**The use of photoperiods to provide year round spawning in lumpfish *Cyclopterus lumpus***

Albert K. Imslanda,b§,Thor Arne Hangstadc, Thor Magne Jonassenc, Sigurd O. Stefanssonb, Tom Ole Nilsenb, Peter Hovgaardd, Tor Anders Elvegårde, Ken Ståle Lindbergf, Bjørn Mikalsenf, Tonje Cecilie Urskogg, Birgitta Norbergh, Eva Anderssonh, Frank Spetlandi, Patrick Reynoldsj

aAkvaplan-niva Iceland Office, Akralind 4, 201 Kópavogur, Iceland; bDepartment of Biological Science, University of Bergen, High Technology Centre, 5020 Bergen, Norway; cAkvaplan-niva, Framsenteret, 9296 Tromsø, Norway; dFjord Forsk Sogn, 6852 Sogndal, Norway; eNordlaks Oppdrett AS, Post box 224, 8455 Stokmarknes, Norway; fLerøy Aurora, Postbox 2123, 9267 Tromsø, Norway; gGrieg Seafood Finnmark AS, Markedsgata 3, Alta, Norway; hInstitute of Marine Research, Postbox 1870 Nordnes, 5817 Bergen, Norwway; iLumarine, Tømmervåg, 6590 Tustna, Norway;  jGIFAS AS, Gildeskål, 8140 Inndyr, Norway

**Running title:** Manipulation of spawning in lumpfish

**§** Corresponding author: Akvaplan-niva Iceland Office, Akralind 4, 201 Kópavogur, Iceland. E-mail address: [albert.imsland@akvaplan.niva.no](mailto:albert.imsland@akvaplan.niva.no)

**Abstract**

In order to provide year round spawning broodstock, lumpfish (initial size 746 g and 24.9 cm) were reared under four different photoperiod regimes from January 2017 to July 2018. One group was reared under simulated natural photoperiod (LDN, control group) for Tromsø (70°N). The second group was transferred to continuous light (LD240) on 30 January 2017 and reared at LD24:0 throughout the trial period. Two compressed and phase advanced photoperiods were also established. Both groups were moved from LDN to LD24:0 on 30 January 2017, and after that reared at compressed natural photoperiods where the annual photoperiod was compressed down to six months (L6) or nine months (L9) for the duration of the study. Spawning time was shifted in both compressed groups during both years of the study. Spawning activity in the second year of the study was higher and followed more closely the expected spawning period in the compressed and the LDN groups. Spawning in the LD240 group was spread out over the experimental period with no distinct peak in spawning. A seasonal and pronounced drop in condition factor was found for females in the L9, L6 and the LDN groups. This post-spawning loss in condition was closely related to the spawning activity of each group. The current findings suggest that photoperiod has a strong influence on the timing of lumpfish maturation and can be used as an efficient and inexpensive tool to secure lumpfish reproduction operations i.e. year-round supply of egg and milt and/or timing with optimal temperature regimes.

*Keywords:*Lumpfish; compressed and phase-shifted photoperiods; growth; maturation

**1. Introduction**

Lumpfish *Cyclopterus lumpus* L. 1758 is widely distributed across a large area on both sides of the North Atlantic Ocean (Vasconcelos et al., 2004, Bañón et al., 2008; Pampoulie et al., 2014; Jónsdóttir et al., 2018). Natural spawning in lumpfish occurs in spring and early summer (March-June, Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018). Spawning of lumpfish often takes place in shallow sub-tidal waters when temperatures reach around 4°C (Collins, 1976; Daborn and Gregory, 1983). Kennedy (2018) investigated the natural spawning cycle and ovary development of lumpfish. The results showed that ovaries of lumpfish had a wide range of oocyte sizes and that lumpfish is a determinate, batch spawner with ovary development taking at least 8 months. They spawn a maximum of two batches per season with a similar number of eggs in each batch. Lumpfish were documented as spawning over a 4-month period (weeks 13-27, March – July), but it is likely that spawning may occur over a greater period.

Recently the lumpfish has been suggested as a cold-water cleaner fish for removal of sea lice from Atlantic salmon, *Salmo salar* (Imsland et al., 2014 a-c; 2015a-b). Interest in use of hatchery reared lumpfish has increased rapidly concurrent with the species use as biological delouser on Atlantic salmon. There is; therefore, a need for year-round production of lumpfish juveniles. To reach that goal development of methods for the management of sexual maturation and spawning are necessary. As a first step for developing methods to manage sexual maturation Imsland et al. (2018) exposed groups of juvenile lumpfish previously reared under simulated natural photoperiod to continuous light from April to January and from April to April the subsequent year followed by 8 week decline in hours of light from 24 to 4 hours (autumn signal) and subsequent 8 week rise from 4 to 24 hours (spring signal). In both groups spawning was seen 3-6 months after the onset of short autumn-short spring photoperiodic signal whereas no spawning was found in the control group reared at simulated natural photoperiod. These findings indicate that spawning control in lumpfish is possible through manipulation of photoperiods.

In temperate regions, teleost reproduction follows a seasonal cycle, which is synchronized by several environmental factors such as photoperiod (Wang et al. 2010; Cyr et al., 2018). These external factors influence/synchronize endogenous rhythms which result in a spawning synchronicity within populations and increase offspring survival (Bromage et al., 2001; Taranger et al., 2010; Cyr et al., 2018). Photoperiod control of the reproductive process has been successfully applied to broodstock to alter the phase of the annual sexual cycles and hence the spawning time in a range of fish species (e.g. Taranger et al., 2010). A range of studies demonstrate that photoperiod manipulation can be an effective tool to control, and synchronize, maturation in farmed fish, e.g. Atlantic salmon (Oppedal et al., 2006), Arctic charr, *Salvelinus alpinus* (Gunnarsson et al., 2012), Atlantic cod, *Gadus morhua* (Norberg et al., 2004; Imsland et al., 2013a), Atlantic halibut, *Hippoglossus hippoglossus* (Norberg et al., 2001; Imsland et al., 2009), turbot, *Scophthalmus maximus* (Imsland et al., 2003, 2013b; Imsland and Jonassen, 2003), Senegalensis sole, *Solea senegalensis* (Garcia-Lopez et al., 2006), common dentex, *Dentex dentex* (Pavlidis et al., 2001) and lumpfish (Imsland et al., 2018), However, the effectiveness of photoperiod protocols differs among species and appears also to be modulated by other factors such as age, feeding, body size, adiposity and the stage of maturation of the fish (Taranger et al., 1999, 2010; Oppedal et al., 2006; Taylor et al., 2008).

