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Effects of continuous light and light intensity on the growth performance and gonadal development of Nile tilapia

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ABSTRACT - Continuous illumination has been known to exert positive effects by stimulating growth and delaying unwanted maturation in seasonal-temperate farmed fish species like salmonids. However, in tropical fish like Nile tilapia (*Oreochromis niloticus*), some studies exist showing inconsistent results and even fewer data is available regarding the effects of light intensity. To clarify some of the inconsistent results in literature and evaluate the effect of different light intensity levels on growth and sexual maturation in Nile tilapia (*Oreochromis niloticus*), we reared twenty days post-hatch Nile tilapia larvae under continuous illumination at three different light intensities and compared against a control photoperiod (12L:12D) up to 118 days post-hatch. A total of 600 fry were used using 75 fry per experimental unit in a previously tested experimental aquarium setup. Fish exposed to high and medium intensity continuous illumination treatments were significantly heavier (13-20%) and longer (6-8%) than fish exposed to the control photoperiod. Importantly, however, the degree of growth enhancement did not vary significantly according to the light intensity used. Feed intake was also higher in all continuous illumination treatments than in the control photoperiod, suggesting that growth benefits might be due to an increase in feed intake, which is not affected by the light intensities used. Gonadal development on the other hand, presented differences between sexes with a delay in spermatogenesis, while an advancement towards ovarian maturation occurred compared with the control fish. These results suggest that continuous illumination can influence both growth and gonadal development in Nile tilapia with no apparent differences between the light intensities tested in this study.

Keywords: gonads, photoperiod, reproduction, tropical species

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1. Introduction

A limited number of studies has addressed the effects of continuous photoperiod using different light intensities in commercially cultured fish even when it has been shown that light intensity and sensitivity threshold vary between species and developmental stages (Villamizar et al., 2011; Aragón-Flores et al., 2017). Nile tilapia (*Oreochromis niloticus*) is an important commercial species worldwide that matures precociously (around six months of age) before reaching market size (Popma and Masser, 1999). It would thus be useful to delay the onset of maturation as currently done in cold-water species, like salmonids, with the use of light technology (Taranger et al., 2010).

Previous studies aiming at this in Nile tilapia have met variable results in metabolic rate, energy loss, and differential growth rates (Biswas and Takeuchi, 2002; Biswas and Takeuchi, 2003; Biswas et al.,

2004; El-Sayed and Kawanna, 2004; Biswas et al., 2005; Rad et al., 2006). Such variation may be due to several reasons, ranging from experimental setup/design to the genetics of fish used; however, it could also be due to the different light intensities and spectra tested. In fact, light intensity and spectra have recently been reported to affect feeding behavior in Nile tilapia (Carvalho et al., 2013; Volpato et al., 2013). Moreover, the circadian light axis in this species appears to be different than in other teleost species, requiring the eyes to translate light information to the pineal gland (Migaud et al., 2007a,b; Martínez-Chávez and Migaud, 2009; Nikaido et al., 2009). Taken together, the effects of continuous light and light intensity warrant further experimental research to assess their impact on sexual maturation and Nile tilapia growth in captivity.

Here, the effects of different light intensities under continuous illumination on growth and gonadal development in Nile tilapia under strict laboratory conditions were investigated. This information could aid in elucidating the differential results reported and help clarify the role of continuous light and intensity thresholds required for optimization of growth in this species under culture.

2. Material and Methods

A total of 600 mixed sex batch of red Nile tilapia strain larvae obtained from a tropical aquarium facility in Stirling, Scotland (Latitude: 56°08'43.80" N), were raised under a 12L:12D photoperiod up to 20 days post-hatch (dph). Afterwards, 75 fry were placed randomly into the experimental system, which consisted in specially designed series of eight tanks or experimental units (200 L) contained within four light boxes (two tanks per light box). Within each tank, a 7-L fry tank was initially used. The fry tanks were cylindrical with an outlet located in the center of each tank. The inlets to the 200-L tanks were modified using additional tubing and reducers to ensure an adequate flow within the fry tanks. Access was gained via two shutter doors on each side of the system so that each tank could be accessed without disrupting the other tanks. Half way through, the fish were transferred out of the 7-L tanks and placed in the main tanks. The tanks were divided in half, and the level of the water was adjusted to be the same as in the 7-L tank so as to maintain similar light intensities at the bottom. The volume of water in these tanks was 40 L.

