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Effect of photoperiod on the productivity factors of the tropical estuarine calanoid copepod, *Acartia tropica*

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Original Article

Abstract

The present study evaluated the effect of photoperiod on the productivity factors of the tropical calanoid copepod *Acartia tropica*. Population growth and composition, intrinsic rate of population increase, individual egg production and egg hatching success (EHS) of *Acartia tropica* were assessed at four different photoperiod regimes [Light (L): Dark (D) hours], viz. 0L: 24D, 8L: 16D, 16L:8D, 24L: 0D. After eight days of culture, the highest mean population count and intrinsic rate of population increase were recorded at 8L:16D photoperiod regime, which was not significantly different ($p>0.05$) from the copepods maintained at 0L:24D photoperiod regime. The result of the population composition study indicates the highest number of adults and naupliar stages in the 8L:16D photoperiod condition. Similarly, the highest mean individual egg production and egg hatching success were also recorded in the 8L:16D photoperiod condition, which was statistically significant ($p<0.05$) compared to others. Percentage nauplii survival does not show any significant difference ($p>0.05$) between 0L: 24D, 8L: 16D, 16L:8D photoperiod regimes. However, 24L: 0D photoperiod regimes recorded the lowest percentage of nauplii survival, which was significantly ($p<0.05$) lower than other treatments. Similarly, different photoperiod regimes did not affect the sex ratio of adult *A. tropica* in the present study. The results of the present study indicate that among the various photoperiod conditions evaluated, 8L: 16D is the optimum photoperiod condition for the culture of *A. tropica,* and that photoperiod has a significant influence on its productivity factors

Keywords: *Photoperiod, Acartia tropica, Population growth, Egg production, Egg hatching success*

Introduction

Copepods are the tiny aquatic organisms contributing a major share of zooplankton in the ocean (Boxshall and Halsey, 2004) and act as an important link in the marine food chain (De-Young *et al*., 2004; Castonguay *et al*., 2008). They form one of the most studied groups of organisms as live feed in aquaculture, especially in marine fish larval rearing. Most of the marine fishes possess an altricial type of larvae characterised by smaller size and little vitelline reserves (Gopakumar *et al*., 2009; Santhosh *et al*., 2018). Thus, on completion of yolk sac absorption, these larvae require smaller live feeds suitable for their mouth-gape size with a good nutritional profile. Different studies have proved the efficiency of copepods as live feed for marine fish larvae in terms of their smaller size, ω3 rich nutritional profile and peculiar jerking movement pattern compared to artemia and rotifers (Jackson and Lenz, 2016; Anil *et al*., 2018; Anil *et al*., 2019; Anzeer *et al*., 2019; Anuraj *et al*., 2021; Suresh Babu *et al*., 2024).

Poor productivity under mass culture is a major drawback with copepods limiting their extensive usage in hatcheries (Santhosh *et al*., 2018). It is proven that factors like salinity, temperature, feed, photoperiod, stocking density, etc. have a significant effect on copepod productivity, which can be enhanced with the optimisation of different culture conditions required for each copepod species (Castro-Longoria, 2003; Chinnery and Williams, 2003; Drillet *et al*., 2015; Wilson *et al*., 2021). Light is one of the structuring factors for life in the ocean (Grassi, 2017) and also an important determinant of the dynamics and trophic efficiency of marine planktonic food webs (Isari *et al*., 2014). It is also studied that photoperiod acts as an important environmental cue regulating the reproduction and population dynamics in marine invertebrates (Moraitou-Apostolopoulou and Verriopoulous, 1982; Miliou, 1992). Hence, copepods being a key part of aquatic food webs, light and photoperiod may also have significant implications on the productivity of copepods.

