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ORIGINAL ARTICLE

Optimization of salinity levels for the culture of cyclopoid copepod *Dioithona oculata* (Farran, 1913) with respect to total population, reproduction, development and adult longevity

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Abstract

Cyclopoid copepod, *Dioithona oculata*, is a common free-living euryhaline species in tropical and temperate waters having potential as live feed in marine fish larval rearing. Here, the effect of salinity on adult and naupliar survival, total population, population composition, clutch production, clutch size, development rate and adult longevity was investigated. Adult copepods survived the abrupt changes in salinities from 15 to 50 ppt (parts per thousand). The highest naupliar survival was at 30 ppt (86.33 ± 2.84%) and the lowest at 15 ppt (12.6 ± 2.34%). The highest production was at 30 ppt (883.0 ± 5.5 individuals/L) and the lowest at 15 ppt (49.0 ± 6.56 individuals/L). The proportion of nauplii was higher at salinities from 20 to 40 ppt, whereas the total population of copepodites and adults was significantly less at 15 and 45 ppt. The highest clutch production was observed at 30 ppt (8.6 ± 0.54 clutches) and the lowest at 45 ppt (2.6 ± 0.54 clutches). Maximum clutch size of *D. oculata* was recorded at 30 ppt (19.2 ± 2.94 eggs/clutch) and minimum at 45 ppt (7 ± 1 eggs/clutch) respectively. Development time from nauplius to adult was significantly ($p < 0.05$) longer at 45 ppt (12.72 ± 0.03 days) and shorter at 20 ppt (9.06 ± 0.02). Adult longevity was significantly higher at 30 ppt (27 ± 1.0 days) and lower at 45 ppt (11.3 ± 1.15). Salinity changes significantly affected the production performance of *D. oculata*. The optimum salinity for mass culture of *D. oculata* was found to be 30 ppt.

KEYWORDS
copepod, cyclopoid, live feed, nauplii production, salinity

1 | INTRODUCTION

Copepods constitute the major component of the zooplankton community and are a critical link between the phytoplankton and higher consumers in the marine habitat (Lee et al., 2010; Sampey et al., 2007; Springer & Roseneau, 1985; Stottrup, 2000; Turner, 2004). Copepods are the natural food for a wide variety of marine fish larvae and crustaceans (Ananthi et al., 2011; Sampey et al., 2007; Toledo et al., 1999). Copepods are superior in nutritional composition and are successfully used in marine fish larviculture (Anzeer et al., 2019; Chesney, 2005; Kim et al., 2020; Rahmati et al., 2020).

Environmental factors, especially temperature and salinity, have potential impacts on the diversity and distribution of marine organisms (Meier et al., 2006). Particularly, salinity is one of the key environmental factors, influencing the distribution and abundance of

zooplanktons in the marine habitat (Cervetto et al., 1999; Devreker et al., 2004; Hall & Burns, 2001). Moreover, the changes in salinity strongly affect the physiological and biological parameters of copepods (Cervetto et al., 1999; Hall & Burns, 2001; Soetaert & Herman, 1994) which in turn affect the abundance and distribution of cyclopoid copepods in aquatic ecosystems (Thompson, 1991). Salinity can be easily maintained at desirable levels without much effort to maximize the production of copepods in the hatchery.

Cyclopoids are one of the most dominant groups among planktonic copepods, widely distributed in all kinds of aquatic environment (Nielsen et al., 1993; Paffenhofer, 1993) and form an important prey for a wide variety of aquatic animals (Drillet et al., 2006; Ostergaard et al., 2005). Many species of cyclopoids are already popular as live feed for larval rearing (Farhadian, 2006; Jepsen et al., 2021; Rahmati et al., 2020). *Dioithona oculata* (Farran, 1913) is a free-living pelagic cyclopoid copepod, which forms swarms near the coral reef lagoons and mangroves of tropical and temperate waters (Ambler et al., 1991; Ara et al., 2017; Buskey et al., 1996; Hamner & Carleton, 1979; Nishida, 1985). These swarms of *D. oculata* are convenient sources of food for larvae of coastal fishes and invertebrates (Ueda et al., 1983). Swarming nature is very common in *D. oculata* which enhances the chances of encounter between males and females (Buskey et al., 1996). *D. oculata* is considered as a good candidate species for mass culture and has been successfully cultured as live feed under monoculture and polyculture with *Brachionus rotundiformis* in outdoor and indoor conditions (Molejon & Alvarez-Lajonchere, 2003). In a recent study, Takayama et al. (2021) confirmed the possibility of cultivation of *D. oculata* in a bioreactor. *D. oculata* has 6 naupliar, 5 copepodites and adult stages (male and female). The eggs are small and spherical, measuring 65–70 μm in size. Mean length of naupliar stages N1 to N6 ranged from 90 to 210 μm and for copepodites C1–C5 ranged from 340 to 670 μm. The adult females ranged from 640 to 800 μm in length and 190 to 260 μm in width and males from 540 to 700 μm in length and 170 to 200 μm in width (Ferrari & Ambler, 1992; Santhosh et al., 2018). Molejon and Alvarez-Lajonchere (2003) also highlighted the potential of *D. oculata* as a live feed for marine fish larval rearing. Copepods of the closely related genera *Oithona* and *Dioithona* are naturally abundant in coastal waters and are subjected to regular salinity fluctuations (Kjerfve, 1994; Zacarias & Zoppi-Roa, 1981). *D. oculata* is also a coastal species, frequently exposed to the changes in physical parameters (Björnberg, 1972; Hamner & Carleton, 1979). In general, cyclopoids are more tolerant and adaptable to wide fluctuations in environmental parameters like temperature and salinity (Santhanam & Perumal, 2012).

