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# Diel cycles of molting, mating, egg sac production and hatching in the swarm forming cyclopoid copepod *Dioithona oculata*

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**Abstract:** Diel periodicity was discovered in 4 life cycle events for the swarming cyclopoid copepod *Dioithona oculata:* the molt to adult stage, mating, egg sac production, and egg hatching. The timing of these events was associated with swarming in which dioithonans form swarms at dawn and disperse at dusk. A laboratory time course experiment revealed that molting of copepodid stage five (CV) to adult (CVI) occurred between midnight and dawn (0600 h). In videotaped experiments of laboratory swarms, mating encounters were greatest at dawn and therefore would occur as soon as CV molted to adults and were present in swarms. In experiments with field collected swarms, 80% of egg sacs were produced by females between midnight and 0820 h the next morning, and 80% of the eggs hatched by the following night between midnight and 0500 h. Egg cycle duration (clutch duration plus inter-clutch interval) was 48 h, and the mean fecundity was 0.56 pairs of egg sacs $d^{-1}$ or 7.6 eggs $d^{-1}$. We suggest that predation is the main selective force for diel cycles of *D. oculata*, but that diel cycles in reproduction benefit the survival of nauplii, whereas diel cycles of molting, mating, and swarming benefit the reproduction and survival of adults.

**Key words:** diel cycles, cyclopoid copepod, egg production, molting, mating

## Introduction

Diel cycles govern many copepod life events by providing proximate cues for their behavior such as vertical migration, swarming, egg production, and feeding (Hamner & Carleton 1979; Haney 1988). We have been studying a tropical swarming cyclopoid copepod, *Dioithona oculata* (Farran 1913), which consistently forms swarms during the daylight hours during all seasons (Ambler et al. 1991). In this study, we focus on diel cycles found for life cycle events which begin with the molt to the adult stage and continue through mating, egg sac production and egg hatching.

*Dioithona oculata* forms dense aggregations in lagoonal waters surrounding mangrove islands off Belize. During the day, adults and immature copepodids occur in swarms among red mangrove prop roots, and densities within swarms ranges from 1–90 copepods $ml^{-1}$ (Ambler et al. 1991; Buskey et al. 1996). Swarms are initiated by phototactic behavior to swarm markers which are light shafts formed by sunlight penetrating through the mangrove canopy. Individual *D. oculata* maintain their positions in swarms by klino-kinetic turning behavior and active swimming to stay within the light shaft swarm markers (Buskey et al. 1995; Buskey et al. 1996). As light intensity decreases at dusk and swarm markers disappear, adults and copepodids disperse from swarms to several meters from the mangrove shoreline overnight (Ambler et al. 1991). Nauplii are never found under the prop roots during the day or night, but occur several meters away from the prop roots in the channels between mangrove islands (Ambler et al. 1991). Thus the daily ambit of the nauplii is much more restricted than that of copepodids and adults which occupy the mangrove channel and prop root habitats.

The consistency and timing of swarming suggested that there were strong selective pressures on *D. oculata* in the mangrove habitat, and led us to consider the timing of other events in their life cycle: molting, mating, egg sac produc-

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tion and egg hatching. Diel cycles of egg production with hatching at night have been reported for many copepod and cladoceran species as reviewed by Haney (1988). More recently Hopcroft & Roff (1996) have reported diel cycles for egg production of 4 cyclopoid copepod species. Our objective was to determine if diel cycles occurred in egg production and events occurring before egg production, and to relate these life cycle events to the diel cycle of swarming.

## Materials and Methods

Swarms of *Dioithona oculata* were collected from several protected shorelines of Twin Cays, which are mangrove islands in the barrier reef lagoon of Belize (16°50'N, 88°05'W) (Fig. 1). Field temperatures varied between 28–30°C during May–July, and 20–26°C in January–February. Copepods formed swarms in the field near dawn: during summer the earliest swarms were observed at 0515 h, and during the winter swarms were observed as early as 0600 h (Ambler et al. 1991). Swarms dispersed near dusk between 1700 and 1800 h during both summer and winter.

For the egg hatching experiments, two types of egg sacs were monitored: (1) egg sacs that females had dropped, and (2) egg sacs still attached to females. *D. oculata* were collected on seven dates between February 1989 to January 1990, and groups of 10 dropped egg sacs or 10 females with a pair of egg sacs were placed in 25-cm-diameter petri dishes with seawater filtered through a 45-$\mu$m mesh. The total number of egg sacs observed for a particular date varied between 30 to 67 (Table 1). Females from May 1990 and July 1991, carried a mean of 7.17 and 6.32 eggs per sac, respectively. Therefore at least 190 eggs were observed during each experimental date. During each experiment, we monitored embryonic stage and the number of egg sacs with complete hatching at 2-h intervals, beginning at 2000 h and usually ending at 0800 h when most of the eggs had hatched.

