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Survival, growth, metabolism and behaviour of *Clarias gariepinus* (Burchell 1822) early stages under different light conditions

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Abstract

African catfish, *Clarias gariepinus* were exposed to total darkness (group D) or continuous light (L) during endogenous feeding. During external feeding some of the fish continued to be reared in darkness (DD) and some in light (LL), whereas two groups were exposed to reversed light conditions (groups DL and LD). Survival to the end of yolk absorption was 22% greater in fish exposed to darkness; during subsequent rearing survival decreased in the sequence DD > LD > DL > LL. The onset of external feeding was delayed by a few hours in the L-group as compared with the D-group. Fish reared in dark were larger than those reared in light; the size difference increased with age. In dark, the ratio of total metabolism to body growth (the R_{tot}/P ratio, both in terms of energy) was depressed, hence in the dark, energy used for locomotor activity may have been low, leading to increased investment in growth. We hypothesised that in juveniles light exerts an indirect effect by increasing locomotor activity which in turn promotes multiple encounters between individuals and enhances cannibalistic behaviour. During the fifth and sixth weeks post-fertilization the biomass of fish reared in the dark was about 175% of that in fish reared in light. Light restriction may be recommended as a simple, low-cost technique for intensification of production of *C. gariepinus* stocking material.

Keywords: *Clarias gariepinus*; Light; Survival; Cannibalism; Growth; Metabolism

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1. Introduction

Yields of *Clarias* catfishes were over 67 000 Mt in 1991 and 125 000 Mt in 1993 (review in Verreth, 1994) and continue to rise. The African catfish, *Clarias gariepinus* (Burchell 1822) is one of the most important of the species currently being farmed. *C. gariepinus* is a native species of tropical and subtropical fresh waters; it has been widely farmed in heated waters outside its natural range (reviews in Hecht and Appelbaum, 1988; Van Weerd, 1995). Its rapid growth at high densities, ability to breath air and to withstand poor water quality, and its tasty flesh make *C. gariepinus* an excellent candidate for aquaculture.

Larval rearing is the bottleneck in *C. gariepinus* production (Verreth, 1994), although progress has been made on the development of larval diets during the last decade (Appelbaum and Van Damme, 1988; Verreth and van Tongeren, 1989; Sermwatanakul, 1993; Hecht, 1996; Hecht et al., 1996). According to Verreth (1994) the above 'feed-oriented approach' needs to be complemented by a more prospective 'fish-oriented approach'. Improvements in rearing conditions might result from studies of behaviour and bioenergetics.

Fish can be classified into species that rely predominantly on vision, and those that rely more on chemical, tactile or electrical senses (Schwassmann, 1971). *C. gariepinus* have been reported to show photophobic behaviour (Hogendoorn et al., 1980; Britz and Pienaar, 1992). The latter authors recorded the highest growth of *C. gariepinus* larvae reared in continuous darkness; cover enhanced growth of larvae reared in continuous light, and territorial aggression was mitigated by darkness, but light conditions had no significant influence on larval mortality. This led to the suggestion that restriction of light may be used in *C. gariepinus* culture for enhancement of growth and stress reduction (Britz and Pienaar, 1992).

The purpose of the study is to find out whether rearing in darkness could be used as a method to improve survival and growth of young *C. gariepinus* under cultivation. We tested the hypothesis that light restriction minimizes mortality by mitigating cannibalism and maximizes growth by reducing metabolic energy expenditures.

2. Materials and methods

2.1. Induced spawning

Fertilized eggs were obtained by hormone-induced reproduction of *C. gariepinus* brood stock originating from Hulagh Swamp, Israel, which had been kept indoors for several years. Two females (weight: 1.5 and 2.1 kg) were injected twice with carp pituitary extract (Dag-Shan, Israel, 0.4 cm^3 per 1 kg body wt.) with an interval of 7 h between injections. Two males (1.0 and 1.4 kg) received one injection at the time of the females' second injection. Eggs were hand-stripped and fertilized 12 h after the last injection; pooled spawn (70 g) was used for the experiments.

2.2. Experimental design

Two groups of embryos and yolk feeding larvae were simultaneously incubated, one under full light (the L-group), and the other in a complete darkness (the D-group). At the end of yolk feeding (age 3.88 days post-fertilization) the two groups were divided among eight tanks to give four treatments, each in duplicate. These were coded as LL1, LL2, LD1, LD2, DL1, DL2, DD1 and DD2 — the first letter (L or D) denotes light or dark conditions during egg incubation and larval endogenous feeding, the second letter shows the conditions during exogenous feeding, and 1 or 2 denotes the replicate. No differences were found in weight, respiration and survival between the two duplicate groups (Mann–Whitney U-test, $P > 0.05$).

The experiment lasted 40 days.

2.3. Incubation of eggs and yolk-sac larvae

The fertilized, sticky eggs were divided into two portions of 35 g each and spread over mosquito nets stretched over wire frames immersed vertically in two 100 dm^3 incubation tanks connected to a recirculation system. One tank was exposed to natural light plus constant artificial illumination (the L-group). Light measurements were performed every 3 h just above water surface, with an LI-185 Photometer (Lambda); there were diurnal fluctuations with midday maxima of about 400 lx, and night minima of about 50 lx. The other tank was kept in continuous darkness (the D-group). Temperature, measured every 2 h, was 26.0 ± 1.1°C (mean $\pm$ S.D.), remaining within the range of 25–28°C which was found to be optimal for the yolk-feeding period of *C. gariepinus* (Kamler et al., 1994). Oxygen concentration was maintained at about 85% of air saturation and NH_4^+–N concentration was kept below 0.01 ppm.

2.4. Larval and juvenile rearing

The eight opaque, blue plastic rearing tanks ($35 \times 30 \times 18$ cm, 7.5 dm^3 water in each), were each stocked with 550 larvae at the end of yolk feeding (age 3.88 days). The rearing tanks were within a recirculating system containing a biological filter and a sedimentation tank, with fresh water being supplemented at a rate of 100 dm^3 h^{-1}. Each rearing tank was supplied with compressed air, and with water from the recirculation system at a rate of 1 dm^3 min^{-1}.