It is essential to study the salinity preferences of *D. oculata* for stable hatchery production and use as live feed. Studies on the effect of salinity on survival and production of cyclopoid copepods are extremely limited (Pan et al., 2016; Peterson, 2001). The present study reports the effect of salinity on survival, total population, population composition, clutch production, clutch size, development rate and adult longevity of *D. oculata* with an aim to standardize its hatchery production as a live feed.

2 | MATERIALS AND METHODS

2.1 | Microalgal culture

Pure stock of microalgae *Isochrysis galbana* and *Pavlova lutheri* were maintained at indoor conditions in 2–4 L haffkine flasks with a temperature of 24–26°C and light intensity of 2500–5000 lux in the algal stock culture facility of the Vizhinjam Regional Centre of ICAR-Central Marine Fisheries Research Institute, Kerala, India. Algal mass cultures were maintained in 20 L carboys under normal indoor conditions of the hatchery at the salinity of 35 ppt. Walne's medium (Walne, 1970) has been used for algal culture. For the different experimental trials, microalgal stock cultures were also acclimated to different salinities (15, 20, 25, 30, 35, 40 and 45 ppt), cultured in 4 L haffkine flasks in the indoor conditions and used for feeding the copepods of respective salinity treatments (Svetlichny & Hubareva, 2014). Algal density was assessed using a Neubauer haemocytometer and a compound microscope Leica DM 1000 (Germany). Algae at its late exponential growth phase, at an approximate cell density of 3×10^5 cells/ml, were used as feed for the copepods (Chen et al., 2006; Hopp & Maier, 2005).

2.2 | Culture of *Dioithona oculata*

Copepods were collected using a plankton net from inshore areas of Vizhinjam (8° 22′ 26.99″ N, 76° 59′ 17.39″ E), Kerala, India during the year 2018. Stock culture and mass culture of *D. oculata* and the whole experiments were carried out in the marine fish hatchery of the Vizhinjam Regional Centre of ICAR-CMFRI, Vizhinjam, Kerala, India. The water temperature and salinity during the collection were 28°C and 35 ppt respectively. Seawater for culture was chlorinated for one time to sterilize, dechlorinated after 24 h and filtered through a 5 μm filter and stored in large tanks. *D. oculata* adults were isolated and cultured in dechlorinated and filtered seawater at a salinity of 35 ppt and a temperature of 28°C under hatchery conditions. Initially, the culture was started in 2 L beakers, gradually transferred to 10 L buckets and 300 L round high-density polyethylene (HDPE) Sintex tanks. Mass culture was maintained in 300 L circular Sintex tanks and is being maintained under the hatchery conditions (Santhosh et al., 2018). Water quality parameters were monitored regularly and if needed, corrected accordingly to ensure the health and density of the culture.

2.3 | Experimental design

All the trials conducted for the present study followed the Completely Randomised Design of statistics. To know the upper and lower salinity ranges, a pilot study was conducted on the abrupt salinity change from 0 to 55 ppt for a period of 24 h. Based on the results of this study, seven different salinity levels (15, 20, 25, 30, 35, 40 and 45 ppt [parts per thousand]) were finalized for

the population study. Furthermore, trials in the salinities below 20 ppt and above 45 ppt were excluded from the subsequent experiments considering the insignificant results obtained from the population study. Furthermore, the effect of salinity on clutch size, clutch production, development rate and adult longevity of *D. oculata* was also evaluated at six different salinity levels (20, 25, 30, 35, 4, and 45 ppt).

For the experiments, low saline water was prepared by diluting the natural seawater (35 ppt) with normal dechlorinated water and high saline water by evaporating the seawater until the required salinities were obtained. The salinities were regularly measured using a portable refractometer (ATAGO, Japan) and adjusted accordingly. Even the minor variations in the salinities were monitored regularly and whenever needed, fresh water was added to compensate the evaporation loss and always maintained same as designated salinities. Copepods, eggs and larval stages were enumerated under a stereo dissecting microscope (Leica S8APO, Germany) and whenever it was required, the compound microscope (Leica DM 1000, Germany) was also used.

2.4 | Effect of abrupt salinity change on *Dioithona oculata*

2.4.1 | Adult survival

To determine the effect of abrupt salinity changes on the survival of *D. oculata*, a 24-h experiment was conducted at 12 different salinities (0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50 and 55 ppt). Adult copepods were collected from the stock culture (35 ppt) by sieving through a 225 μ mesh. From this, six adult copepods were randomly selected and stocked in a 100 ml beaker with 50 ml saline water of corresponding 12 salinities without prior acclimatization. Three replicates were kept for each salinity treatment. The whole experimental setup was maintained at a temperature of 28 ± 1°C. A mixture of microalgae *I. galbana* and *P. lutheri*, cultured at respective salinities, was fed to the copepods in each treatment. After 24 h of incubation, live and dead copepods were enumerated and recorded.

2.4.2 | Naupliar survival

The adult copepods were filtered from the culture tank using a 225 μ mesh and approximately 1000 egg-bearing females were separated and stocked into a new culture tank for nauplii production. After 12 h, the nauplii (N1) stage were collected by serial filtration using sieves of 60 and 45 μ. The separated nauplii were stocked at designated experimental salinities of 10, 15, 20, 25, 30, 35, 40, 45, 50 and 55 ppt without prior acclimatization, at a density of 200 nos/L. Each treatment was replicated three times. The experiment continued till all the nauplii reached the copepodite/adult stage and the copepods that survived were further enumerated. Naupliar survival was calculated by the formula,

$$\text{Naupliar survival}\,(\%) = (\text{Number of copepodites or adults harvested} / \text{Number of nauplii initially stocked}) * 100.$$

2.5 | Effect of salinity on total population and population composition

For the estimation of total population and population composition, late copepodites (copepodites of stage four and five) of *D. oculata* were acclimated in seven different salinities (15, 20, 25, 30, 35, 40 and 45 ppt) following the standard protocol described by Milione and Zeng (2008). From the acclimatized culture, adult copepods of the same age group were separated by draining the copepod culture through a 225 μ mesh. Ten adult pairs (10 female and 10 male) of *D. oculata* were randomly stocked in 2 L containers filled with 1 L of water at designated salinities of 15, 20, 25, 30, 35, 40 and 45 ppt and cultured for 12 days. Three replicates were maintained for each salinity treatment. Gentle aeration was given to each treatment and 20% of the water was replaced daily to maintain the water quality. Microalgae cultured at different salinities were used for feeding the copepods, as described in Section 2.1. At the end of the experiment, the whole sample from each replicate was sieved through a 45 μ mesh and preserved in 4% formalin and then all the life stages (nauplii, copepodites and adults) were counted separately, using a stereo dissecting microscope (Leica S8APO, Germany) and a zooplankton counting chamber.

