [27]. In common with most other catfishes [1, 6, 8, 12, 16, 19, 28, 30, review in 7], vundu feed predominantly at night [2] and may achieve higher growth when fed at night than at other times [24].

Kerdchuen and Legendre [24] studied large (75–220 g) juveniles, cultured at low stocking density (0.01 ind·L⁻¹). Activity rhythms of fish may change with size and age (e.g. [7, 10, 15]), so it is uncertain that nighttime feeding would be the most suitable meal timing for younger juveniles. For example, Avit and Luquet [2] reported that the older the vundu, the higher the proportion of food consumed at night. Kerdchuen and Legendre [24] also reported higher mortality rates, and greater heterogeneity among fish fed at night than amongst those fed during the day, or over

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the entire 24-h cycle. Growth heterogeneity could result in higher risks of cannibalism, and lead to increased mortality [3]. Further, activity of fish may vary with respect to stocking density (e.g. [5]), so it is uncertain whether the advantages of nighttime feeding would persist under the intensive conditions recommended for catfishes that display density-dependent growth patterns (*C. gariepinus* [20], channel catfish *Ictalurus punctatus* [11], *H. longifilis* [25], synthesis in Hecht et al. [18]).

The present study addresses these questions, through a series of experiments designed to examine the effects of meal timing and stocking on growth of juvenile (0.26–85.0 g) *H. longifilis*.

2. MATERIALS AND METHODS

2.1. Fish origin and rearing conditions

Full sibling *H. longifilis* obtained from induced reproduction of captive broodstock were reared in recirculating systems at the Aquaculture Station, University of Liège (Tihange, Belgium; hatching date: April 13, 1995). From the juvenile stage (16–17 d, [26, 31]) onwards, fish were reared in 50-L aquaria, and were transferred to larger enclosures (250 L) at age 80 d (weight ca. 10 g). Water temperature and oxygen concentration were 27.0 ± 1.0 °C and ≥ 5.0 mg $O_2 \cdot L^{-1}$, respectively, and illumination was 12L:12D (light from 08h00; abrupt transitions between dark and light phases). Fish were given artificial feed (45 % protein, 12 % lipid) distributed by automatic feeders during daytime (08h00–20h00), feed delivery commencing about 5 min after the onset of light. The daily (24 h) food ration (DFR, % W) was sub-maximal, being calculated as $DFR = 7.688 W^{-0.322}$, where W was the mean body weight (g) of fish (based on Baras et al. [4]). The food ration was adjusted daily, based on estimated growth, and re-adjusted after each weight control (see below).

2.2. Experimental design

The effects of meal timing on growth, survival and cannibalism of fish of different body weights (mean

initial weights of 0.26, 10.1 and 30.0 g; *table 1*) were examined in three experiments. All three experiments had the same basic design, involving the distribution of food at different times of the day (daytime (D; 08h00–20h00), nighttime (N; 20h00–08h00) or over the entire daily cycle (24)), with food distribution starting less than 5 min after the onset of light (D, 24) or dark (N). All treatments were replicated. In order to avoid any risk of adaptation of fish to schedules other than the routine diurnal schedule, fish studied in any experiment were not re-used later.

Cannibalism is very common amongst catfishes [17]. Fast growing juvenile vundu can ingest conspecific prey of 57 % of their own length (corresponding to a weight of 16.7 % [3]). Consequently fish were size-graded in an attempt to avoid the initial expression of cannibalism; the smallest fish weighed at least 25 % of the body weight of the largest fish. In each experiment, neither the mean initial body weight of fish (W_i), nor the coefficient of variation of the body weight distribution (C_{wi} , %) differed by more than 0.3 % between treatments and replicates (*table 1*). Experimental groups were transferred to 50-L (0.26-g fish) or 250-L aquaria (10.1- and 30.0-g fish), in the same recirculating system as above. No acclimatization period was given when the meal timing was changed from that of routine rearing conditions (during daylight: 08h00–20h00).

A fourth experiment was conducted on 85-g juveniles in 250-L aquaria. In this experiment, the effects of diurnal and nocturnal meal timings were compared for fish held at low (10 fish per aquarium) and high stocking density (40 fish per aquarium). All four treatments were replicated. The use of small fish numbers resulted in the C_{wi} differing by a larger margin (< 3 %) than in the other experiments (*table 1*).