From the egg hatching experiments, we determined that newly formed embryos appeared opaque or gray using transmitted light microscopy, and that 8–10 h later embryos were orange. Four experiments were performed between 31 May and 9 July 1989 to determine the timing of egg sac formation and hatching by distinguishing between newly formed opaque gray embryos and older orange embryos. In the late afternoon (1600 h), 2–3 swarms were collected from Twin Bays (Fig. 1) and placed in a 10.6-liter cooler with water from their mangrove prop root habitat for a final densities around 1 animal $ml^{-1}$. Beginning at 2200 h on the same day, 100-ml samples were removed from the cooler and 100 females were anesthetized with MS222 (tricaine methanesulfonate) and identified to 3 categories: females with new opaque embryos, females with older orange embryos, and females without egg sacs. The 100-ml sample was not returned to the 10.6-liter cooler. Samples of 100 ml were collected at 2-h intervals until 0600 or 0630 h of the following day. Temperature in the cooler decreased by at

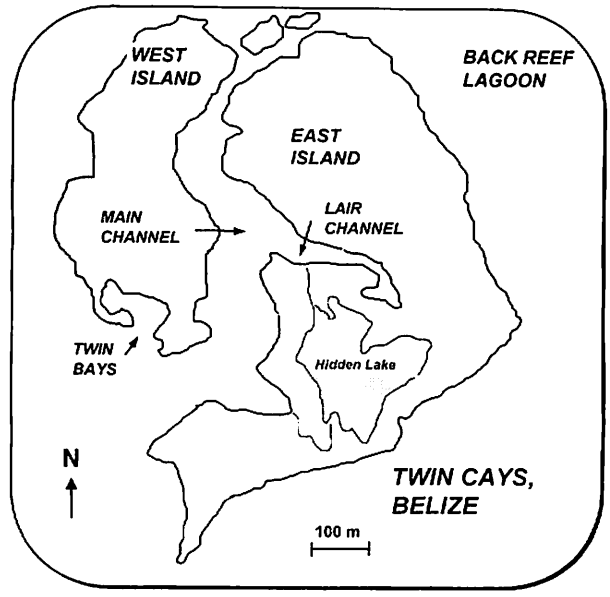


**Fig. 1.** Twin Cays, two mangrove islands (16°50'N, 88°05'W) near the Smithsonian Institution's Field Station at Carrie Bow Cay, Belize. Swarms were collected from Twin Bays, Main Channel, and the Lair Channel.

**Table 1.** *Dioithona oculata*. Estimation of time of 50% hatching of dropped egg sacs (dropped) and paired egg sacs of females (females). For each experiment the following are shown: date, collection time in the field, $r^2$ value, viability of hatching by 0800h the day after collection, the number of egg sacs observed, estimated time of 50% hatch, and the percent eggs hatched at midnight and 0600h the next day.

| Egg sac | Date | Collection time | $r^2$ | Viability (%) | No. of egg sacs | Time of 50% hatch | % eggs hatched 2400 h | % eggs hatched 0600 h |
|---|---|---|---|---|---|---|---|---|
| Dropped | 21 Feb 89 | 1000 h | 0.96 | 100 | 35 | 0144 h | 27 | 94 |
| Dropped | 18 May 89 | 0815 h | 0.85 | 100 | 50 | 0219 h | 5 | 99 |
| Dropped | 20 May 89 | 1145 h | 0.82 | 64 | 67 | 0558 h | 0 | 49 |
| Dropped | 22 May 89 | 1430 h | 0.98 | 100 | 61 | 0158 h | 18 | 99 |
| Females | 21 Feb 89 | | 0.96 | 83 | 132 | 0556 h | 1 | 49 |
| Females | 28 May 89 | | 0.81 | 100 | 30 | 0349 h | 1 | 76 |
| Females | 8 Jan 90 | | 0.99 | 96 | 68 | 0546 h | 1 | 55 |
| | | | | | | Mean | 8 | 74 |

most 1°C during the experimental period.

To determine the percentage and frequency of females producing egg sacs, we followed the egg sac production of individual females fed *Amphidinium klebsii* over a 4-d period during July 1991. On 6 July at 1500 h, swarms of *D. oculata* and water containing a bloom of *A. klebsii* were collected. On 7 July at 0900 h (Day 1), 49 females with newly formed opaque embryos in egg sacs were isolated and each female was put into a single 3-ml well with bloom water. At 0600 h on 8 July (Day 2) through 10 July (Day 4), each female was observed for presence of nauplii indicating hatching and presence of a newly formed egg sac. Nauplii were removed each day.