Four rearing tanks were continuously illuminated (natural and artificial light, 24-h fluctuations from 55 to 65 lx) and four were kept in darkness. Rearing temperature was 27.4 ± 1.0°C. This temperature is close to 28°C which was recommended (Verreth and Den Bieman, 1987) as the optimum temperature for *C. gariepinus* larval rearing. Oxygen concentration was 60–87% of air saturation and NH_4^+–N was kept to below 0.01 ppm.

Food was first offered to the larvae at age 3.88 days post-fertilization (2.73 days post hatching). Larvae were hand fed in excess every 5 h with newly hatched

Artemia nauplii for the first 6 days, then they were gradually, over 4 days, weaned to dry feed (trout starter AquaSTART, Finska Foder, Vasa, Finland, 48% protein) on which they were kept until the end of the experiment. That weaning procedure was recognized as an optimal one by Verreth and van Tongeren (1989).

2.5. Observations

Observations of larval ontogenetic advancement, pigmentation and behaviour were carried out several times per day. Nine observations of the first food in the larval alimentary tract were performed during the 5 h following the time when food was first offered; samples of 5–6 fish from the light-reared group LL and the dark-reared group DD were examined each time. In total, 103 larvae were examined. Survival was assessed 3.8, 14, 19, 27, 34 and 40 days post-fertilization; all fish were removed from each tank and counted, fish sampled for analysis were accounted for. Cranial bones (the cannibalism left-overs) were removed daily and counted.

2.6. Measurements

Measurements of growth and metabolism, both in terms of energy of embryos, larvae and early juveniles were performed during the first 2 weeks from fertilization, i.e. during the period of endogenous feeding and first 10 days of exogenous feeding. This coincides with the usual duration of experiments on *C. gariepinus* (Verreth, 1994). The juveniles continued to be reared and their growth in wet weight was monitored, in parallel with survival (see above) up to the 40th day post-fertilization.

Samples for analysis of chemical composition were air-dried, homogenized in an agate mortar, deep-frozen, homogenized again and dried at 50–60°C to a constant weight in a desiccator over silica gel. All determinations were performed in triplicate. The ash fraction (A, % dry matter) was determined by ashing 20-mg samples in platinum cups at 550°C for 24 h. Elemental analyses were performed in samples of 10 mg using a Carlo Erba (1108) Elemental CHNS-O Automatic Analyser (Milan, Italy) with sulfanilamide as the reference. Oxygen fraction (O, % of O_2 in dry matter) was calculated as:

$$O = 100 - (C + H + N + S + A) \quad (1)$$

Caloric values (cal. val., J mg^{-1} dry wt.) were calculated from C, H, O and S (% dry matter) using the formula for solid fuels given by the analyser's programme:

$$\text{Cal. val.} = 0.004184\ (C \times 82 + H \times 292.69 - O \times 0.25 + S \times 25) \quad (2)$$

The following were analysed (Table 1): (1) initial eggs (1.9 h post-fertilization); (2) dissected yolk sacs (pooled samples taken from groups L and D at hatching and just prior to the onset of exogenous feeding); (3) dissected body tissues of endogenously fed larvae (pooled as above); (4) whole bodies of early juveniles aged 8.2 days post-fertilization (pooled material from all eight tanks); (5) whole bodies of juveniles aged 14 days (the LL, DL, LD and DD groups analysed separately); (6)

dry feed AquaSTART; (7) *Artemia* nauplii pre-washed with water to remove salt. We did not expect any differences in the results of elemental analyses between fish from different light conditions, therefore we analysed pooled materials in (2)–(4); however, to test this hypothesis, we carried out separate analyses for the oldest fish (5).

Wet weight of eggs and fish was measured to the nearest 0.1 mg. They were placed on a nylon net and the adhering water was removed with a paper towel applied from below for a few seconds. Dry weight was taken after drying to constant weight at 50–60°C and cooling in a desiccator over silica gel. Wet and dry

Table 1
Carbon (C), hydrogen (H), nitrogen (N), sulphur (S), oxygen (O) and ash (% dry matter) and caloric value of dry matter (cal. val., J mg^{-1}) of *C. gariepinus* and its food

Material		C	H	N	S	O	Ash	Cal. val.
Eggs	Mean*	52.46^{d}	8.03^{d}	11.62^{c}	0.44^{bc}	19.59^{ab}	7.86^{d}	27.86^{d}
	S.D.	0.29	0.03	0.05	0.17	0.16	0.17	0.12
Yolk	Mean	54.37^{e}	8.13^{d}	11.72^{c}	0.30^{ab}	18.85^{a}	6.63^{a}	28.62^{e}
	S.D.	0.52	0.11	0.20	0.04	0.87	–	0.32
Dissected tissues	Mean	50.83^{c}	7.49^{c}	11.91^{cd}	0.25^{a}	22.53^{d}	7.00^{b}	26.61^{c}
	S.D.	0.53	0.06	0.10	0.09	0.57	–	0.25
Fish 8.2 days	Mean	48.64^{a}	7.29^{ab}	10.51^{b}	0.51^{c}	24.73^{e}	8.32^{e}	25.64^{a}
	S.D.	0.07	0.16	0.06	0.21	0.47	0.13	0.24
Fish 14 days LL	Mean	50.74^{bc}	7.39^{abc}	11.85^{cd}	0.83^{d}	21.51^{cd}	7.69^{cd}	26.52^{bc}
	S.D.	0.08	0.04	0.05	0.01	0.16	0.06	0.07
Fish 14 days DL	Mean	50.51^{bc}	7.29^{ab}	11.79^{cd}	0.92^{d}	21.95^{cd}	7.54^{c}	26.33^{bc}
	S.D.	0.47	0.02	0.08	0.12	0.45	0.23	0.17
Fish 14 days LD	Mean	50.21^{bc}	7.33^{abc}	11.98^{d}	0.86^{d}	21.36^{c}	8.27^{e}	26.27^{bc}
	S.D.	0.39	0.04	0.10	0.02	0.54	0.01	0.18
Fish 14 days DD	Mean	49.93^{b}	7.27^{a}	11.96^{cd}	0.86^{d}	22.08^{cd}	7.91^{d}	26.10^{b}
	S.D.	0.05	0.02	0.04	0.01	0.04	0.50	0.02
Dry feed	Mean	48.04^{a}	7.41^{abc}	11.56^{c}	0.89^{d}	21.62^{cd}	10.47^{f}	25.63^{a}
	S.D.	0.47	0.07	0.03	0.01	0.55	0.30	0.24
Artemia	Mean	48.16^{a}	7.47^{bc}	9.95^{a}	0.56^{c}	20.04^{b}	13.83^{g}	25.70^{a}
	S.D.	0.08	0.01	0.06	0.02	0.34	0.45	0.04
F-value (ANOVA)		90.11	53.49	35.33	18.72	26.60	876.62	79.42