2.3. Measurements, statistical analyses

In each experiment, the aquaria were inspected daily for dead fish. Experiment 1 lasted 15 d, with all surviving fish being counted and weighed (to the nearest 0.001 g) every 5 d. Experiments 2, 3 and 4 lasted 14 d each, with weekly weighings (to the nearest 0.1 g). Mean daily losses due to cannibalism (%) were esti-

Table 1. Synopsis of the four experiments (Exp.) on the effects of meal timing on growth of juvenile vundu *Heterobranchus longifilis*. All experiments were conducted on full siblings, at 27 ± 1 °C under 12L:12D, each treatment being replicated. Meal timings D, N and 24 stand for food distribution by automatic feeders from 08h00 to 20h00, from 20h00 to 08h00, and over the entire 24-h cycle, respectively. N_i : initial number of fish in each group, W_i : mean initial body weight, C_{wi} : coefficient of variation of the initial body weight, $Biom_i$: mean initial biomass, Δ : maximum difference between replicates or treatments.

Exp.	Enclosure	N_i	Age (d)	W_i (g) ($\pm \Delta$)	C_{wi} (%) ($\pm \Delta$)	$Biom_i$ (g·L ⁻¹)	Duration (weighings)	Meal timing
1	50 L	200	31	0.261 (± 0.001)	49.6 (± 0.3)	1.04	15 days (3)	D, N, 24
2	250 L	120	82	10.1 (± 0.2)	33.7 (± 0.2)	4.85	14 days (2)	D, N, 24
3	250 L	100	101	30.0 (± 0.1)	33.2 (± 0.2)	12.00	14 days (2)	D, N, 24
4	250 L	10	157	85.0 (± 0.9)	35.7 (± 2.8)	3.40	14 days (2)	D, N
		40		85.0 (± 0.8)	36.1 (± 1.5)	13.60		

mated by counting survivors and the adding daily recovered dead fish. The apparent specific growth rate (SGR, %·d⁻¹) was calculated as:

$$\text{SGR} = 100 \times [\ln(W_f) - \ln(W_i)] \times \text{time}^{-1}$$

where W_f and W_i are the mean final and initial body weights, respectively. The apparent feed conversion ratio (FCR) was calculated as:

$$\text{FCR} = \text{FR} / [(N_f \times W_f) - (N_i \times W_i)]$$

where FR was the total food ration distributed over the rearing period, N_f and N_i are the final and initial numbers of fish, respectively, and W_f and W_i are as defined above. Growth heterogeneity was assessed from the difference (ΔC_w) between the coefficients of variation of the final and initial distributions of fish body weights (CW_f and CW_i , respectively).

Losses due to cannibalism and mortality from other causes were compared between replicates and treatments by contingency table analyses (df = 1). Growth rates, feed conversion and 'growth heterogeneity' (ΔC_w) were compared by one-way analysis of variance (ANOVA).

3. RESULTS

3.1. Effect of meal timing (exp. 1, 2, 3)

Juvenile catfish of increasing size and age showed significantly ($P < 0.001$) decreasing growth rates (figure 1a), and decreasing rates of cannibalism ($> 1.2 \text{ prey} \cdot \text{d}^{-1}$ among 31-d old fish vs. $\leq 0.2 \text{ prey} \cdot \text{d}^{-1}$, among groups of older fish; figure 1c). Meal timing strongly affected the performance of 31-d old juveniles. Groups of fish fed during the day had significantly ($P < 0.05$) slower growth, higher FCR, higher mortality rates, higher losses due to cannibalism and higher growth heterogeneity (figure 1a–e) than those fed at night or over the entire 24-h cycle. No significant differences were observed between the latter schedules, except for population structure (figure 1e): feeding 24 h a day resulted in a slight increase in size heterogeneity, whereas nighttime feeding resulted in a decrease in size heterogeneity.

A decrease in heterogeneity was also observed when older fish were fed at night, but the differences between meal timings were no longer significant (figure 1e). Similarly, fish fed over 24 h or at night had slightly better growth, lower FCR, and lower daily rates of mortality and cannibalism than those fed during the day, but the differences between treatments were not significant at $P < 0.10$ (figure 1a–d).