Copepods are assumed to have a complex day-night cycle of activity associated with grazing, reproduction, swimming, escape behaviour and other such unidentifiable behaviours (Alekseev and Lajus, 2009). Early studies have noted that copepods primarily feed during the late afternoon and early evening hours (Corkett and McLaren, 1979) and release their eggs during early morning hours (Stearns, 1986; Stearns *et al.*, 1989). There are limited studies related to the effect of light intensity and photoperiod on the various productivity factors of copepods under controlled culture conditions. The available literature on this fact indicates the significant effect of photoperiod on copepod productivity and its ease in manipulation to improve the live feed quality of copepods in marine fish hatcheries (Camus and Zeng, 2008; Fereidouni *et al.*, 2015; Jepsen *et al.*, 2017; Nogueira *et al.*, 2018; Kaviyarasan *et al.*, 2020; Wang *et al.*, 2021; Choi *et al.*, 2022; Kuriakose *et al.*, 2025; Huanacuni *et al.*, 2025).

Among copepods, the calanoids, especially the species of genus *Acartia,* have received wide attention as live feed in marine fish hatcheries (Stottrup, 2000). *Acartia tropica* is a euryhaline tropical estuarine calanoid copepod from the tropical brackish waters in the Indo-West Pacific (Ueda and Hiromi, 1987). They have higher fecundity, smaller naupliar stages and good salinity tolerance, making it a suitable live feed for the larval rearing of marine as well as brackish water fish larvae (Wilson *et al.*, 2021). They also show good density tolerance and high productivity if the adult density is properly maintained with regular harvest and optimum feeding (Wilson *et al.*, 2022a). Similarly, the egg storage study of *A. tropica* has also shown positive attributes, which further increases their live feed potential (Wilson *et al.*, 2022b). Hence, the optimisation of photoperiod may further increase the productivity of *A. tropica* under culture conditions, and therefore, the present study aims to evaluate the effect of photoperiod on the productivity factors of the tropical calanoid copepod *A. tropic*a.

Material and methods

Algal culture

The copepods in the present study were fed with the flagellate microalgae *Dicrateria inornata.* Algal culture was maintained under indoor conditions (23 °C, 12:12 h light and dark regime) using F/2 medium (Guillard and Ryther, 1962) as the nutrient source. The stock culture was maintained in 1 L conical flasks, and the mass culture was maintained in 20 L carboys provided with moderate aeration. The microalgae were harvested at their exponential phase of growth for feeding the copepods. Carbon content of *D. inornata* was measured using a CHNSO elemental analyser (Elementar Vario EL III, Precision > 0.1%abs) employing chromatographic techniques.

Copepod culture

Plankton samples were collected from the brackish water bodies of Moothakunnam region, Kerala, India (10°19′02″ N, 76°20′02′′ E) from which *A. tropica* copepods were isolated (Fig. 1 and 2). The culture was gradually scaled up and maintained in 10 L containers filled with filtered and sterilised water of 15 ppt salinity (Wilson *et al.*, 2021). The copepods were fed with *D. inornata* at a concentration equivalent to 1000 µg carbon/L (Authors' unpublished data). All culture containers were provided with mild aeration. For water quality maintenance, partial water exchange was done every four days interval and total water exchange was done at 12 days.

Experimental design and setup

The experiments in the present study followed a completely randomised design of statistics. Four photoperiod conditions [Light (L): Dark (D) hours] *viz.* 0L: 24D, 8L: 16D, 16L: 8D, 24L: 0D were experimented in the present study to assess their effect on population growth and composition, intrinsic rate of population increase, mean individual egg production, EHS and nauplii survival of *A. tropica*. The copepod density and the feed

Fig. 1. *Acartia tropica* female

Fig. 2. *Acartia tropica* male

concentration of *D. inornata* maintained in all the experiments of the present study were 125 adults/L and 1000 μg C/L, respectively. Enumeration of copepod and developmental stages during the experiments was done using a stereozoom microscope (Leica DM 2000, Germany). The average daily water temperature recorded during the conduct of experiments was 29 ± 2 °C, and the water salinity and light intensity maintained were 15ppt and 1200 lux, respectively. A digital lux meter was used to measure and maintain the light intensity in different treatments.