* Within columns, results followed by the same letters are not significantly different ($P>0.05$), Student–Newman–Keuls Test; chemical composition–arcsine transformation; caloric values–untransformed data (distribution of caloric values does not deviate from normality; Kamler, 1992). ANOVA: all results highly significant ($P<0.0001$).

weights were determined on four samples of 180–220 swollen eggs sampled 1.9 h post-fertilization. Dry weights of larval bodies dissected from yolk sacs (formalin-hardened for 3 h and washed with distilled water) and of remaining yolk were measured from single samples of 50 pooled specimens taken separately from the L and D incubation tanks, at the time when 50% hatching occurred (1.15 days post-fertilization). Triplicate measurements of larval body dry weight (25 pooled specimens in each) were performed at the onset of exogenous feeding (age 3.92 days) for the D- and L-group. Dry weight of exogenously feeding larvae and early juveniles was measured from samples taken daily from each of the eight rearing tanks up to the 13th day post-fertilization. Wet weight of juveniles aged 14, 19, 27, 34 and 40 days was measured individually from samples of $n = 30$ taken from each tank.

Oxygen consumption was measured during 30- to 120-min exposures to 25.5 ± 0.1°C (embryos and pre-fed larvae), or to 27.5 ± 0.1°C (fed larvae and juveniles), in glass constant-pressure volumetric microrespirometers (Klekowski, 1975); in total, 105 measurements were made. In the case of dark-reared groups (D, LD and DD), respiratory chambers were protected from light by aluminium foil. The values of oxygen consumption (mm^3 O_2 $indiv.^{-1}$ h^{-1}) were corrected for STP conditions (0°C, 760 mm Hg). Corrections from the temperature of measurements to the actual rearing temperatures were based on the respiration-to-temperature relationship found by Kamler et al. (1994) for early ontogeny of *C. gariepinus*. The conversion of oxygen consumption values into energy was made using the composite oxycalorific coefficient 13.6 J mg^{-1} oxygen, appropriate for fish catabolizing chiefly fats and protein (Brafield, 1985; Kamler, 1992). In embryos and pre-fed larvae (0–3.92 days), oxygen consumption was measured three times a day in duplicate for the two experimental groups (L and D), whereas in larvae and early juveniles (4–13 days) it was measured once a day in duplicate for the four experimental groups (LL, LD, DL and DD).

Equal numbers of individuals were sampled from every experimental tank.

3. Results

3.1. Observations

The beginning of hatching was observed at the age of 24 h post-fertilization. Three and a half hours later (age 1.15 days) 50% of individuals had hatched; 65% of them had hatched at the age of 1.21 days. The transition, therefore, from an embryo developing within an egg, to a yolk-feeding larva, can be seen at the age of 1.15 days after fertilization. Escape from light was first observed shortly after hatching. Stronger pigmentation of larvae from the L-tank as compared to the D-tank was noted from the age of 3.4 days. At the end of yolk feeding (defined as the time when 50% of individuals have consumed their yolk, age 3.88 days), 2915 live larvae were collected from the D-tank, and only 2275 larvae from the L-tank. Food was first offered to larvae at the age of 3.88 days (time 0 in Fig. 1). Larvae

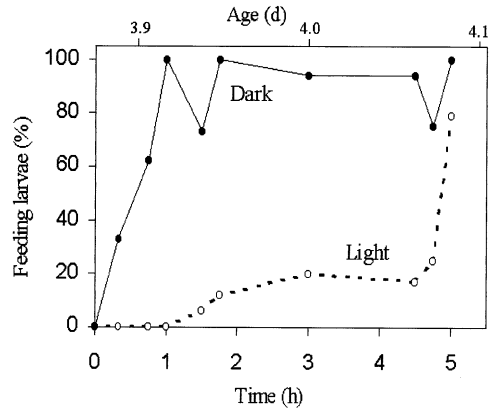

Fig. 1. Beginning of external feeding in *C. gariepinus* larvae reared in light or in dark. First food was offered to larvae aged 3.88 days (time 0 h).

in the D-group started to ingest food immediately, and after 1 h, 75–100% of them had food in their alimentary tracts. The beginning of ingestion was delayed by a few hours in the L-group (Fig. 1); the age of 3.92 days post-fertilization was taken as the onset of external feeding for both groups. Morphological and behavioural observations showed that metamorphosis from a larva into a juvenile occurred at the age of 7.83 days. Cannibalism was first observed at the age of 8.08 days post-fertilization. Catfish of average length of about 11 mm were found to have been attacked by others of similar size: attacks were carried out tail-first. In the course of the experiment, fish carrying signs of attacks (body damages) were found.