The experimental system was performed in a closed water recirculation system at a constant temperature of 27±1 °C as previously described by Campos-Mendoza et al. (2004). Flow rate in each 7-L round tanks was set at 60 L h^{-1} $tank^{-1}$. Weekly partial water changes (10% of total volume) were done to the system with fresh aerated and preheated water. This ensured water quality across the experiment as evidenced by the monitoring of nitrate, nitrite, and ammonia levels (C-Test kits, New Aquarium Systems, Mentor, Ohio, USA), which were observed within safe levels (<10 mg L^{-1}; Monsees et al., 2017) at all times.

Treatments were performed in duplicate as follows: fish were exposed to either a 24-h continuous light (LL) at three different light intensities (LL-High 100%, LL-Medium 15-17%, and LL-Low 1-1.3%) or to a 12-h light and 12-h dark (12L:12D) treatment (control) until they reached 118 dph. The control tank had the same light intensity as the medium LL treatment (Table 1). Incandescent light bulbs (ScrewFix Direct, Yeovil, UK) were used in all cases to provide the broadest spectrum

Table 1 - Light intensities in Watts m^{-2} and lux (mean±SE) measured at the bottom and surface of the tanks for each experimental treatment during daytime

Treatment	Watts m^{-2} (bottom/surface)	Lux (bottom/surface)
LL-H	3.0±0.2/4.6±0.6	684.0±32.0/1031.0±104.0
LL-M	0.5±0.1/0.7±0.1	141.5±17.5/172.5±10.5
LL-L	0.04±0.0/0.05±0.0	4.5±0.5/8.0±1.0
Control (12L:12D)	0.7±0.1/0.9±0.2	172.5±22.5/190.5±30.5

LL-H - high light intensity; LL-M - medium light intensity; LL-L - low light intensity; 12L:12D - 12-h light and 12-h dark.

possible. For the LL-High (LL-H) treatment, four 100-W light units were fitted into the compartment used. The LL-Medium (LL-M) light intensity treatment and the 12L:12D treatment had a single 60-W light unit/compartment whereas the LL-Low (LL-L) intensity treatment had a 10-W bulb with plastic translucent film to achieve the intensity levels shown in Table 1. The 12L:12D control photoperiod was controlled using a digital timer (Smiths Industries, London, UK).

Weight and length of larvae at the beginning of the trial (20 dph) was 0.06 g and 1.30±0.04 cm, respectively. All fish were hand-fed to satiation three times a day at 09.00, 13.00, and 18.00 h. Larvae were weaned on a 1:1 crumb mix (Nutra Trout Fry 02 and Standard Expander 40, Skretting UK) until 72 dph after which normal Nutra Trout Fry 02 was used. Light intensity was measured at the beginning, middle (48 dph) and end of the trial (118 dph), at both the bottom and water surface using Watts and Lux meter sensors calibrated to national standards (Skye Instruments, Ltd, Powys, UK).

Biometric samplings took place every two weeks over a period of four months at 20, 34, 48, 62, 76, 90, 104, and 118 dph. During sampling, fish were either anesthetized (0.1-0.15 g L^{-1}) or sacrificed by a lethal dose (0.5-0.8 g L^{-1}) of benzocaine solution (SIGMA, Poole, UK). Fish (n = 10/replicate/treatment) were sacrificed at the first two sampling points (20 and 34 dph), as they were too small to be anesthetized safely. Thereafter (48-118 dph), both weight-length monitoring of all remaining fish was carried out by anesthesia, and a further sacrifice (n = 5-6/replicate/treatment) at each sampling point was done for histological analysis. Male to female sex ratio from all fish remaining (determined by direct gonad examination of sacrificed fish by the end of the trial) and sampled throughout the experiment was similar in all treatments (1.1, 1.2, 1.4, and 1.1 for LL-H, LL-M, LL-L, and 12L:12D, respectively).

Histological gonadal samples from all fish sacrificed during or at the end of the trial were collected, prepared, and analyzed as previously described (Martínez-Chávez et al., 2008). The stage of oocyte development was visually determined and the leading oocyte cohorts were staged (stages 1-4; S1-S4) according to an adapted classification from Coward and Bromage (1998) for oogenesis and Babiker and Ibrahim (1979) for spermatogenesis (stages 1-5; S1-S5) (Table 2). Image analysis software (ImageProPlus, Media Cybernetics Inc., USA) was used to measure the long and short axis of 30 oocytes/replicate/treatment/sampling point (mean values are presented). Growth performance measurements, specific growth rate (SGR), and feed conversion ratio (FCR) were calculated as in Taylor et al. (2006). Gonadosomatic index (GSI) was calculated for all fish at the end of the trial using the formula GSI = (wet gonad weight (g) × wet body weight^{-1} (g)) × 100. Survival across the trial was also recorded, and personal observations of fish were annotated.