Synchrony in molting of copepodid stage five (CV) to adults (CVI) during the night was documented. Swarms were collected at 1030 h from Twin Bays on 17 June 1995. Between 1230 and 1330 h, 6 groups of 30 CV were sorted from animals which were lightly anesthetized with MS222, and kept in 100-ml beakers with cultures of *Isochrysis galbana* or *Dunaliella salina*. Two groups of 30 animals were preserved at midnight, 0400 and 0630 h. Animals in each group were identified as CV, CVI female or CVI male. Diel periodicity in mating was observed from videotaped laboratory experiments performed during 12–27 January and 24 May–8 June, 1994, and photobehavior from these experiments is described in Buskey et al. (1995). The experimental protocol was to put *D. oculata* collected from swarms in a laboratory aquarium for 5 min in darkness, 10 min in the presence of a vertical light shaft capable of inducing swarming behavior during the day, and 2 min again in darkness. Swarm formation usually occurred within the first 5 min of the light-shaft period. This experiment was repeated at 5 different times during the day: 1600, 2000, 0000, 0600, and 1000 h, and at each time the experiment was replicated 6 times with a different group of animals. For each time, the number of mating pairs was counted during the 10 min of swarming. Matings were distinguished by prolonged contact between 2 copepods, which only occurs between adult males and adult virgin females prior to mating (Ambler et al. 1997).

The percent mating encounters were determined by comparing the number of mated pairs formed per minute to the potential number of copepod pairs encountered per minute. Matings per copepod per minute were determined by dividing the number of observed matings per minute by the observed copepod density. The potential number of encounters per minute was determined by modifying the model of Gerritsen & Strickler (1977) which was developed for predator prey interactions (Buskey 1998). To calculate encounter frequencies, copepod density, swimming speeds of males and females, and encounter distance must be known. Copepod density was calculated using Bioscan Optimas image analysis software, and swimming speeds were calculated using Expertvision Cell-Trak video computer motion analysis. The encounter distance between a male and a female before mating was estimated as 2.5 mm from videotapes of previous experiments (Ambler et al. 1997). Percent mating encounters were calculated as the ratio of the number of observed matings copepod$^{-1}$ min$^{-1}$ to encounter frequency.

Statistical transformations were necessary for fraction CV not molted to adult, fraction gray embryos formed and fraction orange embryos hatched, because these fractions are sigmoidal as a function of time. The fractions were transformed to the arcsine of the square root to produce a linear relationship (Sokal & Rohlf 1981). Linear regressions were performed with EXCEL 97 to describe the time course function and to estimate the times of 10, 50, and 90% molting to adult, egg sac production or egg hatching. Thus we can quantify the time period when 80% of these events occurred, and estimate clutch duration by the difference between times of 50% egg sac production and hatching.

## Results

Diel periodicity of egg hatching was observed to occur at night in experiments with dropped or attached egg sacs (Table 1). By midnight only 8% of the eggs hatched, but by 0600 h the next day, 74% of the eggs hatched. These results were consistent for egg sacs which were either attached to females or dropped. Viability of nauplii was 83–100% in 6 of the 7 experiments. Embryos with attached or dropped sacs developed in the following sequence: (1) 0–14 h: egg sacs form and embryos appear gray in transmitted light and extend to the edges of the egg membrane; egg membranes are pressed together in the sac and do not appear round; (2) 14–20 h: gray embryos become orange embryos inside

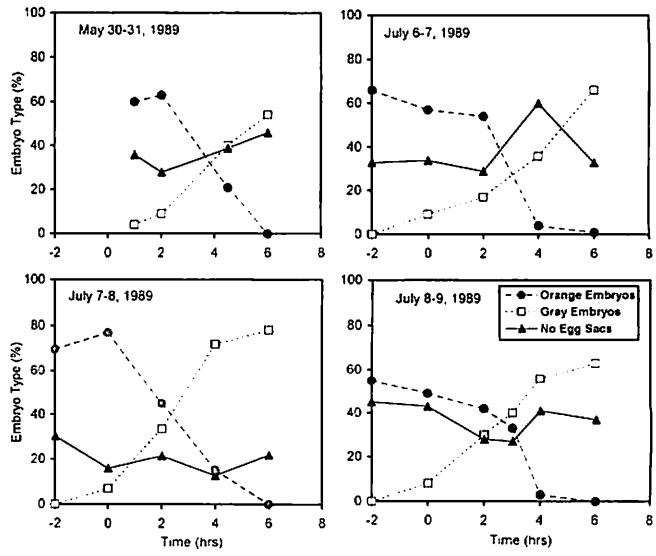


**Fig. 2.** *Dioithona oculata*. Experiments for egg sac formation and egg hatching on 4 different dates. Time course from 2200 h (−2) on the day of swarm collection to 0800 h (8) the following morning for females with new embryos, females with older orange embryos, and females with no egg sacs.

eggs; surface of eggs appears shiny; (3) 20–24 h: eggs hatch; within an hour of hatching the naupliar eye is visible and eggs separate from each other and each egg appears to be attached by a string-like structure.