3.2. Bioenergetics of embryos, larvae and early juveniles

The lowest ash percentage was found in the dry matter of the dissected yolk sacs which, at the same time, had the highest carbon percentage and caloric value (Table 1). The carbon and energy concentrations in newly fertilized eggs were slightly lower than in the yolk. In dissected body tissues of larvae prior to exogenous feeding, the carbon and energy levels were reduced as compared with the yolk and eggs, but they were higher as compared with the body of early juveniles aged 8.2 days. The increase in ash percentage of feeding fish as compared with dissected tissues from yolk-feeding larvae reflects accumulation of minerals for skeleton formation. As expected, different light conditions (LL, DL, LD and DD) had no effect on dry matter elemental composition or caloric values in juveniles aged 14 days, but elevated ash levels were found in the two groups reared in dark during external feeding (LD and DD). The carbon concentration and caloric value of the AquaSTART dry food did not differ from those in *Artemia* nauplii. Nitrogen level was higher and ash was lower in the dry diet than in *Artemia* (Table 1), hence the dry food was not inferior in energy and protein to the live food.

Wet weight of swollen eggs at fertilization was 2.15 ± 0.12 mg (mean $\pm$ S.D.) and dry weight was 0.444 ± 0.014 mg. Shortly after fertilization (age: 1.9 h) embryos consumed 0.0266 ± 0.0082 mm^3 O_2 indiv.$^{-1}$ h^{-1}.

The embryos incubated in the dark hatched with less unresorbed yolk than those reared in the light, and were slightly heavier (by 2%, Table 2). The difference was greater (7%) at the onset of external feeding. Body growth over the period of larval endogenous feeding was slightly higher in the D-group. Although larger larvae in the dark group expended more energy for total metabolism, the amount of energy expended for a unit of production (the R_{tot}/P ratio) was slightly depressed in the D-group. The above differences were not statistically significant, but consistent: more yolk energy consumed accompanied by reduced energy expended for unit of production seem to contribute to more energy channelled into growth in the dark (Table 2).

The growth rate, as expressed in terms of energy in Fig. 2A, differed between exogenously fed larvae (age 4.0–7.8 days) and early juveniles (age 7.9–14.0 days): the slopes of pooled regressions were 0.465 ± 0.058 and 0.231 ± 0.018 ($\pm$ S.E.), respectively, ($t = 3.277$, $P < 0.01$). The flexion point was found at the age of about 7.8 days, thus the time of switch in growth type confirmed the time of metamorphosis based on morphological and behavioural observations (see above). The differ-

Table 2
Development, growth and metabolism during endogenous feeding of *C. gariepinus* larvae, reared in light (L) or in dark (D)

Experimental group	L	D	100D/L(%)
Development			
Hatching time (H, days post-fertilization)	1.15	1.15	–
Onset of external feeding (S, days post-fertilization)	3.92	3.92	–
Duration of larval endogenous feeding (days)	2.77	2.77	–
Weight			
Dry weight of remaining yolk at H (mg)	0.280	0.262	93.6
Dry weight of body tissues at H (Wd_H, mg)	0.0368	0.0375	101.9
Dry weight of body at S (Wd_S, mg)	0.1343	0.1440	107.2
$\pm$S.D.	0.0270	0.0250	–
Growth			
Absolute growth of body (mg Wd indiv.$^{-1}$ per 2.77 days)	0.0975	0.1065	109.2
Absolute growth of body (P, J indiv.$^{-1}$ per 2.77 days)[a]	2.595	2.834	109.2
Metabolism			
Total oxygen consumption (Q_{tot}, mm^3 O_2 indiv.$^{-1}$ per 2.77 days)[b]	98.79	103.79	105.1
Total energy expenditure (R_{tot}, J indiv.$^{-1}$ per 2.77 days)	1.920	2.017	105.1
Ratio			
R_{tot}/P	0.74	0.71	96.0

[a] Converted from dry weight to energy using 26.61 J mg^{-1} (Table 1).
[b] Accumulated from the age 1.15 to 3.92 days according to Klekowski et al. (1967) and Kamler et al. (1998).