2.6 | Effect of salinity on clutch production (number of egg sacs/female)

Newly hatched nauplii (N1) were acclimatized till the fifth copepodite stage in 20, 25, 30, 35, 40 and 45 ppt salinities. From each acclimatized culture, a pair of newly moulted adults (male and female) were transferred to 50 ml containers, with 30 ml water of respective salinities. The copepods were fed with a mixture of *I. galbana* and *P. lutheri*. For each treatment, five replicates were kept. The clutch production was monitored and recorded daily under a stereo dissecting microscope. The nauplii from each newly formed clutch were completely removed whenever the clutch got fully hatched. The experiment continued until the death of female copepod.

2.7 | Effect of salinity on clutch size (number of eggs/egg sacs)

Ovigerous females (5 nos. each) from acclimated populations were randomly selected from all six salinities (20, 25, 30, 35, 40 and 45 ppt), and placed on a Petri dish (5 ml) and treated with 4% sodium hypochlorite solution to separate the eggs from their egg sacs (Ohs et al., 2010). The separated eggs from both sacs were counted under a stereo dissecting microscope.

2.8 | Effect of salinity on naupliar and copepodite development rates

The rate of development from nauplius to adult of *D. oculata* was investigated for six different salinities viz., 20, 25, 30, 35, 40 and 45 ppt. The adult copepods isolated from the stock culture (35 ppt) by filtration (225 μ mesh) were acclimated and reared at each experimental salinity (20 25 30, 35, 40 and 45 ppt). The freshly hatched nauplii (N1) were collected through serial filtration using 45 and 60 μ sieves (Santhosh et al., 2018). A total of 500 nauplii were volumetrically stocked (Ohs et al., 2010) into 500 ml water of the corresponding salinity treatments in triplicate. Daily 10 copepods were sampled from each replicate using a Pasteur pipette and fixed in 4% formalin. The fixed copepods were mounted and observed in a compound microscope and the developmental stages were identified. All treatments were replenished daily with the respective saline water and microalgae as mentioned in 2.5 and maintained at a temperature of 28 ± 1°C. The mean development time from nauplius to adults under each salinity treatment was calculated by a formula described by Camus and Zeng (2008).

$$\text{Mean development time (nauplius to adult)} = \left(\text{no. of copepodites/adults found on day}^{\prime}n^{\prime} \times (n) + \text{no. of copepodites/adults found on day}^{\prime}n+1^{\prime} \times (n+1) + \text{no. of copepodites/adults found on day}^{\prime}n+2^{\prime} \times (n+2) \ldots\right) / \text{total number of copepodites/adults.}$$

2.9 | Adult longevity

Newly moulted adults of *D. oculata* were randomly separated from the acclimatized culture in each salinity treatment. A total of 20 copepods were transferred to each treatment container (500 ml) with 250 ml water with salinities, 20, 25, 30, 35, 40 and 45 ppt, in three replicates and reared at room temperature (29 ± 1 °C). Nauplii produced daily were filtered out (225 μ sieve) from each treatment and the live adults were retained in the designated salinity treatment with fresh microalgae as feed. Daily mortality was recorded in all the replicates and the experiment was terminated when there was no survival. Adult longevity of *D. oculata* was calculated by taking the average of individual lifespans of all replicates in each treatment (Wang et al., 2021).

2.10 | Statistical analysis

All the data were analysed using one-way analysis of variance (ANOVA). Tukey's multiple comparisons test was used to find out the significant differences ($p < 0.05$) between each salinity treatment. All statistical analyses were conducted using SPSS program, version 22. The data for development rate were analysed using two-way factorial ANOVA and the significant differences ($p < 0.05$) in each treatment were tested using Tukey's honest significant difference (HSD) post hoc tests. Data are presented as mean ± standard deviation (mean ± SD).

3 | RESULTS

3.1 | Effect of abrupt salinity change on *Dioithona oculata*

3.1.1 | Adult survival

Dioithona oculata could tolerate a wide range of salinities from 15 to 50 ppt (Figure 1). No mortality was observed from 25 to 35 ppt (100% survival), whereas the survival was 94.4 ± 9.62% at 20 ppt and 88.8 ± 9.62% at 40 ppt. Survival rate was significantly less at 15 and 50 ppt (33.3 ± 16.66% and 44 0.4 ± 9.62% respectively). No survival was observed in the salinities beyond 50 ppt and below 15 ppt.