Diel periodicity of the egg cycle was determined from the time course of embryonic development experiments with swarm samples (Fig. 2). At 2200 h on the day of collection, females were either carrying eggs with orange embryos or not carrying egg sacs. By midnight most egg sacs still contained orange embryos, although 4–9% of females were carrying newly formed gray embryos in egg sacs. At 0200 h the percent females carrying orange embryos in egg sacs was decreasing and the number of females with newly formed gray embryos was increasing. At 0400 h the percentage of females with newly formed embryos was greater than that of females carrying orange embryos. By 0600 h the percentage of females with orange embryos was zero. The percentage of females without egg sacs varied from 20 to 50% during the experimental period from 2200 h on the day of collection to 0600 h the following day.

For all the data in these 4 experiments, 80% of the egg sacs were formed between 0036 and 0820 h, and 80% of the eggs hatched the following day between 0016 and 0509 h (Fig. 3). The clutch or embyronic development time was estimated by the difference between the time of 50% egg sac formation (0428 h) and time of 50% egg hatching (0243 h): 22.25 h. The time of 50% hatch, 0243 h, was in the middle of the range for time of 50% hatch for females with attached egg sacs and for dropped egg sacs (Table 1).

In Fig. 2, 20–50% of the females did not have egg sacs, which might result from all females producing a clutch every other day or only half of the females producing egg sacs every day. The pattern of egg sac production for individual females was determined during the 4-d experiment when 49 individual fertilized females were observed. Thirty eight of the 49 females produced egg sacs only on Days 1 and 3 (Table 2), which means that most females produced a pair of egg sacs every other day. Six of the 49 females produced 3 egg sacs during 4 d, and 3 females produced an egg sac every day. These 49 females produced an average of 1.11 pairs of egg sacs every other day, or 0.56 pairs of egg sacs per day.

Eighty percent of the CV molted to adult overnight between 0057 and 0606 h during the June 1995 experiment (Fig. 4). Only 4% of the CV animals had molted to CVI by midnight, which was about 12 h after they had been anesthetized and isolated from swarms. By 0400 h, 47.7% of the CV were adults; females comprised 52% of adults and 2 females had egg sacs. By 0630 h, 82.5% of copepods were adults with females comprising 51.5% of all adults; there was one female with egg sacs. The estimated time for 50% of the CV to molt was 0330 h.

In more than 200 min of video-taped experiments, 12 episodes of prolonged contact between 2 individuals of *Dioithona oculata* were interpreted as mating. Eleven of these episodes occurred near dawn (0600 h) and one oc-

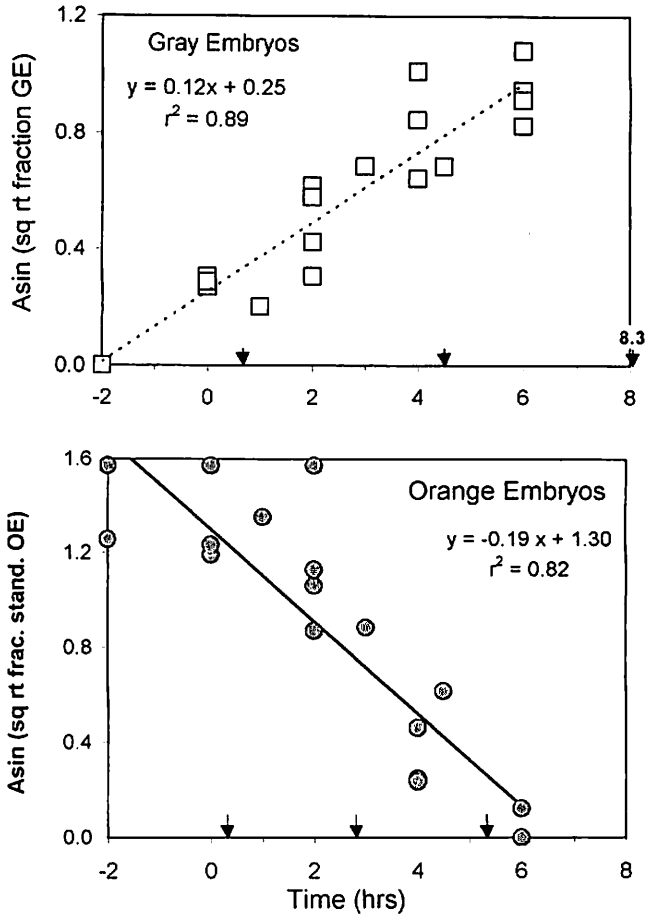


**Fig. 3.** *Dioithona oculata.* Linear regression of arcsine transformation for females with gray embryos GE (top) and females with orange embryos OE (bottom) versus time from 2200 h (−2) to 0600 h (6) the following day. Data from all 4 experiments shown in Fig. 2 combined. Three arrows on the time axis show the estimated times for 10, 50, and 90% egg sac formation (top) and egg hatching (bottom).