Population growth and sex ratio: Stock cultures of *A. tropica* acclimated to four photoperiod conditions were initially developed. From the acclimatised stock cultures, eggs produced over a period of 24 h were collected by siphoning and simultaneous sieving through 100 μm and 25 μm meshed sieves. The eggs collected in the 25 μm mesh were then incubated at the corresponding photoperiod condition so that adults of the same age group could be developed from those eggs under each photoperiod treatment. From the newly reproducing adults, groups of seven adults (4 females: 3 males) were randomly selected and stocked in four replicate 1L beakers maintained under different photoperiod conditions and fed with *D. inornata* @ 1000 μg C/L. After 8 days of culture, the whole population in replicate beakers were sieved out through a 25 μm screen and fixed in 10% formalin. Later, each developmental stage of copepods was enumerated separately, and the adults were segregated according to their sex to determine the sex ratio. The average population count of four replicates of each treatment was taken as the final population count, and the intrinsic rate of population increase (r) was calculated using the following formula.

$$r = \ln(N1/N0)/t$$

where, N0 = the population size at the beginning of the experiment, N1 = the population size at the end of the experiment and t = duration of the experiment in days (Siqwepu *et al.*, 2017).

Mean individual egg production: Adults of the same age group acclimated to different photoperiod conditions were developed as per the procedure described in section 2.3.1. The adults from each photoperiod treatment were then randomly distributed at a density of 31 per 250 ml containers kept floating in individual 1 l beakers in triplicate. The 250 ml containers were open at both ends and fitted with 100 μm sieve at the bottom end to retain the adults and help the eggs and nauplii to pass through and remain in the 1 l beaker. Every day, the 250 ml containers were shifted to fresh 1 l beakers, and the contents in the earlier 1 l beaker were sieved through 25 μm screen to collect and preserve the eggs and the nauplii produced on that particular day for further enumeration (Alajmi and Zeng, 2014; Wilson *et al.*, 2022a). Assuming a constant sex ratio across all treatments, uninfluenced by photoperiod, we calculated the total eight-day and mean individual egg production per female using the collected data.

Egg hatching success: From the cultures of *A. tropica* maintained at different photoperiod conditions, the eggs produced over a period of 12 h were collected by sieving the cultures simultaneously through 100 μm and 25 μm sieves and the eggs collected on 25 μm sieves were dipped in fresh water for a few minutes to kill the post-egg stages, if any (Knuckey *et al.*, 2005). The eggs from each photoperiod condition were then stocked (1 egg / mL) into the four replicate 50 mL containers and placed under the respective photoperiod condition. After 24 h, the contents from each 50 mL container were filtered (using 25 μm sieve) and the number of nauplii and unhatched eggs in each treatment replicate was enumerated to calculate the EHS.

EHS (%) = [(No. of eggs stocked – No. of unhatched eggs) / No. of Eggs stocked] × 100

Nauplii Survival: Eggs were collected from the copepod cultures acclimatised to different photoperiod conditions and followed the stocking procedure described in section 2.3.3. The containers were maintained under the respective photoperiod conditions for three days, and thereafter filtered and enumerated the number of live individuals in each container in order to calculate the percentage survival of naupliar stages.

Statistical analysis: All statistical analyses were conducted using SPSS 20.0 software. The population growth, egg production, EHS and nauplii survival data were tested for differences between photoperiod treatments by one-way analysis of variance (ANOVA). Tukey's HSD post-hoc tests at the 0.05 level of significance were carried out to determine differences between the treatments.

Results

Population growth and sex ratio

Photoperiod had a significant ($p<0.05$) effect on the final population count and intrinsic rate of population increase of *A. tropica* (Table 1). The 8L:16D photoperiod produced the highest final population count (7811 ± 189) and highest intrinsic rates of whole and live population increase (0.66 ± 0.003; 0.65 ± 0.004), though these were not significantly different ($p>0.05$) from the 0L:24D condition. Critically, the intrinsic rate of adult population increase (0.38 ± 0.006) was highest and significantly different ($p<0.05$) under 8L:1 6D compared to all other treatments. Photoperiod also significantly ($p<0.05$) influenced life stage counts (Table 2). The number of nauplii was highest in 8L :1 6D treatment, statistically comparable to 0L:2 4D treatment. The number of adults was significantly highest in the 8L: 16D group (870±39). Counts for eggs and copepodites showed no significant differences ($p>0.05$) across experimental groups. The sex ratio remained statistically unchanged ($p>0.05$) regardless of the photoperiod treatment (Table 1).