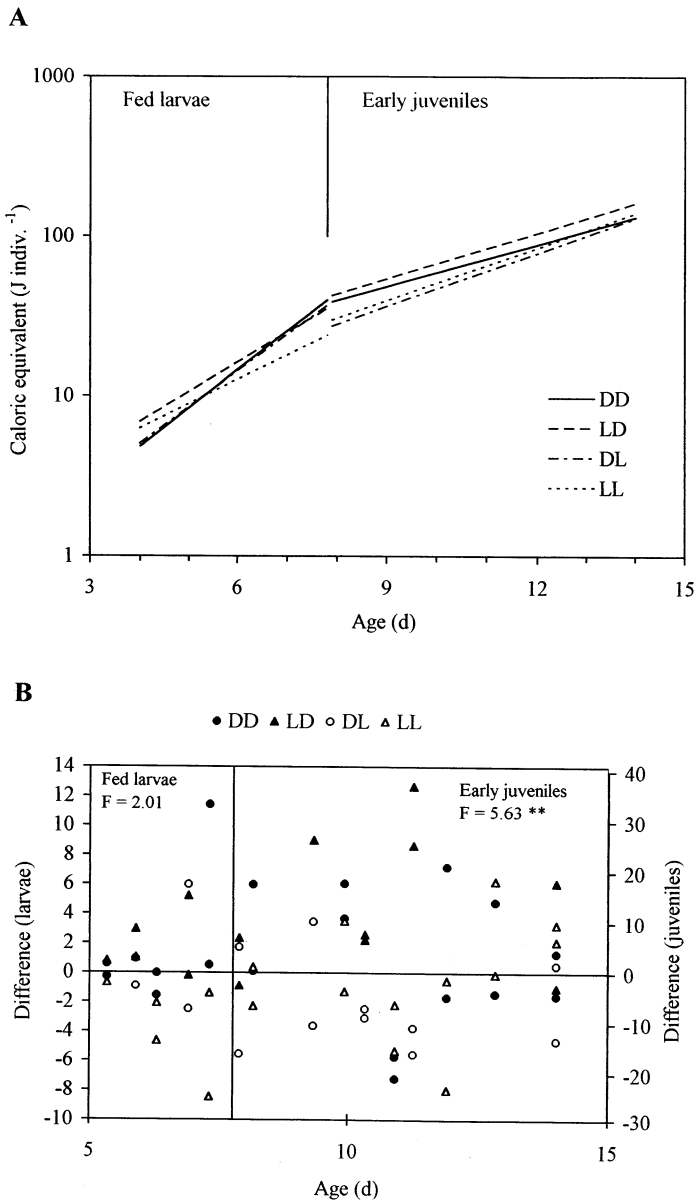

Fig. 2. Age-dependence of size (caloric equivalent, C.e., J indiv.$^{-1}$) in *C. gariepinus* fed larvae and early juveniles reared in four experimental groups DD, LD, DL and LL. A, regression lines of C.e. on age (τ, days): C.e. $= ae^{b\tau}$; B, differences taken from: $\text{C.e.}_{\text{meas.}} - \text{C.e.}_{\text{theor.}}$ where $\text{C.e.}_{\text{theor}}$ are computed from two regressions pooled for all the four experimental groups: C.e. $= 0.883e^{0.465\tau}$, $n = 20$, $r = 0.884$, $P < 0.001$ for fed larvae, and C.e. $= 5.500e^{0.231\tau}$, $n = 44$, $r = 0.897$, $P < 0.01$ for early juveniles. Note different scales for larvae and juveniles. Statistical treatment was done among experimental groups within developmental periods, F-values are shown (single classification ANOVA with unequal sample sizes, Sokal and Rohlf, 1969), $^{**}P < 0.01$.

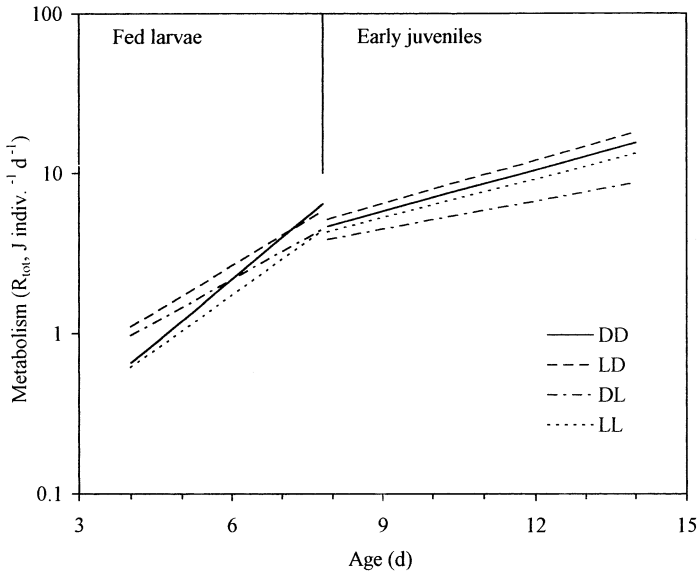

Fig. 3. Age-dependence of total metabolism (R_{tot}, J indiv.$^{-1}$ day^{-1}) of *C. gariepinus* fed larvae and early juveniles. Regression lines $R_{tot} = ae^{b\tau}$ are shown for each experimental group DD, LD, DL and LL; the regression coefficients b (slopes) were ($\pm$ S.E.) 0.602 ± 0.065, 0.440 ± 0.063, 0.405 ± 0.071 and 0.520 ± 0.069, respectively for larvae, and 0.197 ± 0.055, 0.207 ± 0.061, 0.135 ± 0.076 and 0.185 ± 0.089, respectively for juveniles.

ence in size between experimental groups was not significant for feeding larvae (Fig. 2B), but there was a tendency towards greater size in larvae reared in the dark during external feeding (groups DD and LD) as compared with that in fish reared in the light (DL and LL) (Fig. 2B). For example, caloric equivalents for larvae aged 6 days (estimated from the regressions shown in Fig. 2A) were 14.70, 16.35, 14.42 and 12.75 J indiv.$^{-1}$ for DD, LD, DL and LL, respectively, thus the ratio 100(DD + LD)/(DL + LL) amounted to 114%. Highly significant differences ($P < 0.01$) were found between groups of early juveniles (Fig. 2B). The caloric equivalents estimated for juveniles aged 11 days were 72.19, 83.74, 60.50 and 65.54 J indiv.$^{-1}$, respectively for the DD, LD, DL and LL groups, the ratio (computed as above) being 124%.

A change in the metabolism-on-age relationship lends further support to the conclusion that the transition from larvae to juveniles occurred at the age of 7.8 days (Fig. 3): the slopes b were steeper in larvae (mean values ranged from 0.405 to 0.602) than in juveniles (0.135–0.207); the difference was significant ($P < 0.05$) for the DD group, only. The total metabolic expenditures of the larger fish reared in the dark during external feeding (Fig. 3) were, like their size (Fig. 2), slightly greater than those reared in the light, but the amount of energy expended for overall metabolism related to the unit of body production (the R_{tot}/P ratio, Fig. 4) was suppressed in the dark-reared fish during external feeding. Thus, more energy is channelled into growth and less expended on metabolism in the dark.

3.3. Survival and growth of juveniles 2–6 weeks post-fertilization

Survival decreased in the sequence DD, LD, DL and LL (Fig. 5A). Significant differences were found in all the comparisons (Fig. 5B), suggesting that survival rate was depressed not only by rearing in light during external feeding (LL < DD, DL < DD, DL < LD and LL < LD) but also exposure to light during yolk-feeding period had a negative effect on survival of juveniles later on (LL < DL and LD < DD).