In salmonids (autumn spawners) long photoperiods or continuous light early in the season are believed to phase advance circannual rhythms that control the seasonal timing of onset and completion of puberty, whereas long photoperiods or continuous light from midsummer onwards delay such rhythms (Bromage et al., 2001; Taranger et al., 2010). For spring spawning species as Atlantic cod continuous light treatment has been found to arrest or delay pubertal development when applied from around mid-summer and onwards (Hansen et al., 2001; Davie et al., 2003, 2007a; Karlsen et al., 2006; Imsland et al., 2013a). A similar delay of maturation by applying continuous light one year before first maturity has been found in the Atlantic halibut (Imsland et al., 2009). The effect of compressed and phase-shifted photoperiod is less documented but in general such treatment seems to advance spawning allowing for synchronizing spawning time for year round production of gametes (Bromage et al., 2001; Morehead et al., 2000; Norberg et al., 2004; Guerrero-Tortolero et al., 2010; Newman et al., 2010; Cyr et al., 2018).

At present only one published study exists on the effect of continuous light or other light regimes on growth in lumpfish (Imsland et al., 2018). Here, exposure of lumpfish to continuous light in spring for 9-12 months followed by an autumn-spring signal stimulated somatic growth especially in females. The growth enhancing effect of continuous light lasted for approximately six months in females compared to one month in the males. In other marine species, there are indications that exposure to continuous light during the juvenile stage may significantly affect subsequent growth and thereby age at maturity (Imsland and Jonassen, 2003, 2005; Imsland et al., 2009, 2013a-b). However, in some cases prolonged exposure to continuous or extended light regimes may reduce growth and food conversion efficiency (e.g. Stefánsson et al., 2002), so the period of extended or continuous light must be synchronized with the internal rhythms of the fish and the season in order to achieve increased growth and/or lower maturity. Based on findings from other marine species and the recent study of Imsland et al. (2018) we hypothesize that rearing juvenile lumpfish at continuous light will enhance growth during the late juvenile phase. If maturation is triggered at a certain size threshold as seen in many teleosts (Imsland et al., 1997a) the enhanced growth will alter the age at 1st maturation in lumpfish.

The rationale behind the chosen light regimes in the current trial, was to investigate possible effect of phase advanced and compressed photoperiods on growth and maturation in lumpfish. Accordingly, a study was performed where 1+ juvenile lumpfish (initial weight 746 g) were reared under simulated natural photoperiod for Tromsø, (LDN, control group) with expected first spawning in spring 2017 based on the natural spawning cycle for the species (Collins, 1976; Daborn and Gregory, 1983; Kennedy, 2018). In addition, there were three groups exposed to continuous light from late January 2017, two of those (L6 and L9) were thereafter reared on phase advanced compressed annual photoperiod (12 months cycle compressed to 6 and 9 months, respectively) and the third group reared under continuous light (LD240) throughout the trial period.

The objective of this study was to investigate if it is possible to change the annual spawning season in lumpfish by rearing the fish under phase advanced and compressed photoperiods. A second objective was to investigate how rearing at continuous light affects the growth properties of lumpfish during the late juvenile phase and whether 24L brings spawning of the individual fish out of synchrony within the group and with the normal season. Based on the effect of photoperiod on controlling maturity and the effect of phase advancing and compressing photoperiods in other species we predict that spawning time will shift in the compressed photoperiods with spawning starting once hours of light per day in the artificial spring reach 8-10 h and continuing for 3-5 months.

**2. Materials and Methods**

*2.1 Pre-experimental protocol*

Sexually mature wild lumpfish (10 females and 2 males) were caught by local fishermen in gill nets at Hekkingen, Sommarøy, Troms County, Norway during September-October 2015. The fertilized eggs were incubated at 8.5-9.7°C at Akvaplan-niva research station at Kraknes (APN-K) and later transferred to Senja Akvakultursenter, Senja, Troms County where they hatched in December 2015 and were reared in 8-10 m3 tanks at 10-11°C. In June 2016 1500 lumpfish juveniles were transported back to APN-K and reared at 8-10°C and simulated natural photoperiod (LDN) for Tromsø (N 69° 40`) to experimental start-up in January 2017. The juveniles were initially fed with Gemma Micro (150 -500 µm, Skretting, Norway). After 30 days, the juveniles were fed with 500-800 µm dry feed pellets (Gemma Wean Diamond, Skretting, Norway). After approximately 120 days the juveniles were fed with Gemma Wean diamond 2.0 mm (Skretting AS, Stavanger, Norway) and pellet size increased according to size following the producers recommendation.

*2.2 Experimental set-up and rearing conditions*

Two tanks were reared under simulated natural photoperiod for Tromsø prior to start of the experiment in January 2017. On 30 January 2017 four experimental groups (Fig. 1) with a mean (± SD) weight of 746 g (±175) and length 24.9 cm (±1.6) were established. One group remained on LDN (control group) and one group was transferred to continuous light (LD240) and reared under this regime throughout the trial period. Two phase advanced and compressed photoperiods were also established on 30 January. Both groups were moved to continuous light and after that reared at compressed natural photoperiods where the annual photoperiod was compressed down to six months (L6) or nine months (L9). The trial was terminated on 12 July 2018.

On 19-21 June 2017 all lumpfish (N=300) with an average (± SD) weight of 1267 g (± 324 g) and length of 28.01 cm (± 3.2 g) (were anaesthetized (Finquel® 150 mg L-1)and tagged intraperitoneally with a Trovan® Passive Integrated Transponder and distributed among eight 12 m3 tanks at APN-K with 37-38 fish in each tank. Light in all tanks was supplied using two 18W fluorescent daylight tubes positioned in the centre of the tank-cover. Photoirradiance at the tank bottom was approximately 15.3 mol m-2 s-1.

The fish were reared under ambient water conditions (Fig. 2) with minimum temperatures around 3.0°C in February and maximum around 9.0°C in September-October and annual average temperature of 5.8°C. Salinity was around 34.1 ppt. throughout the study period. Dissolved oxygen ranged between 8.9 mg l-1 and 11.1 mg l-1 during the trial period. The fish were fed to satiationwith a commercial formulated feed (4-7 mm, Skretting Amber Neptun, Stavanger, Norway) containing 16% fat and 52% protein during light hours in the LDN.

*2.4 Growth and maturation*

All fish were individually weighted and their length measured at the following dates: 30-31 January 2017, 20-21 June 2017, 15-16 November 2017, 27-28 March 2017, 30-31 May 2017, 10-12 July 2018. Specific growth rate (SGR) of individual lumpfish was calculated according to the formula of Houde and Schekter (1981):

SGR = (eg-1) ×100

where g = (ln (W2)-ln (W1) / (t2-t1) and W2 and W1 are weights on days t2 and t1, respectively.

The condition factor (K) of individual lumpfish (calculated at each sampling interval) was defined as:

K =100 \* W / L3

where W is the weight (g) of the fish and L the corresponding total length (cm).

