

THE REVERSIBILITY OF SUBITANEOUS AND DIAPAUSE EGG PRODUCTION BY INDIVIDUAL FEMALES OF *LABIDOCERA AESTIVA* (COPEPODA: CALANOIDA)

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ABSTRACT

In Vineyard Sound, Massachusetts the calanoid copepod, *Labidocera aestiva* undergoes a period of facultative diapause that is induced by short daylength photoperiods. This study examines egg production by individual females. It is shown that some, if not all, females can switch the type(s) of egg produced. The results indicate that in Vineyard Sound females adjust to the decreasing daylengths experienced during the fall by switching production from subitaneous to diapause eggs. I suggest that a female is triggered to switch the type of eggs produced after perceiving a specific number of short daylength photoperiods. The conversion is not instantaneous, however, and during this transition phase a female produces both subitaneous and diapause eggs. It is suggested that the reproductive capacity of the population is enhanced by this type of flexible diapause response.

INTRODUCTION

The marine calanoid copepod, *Labidocera aestiva* undergoes a period of facultative diapause in Vineyard Sound, MA (Grice and Gibson, 1975; Marcus, 1979, 1980). Adults of *L. aestiva* are in the plankton from June through mid-December, during which time females produce subitaneous eggs. These eggs hatch within 2–3 days at 20.0°C. Diapause egg production commences in early September, gradually increases throughout the fall, and is accompanied by a decrease in subitaneous egg production. The diapause eggs overwinter on the sea-bottom and hatch the following spring. The production of subitaneous and diapause eggs is regulated by a temperature compensated photoperiodic response (Marcus, 1980, 1982).

Previous investigations of proportionate changes in subitaneous and diapause egg production of *L. aestiva* have been based on eggs obtained from groups of females. This study examines egg production by individuals to determine whether the type(s) of eggs produced by a female is fixed or reversible. The results indicate that *L. aestiva* females can switch the type of egg produced as a result of the photoperiodic regimen experienced by the mature animal. The impact of this flexibility on the population biology and evolution of *L. aestiva* is discussed.

MATERIALS AND METHODS

Egg production by individuals before acclimation

Labidocera aestiva adults were collected from June 1979 through December 1979 from a 1–2 m depth in Vineyard Sound by towing a 1 m, 243 μ mesh net for 10 minute periods. Adult females were removed from the tow samples by pipette

Received 18 May 1981; accepted 16 November 1981.

Contribution No. 4891 from the Woods Hole Oceanographic Institution

and placed individually into separate 100 ml dishes containing filtered seawater (glass fiber). The dinoflagellate, *Gymnodinium nelsoni*, was added as food (5×10^2 cells/ml). The dishes then were covered and placed overnight in an incubator at 19.0°C, with a 12L:12D photoperiod. The following morning, eggs produced by each female were counted and transferred to another set of dishes containing clean filtered seawater. The identification of eggs as subitaneous, diapause, or non-viable was determined by the protocol described by Marcus (1979, 1980).

Egg production by individuals after acclimation to antagonistic photoperiodic regimens for 1 to 2 weeks

The procedures for maintaining and rearing *L. aestiva* in the laboratory described by Marcus (1980) were followed in this study, using the same schedule for feeding and transfer of adults to clean filtered seawater. Each day that eggs were collected from a carboy the type(s) of eggs produced were identified using samples of 100–120 eggs of the total number collected, according to the protocol of Marcus (1980).

A preliminary experiment (Table I, #19) used 25 females and 25 males reared to reproductive maturity at 13.5°–15.5°C and 8L:16D in the laboratory. At the onset of egg production the photoperiodic regimen was altered to 12L:12D. The

TABLE I

Temporal changes in the percentage of subitaneous, diapause and non-viable eggs produced in each carboy following exposure to an antagonistic photoperiodic regimen.