Table 2 - Classification scheme used to identify the stages of oogenesis and spermatogenesis[1]

	Stage	Definition	Size range (µm)	Appearance
Oogenesis	S1	Pre-vitellogenic	7-345	Nucleus containing chromatin strands. Developing follicular layer. Vesicle at near edge of oocyte. Stains dark pink reducing to pale pink as less basophilic.
	S2	Early stages of vitellogenesis	224-658	Small yolk granules starting at periphery. Vesicles seen throughout oocyte. Follicular layer can be seen to be more developed.
	S3	Late stages of vitellogenesis	428-1416	Yolk granules become larger yolk globules and empty vacuoles throughout oocyte. Very developed follicular wall. Nucleus central.
	S4	Mature	428-1416	Same as S3 but vesicle migration can be seen.
Spermatogenesis	S1	Immature	-	Mostly spermatogonia with some spermatocytes.
	S2	Maturing	-	Clusters of spermatocytes and a few spermatids.
	S3	Mature	-	Spermatogonia, spermatocytes, and spermatids all present and few spermatozoa in the middle.
	S4	Ripening	-	All stages present with abundant spermatozoa.
	S5	Ripe	-	Sperm ducts distended with spermatozoa and seminal fluid.

[1] Adapted from Coward and Bromage (1998) and Babiker and Ibrahim (1979).

All data were analyzed by non-parametric statistical tests (Kruskal-Wallis ANOVA on Ranks) before a Dunn's pair wise comparison at each sample point. All stats and graphs were created using Sigma Plot (Version 10.0 Systat Software Inc., London, UK). For all tests, significance was set at $P<0.05$.

3. Results

Clear growth and gonadal development effects were observed between fish exposed to continuous illumination (LL-H, LL-M, LL-L) compared with a 12L:12D photoperiod. Specifically, fish under LL-H and LL-M treatments were significantly heavier (13-20%) and longer (6-8%) than fish exposed to 12L:12D photoperiod by the end of the trial (118 dph) (Table 3, Figure 1). Importantly, the degree of growth enhancement did not vary according to the light intensity at this stage; interestingly, however, the highest mortality rate in this study (12%) was found at the highest intensity applied (LL-H; Table 3), but it was traced to a single unknown mortality event.

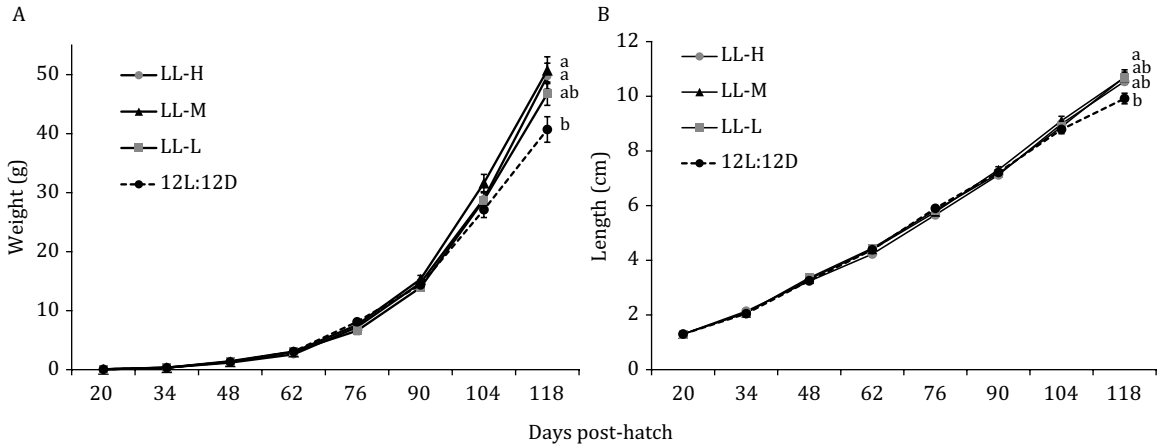
Feed intake by fish in LL treatments was 13-16% higher than in the control, while FCR and SGR were found to be similar among all treatments (Table 3).