All fish were sexed as it is possible to sex lumpfish based on skin coloration from early juvenile age (Davenport and Bradshaw, 1995). From beginning of the trial all fish were checked regularly for sexual maturation by examining external morphology. Fish in later stages of their sexual maturation were gently hand-stripped. Each experimental tank was examined daily and any eggs removed. When in the ovary-oviduct, lumpfish eggs are invariably rose pink in colour, but after discharge to the environment they change to a variety of yellow, green, purple, violet, blue and grey colours each mass being of fairly homogenous colour (Davenport, 1985). Accordingly, it was possible to distinguish individual spawnings in the tank based on coloration of the eggs sampled (Davenport, 1985; Armand Nes, Akvaplan-niva, Kraknes research station, pers. comm.). The fish were slaughtered after termination of the trial in July 2018 and sex of all individuals confirmed and all fish categorized into eight groups with the sampling size in each group as follows: L6-males (N=28), L6-females (N=47); L9-males (N=31), L9-females (N=44); LND-males (N=32), LND-females (N=43); LD240-males (N=30), LD240-females (N=45).

*2.6. Statistics*

All statistical analyses were conducted using Statistica™ 13.3 software. A Kolmogorov-Smirnov test (Zar, 1984) was used to assess for normality of distributions. The homogeneity of variances was tested using the Levene’s F test (Zar, 1984 Data on mortality and spawning activity was tested with a 2 test with the LDN group as expected value. A three-way nested analysis of variance (ANOVA, Searle et al., 1992) where replicates are nested within photoperiod group and sex was applied to calculate the effect of different photoperiods and sex on mean weights, condition factor and specific growth rates. The model equation of the nested ANOVA had the form:

1. X*ijk* =  + *i* + *j* + *ij* + C*ijk* + *ijkl*

where  is the general level; *i* is the photoperiod effect; *j* is the sex effect; *ij* is the interactive effect between photoperiod and sex; C*ijk* is the contribution caused by replicate (tank) *k* in photoperiod *i* and sex *j* and *ijkl* is the error term. We assume that *ijkl* ~ Normal distributed (0, 2). Possible changes over time in condition factor was tested with a linear regression.

Mean individual growth trajectories were analysed using a growth curve multivariate analysis (GCM) of variance (MANOVA) model (Timm, 1980; Chambers and Miller, 1995). The model equation of the GCM had the form:

1. **Y** (n  p) = **X** (n  q) **B** (q  p) + **E** (n  p)

Where **Y** (n  p) are the growth at age vectors

1. **y** = (y1, y2, …, yp)

for each p (age) measurements on n individual fish; **X** (n  q) is the design matrix or the set of extraneous variables measured for each individual, i.e., q = agei+ photoperiod regimej (j = L6; L9; LDN; LD240) + sexk (k = female; male) + replicatej (j = replicate a; replicate b); **B** (q  p) is the matrix of parameters estimated by the model; **E** (n  p) is the matrix of deviations for each individual from the expected value of **Y** = **XB**

Significant differences revealed in MANOVA or ANOVA were followed by Student-Newman-Keuls (SNK) post hoc test to determine differences among experimental groups. A significance level () of 0.05 was used if not stated otherwise. In cases with non-significant statistical tests, power (1-) analysis was performed in Statistica using  = 0.05.

**3. Results**

*3.1 Growth and mortality*

A total of 37 (12%) fish died during the experiment. The mortality did not vary among the groups (2 ≤ 2.7, p > 0.10) and occurred mainly during the spawning period in each experimental group. The overall initial mean weight (SD) was 746 (175) g and did not differ (three way nested ANOVA, p> 0.6, Power (1 – ) > 0.7, Fig. 3) among sex and photoperiod groups. From June 2017 and throughout the study all male groups displayed lower mean weights (SNK test, p< 0.05, Fig. 3) compared to the females. Significant effect of photoperiod (three way nested ANOVA, *F*3, 254 = 5.1 p< 0.05) was seen from November to March as LDN males were larger than the three other male groups (SNK test, p< 0.05). A significant interactive effect of photoperiod and sex (three way nested ANOVA, *F*3, 216 = 4.7, p< 0.05) was seen in May 2018 as female LD240 were largest of the four female groups whereas LD240 males were the smallest of the males (Fig. 3). No significant differences between the photoperiod groups within each sex was seen at the termination of the trial (SNK test, p > 0.30).

The fish reared on the different photoperiod regimes differed in their growth patterns, as the GCM analyses revealed differences between the individual growth trajectories of the photoperiod regimes (MANOVA (PHOTOPERIOD), Wilk's 12, 262 = 0.61, p < 0.001, Fig. 4), sex (MANOVA (SEX), Wilk's 4, 99 = 0.65, p < 0.001) and interaction between photoperiod and sex (MANOVA (PHOTOPERIOD X SEX), Wilk's 12, 262 = 0.72, p < 0.001). Growth rates varied between the sexes from onset of the trial (three ways nested ANOVA, p < 0.05), whereas photoperiod effects were found from June 2017 to May 2018, and interactive effect of sex and photoperiod between June and November 2017 (Fig. 4). The L6 females displayed the highest growth of all groups between June and November (SNK post hoc test, p < 0.01). Average negative growth (weight loss) was seen for the LDN females and males from March 2018 onwards as well as for females in the L6 group and females and males in the LD240 group during the final period of the trial (Fig. 4).

Initial condition factor (K) did not vary between the experimental groups (three way nested ANOVA, *P* > 0.3, (1 – ) > 0.7, Fig. 5). The effect of photoperiod on K was significant in May 2018 as the females in the LD240 group displayed higher K (SNK test, p< 0.05) compared to the LDN and L9 female groups. A significant interactive effect of photoperiod and sex (three way nested ANOVA, p< 0.05) was seen in in November 2017 and July 2018 as female L6 (November) and LD240 (July) had the highest K of the female groups but no such trend was seen in the males at these dates (Fig. 5). The K sank significantly from June to November for the L9 females (linear regression,  = -0.31, p < 0.001, Fig. 5), from November onwards for the L6 females (linear regression,  = -0.29, p < 0.001) and from March to July 2018 for the LDN females (linear regression,  = -0.41, p < 0.001).

*3.2 Maturation*

Spawning colouration and running milt was seen for males in all four photoperiod groups from June 2017 onwards. In the females, spawning time varied between the photoperiod groups (Fig. 6, Table 1). Spawning in the LDN group was about 3 months delayed in relation to expected spawning time in 2017, but spawning increased for this group in 2018 and was observed between March and July in line with expected spawning time (Fig. 6). In both phase advanced compressed groups spawning took place around the expected spawning periods in both years of the trial. Few females in the L6 group spawned in June and July 2017 (Table 1), but higher spawning activity was seen in this group between January and May in 2018 according to their spring-summer photoperiod. High proportion of spawning females was found in the L9 group between July and September 2017 and from February to June in 2018, according to their spring photoperiod. Spawning in the LD240 female group occurred sporadically throughout the trial period and did not show any apparent pattern. Spawning activity was significantly higher in the L9 group compared to the control group (LDN) during spring 2018 (2 = 4.0, p < 0.05, Table 1) and significantly lower for the LD240 group compared the L9 and LDN groups during 2018 (2 > 5.1, p < 0.05). Spawning activity was marginally lower in the L6 group compared to the L9 group during summer 2017 (2 = 3.8, p < 0.05).