Individual wet weight was greater in the experimental groups reared in the dark during endogenous feeding (DD and LD) as compared with the light groups (DL and LL) — Table 3. From the 19th day onwards, the ratio 100(DD + LD)/(DL + LL) ranged from 128 to 151% with significant differences between dark and light groups; the non-significant result on 40th day is surprising. No effect of light conditions during yolk-feeding period on juvenile growth could be detected: in nine out of 10 comparisons (five for DD vs. LD and five for DL vs. LL), no significant difference was found. The variability in size, as expressed by the relative weight difference between the largest and smallest individuals (W_{max}/W_{min} ratio) in each of eight tanks, ranged from 2.5 to 4.0, 2.6 to 6.4, 2.9 to 6.6, 3.6 to 11.3 and 4.0 to 13.7 on the 14th, 19th, 27th, 34th and 40th days, respectively. Thus, the variability in size up to the 27th day was relatively small and increased slowly with age, but it increased dramatically thereafter. The largest W_{max}/W_{min} ratios of 11.3 on the 34th day and 13.7 on the 40th day were found in tanks exposed to light during external feeding, LL1 and DL1, respectively.

Total biomass in the experimental tanks (Table 4), as a combined effect of survival and growth, was higher in groups reared in the dark during external

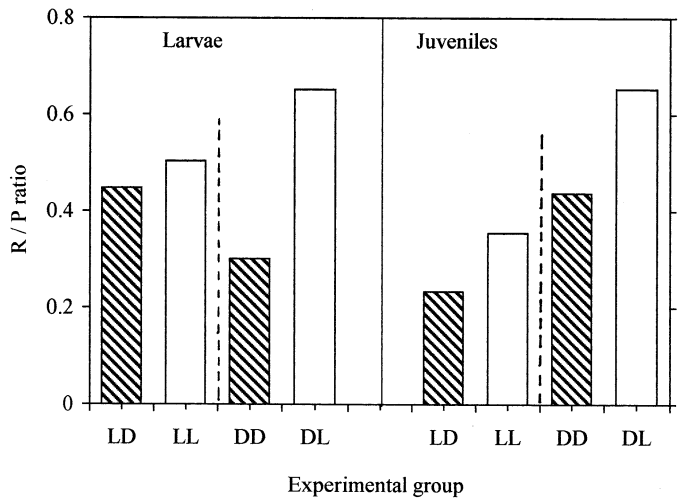

Fig. 4. Ratio of total metabolism (R_{tot}) to growth (P) (both in J indiv.$^{-1}$ day^{-1}) of *C. gariepinus* externally fed larvae (age 4.0–7.8 days) and early juveniles (age 7.9–14 days). Conditions during external feeding: dark, hatched bars; light, open bars. Mean values from individual measurements.

Table 3
Time course of wet weight (mg indiv.$^{-1}$) of juvenile *C. gariepinus*[a]

Experimental group	Light conditions during external feeding	Age (days)				
		14	19	27	34	40
DD	Dark	43[a]	130[b]	460[b]	975[b]	1787[a]
LD	Dark	44[a]	135[b]	425[b]	1104[c]	1895[a]
DL	Light	41[a]	97[a]	271[a]	701[a]	1181[a]
LL	Light	42[a]	110[a]	315[a]	722[a]	1449[a]
ANOVA	*F*-value	0.592	12.528	17.415	45.126	4.551
	P-value	0.652	0.017*	0.009**	0.001**	0.089
Ratio 100(DD+LD)/(DL+LL)		105	128	151	146	140

[a] Mean values are shown from two tanks for each light condition. Within columns, results followed by the same letters are not significantly different ($P>0.05$), Student–Newman–Keuls Test.
* ANOVA: significant ($P<0.05$) result.
** ANOVA: highly significant ($P<0.01$) result.

feeding. Significant differences were observed from the 19th day onwards; at 4–6 weeks post-fertilization the ratio amounted to about 175%. Light conditions during yolk-feeding had no effect on juvenile biomass.

4. Discussion

Our morphological and behavioural observations indicated that the transition from a larva into a juvenile occurred at the age of about 7.8 days post-fertilization, which coincided with a switch in growth (Fig. 2) and metabolism (Fig. 3). From the ultrastructure of gland cells, the [^{3}H]thymidine labelling index and the onset of acid production, Stroband and Kroon (1981) inferred that a functional stomach was formed in *C. gariepinus* aged about 12 days post-fertilization at 23–24°C. Using the equation describing the acceleration of developmental rate by temperature (Kamler, 1992) and assuming $Q_{10}=3$ (appropriate for the lower part of the optimum temperature range, Kamler et al., 1994) we found that the age of 12 days at 23.5°C corresponds to the age of 7.7 days at 27.5°C — the rearing temperature in the present experiment. Terjesen et al. (1997) found that the relative urea nitrogen excretion (expressed as % of the total nitrogen excretion) increased in exogenously feeding *C. gariepinus* larvae up to the age of 7.5 days at 28°C ($=7.85$ days at 27.5°C) and stabilized thereafter; in their Fig. 1 they indicated this age as a beginning of metamorphosis. Therefore, the age of 7.7–7.9 days at 27.5°C was an important turning point for *C. gariepinus*, possibly equivalent to metamorphosis.