Regarding gonad maturation, females of all treatments were at S1 and S2 stages between 62 and 76 dph. The S3 oocytes appeared first at 90 dph in LL-H and at 104 dph in 12L:12D and at 118 dph for both

Table 3 - Summary of final (118 dph) weight, length, gonadosomatic index (GSI), and overall (20-118 dph) specific growth rate (SGR), feed conversion rate (FCR), feed intake, and mortality

	Treatment				P
	High	Medium	Low	Control	
Final weight	49.7±2.2a	50.8±2.3a	46.8±2.0ab	40.7±2.2b	0.007
Final length	10.5±0.2a	10.7±0.2ab	10.7±0.3ab	9.9±0.2b	0.012
Total feed intake (g)	3539	3533	3468	3050	
SGR	7.6	7.6	7.5	7.4	
FCR	0.7	0.8	0.7	0.7	
GSI (F/M)	0.9±0.4/0.4±0.1	1.4±0.3/0.6±0.1	2.0±0.6/0.5±0.1	1.1±0.4/0.4±0.05	
% Mortality	12.0±2.7	2.0±0.7	1.0±0.7	5.3±1.3	

F - female; M - male.
Final weights and lengths are expressed as mean±SE. Where appropriate, P-values are shown and letters indicate significant differences across treatments.



LL-H - high light intensity; LL-M - medium light intensity; LL-L - low light intensity; 12L:12D - 12-h light and 12-h dark, control.
Values are expressed as mean±SE (33-75 individuals/replicate/time point).
Lowercase letters indicate significant differences between treatments at a given time point.

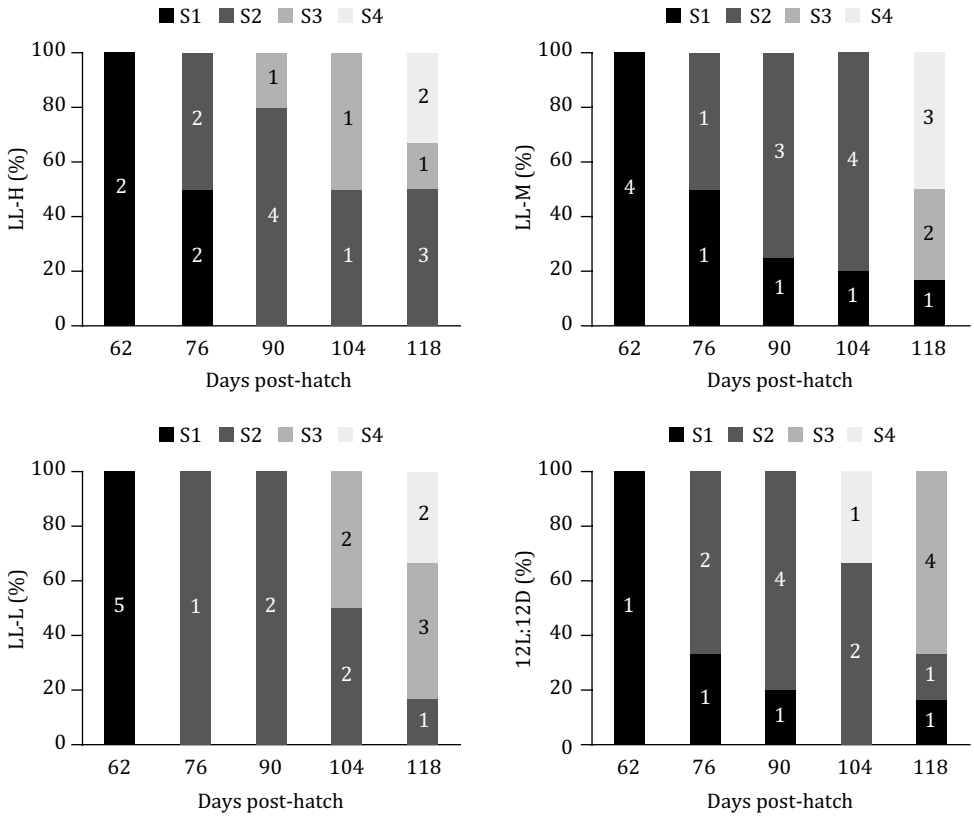
Figure 1 - Weight (A) and length (B) over time in Nile tilapia raised from 20 to 118 days post-hatch under different light intensities.

remaining treatments (LL-M and LL-L). At 118 dph, 33 to 50% of females sacrificed were at S4 stage in all LL treatments but none had reached this stage of gonadal development under 12L:12D, in which 66% were at S3 (Figure 2).