**4. Discussion**

*4.1 Maturation*

The efficiency of photoperiod manipulation as a tool for regulating reproduction in lumpfish is demonstrated by the shift in spawning cycle caused by the altered light regimes. Expected spawning times based on earlier trials and lumpfish natural spawning time in the LDN group is between March-June (Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018) whereas spawning commenced in the LDN group in July 2017 i.e. 3-5 months delayed. An explanation for the delayed response could be that the developmental stage or size threshold needed to respond to photoperiod was not reached until summer 2017. Such size related threshold of maturation has previously been indicated by Imsland et al. (2018) where female lumpfish spawned at approximately 1.5 kg. This size was reached in June-July 2017 concomitant with onset of spawning in the LDN group. Spawning activity in the second year of the study was higher and followed more closely the expected spawning period in the compressed and the LDN groups.

Earlier studies have shown that phase advanced and compressed natural photoperiods treatment seem to advance spawning allowing for synchronizing spawning time for year round production of gametes. Morehead et al. (2000) reared sexually mature striped trumpeter *Latris lineata* on either a 12-month cycle of ambient temperature (9-18°C) and photoperiod, or a 9-month compressed temperature and photoperiod cycle and found that the compressed cycle advanced spawning by 1 and 4 months during consecutive seasons. Norberg et al. (2004) compressed the annual photoperiod cycle of Atlantic cod into 6 or 9 months, held at 12 months, or extended to 18 months, in each case followed by one 12-month cycle (termed 6+12, 9+12, 12+12, and 18+12, respectively). Photoperiod alterations caused shifts in the cyclic patterns of plasma calcium, sex steroid, and thyroid hormones, and also produced correlative changes in the timing of spawning. Initial spawning was advanced in the compressed (6+12) photoperiod group, followed by further advancement in the timing of the second spawning. Conversely, spawning was delayed in the 18+12 group. Guerrero-Tortolero et al. (2010) compressed the yearly photoperiod down to 3 month period in yellowtail snapper, *Lutjanus argentiventris* and achieved spawning, in this group during winter approximately 6 months prior to the natural spawning season. Newman et al. (2010) investigated the effect of phase advancing the photoperiod for three months in Murray cod, *Maccullochella peelii peelii*, and found that maturation was advanced for three-four months. In common wolffish, *Anarhichas lupus*, and spotted wolffish, *Anarhichas minor* fish subjected to a 8-month compressed photoperiod spawned 2-6 months earlier than the controls (Cyr et al., 2018). Overall, present data are in line with the published earlier findings, showing that many teleost species will readily react to phase advanced and compressed photoperiod cycle by advancing the annual timing of spawning. However, the effect is also dependent on the prior maturation stage of the fish and other external factors such as temperature.

As the fish were reared under ambient temperature in the present trial it may also be speculated if temperature had a confounding or masking effect for spawning in lumpfish. Notable the minimum temperatures in the second year of the trial were about 2°C lower (2.7°C vs- 4.8°C). This was due to colder sea water conditions near the water inlet for the experimental station. Despite these low temperatures spawning was not delayed in the experimental groups during this period of low temperature. In nature spawning of lumpfish often takes place in shallow sub-tidal waters when temperatures reach around 4°C (Collins, 1976; Daborn and Gregory, 1983) and current data indicate that temperatures as low as 2.7-3.3°C for a 4-5 week period in early spring does seemingly not interfere with the natural spawning progression of lumpfish. Natural spawning in lumpfish occurs in spring and early summer (April-July, Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015) when low sea water temperatures in line with those seen in the current study can be expected.

Lower spawning activity was seen in the L6 compared to the L9 group in the first half of the study (2017). A possible explanation could be that the phase advanced compressed photoperiodic signal from winter to summer solstice that naturally is 6 months long was compressed to 3 months. Although the fish can perceive the light signals it may still need more than 3 months to finalize the maturation process. This could explain the higher spawning activity in the L9 group during this period where the same photoperiodic signal was 4.5 month. Overall, our findings indicate that exposure to phase advanced compressed natural photoperiod signal can be used to control the spawning time in lumpfish. Although the female lumpfish display a positive response to photoperiod in relation to growth it is more unclear how the females utilize photoperiod signal to synchronize the spawning. It may be speculated that lumpfish do not synchronize for a narrow spawning season as the natural spawning period extends from early spring to autumn (Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018).

Rearing lumpfish under continuous light resulted in infrequent and non-rhythmic spawning, i.e. free-running, throughout the study period. It is well established that continuous light modulates the endocrine regulations and regulatory pathways from the brain-pituitary-gonad axis (Taranger et al., 2010) thereby modulating the onset of puberty. Rearing fish without photoperiod cue as done under continuous light may also lead to absence of the melatonin rhythm (Davie et al., 2007b; Bayarri et al., 2009), which in turn can alter the circadian variations of reproductive hormones causing irregularities in the reproductive process (Bayarri et al., 2009). Under continuous light fish may enter into a free running rhythm (as seen in present study) or block or delay the onset of gametogenesis (Karlsen et al., 2014). However, the response towards continuous light can be stage-dependent (Hansen et al., 2001). Such stage-dependent response towards continuous light was seen in the study of Imsland et al. (2013a) where maturation in juvenile Atlantic cod was postponed 6-12 months in groups exposed to continuous light during juvenile stages (600-800 g) whereas later exposure (> 1000 g) did not have any effect on maturation. Findings for Atlantic salmon reared in sea cages have also highlighted the importance of the timing of exposure to continuous light in the control of maturation (Hansen et al., 1992; Porter et al., 1999; Taranger et al. 1999), as exposure to continuous light out of phase with the natural light cycle, i.e. during winter, resulted in fewer fish reaching maturation. Delayed maturation in turbot exposed to continuous light during the juvenile stage has also been documented for first time spawners (Imsland et al., 1997a-b). This may indicate that the timing of continuous light exposure is important with respect to subsequent maturation and that the decision to mature is a gated rhythm (Taranger et al., 1998; Bromage et al., 2001). It is possible that the “gate open” position can vary between species (Imsland et al., 2003) according to their natural spawning season and timing of the initiation of the maturation process. This could help to explain the different effects of exposure to compressed photoperiods on timing of sexual maturation in different species (Norberg et al., 2004; Cyr et al., 2018 present study).