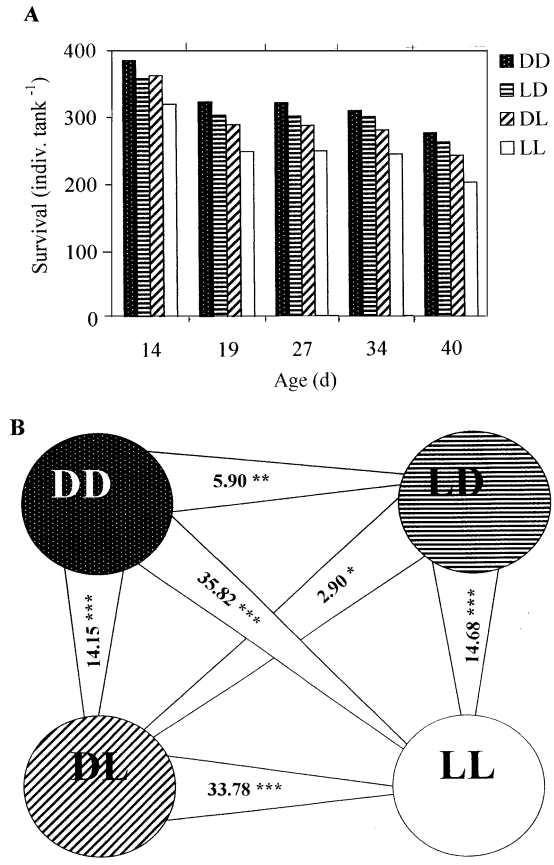

Fig. 5. Survival of *C. gariepinus* juveniles aged 14–40 days. A, mean values from two tanks of each experimental group; B, statistical evaluation, *t*-values are shown (*t*-test for paired comparisons, Sokal and Rohlf, 1969), $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, the edges point at the lower values.

C. gariepinus larvae are photophobic (Hogendoorn et al., 1980). They live in covered habitats on the edges of lakes and rivers (review in Britz and Pienaar, 1992). Photophobic behaviour is initiated shortly after hatching (present work). Hecht and Appelbaum (1988) demonstrated that in this species eyes were less important for prey capture, while the circum-oral barbels were essential. In contrast with many fish species, *C. gariepinus* are tactile and possibly chemoreceptive predators rather than visual predators. Hence, rearing in darkness was not expected to exert a negative effect on *C. gariepinus* survival and growth.

Negative effects of light on fish during endogenous feeding, i.e. precocious hatching, reduced hatching success, smaller body size, and elevated percentage of deformities and mortality were reported by Leshchinskaya (1954) for *Engraulis encrasicolus maeoticus* Pusanov, Leitritz and Lewis (1976) for *Oncorhynchus nerka* (Walbaum), and by Appelbaum et al. (1995) for *Ophiodon elongatus* Girard. In

juvenile *Salvelinus alpinus* (L.), density-dependent suppression of growth and elevated size variability observed under continuous lighting were eliminated by feeding in the dark under short-day (8 h light, 16 h dark) conditions, probably by mitigation of social interactions and resulting reduction of energy expenditure during feeding (Jørgensen and Jobling, 1993). On the other hand, no effects of different light conditions (continuous light, total darkness or natural photoperiod) on hatching time and size of newly-hatched larvae of *Rutilus rutilus heckeli* (Nordman) and *Stizostedion lucioperca* (L.) were found by Belyj (1961). In contrast, newly-hatched *Acipenser stellatus* Pallas were heavier after incubation in daylight than in darkness (Detlaf et al., 1981). Feeding rates of *Salmo salar* L. juveniles during daylight hours were greater than during darkness by a factor of 3.1–7.5 (Jørgensen and Jobling, 1992). An ontogenetic shift in the rates of food consumption, growth and metabolism, and in efficiency of food utilization, in relation to light conditions was demonstrated by Ryzhkov (1976) for four salmonid species; during embryogenesis a better performance was achieved in darkness than in light, but this tendency was reversed in larvae and juveniles. In summary, the above examples and an extensive review by Zhukinskij (1986) demonstrate that in fish early ontogeny the response to light is extremely variable. It can be negative, positive, or without effect, and is related to environmental adaptations. Thus it is species- and age-specific.

We found that survival of *C. gariepinus* throughout endogenous feeding was suppressed in the light tank. Negative effects of ultraviolet radiation on embryogenesis include morphological deformities and elevated mortality (reviews in Blaxter, 1969 and Zhukinskij, 1986). Irradiation of *Brachydanio rerio* (Hamilton-Buchanan) early embryos impaired epiboly, thus preventing blastopore closure, but gastrula-

Table 4
Time course of total biomass (g wet wt. tank^{-1}) of juvenile *C. gariepinus* populations[a]

Experimental group	Light conditions during external feeding	Age (days)				
		14	19	27	34	40
DD	Dark	16.4[a]	41.7[b]	146.6[b]	299.1[b]	486.7[b]
LD	Dark	15.6[a]	40.6[b]	126.9[b]	332.6[b]	487.5[b]
DL	Light	14.7[a]	28.1[a]	77.4[a]	194.9[a]	280.0[a]
LL	Light	13.5[a]	27.2[a]	78.3[a]	172.0[a]	289.0[a]
ANOVA	*F*-value	2.593	9.582	25.552	12.443	13.849
	P-value	0.190	0.027*	0.004**	0.017*	0.014*
Ratio 100(DD+LD)/(DL+LL)		113	149	176	172	171

[a] Mean values are shown from two tanks for each light condition. Within columns, results followed by the same letters are not significantly different ($P>0.05$), Student–Newman–Keuls Test.

* ANOVA: significant ($P<0.05$) result.

** ANOVA: highly significant ($P<0.01$) result.

tion was less affected by ultraviolet radiation (Straehle and Jesuthasan, 1993). In *Carassius auratus* (L.) UV radiation for 10–20 min resulted in caudal fin abnormalities, but radiation after the 16-cell stage had almost no effect (Cai, 1993). Embryos and newly-hatched larvae of *Phoxinus phoxinus* (L.) and *R. rutilus* (L.) were sensitive to UV-B radiation of intensity that corresponded to the local mid-summer conditions, but in older larvae resistance against UV-B increased progressively; a substance acting as a sun screen was identified and its concentration was found to increase during larval development (Hofer and Kaweewat, 1998). Thus, suppressed survival of yolk-feeding *C. gariepinus* in light might be attributed to direct effects of ultraviolet radiation on early embryogenesis, when the differentiation rate is at its highest.