**Table 2.** *Dioithona oculata.* Patterns of egg sac production for 49 females collected at 1500 h on 6 July, 1991 and fed dinoflagellates collected from the field for 4 d. ×=new pair of egg sacs observed at 0600 h of each day. See text for methods.

| No. Females | Days | | | | Total no. clutches |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | |
| 38 | × | | × | | 2 |
| 3 | × | × | × | × | 4 |
| 3 | × | × | × | | 3 |
| 2 | × | | × | × | 3 |
| 1 | × | × | | × | 3 |
| 1 | × | × | | | 2 |
| 1 | × | | | | 1 |
| 49 Total females | 49 | 8 | 46 | 6 | 109 Total |

Mean=2.22 pairs of egg sacs $(4\,d)^{-1}$, or 0.56 pairs of egg sacs $d^{-1}$

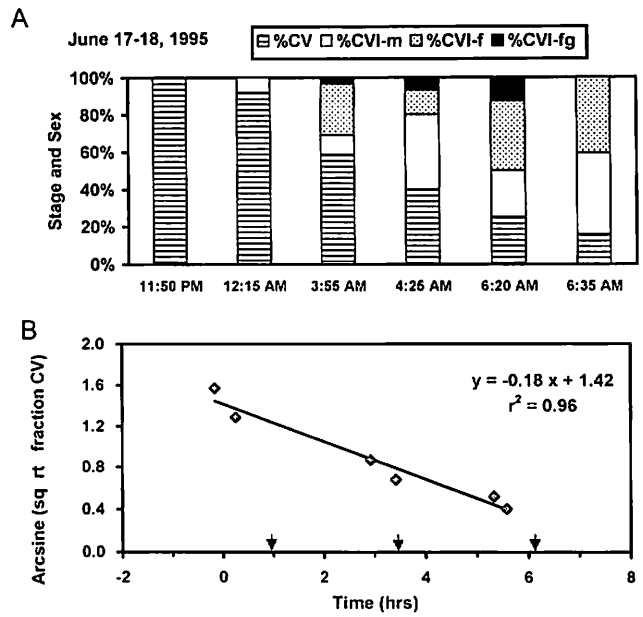


**Fig. 4.** *Dioithona oculata*. Molting of CV to adult during the night. **A.** Relative abundance CV, and adult males (CVIm), adult females (CVIf), and ovigerous females (CVIfg). **B.** Regression of arcsine transformation of CV as a function of time from midnight (0) to 0600 h (6). Three arrows in (B) show the time of 10, 50, and 90% molting from CV to adult.

curred at 1000 h (Table 3). Within the center of the light shaft, copepod density increased from 0.64 copepods $ml^{-1}$ at midnight to 11.22 copepods $ml^{-1}$ at 1600 h, a 17-fold increase. The rate of encounters between 2 individuals also varied by 17-fold: from 2.0 encounters $copepod^{-1}\,min^{-1}$ at midnight to 35.2 encounters $copepod^{-1}\,min^{-1}$ at 1600 h. Obviously, encounter rates were much greater during the day when copepods formed swarms. Therefore mating encounters were not a function of copepod density but time of day, since the highest percent mating encounters, 0.9%, occurred at dawn.

## Discussion

We detected diel cycles of egg production by identifying 2 distinct stages in embryonic development: new gray non-differentiated embryos and older orange embryos with distinct features including naupliar eyes. These stages were distinct because we observed live rather than preserved animals and could easily distinguish colors of embryos. This technique allowed us to focus on the time period when egg hatching and egg-sac formation were occurring. Hopcroft & Roff (1996) observed females at 1–2-h intervals, and sometimes missed egg hatching. If other cyclopoid species have distinct color changes in embryonic development, then the time of egg hatching could be estimated by observing the proportion of females with and without colored embryos. Tessier (1984) reported diel cycles of egg production in cladoceran species by observing that the frequency of embryonic development stages remained constant.