*4.2 Growth*

In the present study, exposure of lumpfish to compressed photoperiods changed the growth pattern compared to the control group and affected age at first maturity in females. Growth in the males in all four photoperiod groups was very slow or halted once they reached approximately 1200 g (around 28 cm). Previous research has demonstrated the sexual dimorphism in size (Imsland et al., 2018) and skin colouration of lumpfish (Goulet et al., 1986). Mature females range from 35-45 cm and are often bluish grey or green in colour, while males are 17-38 cm and display nuptial colour of pink, orange and deep red (Daborn and Gregory, 1983; Davenport, 1985). Sexual maturation influences the growth differently between the sexes (Imsland et al., 1997b; Imsland and Jonassen, 2005). First signs of maturation in the males were apparent from 600 g resulting in stagnation of growth as previously seen in Imsland et al. (2018), whereas the females started to mature at a much larger size (approx. 1500 g). These findings are in line with data from wild lumpfish where males mature one year prior, and at a much smaller size, compared to females (Hedeholm et al, 2014). For the females growth increased with increasing day-length. During summer and autumn of 2017 the L6 female group displayed higher growth compared to other female groups. Part of the explanation could be that the higher maturation seen in the L9 and LDN groups as maturation in lumpfish will slow or halt the growth (Hedeholm et al., 2014). The stunted growth seen for both sexes in the LDN and LD240 groups as well as for L6 females during the final stages of the trial may reflect the energy costs of reproduction as confirmed in previous photoperiod trials in other marine teleosts (Karlsen et al., 2006; Imsland et al., 2003, 2009, 2013a-b; Taranger et al., 2010).

The seasonal and pronounced drop in condition factor found for females in the L9, L6 and the LDN groups (Fig. 4) suggests a post-spawning loss in condition as it was closely related to the spawning activity of each group (Fig. 6). In nature seasonal changes in growth have been seen in juvenile lumpfish (Moring, 2001), with higher K in autumn prior to spawning period compared to the post-spawning period during summer. Studies on other marine species in the northeast Atlantic have shown similar seasonal change in K with lower K during winter (Haug et al., 1989; Imsland et al., 1995). The results from the present study indicate seasonal changes in growth and condition factor in lumpfish, in accordance with earlier findings on juvenile lumpfish in nature.

**5. Conclusions**

Photoperiod has a strong influence on the timing of lumpfish maturation and can be used as an efficient and inexpensive tool to secure lumpfish reproduction operations. Males in all experimental groups reached maturation at 600–800 g independent of photoperiod regime indicating that final maturation started prior to the photoperiod treatment in present study. Spawning time was shifted in both compressed groups during both years of the study indicating that a year round supply of eggs can be achieved in commercial operations of lumpfish production. Spawning in the LD240 group was spread out over the experimental period with no distinct peak in spawning.

**Acknowledgements**

The authors would like to thank Lauri Kapari and Armand Moe Nes and the technical staff at the Kraknes Aquaculture Research Station at Kraknes, Tromsø for valuable assistance prior to and during the experimental period. Financial support was given by the Norwegian Research Council (LUSINFER 256199, STAMINA 269043).

**References**

Bañón, R., Garazo, A., Fernández, A., 2008. Note about the presence of the lumpsucker *Cyclopterus lumpus* (Teleostei, Cyclopteridae) in Galician waters (NW Spain). J. Appl. Ichthyol. 24, 108-109.

Bayarri, M. J., Zanuy, S., Yilmaz, O., Carrillo, M., 2009. Effects of continuous light on the reproductive system of European sea bass gauged by alterations of circadian variations during their first reproductive cycle. Cronobiol. Int. 26, 184-199.

Bromage, N., Porter, M., Randall, C., 2001. The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. Aquaculture 197, 63-98.

Chambers, R.C., Miller, T.J., 1995. Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, South Carolina, pp. 155-175.

Collins, M.A.J., 1976. The lumpfish (*Cyclopterus lumpus* L.) in Newfoundland waters. Can. Field Nat. 90, 64-67.

Cyr, B.A.D., Tveiten, H., Maltais, D., Vandenberg, G.W., Le Francois, N.R., 2018. Photoperiod manipulation for the reproductive management of captive wolffish populations: *Anarhichas minor* and *A. lupus*. Aquac. Int. 26, 1051-1065.

Daborn, G.R., Gregory, R.S., 1983. Occurrence, distribution, and feeding habits of juvenile lumpfish, *Cyclopterus lumpus* L in the Bay of Fundy. Can. J. Zool. 61, 797-801.

Davenport, J., 1985. Synopsis of biological data of the lumpsucker *Cyclopterus lumpus* (L 1758). FAO Fisheries synopsis No. 147. 31 pp.

Davenport, J., Bradshaw, C., 1995. Observations on skin color changes in juvenile lumpsuckers. J. Fish Biol. 47, 143-154.

Davie A., Porter M.J.R., Bromage N.R., 2003. Photoperiod manipulation of maturation and growth of Atlantic cod (*Gadus morhua*). Fish Physiol Biochem. 28, 399-401.

Davie, A., Porter, M.J.R., Bromage, N.R., Migaud, H., 2007a. The role of seasonally altering photoperiod in regulating physiology in Atlantic cod (*Gadus morhua*). Part I. Sexual maturation. Can. J. Fish Aquat. Sci. 64, 84-97.

Davie, A., de Quero, C. M., Bromage, N., Treasurer, J., Migaud, H., 2007b. Inhibition of sexual maturation in tank reared haddock (*Melanogrammus aeglefinus*) through the use of constant light photoperiods. Aquaculture 270, 379-389.

Garcia-Lopez, A., Anguis, V., Couto, E., Canario, A.V.M., Canavate, J.P., Sarasquete, C., Martinez-Rodriguez, G., 2006. Non-invasive assessment of reproductive status and cycle of sex steroid levels in a captive wild broodstock of Senegalese sole *Solea senegalensis* (Kaup). Aquaculture 254, 583-593.

Goulet, D., Green, J.M., Shears, T.H., 1986. Courtship, spawning, and parental care behavior of the lumpfish, *Cyclopterus lumpus* L, in Newfoundland. Can. J. Zool. 64, 1320-1325.

Guerrero-Tortolero, D. A., Campos-Ramos, R., Burgos-Aceves, M. A., Perez-Urbiola, J. C., Colado-Duran, G., 2010. Effects of compressed seasonally changing day-length cycles on spawning performance, production of viable eggs and levels of vitellogenin in plasma in female yellowtail snapper *Lutjanus argentiventris*. J. Fish Biol. 77, 2285-2297.

Gunnarsson, S., Imsland, A.K., Arnarson, I., Siikavuopio, S.I., Gústavsson, A. Thorarensen, H., 2012. Enhanced growth of farmed Arctic charr (*Salvelinus alpinus*) following a temporal treatment of short day photoperiod. Aquaculture 350-353, 75-81.

Hansen, T., Stefansson, S.O., Taranger, G.L., 1992. Growth and sexual maturation in Atlantic salmon, *Salmo salar* L., reared in sea cages at two different light regimes. Aquac. Fish. Managem. 23, 275-280.

Hansen, T., Karlsen, Ø., Taranger, G.L., Hemre, G.I., Holm, J.C., Kjesbu, O.S., 2001. Growth, gonadal development and spawning time of Atlantic cod (*Gadus morhua*) reared under different photoperiods. Aquaculture 203, 51-67.

Haug, T., Huse, I., Kjørsvik, E., Rabben, H., 1989. Observations on the growth of juvenile Atlantic halibut (*Hippoglossus hippoglossus* l.) in captivity. Aquaculture 80, 79-86.