3.1.2 | Naupliar survival

Sudden changes in salinities significantly ($p < 0.05$) affected the naupliar survival of *D. oculata* and the results are summarized in Figure 2. Among the salinities tested (10, 15, 20, 25, 30, 35, 40, 45, 50 and 55 ppt), the highest naupliar survival (86.33 ± 2.84%) was observed at 30 ppt, which was not significantly different to naupliar survival

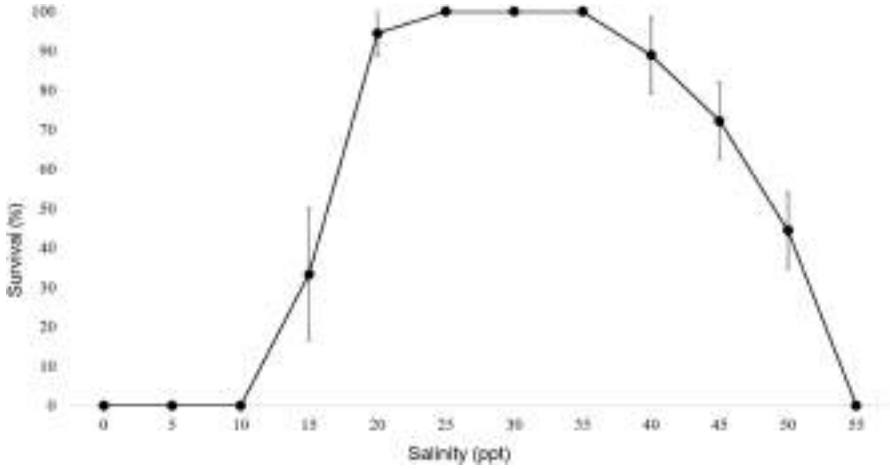

FIGURE 1 Effect of abrupt salinity change on adult survival (%) of *Dioithona oculata* after 24 h exposure under different salinities (0–55 ppt). Data are presented as mean ± SD.

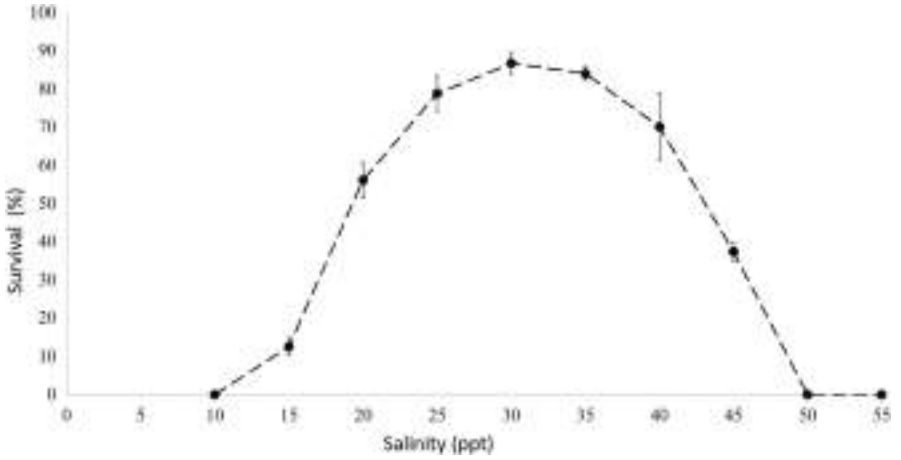

FIGURE 2 Survival (%) of *Dioithona. oculata* nauplii under different salinity treatments (10–55 ppt). Data are presented as mean ± SD.

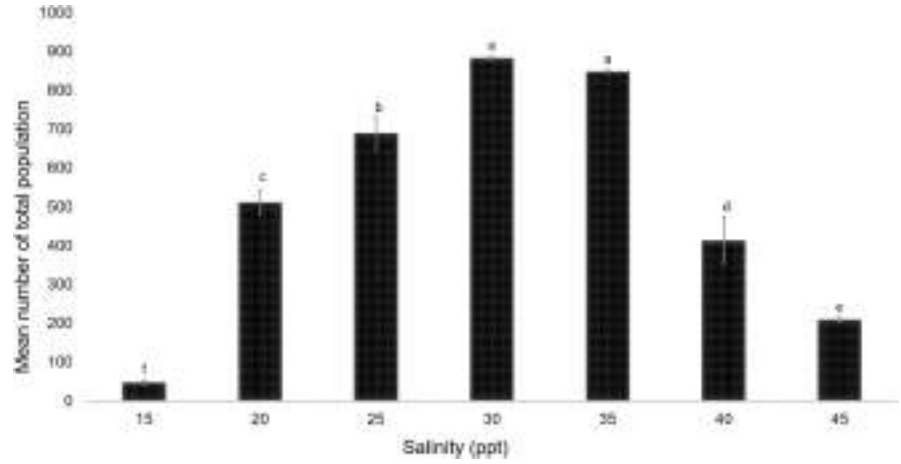

FIGURE 3 Mean total population of *Dioithona oculata* at seven different salinity treatments (Mean ± SD). Means with different superscript letters are significantly different ($p < 0.05$).

at 25 ppt (78.83 ± 4.64%) and 35 ppt (84.16 ± 1.75%). The lowest naupliar survival (12.6 ± 2.34%) was recorded at 15 ppt. No naupliar survival was observed at salinities beyond 45 ppt and below 15 ppt.

3.2 | Effect of salinity on total population and population composition

Salinity had a significant ($p < 0.05$) effect on population growth and population composition of *D. oculata* (Figures 3 and 4). Numerically, the highest value for population was recorded at 30 ppt (883.0 ± 5.5 individuals/L), which was not significantly different ($p > 0.05$) from 35 ppt (849.66 ± 4.5 individuals/L). However, a marked reduction was observed when the salinity decreased below 30 ppt or increased above 35 ppt (Figure 3). The lowest final population count was recorded at 15 ppt (49.0 ± 6.56 individuals/L), which was significantly lower than all other salinity treatments (20, 25, 30, 35, 40 and 45 ppt).

Nauplii contributed a relatively higher proportion of the population at 20, 25, 30, 35 and 40 ppt (298.33 ± 18, 371.66 ± 28, 535.0 ± 10, 503 ± 10 and 248 ± 43 individuals/L respectively) compared with the copepodites and adults (Figure 4). The lowest number of nauplii was recorded at 15 ppt (12.33 ± 2.51individuals/L). There was no significant difference in the mean population of copepodites and adults ($p > 0.05$) at 25, 30 and 35 ppt. The total population of copepodites and adults at salinities of 15 and 45 ppt was significantly less ($p < 0.05$) than that of all other salinities.