Egg production

Individual egg production by *A. tropica* across all photoperiod treatments over 8 days increased sharply from Day 1 to Day 4, then subsequently declined (Fig. 3). The mean individual egg production over the 8-day period varied significantly among treatments ($p<0.05$, Table 3). It was recorded highest under the 8L: 16D photoperiod (62 ± 2), which was not significantly different ($p>0.05$) from the 0L: 24D regime (54 ± 2). The lowest mean individual egg production was observed in the 24L:0D treatment (49.93 ± 0.89).

Egg hatching success (%): The 24 h egg hatching success was recorded to be highest for the copepod raised at the

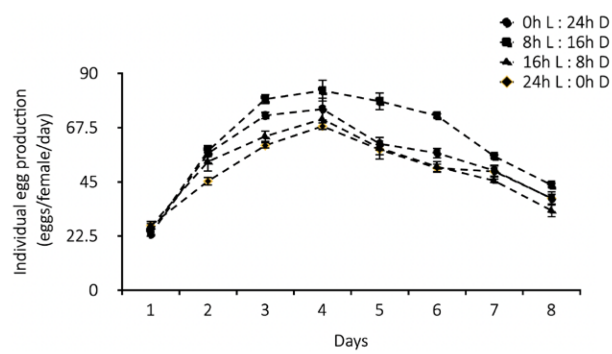

Fig. 3. Individual egg production (eggs/female/day) of *A. tropica* over a period of 8 days at different photoperiod regimes (Mean ± SE)

Table 1. Comparative analysis of total population count, intrinsic rate of population increase (r), and sex ratio in *A. tropica* cultured across different photoperiods

Photoperiod (Light: Dark) (hour)	0 : 24	8 : 16	16 : 8	24 : 0
Total population count (Ind./l)	6936.75^{b} ± 182.71	7810.75^{b} ± 189.10	4875.75^{a} ± 330.81	4603^{a} ± 288.49
Adult sex ratio (Male: Female)	0.83^{a} ± 0.038	0.80^{a} ± 0.027	0.82^{a} ± 0.030	0.84^{a} ± 0.016
Intrinsic rate of population increase (r)				
Whole population	0.644^{b} ± 0.003	0.66^{b} ± 0.003	0.60^{a} ± 0.008	0.60^{a} ± 0.008
Live population	0.638^{b} ± 0.003	0.65^{b} ± 0.004	0.60^{a} ± 0.008	0.59^{a} ± 0.007
Adults	0.33^{a} ± 0.008	0.38^{b} ± 0.006	0.31^{a} ± 0.006	0.31^{a} ± 0.006

Values with different superscripts in the same row differ significantly ($p < 0.05$), and data are expressed as Mean ± SE

Table 2. Changes in population composition of *A. tropica* over 8 days under various photoperiod regimes

Photoperiod (Light: Dark) (hour)		0 : 24	8 : 16	16 : 8	24 : 0
Population composition (Ind./l)	Egg	336.25^{a} ± 83.09	340^{a} ± 33.98	188.5^{a} ± 19.16	146^{a} ± 20.02
	Nauplii	3132.75^{b} ± 152.89	3725.75^{b} ± 231.97	1878.5^{a} ± 119.21	1685.75^{a} ± 204.62
	Copepodite	2882.25^{a} ± 186.95	2875.5^{a} ± 134.77	2429.75^{a} ± 221.6	2285.25^{a} ± 98.93
	Adult	585.5^{a} ± 37.64	869.5^{b} ± 38.59	479^{a} ± 21.21	486^{a} ± 21.28

Values with different superscripts in the same row differ significantly ($p < 0.05$) and data is expressed as Mean ± SD

Table 3. Influence of photoperiod regimes on fecundity, egg viability, and larval survival in *A. tropica*

Photoperiod (Light: Dark) (hour)	0 : 24	8 : 16	16 : 8	24:0
Mean individual egg production over 8 days (eggs/female/day)	$54.21^{ab} \pm 2.18$	$61.71^{b} \pm 2.16$	$50.82^{a} \pm 2.25$	$49.93^{a} \pm 0.89$
24 h Egg hatching success (%)	$76.28^{b} \pm 12.12$	$83.11^{b} \pm 1.93$	$71.39^{ab} \pm 8.34$	$56.39^{a} \pm 4.07$
Nauplii survival (%)	$67.55^{b} \pm 16.85$	$76.28^{b} \pm 5.57$	$64.94^{b} \pm 9.18$	$33.73^{a} \pm 13.04$