3.2. Effect of stocking density and meal timing (exp. 4)

When held at high stocking density, catfishes fed at night tended to have faster growth, lower mortality rate

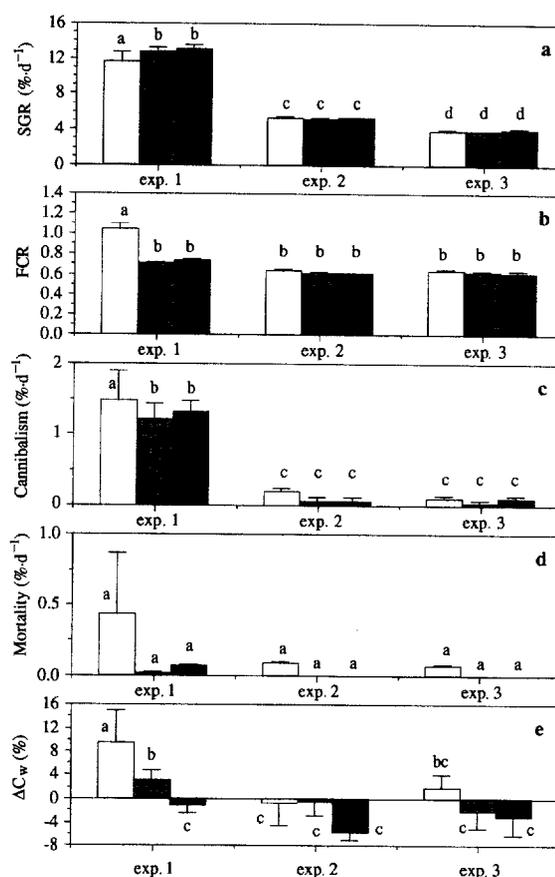


Figure 1. Specific growth rate (SGR, a), feed conversion ratio (FCR, b), daily rates of cannibalism (c), of mortality (excluding cannibalism, d) and growth heterogeneity (differences between initial and final coefficient of variation of fish body weight, ΔC_w , e) among juvenile *Heterobranchus longifilis* reared under 12L:12D at 27 ± 1 °C, depending on meal timing: □: diurnal (08h00–20h00); ■: nocturnal (20h00–08h00); ▒: continuous (08h00–08h00). Growth heterogeneity is deduced from the difference (ΔC_w) between the coefficients of variation of the final and initial mean body weights. Age, body weight, biomass of fish as in table 1 (exp. 1, 2 and 3). Values are means of replicates, and error bars indicate their range. For each graph, values sharing at least one common superscript are not significantly different, whereas other comparisons differ at $P < 0.05$.

and lower growth heterogeneity than those fed during the day, but differences between treatments were not significant (figure 2). Fish reared at low density had significantly ($P < 0.001$) slower growth and higher feed conversion ratios than those fed at high density, but the impairment was substantially mitigated under nighttime feeding.

4. DISCUSSION

Throughout these experiments, juvenile vundu had growth rates and feed conversion ratios (≤ 1.00) that were similar to or better than those reported earlier