Hedeholm, R., Blicher, M.E., Grønkjær, P., 2014. First estimates of age and production of lumpsucker (*Cyclopterus lumpus*) in Greenland. Fish. Res. 149, 1-4.

Houde, E.D., Schekter, R.C., 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-v. Réun. Cons. Int. Explor. Mer.178, 441-453.

Imsland, A.K., Jonassen, T.M., 2003. Effects of exposure to extended photoperiods on long-term growth and age at first maturity in turbot and Atlantic halibut. Aquac. Int. 11, 463-475.

Imsland, A.K. and Jonassen, T.M., 2005. The relation between age at first maturity and growth of Atlantic halibut (*Hippoglossus hippoglossus* L.) reared under four different light regimes. Aquac. Res. 36, 1-7.

Imsland, A.K., Folkvord, A., Stefansson, S.O., 1995. Growth, oxygen consumption and activity of juvenile turbot (*Scophthalmus maximus*) reared under different temperatures and photoperiods. Neth. J. Sea Res. 34, 149–159.

Imsland, A.K., Folkvord, A., Jónsdóttir, Ó.D.B., Stefansson, S.O., 1997a. Effect of exposure to extended photoperiods during the first winter on long-term growth and age at first maturity in turbot (*Scophthalmus maximus* L.). Aquaculture 159, 125-141.

Imsland, A.K., Folkvord, A., Grung, G.L., Stefansson, S.O., Taranger, G.L., 1997b. Sexual dimorphism in growth and maturation of turbot, *Scophthalmus maximus* (Rafinesque 1810). Aquac. Res. 28, 101-114.

Imsland, A.K., Dragsnes, M., Stefansson, S.O., 2003. Exposure to continuous light inhibits maturation in turbot (*Scophthalmus maximus*). Aquaculture 219, 911-919.

Imsland, A.K., Roth, B., Foss, A., Vikingstad, E., Stefansson, S.O., Pedersen, S., Sandvik, T., Norberg, B., 2009. Long term effect of photoperiod manipulation on growth, maturation and flesh quality in Atlantic halibut. Aquaculture Research 40, 1260-1269.

Imsland, A.K., Hansen, H., Roth, B., Foss, A., Vikingstad, E., Bjørnevik, M., Powell, M., Solberg, C., Norberg, B., 2013a. Short term exposure to continuous light delays sexual maturation and increases growth of Atlantic cod in sea pens. Aquaculture Research 44, 1665-1676.

Imsland, A.K., Gunnarsson, S., Roth, B., Foss, A., Le Deuff, S., Norberg, B., Thorarensen, H., Helmvig, T., Kristjánsson, B., 2013b. Long term effect of photoperiod manipulation on growth, maturation and flesh quality in turbot. Aquaculture 416-417, 152-160.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Foss, A., Vikingstad, E., Elvegård, T.A., 2014a. The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo sala*r L.). Aquaculture425-426, 18-23.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2014b. Notes on behaviour of lumpfish in sea pens with and without Atlantic salmon. J. Ethol.32, 117-122.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2014c. Assessment of growth and sea lice infection levels in Atlantic salmon stocked in small-scale cages with lumpfish. Aquaculture433, 137-142.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2015a. Feeding preferences of lumpfish (*Cyclopterus lumpus* L.) maintained in open net-pens with Atlantic salmon (*Salmo salar* L.) Aquaculture436, 47-51.

Imsland, A.K., Reynolds, P., Eliassen, G., Hangstad, T.A., Nytrø, A.V., Foss, A., Vikingstad, E., Elvegård, T.A., 2015b. Assessment of suitable substrates for lumpfish in sea pens. Aquac. Int. 23, 639-645.

Imsland, A.K., Jonassen, T.M., Hangstad, T.A., Stefansson, S.O., Elvegård, T.A., Lemmens, S.C.A., Urskog, T.C., Nytrø, A.V., Reynolds, P., 2018. The effect of continuous light and compressed photoperiods on growth and maturation in lumpfish *Cyclopterus lumpus*. Aquaculture 485, 166-172.

Jónsdóttir, Ó.D.B., Schregel, J., Hagen, S., Tobiassen, C., Aarnes, S.G., Imsland, A.K.D., 2018. Population structure of lumpfish along the Norwegian coast: aquaculture implications. Aquac. Int. 26, 49-60.

Karlsen, Ø., Norberg, B., Kjesbu, O.S., Taranger, G.L., 2006. Effects of photoperiod and exercise on growth, liver size, and age at puberty in farmed Atlantic cod (*Gadus morhua* L.). ICES J. Mar. Sci. 63, 355–364.

Karlsen, Ø., Mittelholzer, C., Andersson, E., Norberg, B., Taranger, G.L., 2014. Continuous light affects onset of puberty and associated changes in pituitary gonadotropin subunit transcript levels, and plasma estradiol-17 beta and testosterone levels in Atlantic cod (*Gadus morhua* L.) females. Aquaculture 424, 95-103.

Kennedy, J., Jonsson, S.P., Kasper, J.M., Olafsson, H.G., 2015. Movements of female lumpfish (*Cyclopterus lumpus*) around Iceland. ICES J. Mar. Sci. 72, 880-889.

Kennedy, J., 2018. Oocyte size distribution reveals ovary development strategy, number and relative size of egg batches in lumpfish (*Cyclopterus lumpus*). Polar Biol. 41, 1091-1103.

Mitamura, H., Thorstad, E.B., Uglem, I., Bjørn, P.A., Okland, F., Naesje, T.F., Dempster, T., Arai, N., 2012 Movements of lumpsucker females in a northern Norwegian fjord during the spawning season. Env. Biol. Fish. 93, 475-481.

Morehead, D.T., Ritar, A.J., Pankhurst, N.W., 2000. Effect of consecutive 9-or 12-month photothermal cycles and handling on sex steroid levels, oocyte development, and reproductive performance in female striped trumpeter *Latris lineata* (Latrididae). Aquaculture 189, 293-305.

Moring, J.R., 2001. Intertidal growth of larval and juvenile lumpfish in Maine: A 20-year assessment. Northeastern Nat. 8, 347-354.

Newman, D.M., Jones, P.L., Ingram, B.A., 2010. Advanced ovarian development of Murray cod *Maccullochella peelii peelii* via phase-shifted photoperiod and two temperature regimes. Aquaculture 210, 206-212.

Norberg B., Weltzien F.A., Karlsen Ø., Holm J.C., 2001. Effects of photoperiod on sexual maturation and somatic growth in male Atlantic halibut (*Hippoglossus hippoglossus* L.). Comp. Biochem. Physiol. 129(B), 357-365.

Norberg. B., Brown, C. L., Halldorsson, O., Stensland, K., Björnsson, B. Th., 2004. Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in the Atlantic cod (*Gadus morhua*). Aquaculture 229, 451-467.

Oppedal, F., Berg. A., Olsen, R.E., Taranger, G.L., Hansen, T., 2006. Photoperiod in seawater influence seasonal growth and chemical composition in autumn sea-transferred Atlantic salmon (*Salmo salar* L.) given two vaccines. Aquaculture 254, 396-410.