Values with different superscripts in the same row differ significantly ($p < 0.05$) and data is expressed as Mean ± SD

photoperiod regime of 8L: 16D (83 ± 2), which was not significantly different (p>0.05) from those raised at 0L: 24D (76 ± 12) and 16L: 8D (71 ± 8) photoperiod regime. The lowest 24 h EHS was recorded when the copepods were raised at a 24L: 0D (56 ± 4) photoperiod regime (Table 3).

Nauplii survival (%): The survival of *A. tropica* nauplii varied significantly (p<0.05) across different photoperiod regimes (Table 3). The highest nauplii survival was recorded under the 8L: 16D photoperiod (76 ± 6). This rate was statistically similar (p>0.05) to the survival observed in the 0L: 24D (68 ± 17) and 16L: 8D (65 ± 9) regimes. Conversely, the lowest nauplii survival was measured at the 24L: 0D photoperiod (34 ± 13), which was significantly lower (p<0.05) than all other experimental groups.

Discussion

Reproduction in aquatic animals, including copepods, is known to be light-dependent and regulated by photoperiod (Segal, 1970; Camus and Zeng, 2008). Specifically, the findings in temperate copepod species indicate temperature-compensated photoperiodic effect in inducing dormant egg production (Marcus, 1980, 1982). Marine copepod functions and activities often reach their maximum occurrence at specific times of the day or night as determined by photoperiod regimes (Marcus, 1986). Understanding the significance of photoperiod in copepod production, along with other environmental factors, is crucial for enhancing copepod productivity in the mass culture systems. Copepods with a superior nutritional profile, appropriate size, and peculiar swimming behaviour form an indispensable live feed for the early larval forms of many commercially important fish species (Santhosh *et al.*, 2018). Therefore, to advance the seed production of such fish species and, consequently, mariculture, commercial-scale copepod production is crucial. *A. tropica* is a tropical estuarine calanoid copepod with good productivity and salinity tolerance, and the present study investigates how different photoperiod regimes influence the egg production, egg hatching success, nauplii survival, and overall population dynamics of *A. tropica* under culture conditions.

Photoperiod significantly influenced the population dynamics of *A. tropica*. Short durations of light exposure (8L: 16D and 0L: 24D) enhanced population development more effectively than longer light hours (16L: 8D and 24L: 0D), with 8L: 16D being the most suitable photoperiod regime for growth. This finding aligns with Nogueira *et al.* (2018) and Huanacuni *et al.* (2025), in which the lowest population numbers for *Acartia grani* and *Oithona nana* respectively, were recorded under constant light conditions. Increased metabolic rates and depletion of energy reserves in copepods when exposed to longer light hours may affect the population increase compared to longer dark hours. Similarly, Marshall and Orr (1972) have reported increased respiration rate and stressed condition in *Calanus* spp. during bright sunshine hours. Miliou (1992) also noted a similar pattern in *Tisbe holothuriae*, recording varied total offspring production per female under different photoperiod conditions. Regarding sex ratio, different photoperiod regimes did not show any noticeable effect on *A. tropica* adults in the present study. However, the sex ratio was consistently skewed in favour of females across all treatments. This female-biased population response to photoperiod is consistent with previous reports, including those by Camus and Zeng (2008) in *Acartia sinjiensis*, Fereidouni *et al.* (2015) in *Mesocyclops* spp., and Nogueira *et al.* (2018) in *A. grani*.