3.3 | Effect of salinity on clutch production (number of egg sacs/female)

The mean clutch production per female was higher at 30 ppt (8.6 ± 0.54 clutches) and 35 ppt (7.8 ± 0.83 clutches) which was significantly different ($p < 0.05$) from other salinity treatments (Figure 5). The lowest clutch production was at the highest salinity of 45 ppt (2.6 ± 0.54 clutches) tested.

3.4 | Effect of salinity on clutch size (number of eggs /sacs)

Clutch size was significantly higher ($p < 0.05$) at salinities of 30 and 35 ppt (19.2 ± 2.94 and 19 ± 2.12 eggs/clutch respectively) and gradually decreased when exposed to salinities lower than 30 ppt and higher than 35 ppt (Figure 6). The lowest clutch size was at 45 ppt (7.0 ± 1 eggs/clutch). No significant difference was observed between the treatments using salinities of 20 ppt (11.8 ± 2.04 eggs/clutch), 25 ppt (15.0 ± 2 eggs/clutch) and 40 ppt (11.2 ± 1.09 eggs/clutch).

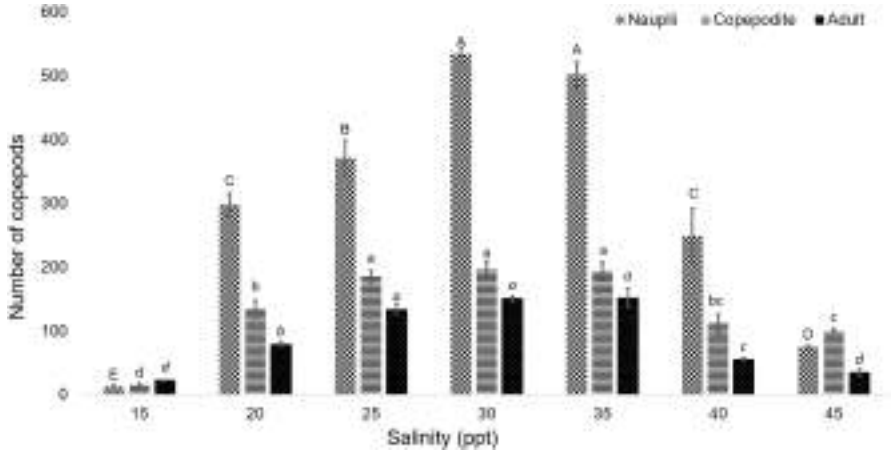

FIGURE 4 Total number of nauplii, copepodites and adults of *Dioithona oculata* reared under different salinities (Mean ± SD). Means with different superscript letters are significantly different ($p < 0.05$).

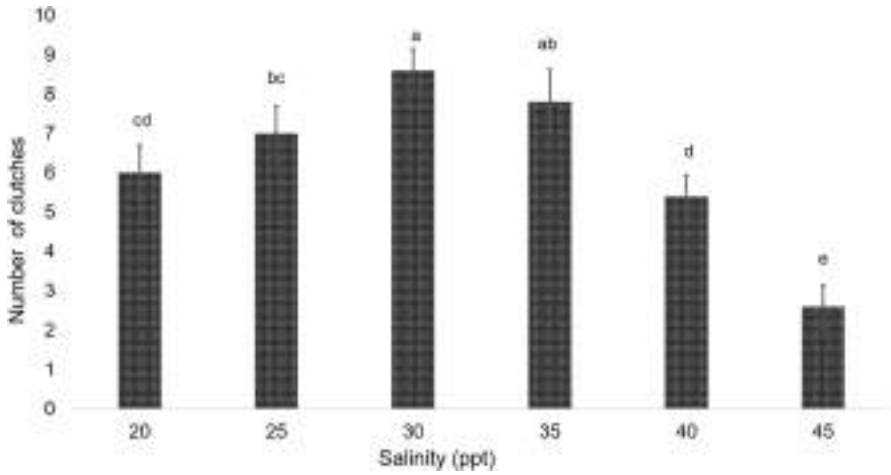

FIGURE 5 Number of clutches produced per female *Dioithona oculata* during its reproductive period at different salinity treatments. Data are presented as the mean ± standard deviation. Means with different superscript letters are significantly different ($p < 0.05$).

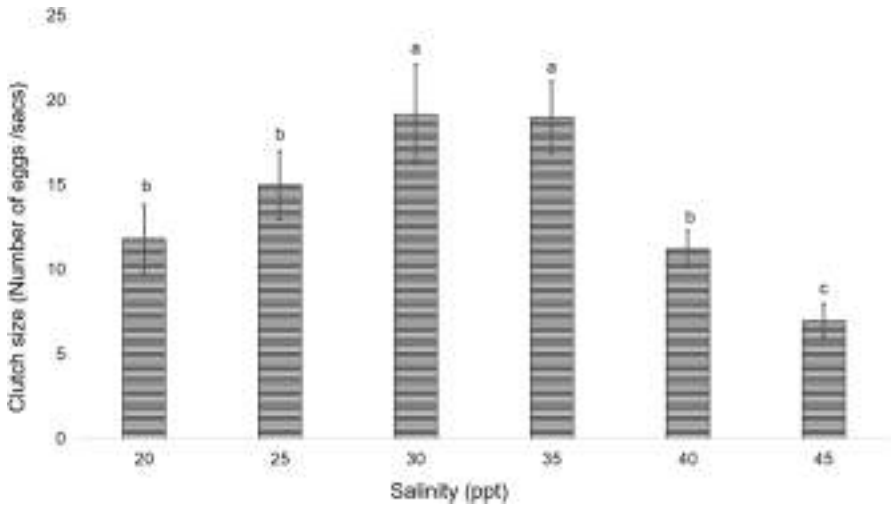

FIGURE 6 The mean clutch size of *Dioithona. oculata* reared under six salinity treatments (Mean ± SD). Means with different superscript letters are significantly different ($p < 0.05$).