Pampoulie, C., Skirnisdottir, S., Olafsdottir, G., Helyar, S.J., Thorsteinsson, V., Jónsson, S.Þ., Fréchet, A., Durif, C.M.F., Sherman, S., Lampart-Kalużniacka, M., Hedeholm, R., Ólafsson, H., Daníelsdóttir, A.K., Kasper, J.M., 2014. Genetic structure of the lumpfish *Cyclopterus lumpus* across the North Atlantic. ICES J. Mar. Sci. 71, 2390-2397.

Pavlidis, M., Keravec, S., Greenwood, L., Mourot, B., Scott, A.P., 2001. Reproductive performance of common dentex, *Dentex dentex*, broodstock held under different photoperiod and constant temperature conditions. Fish Physiol. Biochem. 25, 171-180.

Porter, M., Duncan, N., Mitchell, D., Bromage, N., 1999. The use of cage lighting to reduce plasma melatonin in Atlantic salmon (*Salmo salar*) and its effects on the inhibition of grisling. Aquaculture 176, 237-244.

Searle, S.R., Casella, G., McCulloch, C.E., 1992. Variance components*.* John Wiley & Sons, New York, 501 pp.

Stefánsson, M.Ö., FitzGerald R.D., Cross T.F., 2002. Growth, feed utilization and growth heterogeneity in juvenile turbot *Scophthalmus maximus* (Rafinesque) reared under different photoperiod regimes. Aquac. Res. 33, 177-187.

Taranger, G.L., Haux, C., Stefansson, S.O., Björnsson, B.Th., Walther, B.Th., Hansen, T., 1998. Abrupt changes in photoperiod affect age at maturity, timing of ovulation and plasma testosterone and oestradiol 17 profiles in Atlantic salmon (*Salmo salar*). Aquaculture 162, 85-98.

Taranger, G.L., Haux, C., Hansen, T., Stefansson, S.O., Björnsson, B.Th., Walther, B.Th., Kryvi, H., 1999. Mechanisms underlying photoperiod effects on age at sexual maturity in Atlantic salmon, *Salmo salar.* Aquaculture 177, 47-60.

Taranger, G.L., Carrillo, M., Schulz, R.W., Fontaine, P., Sanuy, S., Felip, A., Weltzien, F.A., Dufour, S., Karlsen, Ø., Norberg, B., Andersson, E., Hansen, T., 2010. Control of puberty in farmed fish. Gen. Comp. Endocrinol. 165, 483-515.

Taylor, J.F., Porter, M.J.R., Bromage, N.R., Migaud, H., 2008. Relationships between environmental changes, maturity, growth rate and plasma insulin-like growth factor-I (IGF-I) in female rainbow trout. Gen. Comp. Endocrinol. 155, 257-270.

Timm, N.H., 1980. Multivariate analysis of variance of repeated measurements. In: Krishnaiah, P.R. (Ed.), Handbook of Statistics, Vol. 1, Analysis of Variance. North-Holland Publishing Company, Amsterdam, Netherlands, pp. 41-87.

Vasconcelos, P., Monteiro, C.C., Santos, M.N., Gaspar, B., 2004. First record of the lumpfish (*Cyclopterus lumpus* Linnaeus, 1758) off the Algarve coast (southern Portugal): southward extension of the species distributional range. J. Appl. Ichthyol. 20, 159-160.

Wang, N., Teletchea, F., Kestemont, P., Milla, S., Fontaine, P., 2010. Photothermal control of the reproductive cycle in temperate fishes. Rev. Aquaculture 2, 209–222.

Zar, J.H., 1984. Biostatistical Analysis, 2nd edition, Prentice-Hall, Inc., Englewood Cliffs, N.J., 718 pp.

**Figure captions**

**Fig 1.** Photoperiods applied in the experiment. The control group was reared at LDN (Simulated natural photoperiod of Tromsø, N-Norway, 69º40´N) throughout the experimental period (30 January 2017 – 12 July 2018). The L6 and L9 groups were transferred to continuous light on 30 Jan. 2017 and then reared under a 6 and 9 month, respectively, compressed and phase shifted LDN regime throughout the trial. The LD240 group was reared under continuous light from 30 Jan. 2017 onwards.

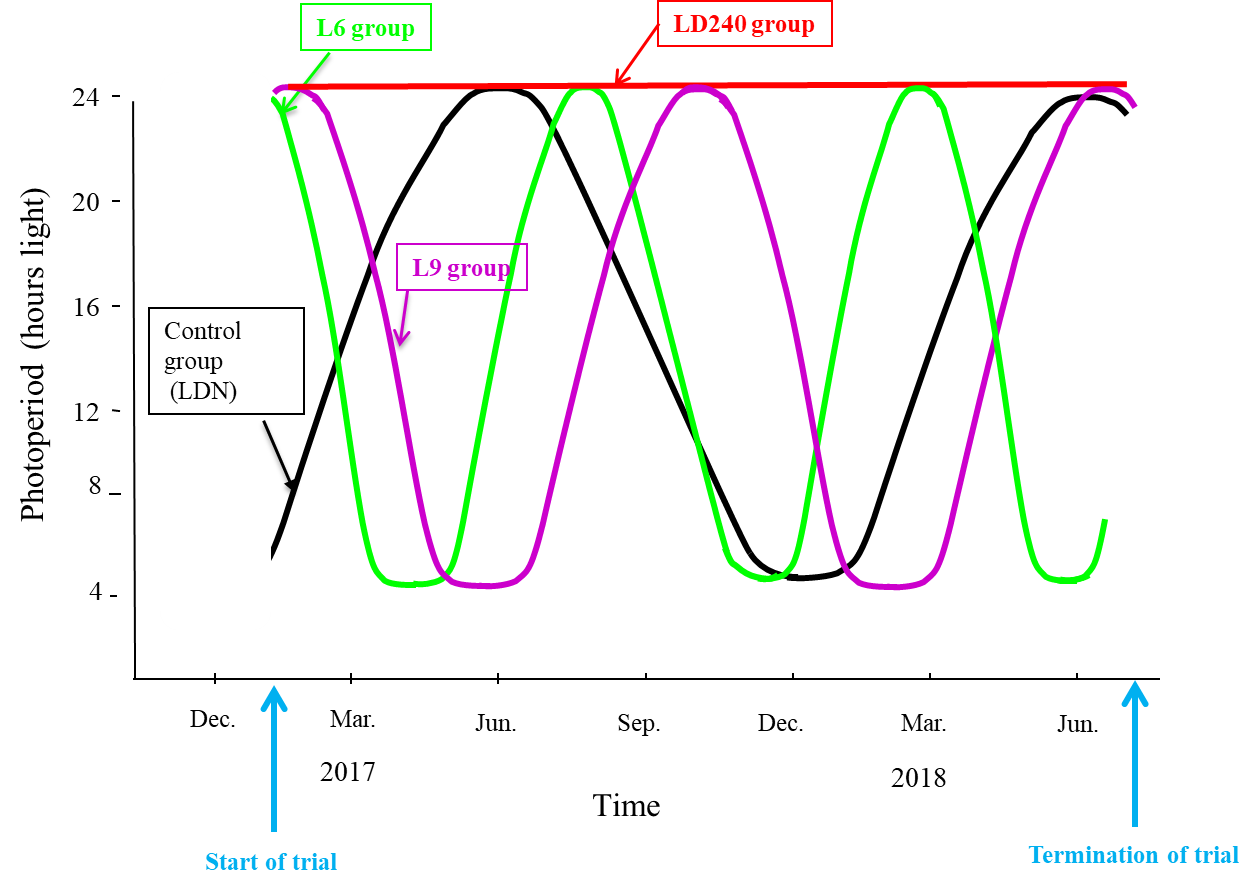
**Fig. 2.** Temperature profile during the experimental period.