Most male gonads at 62 dph were at S1 with only few individuals of treatments LL-H, LL-M, and 12L:12D progressing to stage S2. First signs of S4 stage were observed in the control group at 76 dph. At 90 dph, all treatments showed 40-60% of sacrificed individuals in S4 with no apparent differences among treatments. However, by 104 dph, while most fish sampled in the 12L:12D treatment were spermiating (S5), only 10-33% of the fish under LL treatments were at the same stage with the remaining fish in S4. At 118 dph, the percentage of spermiating fish increased slightly in the LL-treated groups (33-50%) and, importantly, male fish were still observed at stage 3 (all LL treatments) as opposed to the 12L:12D, in which fish were only found at more advanced S4-S5 stages (Figure 3). The GSI values for all treatments were not significantly different between males and females, while mortality ranged from 1-12% (Table 3).

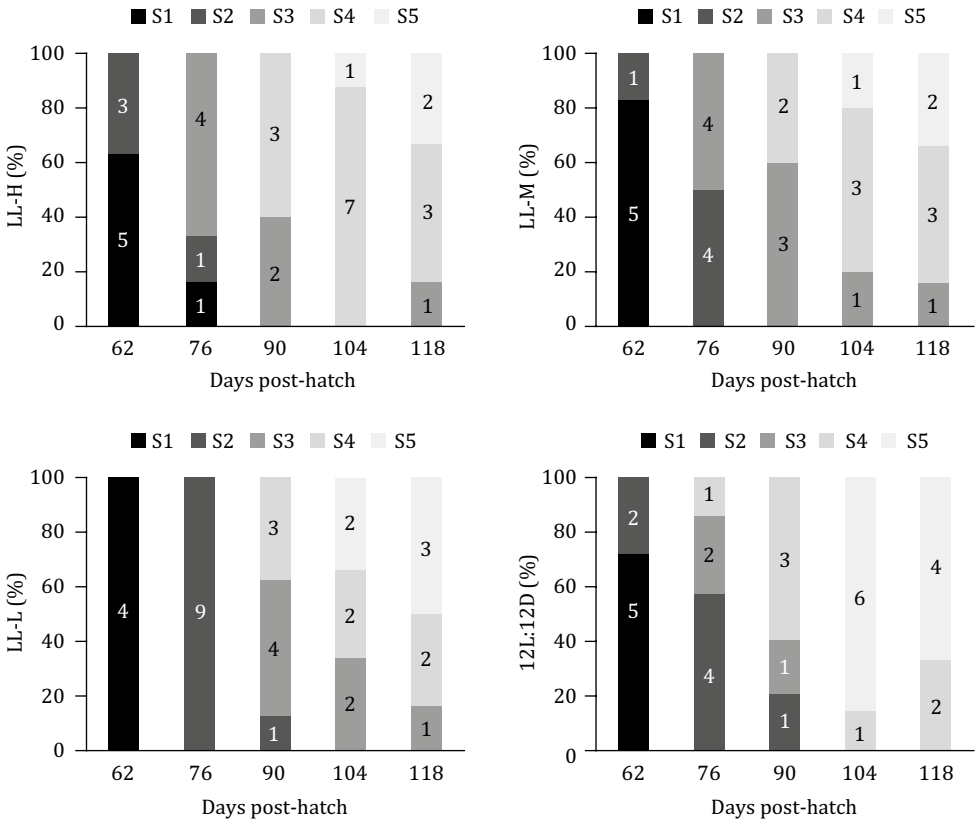
4. Discussion

Enhanced growth and gonadal development effects were observed between fish exposed to continuous illumination as previously shown by El-Sayed and Kawanna (2004) and Rad et al. (2006), in which higher percentages of enhanced growth (59 and 23%, respectively) in similar conditions (long day or LL, but not testing different light intensities) for the same species were found, although fish in the present study achieved double the weight almost a month earlier, suggesting a suboptimal growth of fish in previous studies. These differences can be attributed to methodology used such as



LL-H - high light intensity; LL-M - medium light intensity; LL-L - low light intensity; 12L:12D - 12-h light and 12-h dark, control.
S1: stage 1; S2: stage 2; S3: stage 3; S4: stage 4.
The number of individuals for each sampling time is indicated on the graph. Staging adapted from Coward and Bromage, 1998.

Figure 2 - Relative proportion of each stage of oogenesis in Nile tilapia fry reared under different light intensities from 62 to 118 days post-hatch.