3.5 | Effect of salinity on naupliar and copepodite development rates

The progress of development from the naupliar to adult stage under different salinity treatments is represented in Figure 7. The rate of development in *D. oculata* was delayed with increasing salinity. On 4th day, the proportions (%) of *D. oculata* reaching the copepodite stage were 46.66 ± 5.77, 16.66 ± 5.77, 10, 10, 6.66 ± 5.77 and 0 at salinities of 20, 25, 30, 35, 40 and 45 ppt respectively. On the 10th day of the experiment, the proportion (%) of *D. oculata* reaching the adult stage was 100, 100, 96.66 ± 5.77, 93.33 ± 5.77, 90 ± 10 and 0 at 20, 25, 30, 35, 40 and 45 ppt respectively. The effect of salinity on the development of *D. oculata*

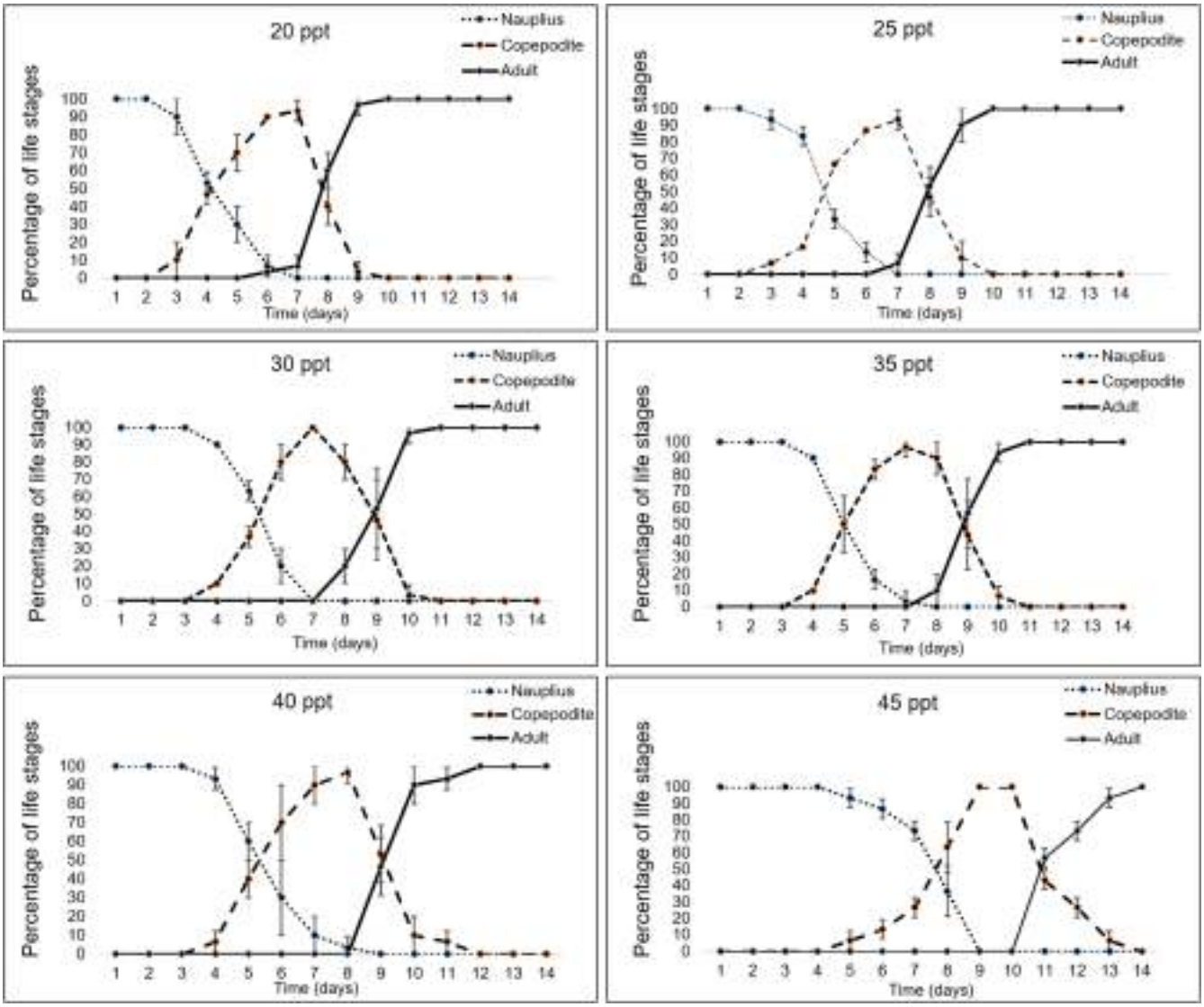

FIGURE 7 Development rate of *Dioithona oculata* reared at six salinity treatments (20, 25, 30, 35, 40 and 45 ppt). The various developmental stages (nauplii, copepodites and adults) were recorded daily and converted into percentage of the total population. Data are presented as the mean ± standard deviation.

was clearly evident when average development time from nauplii to copepodites and that from nauplii to adults were compared (Table 1). Mean development time from nauplii to copepodites (8.73 ± 0.15) and that from nauplii to adults (12.72 ± 0.03 days) were longest at 45 ppt and the shortest corresponding development time was at 20 ppt (4.86 ± 0.4 and 9.06 ± 0.02 days respectively) (Table 1).

3.6 | Effect of salinity on adult longevity

The adult longevity was maximum at salinity 30 ppt (27.0 ± 1.0 days) and found to decrease at salinities above and below 30 ppt (Table 1). On the 11th day of treatment, 100% mortality was observed at 45 ppt. The effects of salinities higher than 35 ppt on adult longevity were more adverse (15 ± 1.0 and 11.3 ± 1.15 days at 40 and 45 ppt respectively) when compared with the effects of lower salinities.