**Fig. 3**. Mean weight of individually tagged male (M) and female (F) lumpfish reared at four different photoperiods. Vertical lines indicate SE. Solid lines=females; broken lines=males. Squares=L6; triangles=L9; circles=LD240; diamonds=LDN. Capital letters at top of the plot indicate significant effect (three way nested ANOVA, *P* < 0.05) of photoperiod (P), sex (S) and interaction between photoperiod and sex (PxS), N.N., not significant.

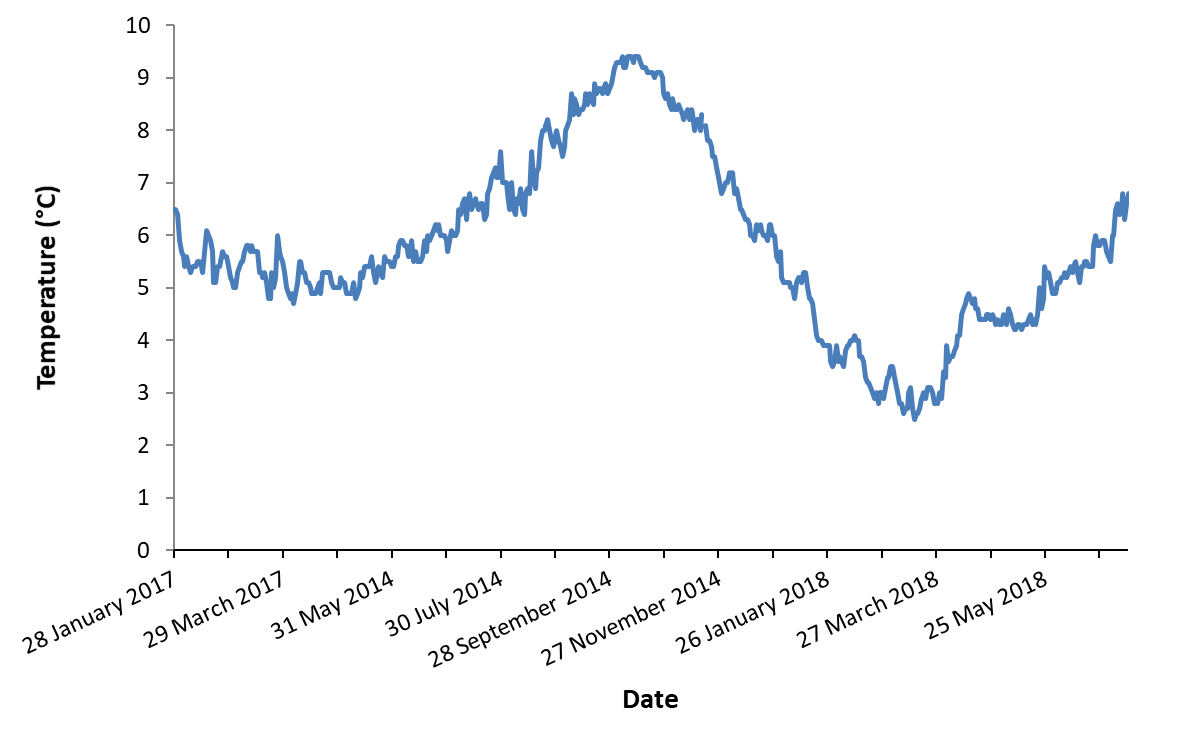
**Fig. 4.** Growth rates of individually tagged male (M) and female (F) lumpfish reared at four different photoperiods. Vertical lines indicate SE. Capital letters below plot indicate significant effect (three way nested ANOVA, *P* < 0.05) of photoperiod (P), sex (S) and interaction between photoperiod and sex (PxS), .N.S., not significant.

**Fig. 5.** Mean condition factor of individually tagged male (M) and female (F) lumpfish reared at three different photoperiods. Vertical lines indicate SE. Whole lines=females; broken lines=males. Squares=L6; triangles=L9; circles=LD240; diamonds=LDN. Capital letters at top of the plot indicate significant effect (three way nested ANOVA, *P* < 0.05) of photoperiod (P), sex (S) and interaction between photoperiod and sex (PxS), N.N., not significant.

**Fig. 6.** Individual spawning time for female lumpfish reared at four different photoperiods. Spawnings are marked with different symbols for each group: squares=L6; triangles=L9; circles=LD240 and diamonds=LDN. Expected spawning times based on earlier trials and lumpfish natural spawning time in the LDN group (March-June, Davenport, 1985; Mitamura et al., 2012; Kennedy et al., 2015; Kennedy, 2018) and for similar light conditions (i.e. spring to early summer) in the L6 and L9 groups are indicated in the vertical boxes.



**Fig. 1.** Imsland et al.



**Fig. 2.** Imsland et al.



**Fig. 3.** Imsland et al.



**Fig. 4.** Imsland et al.



**Fig. 5.** Imsland et al.

**Fig. 6.** Imsland et al.

**Table 1.** Overview of the experimental photoperiods, size of fish at start and end, spawning period (# of egg batches) and temperatures in the spawning period for both experimental years.

|  |  |  |  |
| --- | --- | --- | --- |
| Experimental group | Size (g) | Female spawning period (# of egg batches) | Temperature (°C) in spawning period |

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Males |  | Females |  | 2017 | 2018 | 2017 | 2018 |
|  | Start | End | Start | End |  |  |  |  |
| LDN | 753 | 1375 | 775 | 3140 | 24.07-31.10 (10) | 05.02-07.07 (18) | 6.8-7.4 | 3.8-6.5 |
| LD24:0 | 745 | 1183 | 763 | 3529 | 13.05-31.12 (12) | 16.03-12.07 (7) | 5.2-9.4 | 3.5-7.8 |
| L6 | 770 | 1363 | 736 | 3039 | 17.06-26.07 (6) | 20.01-06.07 (14) | 5.9-7.1 | 5.3-6.5 |
| L9 | 755 | 1476 | 769 | 3658 | 20.06-30.09 (13) | 18.02-23.06 (25) | 5.7-8.8 | 3.6-5.7 |