The present study assessed the mean daily individual egg production (eggs/female/day) of *A. tropica* over eight consecutive days under different photoperiod conditions. Photoperiod significantly influenced egg production, with the maximum individual egg production recorded at the 8L: 16D regime. A steady increase in the individual egg production of *A. tropica* was observed in all the photoperiod regimes from day 1 to 4 and subsequently declined. Our findings confirm that longer durations of illumination significantly reduced offspring production in *A. tropica*. This is consistent with multiple studies reporting the detrimental effects of longer light hours on the reproductive capacity of copepods (Miliou, 1992; Matias-Peralta *et al.*, 2005; Camus and Zeng, 2008; Fereidouni *et al.*, 2015; Jepsen *et al.*, 2017; Nogueira *et al.*, 2018; Choi *et al.*, 2022; Kuriakose *et al.*, 2025). The lower egg production observed during longer illumination periods in *A. tropica* supports the proposed positive correlation between nocturnal feeding habits and increased egg production during dark hours, as suggested by Stearns (1986, 1989) for *A. tonsa*. Similar results were also reported by Calbet and Alcaraz (1996, 1997) in *A. grani*. However, copepods also show species-specific responses in productivity factors to various photoperiod regimes (Peck and Holste, 2006; Nogueira *et a*l., 2018).

Different photoperiod regimes had discernible effects on the egg hatching success of *A. tropica*, with the highest hatching success recorded at the 8L: 16D treatment. These results align with the findings of Nogueira *et al.* (2018) and Choi *et al.* (2022), who observed lower egg hatching rates in *A. grani* and *Eurytemora Pacifica* respectively, when subjected to long-day photoperiod regimes compared to short-day photoperiod regimes. However, this response contrasts with previous work showing increased hatching rates with longer light hours for both *A. tonsa* (Peck and Holste, 2006; Peck *et al*., 2008) and *A. sinjiensis* (Camus and Zeng, 2008). Landry (1975) observed that darkness completely and immediately suppresses the hatching of *A. clausi* eggs. According to them, the increased egg hatching during daylight hours is a mechanism that would decrease the distributional co-occurrence of females and the first nauplii, thereby reducing the cannibalism of nauplii by adults. This separation occurs because nauplii are positively phototropic, and during daylight hours, they are attracted to surface waters, while adults remain in deeper layers. The lower egg hatching success observed during longer light hours in the present study may be correlated with the estuarine distribution and adaptation of *A. tropica* (Ueda and Hiromi, 1987). Estuarine environments typically have less dense water and a turbid bottom, enabling the complete sinking of copepod eggs to the bottom, where they experience longer durations of darkness, and where hatching occurs. Conversely, Jepsen *et al.* (2017) revealed no observed effect of photoperiod on the egg hatching success of copepods exposed to continuous light or darkness, highlighting the species-specific nature of this response.

Photoperiod significantly influenced the nauplii survival of *A. tropica* in the present study, with the maximum nauplii survival recorded at an 8L: 16D Photoperiod regime. The lower nauplii survival recorded at longer durations of illumination is in line with the findings of Matias Peralta *et al.* (2005) in *Nitokra affinis* where they reported total mortality of offspring after few hours of hatching under continuous light condition (24:00). This can be attributed to the higher metabolic rates and depletion of energy reserves under constant light conditions which could explain the higher mortality of nauplii. However, it is reported that continuous light had no drastic harmful effects on the nauplii survival of Mesocyclops sp (Fereidouni *et al*., 2015).

Conclusion

The present study concludes that photoperiod had a significant effect on the productivity factors of *A. tropica*. Our results indicate that, 8: 16 light: dark photoperiod regime supports the maximum productivity of *A. tropica.* The major limitation with copepods as a live feed in hatcheries is their poor productivity under mass culture, and it can only be balanced by optimising their preferred culture conditions. Hence, the findings of the present study have wide applications in increasing the productivity of *A. tropica* in culture conditions and thereby improving their live feed quality.

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Author contributions

Conceptualisation: JMW, BI; Methodology: JMW, BI, BS, PBS; Writing Original Draft: JMW; Data Analysis: JMW, BI; Supervision: BI, BS, PBS; Data Collection: JMW, NR, ASS.

Data availability

The data are available and can be requested from the corresponding author.

Conflict of interest

The authors declare that they have no conflict of financial or non-financial interests that could have influenced the outcome or interpretation of the results.

Ethical statement

No ethical approval is required as the study does not include activities that require ethical approval or involve protected organisms/ human subjects/ collection of sensitive samples/ protected environments.

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