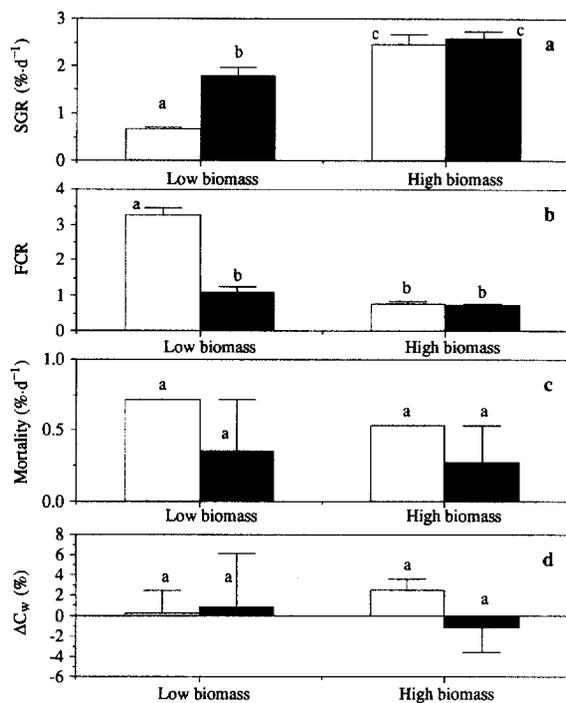


Figure 2. Specific growth rate (SGR, a), feed conversion ratio (FCR, b), daily rates of mortality (c) and growth heterogeneity (d) in juvenile *Heterobranchus longifilis* reared at 27 ± 1 °C under 12L:12D, depending on stocking biomass and meal timing. Low biomass: $3.4 \text{ g}\cdot\text{L}^{-1}$; high biomass: $13.6 \text{ g}\cdot\text{L}^{-1}$. □: Diurnal (08h00–20h00); ■: nocturnal (20h00–08h00). Growth heterogeneity is deduced from the difference (ΔC_w) between the coefficients of variation of the final and initial mean body weights. Age and weight of fish as in table 1 (exp. 4). Values are means of replicates, and error bars indicate the difference between these. For each graph, values sharing at least one common superscript are not significantly different, whereas other comparisons differ at $P < 0.001$.

[2, 24]. This gives further evidence of the potential of this species for aquaculture [18, 29], and suggests that differences between treatments did not originate from poor feeding conditions.

When reared under 12L:12D, fish of all sizes and ages had better growth when fed at night, supporting the conclusions of Kerdchuen and Legendre [24], and suggesting that this tendency applies to the entire juvenile stage. This is presumably because vundu are nocturnal throughout this stage (see [2]). Kerdchuen and Legendre [24] found that the adiposomatic index of vundu was proportional to the proportion of food distributed out of phase (during the day), and similar relationships were reported for channel catfish receiving a single meal in phase or out of phase with their natural feeding rhythm [27]. By analogy with the findings of Gélineau et al. [13, 14] on rainbow trout *Oncorhynchus mykiss*, it is possible that catfish may also suffer from a lower capacity for protein synthesis, and thus from a higher magnitude of protein wastage when fed out of phase. Furthermore, the deposit of fat requires less water fixation than the deposit of proteins (synthe-

sis in Jobling [21]), and this may also contribute to the lower weight gain of vundu fed during the day.

No analysis of food wastage was made, either in the present study, or in the study by Kerdchuen and Legendre [24], so ingestion is not known. Differences in performance between fish fed according to different meal timings could have resulted from different ingestion rates due to different levels of agonistic interactions. Aggression and cannibalism between catfishes are usually higher in hungry than in fed fish, and higher during daylight than in darkness [3, 4, 17]. Agonistic interactions were not quantified, but mortality, cannibalism and size heterogeneity were lower among vundu fed in darkness, suggesting that aggression was also lower. This was not detected in Kerdchuen and Legendre's [24] study on juvenile vundu (highest size heterogeneity amongst fish fed at night), but Hogendoorn [19] observed trends that were similar to those seen here with respect to growth heterogeneity when juvenile (0.5 g) sharptooth catfish were fed at different times. However the juvenile sharptooth catfish fed at night grew significantly slower than those fed over the entire 24-h cycle.

Consistent with the findings of Kerdchuen and Legendre [25], we observed that vundu showed slower growth and suffered higher mortality when stocked at low density. Density-dependent growth rates may result from lower levels of agonistic interactions under higher stocking densities (channel catfish [11], Arctic charr *Salvelinus alpinus* [9, 22]), and this was the conclusion reached by Kerdchuen and Legendre [25] for juvenile vundu. In the present study, we observed that the negative effects of low stocking density on growth were mitigated when juvenile vundu were fed at night. Jørgensen and Jobling [23] reported density effects on growth of Arctic charr fed during the day, but they observed no feeding and growth differences when the fish were fed in darkness. This suggests that stocking density, time of feeding and illumination may act through similar mechanisms that involve changes in the level of aggression.

The alleviation or suppression of density-dependent growth of vundu by the provision of food during the hours of darkness would also account for the variable advantage of nighttime feeding in fish of increasing age and weight [present study, 24]. In experiments where nighttime feeding provided a substantial advantage over daytime feeding, stocking biomasses were $< 3.5 \text{ g}\cdot\text{L}^{-1}$, whereas minimal treatment differences were observed for stocking biomasses $> 4.8 \text{ g}\cdot\text{L}^{-1}$. Hence, it is suggested that nighttime feeding may have limited application in high-density intensive catfish culture, and that such a regime could be replaced by 24-h feeding under conditions of permanent darkness. This would be predicted to suppress any detrimental effects of day-night transitions, such as the promotion of cannibalism in fast growing juveniles (Baras, unpubl.).

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