*Dioithona oculata* females collected from swarms reproduced synchronously with a diel cycle, with eggs hatching between midnight and 0600 h the next morning (Table 1, Fig. 2). The egg cycle duration, which includes the clutch duration (22.25 h) and the inter-clutch duration was usually 48 h, although some individual females produced egg sacs within a few hours after egg hatching which resulted in a 24-h clutch duration (Table 2). Hopcroft & Roff (1996) observed diel cycles of clutch duration for the tropical cyclopoid species: *Oithona nana*, *Oithona simplex*, and *Corycaeus amazonicus*, and for the harpacticoid *Euterpina acutifrons*. *Oithona nana* and *O. simplex* had diel cycles with the same timing as *D. oculata*: egg hatching occurred between 0300 and 0600 h. However, the majority of *O. nana*, *O. simplex*, and *E. acutifrons* females produced egg sacs soon (within 1 h) after egg hatching, so that most females carried egg sacs (Hopcroft & Roff 1996). This 24-h egg-cycle duration contrasts with *D. oculata* which usually produced egg sacs the next day after egg hatching and therefore had a 48-h egg-cycle duration (Table 2). Hopcroft & Roff (1996) also observed longer egg-cycle durations for *Oithona plumifera* which they collected further offshore than other oithonids. Thus diel cycles of egg production have been observed for 5 cyclopoid and one harpacticoid species with hatching occurring near dawn (Hopcroft & Roff 1996; present study). One exception was *C. amazonicus* whose eggs hatched in late afternoon (Hopcroft & Roff 1996).

Egg-cycle duration, clutch size, and egg-production rates

**Table 3.** *Dioithona oculata*. Diel mating pattern for females in laboratory experiments, in which copepods were filmed for 5 min in dark, 10 min in the center of a light shaft formed by fiber optic probe, and 5 min in dark. Recordings began at 1600 h on the day of field collection.

| Time (h) | Density copepod $ml^{-1}$ | no. matings in 10 min | no. matings copepod$^{-1}$ min$^{-1}$ | no. encounters copepod$^{-1}$ min$^{-1}$ | Mating encounters (%) |
|---|---|---|---|---|---|
| 1600 | 11.22 | 0 | 0 | 35.2 | 0 |
| 2000 | 1.03 | 0 | 0 | 3.23 | 0 |
| 0000 | 0.64 | 0 | 0 | 2.02 | 0 |
| 0600 | 3.67 | 11 | 0.1 | 11.5 | 0.87 |
| 1000 | 9.97 | 1 | 0.0033 | 31.3 | 0.011 |

**Table 4.** Maximum egg production rates calculated from clutch size divided by experimental or best estimate of minimum egg-cycle duration for a given temperature. Cycle duration is the time between clutches and equals clutch duration (egg developmental time) plus inter-clutch duration. If cycle duration was not available from the literature, then a best estimate of cycle duration is clutch duration times the mean ratio of cycle to clutch duration (1.22). NA=not available.

| Species | Temp (°C) | Clutch duration (d) | Minimum cycle duration (d) | Ratio cycle/clutch | Best estimate cycle duration | Clutch size (eggs pair $^{-1}$) | Egg prod (eggs female$^{-1}$d$^{-1}$) | Reference |
|---|---|---|---|---|---|---|---|---|
| *Corycaeus amazonicus* | 28 | 0.91 | 1.0 | 1.10 | 1.00 | 43.0 | 43.0 | Hopcroft & Roff 1996 |
| *Dioithona oculata* | 28 | 0.84 | 1.0 | 1.19 | 1.00 | 13.5 | 13.5 | This Study |
| *Oithona colcarva* | 15 | 4.00 | NA | NA | 4.87 | 15.0 | 3.1 | Lonsdale 1981 |
| *Oithona colcarva* | 20 | 1.68 | NA | NA | 2.05 | 20.0 | 9.8 | Lonsdale 1981 |
| *Oithona colcarva* | 25 | 0.86 | NA | NA | 1.05 | 16.8 | 16.0 | Lonsdale 1981 |
| *Oithona davisae* | 20 | NA | 2.7 | NA | 2.70 | 10.0 | 3.7 | Uchima 1985 |
| *Oithona davisae* | 28 | 0.77 | NA | NA | 0.94 | 20.0 | 21.3 | Uye & Sano 1995 |
| *Oithona nana* | 28 | 0.98 | 1.0 | 1.02 | 1.00 | 18.5 | 18.5 | Hopcroft & Roff 1996 |
| *Oithona plumifera* | 20 | NA | 3.2 | NA | 3.20 | 12.2 | 3.8 | Paffenhöfer 1993 |
| *Oithona plumifera* | 28 | 1.60 | 2.2 | 1.38 | 2.20 | 8.0 | 3.6 | Webber & Roff 1995 |
| *Oithona plumifera* | 28 | 1.50 | 2.5 | 1.67 | 2.50 | 12.9 | 5.2 | Hopcroft & Roff 1996 |
| *Oithona similis* | 10 | NA | 6.0 | NA | 6.00 | 9.3 | 1.6 | Eaton 1971 |
| *Oithona similis* | 15 | 3.00 | 3.4 | 1.13 | 3.40 | 14.9 | 4.4 | Sabatini & Kiørboe 1994 |
| *Oithona simplex* | 28 | 0.96 | 1.0 | 1.04 | 1.00 | 7.0 | 7.0 | Hopcroft & Roff 1996 |
| | | | Mean ratio | 1.22 | | | | |