Also, survival of *C. gariepinus* juveniles was found to be suppressed by light (Fig. 5). In contrast, Britz and Pienaar (1992) did not detect any differences in survival rate of *C. gariepinus* larvae reared for 13 days in continuous dark or light, with or without cover; nevertheless, they concluded that stress, aggression and cannibalism are reduced under dark conditions. Coeval cannibalism (i.e. cannibalism among similar-aged individuals) is a common feature in larval and juvenile fish (review in Folkvord, 1997). Cannibalism in *C. gariepinus* falls into the category of sibling intracohort cannibalism of post-hatching stages (Smith and Reay, 1991). In earlier experiments with *C. gariepinus* larvae and juveniles, cannibalism was found to contribute to 70–83% of total mortality accumulated during 46–50 days of rearing (Hecht and Appelbaum, 1987; Appelbaum and Van Damme, 1988). In the present experiment, cannibalistic behaviour was first observed at the age of 8.08 days post-fertilization (4.16 days after the onset of external feeding). Hecht and Appelbaum (1988) found that cannibalism in *C. gariepinus* started 3.5 days and ceased 47 days after the onset of external feeding; it was the response to tactile stimuli between individuals. In their experiment the rate of cannibalism was found to be significantly reduced by provision of shelters that increased the proportion of time spent resting. Rearing in darkness suppressed swimming activity of *Ophiodon elongatus* yolk-sac larvae (Appelbaum et al., 1995). In the present work, reduced locomotor activity in the dark was deduced from the smaller ratio of total metabolism to growth (R_{tot}/P ratio, Fig. 4). It seems that light exerts an indirect effect on juvenile *C. gariepinus* mortality by increasing locomotor activity which in turn promotes multiple encounters between individuals and enhances cannibalistic behaviour.

Cannibalism is a size-dependent process, usually limited by the mouth width of the predator (data for *C. gariepinus* in Hecht and Appelbaum, 1988). Increased variability in size among individuals promotes cannibalism; for example, size-sorting suppressed cannibalism in *Perca fluviatilis* (L.) larvae (Melard et al., 1996). The commonly used measure of body size variability, the coefficient of variation ($CV = 100$ S.D. mean^{-1}), does not seem to be particularly useful in describing the risk of cannibalism; the relative size difference between the largest and smallest individual may be a better measure of cannibalism risk (Folkvord, 1997). The largest individuals are important in cannibalism (Van Damme et al., 1989;

Folkvord, 1997). We found that variability in size, as expressed by the W_{max}/W_{min} ratio, was relatively small and increased slowly between the 14th and 27th days post-fertilization, but it increased dramatically after the 34th day in the tanks exposed to light during external feeding. The same pattern of variability in *C. gariepinus* total length was demonstrated by Hecht and Appelbaum (1988). A sudden rise of size variability after the 35.5th day coincided with the transition from Type I cannibalism (the prey is caught tail-first, the head is bitten off and discarded) to type II (the prey is caught head-first and swallowed whole). Type I cannibalism does not require large size differences between prey and predator, while Type II does. Thus, our observation of a sudden increase in the W_{max}/W_{min} ratio found in the light tanks after the 34th day confirms an elevated risk of cannibalism when rearing in light.

Not only did light impair survival of juvenile *C. gariepinus* when applied during external feeding, but also the 'light history' was of significance. Suppressed survival was recorded in juveniles reared under the same conditions during external feeding, but incubated in light during yolk feeding: LL < DL and LD < DD (Fig. 5). A possible explanation may be that there were individuals in the L-group that, although they survived exposure to light during yolk feeding, were nevertheless slightly damaged by ultraviolet light during embryogenesis; these less viable individuals could later be an easy target for cannibals.

Rearing in the dark resulted in larger sized *C. gariepinus* than rearing in light, by 2, 7, 14, 24*, 28*, 51*, 46* and 40% at the age of 1.15, 3.92, 6, 11, 19, 27, 34 and 40 days post-fertilization, respectively (Fig. 2, Tables 2 and 3). This tendency was weak and non-significant at early stages of development but increased with age (significant results are marked with an asterisk).

The energy budget of a growing, non-reproducing organism is usually defined as:

$$C = P + R_{tot} + F + U \tag{3}$$

where some of the energy ingested in food (C) is incorporated as chemical energy in new tissues (P), some is used for biological work (R_{tot}) and the remainder is lost in the form of faeces (F) and nitrogenous excretory products (U). The three subcomponents of R_{tot} are: resting metabolism, activity (associated with locomotion, foraging and predator avoidance), and costs of growth. Costs of growth of 10.6 and 8.2–9.4 mmol O_2 per 1 g dry wt. deposited were reported for *C. gariepinus* yolk-feeding larvae and externally feeding larvae of 0.56–5.02 mg dry wt., respectively (Conceição et al., 1997). Costs of growth are negatively associated with growth rate (Wieser, 1994; Conceição et al., 1997). There is a trade-off in fishes between energy expended to pay the costs of activity and that channelled into growth (Calow, 1985), and this conflict is maximum in larvae fish (Conover and Schultz, 1997). Therefore, the lower R_{tot}/P ratio in the dark (Table 2, Fig. 4) may perhaps explain the better growth in dark conditions: energy used for locomotor activity was minimized while energy used for growth was maximized.

An elevated ash level in dark-reared 14-day-old fish (groups LD and DD in Table 1) indicates more advanced skeleton formation. Likely the fish in the dark ate more and therefore grew better.

Mortality and growth, the two most important processes in fish early life, are strongly coupled (Houde, 1997). From the present work, it can be concluded that during the early life of *C. gariepinus*, rearing in the dark affects both survival and growth positively, which in turn results in biomass 175% greater than in light after 4 weeks of rearing (Table 4). Thus, the implied application of the results of this study is in conformity with the suggestion given by Britz and Pienaar (1992): light restriction may be recommended as a simple, low-cost technique for intensification of production of *C. gariepinus* stocking material.

However, several questions remained unanswered. Is complete darkness really the best solution? If not, what light intensity and wavelength are optimal? Is meat quality unaffected by absence of light? Further research is required to answer these questions.

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