4 | DISCUSSION

4.1 | Effect of abrupt salinity change on *Dioithona oculata*

4.1.1 | Adult survival

Survival of copepod to sudden changes in the salinity will help to assess its range of utilization as live feed in larval rearing trials. No mortality was observed in the sudden change of salinity from 35 ppt to 25 ppt, which clearly indicates its utilization in direct

TABLE 1 Mean development time (nauplius to copepodites and adults) and adult longevity of *Dioithona oculata* at six salinity treatments. The data were represented as mean ± SD. Means with different superscript letters are significantly different ($p < 0.05$)

Salinity (ppt)	Development time from nauplius to copepodite (days)	Development time from nauplius to adult (days)	Adult longevity (days)
20	4.86 ± 0.4^{d}	9.06 ± 0.02^{e}	22 ± 1.0^{b}
25	5.53 ± 0.35^{cd}	9.11 ± 0.04^{d}	26.3 ± 1.5^{a}
30	$6.12 \pm 0.05b^{c}$	9.99 ± 0.16^{c}	27 ± 1.0^{a}
35	$6.2 \pm 0.3b^{c}$	10.07 ± 0.14^{c}	23 ± 1.0^{b}
40	6.77 ± 0.1^{b}	10.73 ± 0.11^{b}	15 ± 1.0^{c}
45	8.73 ± 0.15^{a}	12.72 ± 0.03^{a}	11.3 ± 1.15^{d}

feeding in these salinities. In general, more than 50% survival was observed between 20 and 45 ppt range giving a better scope for wider utilization. Reports on the distribution and swarming of *D. oculata* in coastal, marine and estuarine habitats confirm its ability to tolerate changes in salinities (Araujo et al., 2016; Hamner & Carleton, 1979; Kurt, 2018, 2020; Lopes et al., 1998; Sterza & Fernandes, 2006).

Swarms of *D. oculata* have also been reported from areas with high salinity fluctuations (Kurt, 2018; Thompson, 1991). Another cyclopoid copepod often reported from a similar habitat *Oithona davisae* could withstand a wider range of salinity from 6 to 40 ppt (Svetlichny et al., 2021). The adaptation of copepods to highly fluctuating salinity conditions is facilitated through osmoregulation (Bayly & Boxshall, 2009; Svetlichny & Hubareva, 2014) by regulating the concentration of intracellular free amino acids in their body (Burton & Feldman, 1982; Goolish & Burton, 1989) and the capacity to survive at different salinity levels is mostly species specific.

4.1.2 | Naupliar survival

Copepod nauplii are comparatively more sensitive and vulnerable to changes in salinity (Devreker et al., 2004; Nagaraj, 1992; Pandori & Sorte, 2019; Tester & Turner, 1991). Often nauplii alone are filtered and used for larval rearing. Here, maximum nauplii survival of *D. oculata* was recorded at a salinity range of 25–35 ppt. Nauplii did not survive at salinity levels below 15 ppt and above 45 ppt. Salinity has more direct influence on the survival of copepod nauplii than adults (Chen et al., 2006; Chinnery & Williams, 2004; Karlsson et al., 2018). Nauplii of other cyclopoids like *Dioithona rigida* (Santhanam et al., 2018) and *Oithona simplex* (Noor et al., 2018) were reported to give better survival in lower salinities than the higher salinity ranges from the mean seawater salinity (35 ppt). Cyclopoids, particularly the members of *Oithona* and *Dioithona*, have better survival in lower salinities (Magouz et al., 2021). Salinity stress induces the degradation of more amino acids to meet the energy requirements for osmoregulation which in turn causes depletion in protein reserves and thereby adversely affects the survival of nauplii, especially the non-feeding initial naupliar stages (Farmer & Reeve, 1978; Kimmel & Bradley, 2001).

4.2 | Effect of salinity on total population and population composition

The success of copepod culture as live feed depends on the population growth and population composition and *D. oculata* is a common copepod forming swarms in the euryhaline environments (Ambler, 2002; Ambler et al., 1991; Kurt, 2018; Sander & Moore, 1979; Sterza & Fernandes, 2006). But salinity has significantly influenced the total population and the population composition of *D. oculata*. The total population of *D. oculata* was significantly higher at 30 and 35 ppt compared with other salinity treatments. This may be the reason why *D. oculata* was seen to be popularly reported in coastal lagoons and estuarine waters where the salinity will be always slightly lesser than the normal seawater (Björnberg, 1972; Kurt, 2018; Thompson, 1991; Ueda et al., 1983). Even though, most of the cyclopoid copepods survive in a euryhaline environment, their productivity varies with the changes in salinity (Pan et al., 2016). In *Oithona nana*, the total population was maximum at a salinity of 20 ppt (Magouz et al., 2021) and in *O. rigida*, the maximum production was observed at a range from 28 to 34 ppt (Santhanam & Perumal, 2012).

Salinity changes also affected the population composition of *D. oculata*. Generally, the proportion of nauplii and copepodites in a culture specifies the advancement of culture (Vanderlugt et al., 2009). Naupliar stages of *D. oculata* were relatively higher in number than other developmental stages in all tested salinities, except 15 and 45 ppt. At 15 ppt and 45 ppt, the percentage composition of adults and copepodites was higher due to the lack of naupliar production and poor survival rate. This also supports the findings of Magouz et al. (2021), where a significantly higher percentage composition of nauplii and copepodites is reported in *O. nana* at the salinity levels from 20 to 30 ppt. There are various reports suggesting that higher the number of nauplii in a culture reflects the higher reproductive rate of the females which consequently enhances the final population (Vanderlugt et al., 2009; Wilson et al., 2021). Production of higher number of nauplii is always a promising feature of a copepod which benefits aquaculture sector by ensuring higher quantity of live feed for fish larvae (Stottrup & Norsker, 1997).