of *D. oculata* were comparable to other cyclopoid copepod species (Table 4). The minimum egg-cycle duration was a few hours longer than clutch duration (embryonic development time), and decreased exponentially with temperature for 7 species (Fig. 5). These minimal times for egg-cycle duration may represent optimal conditions with no food limitation, since Sabatini & Kiørboe (1994) found that egg-cycle duration decreased with increasing food concentrations for a given temperature. Egg-production rates were calculated by dividing clutch size by egg-cycle duration. In contrast to a fairly uniform temperature function for egg-cycle duration, the temperature function for daily egg-production rates was more variable due to lower clutch sizes for *O. simplex* and *D. oculata*, and longer egg-cycle durations for the coastal species *O. plumifera* (Paffenhöfer 1993; Webber & Roff 1995; Hopcroft & Roff 1996). Egg-production rates for *Oithona davisae* fed natural food at 28°C followed the maximal temperature curve, but *O. davisae* fed two flagellate cultures at 20°C were lower than maximal rate for that temperature (Uchima 1985; Uye &

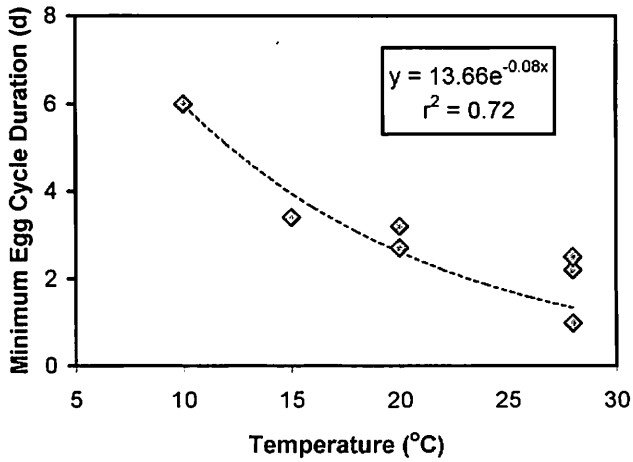


**Fig. 5.** Seven species in Order Cyclopoida. Experimental data for minimum egg-cycle duration (time from clutch to clutch) as a function of temperature.

Sano 1995). *Corycaeus amazonicus* had a much higher clutch size than the oithonids, which resulted in higher egg-production rates (Table 4). Although egg-production rates follow a general temperature function, they are characterized by differences between species and food availability.

Male-female pairs of *D. oculata* were more often found mating early in the morning (Table 3), and this timing of copulation may result directly from CV molting to adult before dawn, and male preference for mating with virgin females (Ambler et al. 1997). Mated females may produce egg sacs shortly after copulation, or wait until the following day at 0400 h. Uchima (1985) found that for *O. davisae*, hatching success of viable nauplii was highest for females that produced egg sacs within a day of copulation. Timing of copulation at dawn may also result from an adaptive advantage for diel periodicity for later reproductive events such as egg laying or hatching of nauplii. However, Volkmann-Rocco (1972) found that harpacticoid copepods in genus *Tisbe* could delay fertilization. Therefore, selective pressures for the timing of copulation may not influence timing for egg sac production and egg hatching.

Although mating encounters were greatest for the dawn experiment, 0.9% is a low percentage. The average composition of field collected swarms is 24% males, 36% females, 9% female CV, 6% male CV, and 25% younger copepodid stages (Ambler et al. 1991). For a swarm collected during the day and kept overnight, 9% of the animals would be virgin females if all CV females molted between midnight and 0630h (Fig. 4). Therefore most of the encounters between copepods are not potential mating pairs.

Reproduction of female *D. oculata* included the following diel episodic events: molt to adult before dawn (E1), mating at early dawn on the same day as E1 after swarm formation (E2), egg sac production probably the night after mating (E3), egg hatching 22.25 h after E3 (E4), and events E3 and E4 repeat several times until females die (Fig. 6). Longevity of adult females is unknown but females may live 3–4 d longer than CV copepodids, because the percentage of adults found under the mangroves but not in swarms during the day is a ratio of 4 adults to 1 copepodid (Ambler et al. 1991). This estimate assumes a stable age distribution in the population of *D. oculata*. We do not know if females spawn continuously until they die, but most females were probably producing egg sacs since the percentage of ovigerous females in a swarm population was usually at least 50% (Fig. 2) and most females produced a pair of egg sacs every other day (Table 2).