LL-H - high light intensity; LL-M - medium light intensity; LL-L - low light intensity; 12L:12D - 12-h light and 12-h dark, control.
S1: stage 1; S2: stage 2; S3: stage 3; S4: stage 4; S5: stage 5.
The number of individuals is indicated on the graph. Staging adapted from Babiker and Ibrahim, 1979.

Figure 3 - Relative proportion of each stage of spermatogenesis in Nile tilapia fry reared under different light intensities from 62 to 118 days post-hatch.

initial age of exposure and weight, feeding regime (i.e., feeding time and frequency), feeding type (i.e., % biomass versus satiation), nutritional composition of feed, stocking density, and light intensities used, but also to more inconspicuous differences such as the genetic background and strain of fish (Migaud et al., 2010). This illustrates the difficulties of comparing datasets from different trials even in a single species when not enough information on such variables is reported and results cannot be replicated or could potentially be under- or overestimated.

In this study, the degree of growth enhancement did not vary according to the light intensity used, despite the fact that fish were exposed to photoperiod treatments as suggested for annual temperate species (Taylor et al., 2006). This could be related to the timing/age of exposition in this study (20 dph) or differences in the circadian axis transduction/sensitivity in this species (Migaud et al., 2007b; Martínez-Chávez and Migaud, 2009; Nikaido et al., 2009); however, this requires further confirmation.

The current results thus demonstrate that the different light intensities tested would not play an important role in the growth enhancement effect observed in Nile tilapia exposed to continuous illumination at this stage. However, the highest mortality rate in this study was found at the highest intensity applied and was correlated to direct observations that fish showed more aggressiveness and a general heightened state of alert, which may have caused the single recorded mortality event. This agrees with data from other species, in which higher intensities are known to be detrimental to fish (Migaud et al., 2007a; Villamizar et al., 2011). Therefore, these results have implications for the use of artificial lighting in tilapia culture as low to medium intensity continuous illumination regimes may provide safer conditions for fish welfare (Table 3). Long-term studies are required as it is possible that higher light intensities could have a greater effect in latter growth stages as shown in temperate

teleosts, in which, in some cases, growth effects were only shown three months after onset of continuous illumination (Johnston et al., 2003; Taylor and Migaud, 2009).

According to the feed intake, FCR, and SGR found in this study, it can be suggested that continuous lighting would not enhance any of these parameters but rather have an orexigenic effect as suggested recently for this and other teleost species (Volkoff et al., 2010; Volpato et al., 2013). Studies are required at both endocrine and molecular levels to confirm such a theory, especially focusing on the somatotropic axis, which regulates feed intake, somatic growth, and its effects on energy distribution towards reproduction.

In agreement with previous studies in Nile tilapia (Rad et al., 2006) and seasonal species such as Senegalese sole (*Solea senegalensis*) and European sea bass (*Dicentrarchus labrax*) (García-López et al., 2006), male spermatogenesis in this study appeared to be delayed under continuous illumination regimes compared with 12L:12D. In contrast, females appeared to be at more advanced gonadal stages under all continuous illumination treatments compared with the 12L:12D photoperiod, which agrees with previous investigations (Martínez-Chávez et al., 2008). The fact that females of this species under continuous illumination treatments seem to reach advanced stages of maturation earlier is quite interesting, as most of the previous studies have been performed in seasonal spawners that have clear windows of oocyte recruitment and maturational commitment that can be suppressed or delayed with the use of long days and/or continuous illumination (Bromage et al., 2001; Hansen et al., 2001; Davie et al., 2007). The fact that female Nile tilapia seem less affected by one of the most important drivers of maturation (photoperiod) deserves further investigation as to whether genetic or other phenotypic variables, such as endogenous clocks, are at play.

5. Conclusions

This study shows a clear effect of continuous illumination on growth of Nile tilapia, which is higher than previous reports.

Clear gonadal maturation effects between male (delay) and females (advancement) of Nile tilapia are observed under continuous illumination regimes.

No significant differences in growth is observed within continuous illumination treatments, suggesting that light intensity at thresholds tested might not be affecting these variables. However, care should be taken if light intensity is increased as it could provide negative welfare conditions for Nile tilapia.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: C.C. Martínez-Chávez. Data curation: D.V. Parke. Formal analysis: D.V. Parke. Methodology: C.C. Martínez-Chávez. Supervision: H. Migaud. Writing-original draft: C.C. Martínez-Chávez and P. Navarrete-Ramírez. Writing-review & editing: P. Navarrete-Ramírez.

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