4.3 | Effect of salinity on clutch production (egg sacs/female)

Clutch production and number of eggs/clutch are a direct indication of the reproductive potential for that particular salinity. In the current study, higher clutch production and the number of eggs/clutch of *D. oculata* were observed at the salinities of 30 and 35 ppt, suggesting this as the ideal salinity for mass production. Salinity is a significant parameter in the clutch production of copepods and the variations from optimal salinity conditions lead to physiological changes for maintaining the osmotic balance in copepods and reduce the energy available for reproduction (Cailleaud et al., 2007; Chen et al., 2006; Dexter, 1993; Peck et al., 2015; Svetlichny & Hubareva, 2014). Noor et al. (2018) reported 30 ppt as ideal for maximum clutch production in *Oithona simplex*. *Apocyclops* spp. in general are more euryhaline and in *Apocyclops royi*, there was no significant difference in clutch production in salinities from 10 to 30 ppt (Pan et al., 2016) but in case of *Apocyclops dengizicus*, Farhadian et al. (2014) reported a reduction in clutch production at salinities above and below 25 ppt. However, in a recent study, Wilson et al. (2021) indicated that the multigenerational acclimatization at different salinities has significantly improved the mean daily egg production in a typical estuarine species (*Acartia tropica*) collected and reared from Cochin backwaters.

4.4 | Effect of salinity on clutch size (number of eggs/sacs)

Salinity changes strongly influenced the clutch size of *D. oculata* in the present study. According to Ambler et al. (1999), clutch size is considered as an ideal indicator to assess the egg production rate in *D. oculata*. The maximum clutch size in *D. oculata* was found in 30 and 35 ppt. But the clutch size was reduced beyond 35 ppt which could be the result of physiological stress at higher salinities. Pan et al. (2016) conveyed that suboptimal salinities result in fewer egg production compared with its optimum salinity in *A. royi*. Due to the abnormal change in salinities, copepods demand more energy for osmoregulation which in turn affects their egg production (Goolish & Burton, 1989; Kimmel & Bradley, 2001).

4.5 | Effect of salinity on naupliar and copepodite development rate

The development rate of copepods is reported to be strongly influenced by salinity (Devreker et al., 2012). Here, increase in salinity retarded the naupliar and copepodite development of *D. oculata*. The rate of development of nauplii of *D. oculata* lasted 4.86 days at 20 ppt but was prolonged to 8.73 days at 45 ppt. Both naupliar and copepodite development rates were relatively lower at the salinity levels of 20, 25, 30 and 35 ppt compared with the higher salinity levels of 40 and 45 ppt. According to Devreker et al. (2004), the sensitive nauplii stage in adverse environment generally exhibits a delay in development. Though the development time in response to salinity is species specific (Karlsson et al., 2018), lower salinity conditions did not affect the nauplii and copepod development rates in cultured cyclopoid copepods as reported in case of *A. royi* (Lee et al., 2005), *Paracyclopina nana* (Lee et al., 2016) and *D. rigida* (Santhanam et al., 2018). But in case of most of the calanoids cultured, lower salinity conditions significantly affected the larval development time as in case of *Acartia bifilosa*, *Acartia clausi*, *Acartia discaudata* and *Acartia tonsa* (Chinnery & Williams, 2004), *Eurytemora affinis* (Karlsson et al., 2018) and also in harpacticoid copepod *Nitocra affinis* (Matias-peralta et al., 2005). The delay in development of nauplii is often an added advantage in the rearing of fish larvae with a small mouth gape, especially during the coculture of copepods with fish larvae.

4.6 | Effect of salinity on adult longevity

Adult longevity has great significance in population dynamics and productivity of copepods (Peterson, 2001). Though *D. oculata* can tolerate a salinity range of 20–45 ppt, the longest lifespan was observed at 30 ppt. Noor et al. (2018) reported a reduction in adult longevity of *O. simplex* above its optimum salinity (30 ppt). In addition, Farhadian et al. (2014) also reported maximum longevity (71 days) at 30 ppt for *Apocyclops dengizicus*. Therefore, it is confirmed that the salinity (30 ppt) with longest longevity (30 ppt) is ideal for the mass production.

5 | CONCLUSION

Though, *D. oculata* is commonly reported to form huge swarms in coastal waters with varying salinities, it can be cultured ideally in 30 to 35 ppt salinities without affecting the parameters like total population, clutch production, clutch size, development rate and adult longevity. In order to produce a large number of nauplii, the culture needs to be maintained at 30 ppt salinity. It can be very well utilized for larval feeding at salinity ranges of 25 to 35 ppt. Considering its highest longevity at 30 ppt, the stock culture of this species can be ideally maintained at 30 ppt. Considering its potential and suitability for production in a salinity ranges of 25–35 ppt, it can be mass cultured in these salinities and used as an efficient live feed for marine fish larvae.

AUTHOR CONTRIBUTIONS

S. Darsana contributed to investigation, formal analysis, writing – original draft; B. Santhosh to conceptualization, supervision, identification, review and editing; F. Muhammed Anzeer to collection, isolation and basic culture; K. S. Aneesh to Microalgae culture and feeding trials; Ritty Maria Thomas to statistical analysis; Divya Grace Dilip to copepod maintenance; C. Anushree to water quality monitoring and laboratory analyses; M. K. Anil to review and editing.

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CONFLICT OF INTEREST

All the authors have contributed equally and extended full support towards implementing the project and preparation of the manuscript. Therefore, as a corresponding author I declare that the authors have no conflict of interest in publishing this research work. The work described in this manuscript was original research that has not been published previously, and not under consideration for publication elsewhere, in whole or in part.

DATA AVAILABILITY STATEMENT

The data sets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

ETHICS STATEMENT

Different experiments with live animals were conducted in compliance with the guidelines of standard operating procedure guidelines established by the Institutional Animal Ethics Committee (IAEC) of ICAR-CMFRI, Kochi, India. Therefore, this article does not contain any studies that are against ethics and the authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to.

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