Naupliar hatching occurs at night when many females are 3–5 m away from the mangrove prop roots. Thus nauplii are not released into water near the mangrove prop roots, where copepodids and adults swarm. This corresponds to the absence of nauplii from swarm samples and their presence in samples from offshore waters (Ambler et al. 1991). Older copepodid stages and adults, including mothers of the nauplii, are able to cannibalize the nauplii (Unpublished results). Because there is a difference in copepodid and adult densities of about 2 orders of magnitude between swarms during the day and offshore waters at night, diel episodic hatching into offshore water should decrease cannibalism by reducing the probability of naupliar encounters by older copepods.

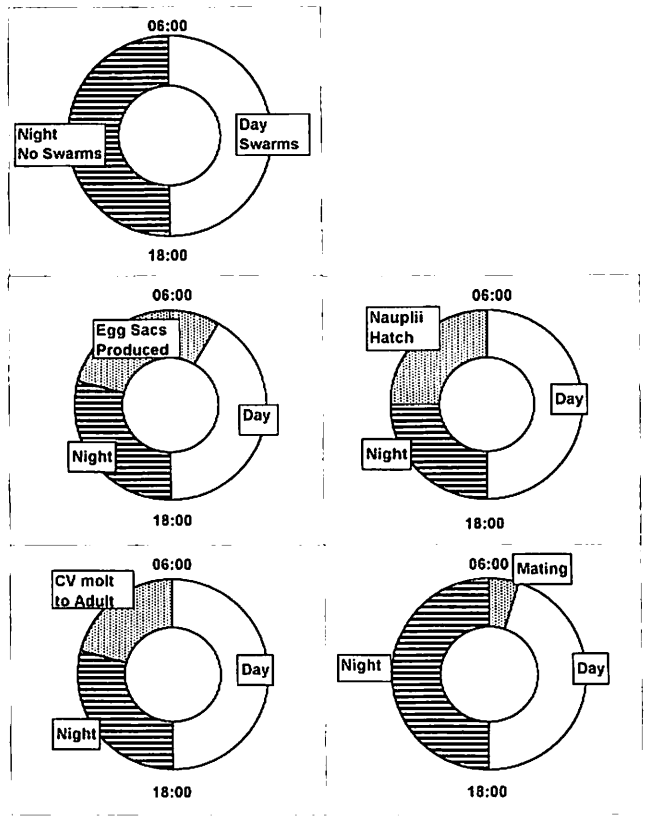


**Fig. 6.** *Dioithona oculata*. Schematic diagram portraying diel cycles for 4 life history events.

Release of *D. oculata* nauplii in water offshore of the mangroves should also reduce predation by the mangrove mysid *Mysidium columbiae*, which occupies the mangrove prop root habitat during the day and night (Modlin 1990). Juveniles of this mysid species probably can capture nauplii, since exoskeletons of *D. oculata* copepodids have been recovered from stomachs of adult *M. columbiae* (F. D. Ferrari, unpublished data). Aser et al. (1995) have shown that *Neomysis integer* can capture both nauplii and copepodids of the calanoid copepod *Eurytemora affinis*. Other potential predators of copepod nauplii in the mangrove habitat include numerous sessile filter feeders such as oysters and anemones attached to prop roots (Ambler et al. 1994).

Diel cycles of egg-sac production and egg hatching are more widespread phenomena than swarming for species of Oithonidae. *Oithona simplex*, *O. nana* and *O. fonsecae* have also been collected in Twin Cays, but never with the swarms of *D. oculata* (unpublished data). Although diel cycles of egg hatching appear to protect nauplii from predation, about 50% of the *D. oculata* females are always carrying egg sacs (Fig. 2), which should cause them to be more visible to predators. Swarming of *D. oculata* may be a de-

terrent to fish predation, and restricted to this species since they are larger than other *Oithona* spp. Mating pairs of *D. oculata* are probably especially visible to predators because mating pairs have distinctive swimming patterns (Ambler et al. 1997). If mating is restricted to an hour at dawn, then mating pairs have less risk from predation. Swarming may allow more encounters for mates, but if this is the primary cause, then the closely related *Oithona* spp. should also benefit from this behavior and swarm. However, *Oithona* spp. may have other methods of locating and identifying mates such as female release of distance pheremones which were hypothesized for *O. davisae* (Uchima & Murano 1988). Predation appears to be the main selective force for diel cycles of *D. oculata*, but diel cycles in reproduction probably increase the survival of nauplii, whereas diel cycles of molting, mating, and swarming may insure higher fecundity and increase survival of adults.

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