Experiment	Antagonistic photoperiodic regimen	Day	Percent subitaneous	Percent diapause	Percent non-viable
19	12L:12D	2	14	66	20
		5	23	64	13
		7	27	61	12
		9	38	35	27
		12	44	51	5
		14	43	48	8
		16	43	44	13
33	8L:16D	1	90	0	10
		11	75	15	10
		13	65	32	3
34	8L:16D	1	91	0	9
		6	62	25	13
		15	43	37	20
		19	4	80	16
		21	27	42	31
36	8L:16D	1	84	0	16
		6	21	70	9
		10	14	83	3
		12	8	85	7
41	18L:6D	1	0	100	0
		11	39	55	6
		13	35	26	39
		15	92	—	—
		17	93	—	—

temperature regimen was not changed. The type(s) of eggs produced after the change was monitored every 2–3 days for 16 days.

Next, in three experiments (Table I, #s 33, 34, and 36) begun 5 August, 14 August, and 5 September 1980, adult copepods were collected from Vineyard Sound according to the procedure outlined above and the type(s) of eggs produced overnight by isolated females was ascertained. During the few days needed to determine the type(s) of eggs produced by each female, males collected at the same time as the females were maintained in 1800 ml beakers containing filtered seawater at 19.0°C, and 8L:16D, and fed *Gymnodinium nelsoni*. Females that produced mostly subitaneous eggs as part of the first overnight clutch (*i.e.*, no diapause eggs, but some non-viable eggs) then were placed with the males in a 19 l glass carboy containing filtered seawater, and dinoflagellates (*Gymnodinium nelsoni*, *Gonyaulax polyedra*, *Prorocentrum micans*, and *Peridinium trochoideum*). Ten to 20 adults of each sex were used for each experiment. The carboy was mounted on a mechanical rotator (Marcus, 1980), in an incubator set at 17.0°–19.0°C and 8L:16D. Thereafter, the type(s) of eggs produced in each carboy was monitored every few days for a minimum of 12 days.

A fourth experiment (Table I, #41) used adults collected in October 1980. The procedure was as described above except that females producing mostly diapause eggs (*i.e.*, no subitaneous, but some non-viable) were used, and conditions in the incubator were 17.0–19.0°C and 18L:6D.

RESULTS

Egg production prior to acclimation

During 19 June–13 August 1979, the type(s) of eggs produced by individuals was determined for 70 females collected from Vineyard Sound. Most eggs produced by these females hatched within 4–5 days, and hence were classified as subitaneous. Eggs that did not hatch within 4–5 days were identified as non-viable according to the criteria of Marcus (1979, 1980). No diapause eggs were obtained.

Diapause eggs were first obtained on 27 August 1979. Their production persisted until 12 December 1979, when collecting was terminated because adults could no longer be obtained in Vineyard Sound. During this period, 64 of the females collected, isolated, and studied as individuals produced no eggs after 1 night of incubation. The initial (within 4–5 days) hatch of eggs at 25.0°C varied among the 131 remaining females. For 76 no eggs hatched within 4–5 days. For 20, more than 80% hatched. For the remaining 35, less than 80% hatched. The unhatched eggs of 73 females were chilled at 5.0°C for a minimum of 30 days, and then warmed at 25.0°C to determine if they were diapause or non-viable eggs. Of these females, 25 produced heterogeneous (*i.e.*, consisting of both subitaneous and diapause eggs) overnight clutches, 45 produced homogeneous (*i.e.*, subitaneous or diapause eggs) overnight clutches, and 3 produced non-viable eggs.

Egg production after acclimation

Table I shows the results of the laboratory acclimation study. The percentages of subitaneous and diapause eggs changed in each experiment after the photoperiodic regimen was altered. In the preliminary experiment (#19) subitaneous egg production was low (14%) when the animals were first exposed to 12L:12D. Subsequently the percentage of subitaneous eggs produced increased gradually and stabilized at 43% after 2 weeks of exposure to 13.5°–15.5°C and 12L:12D.

Experiments #33, 34, 36, and 41 indicate that the type(s) of eggs produced by a female change in response to a change in photoperiodic regimen. In experiments 33, 34, and 36 females that initially produced only subitaneous eggs were maintained with males under photoperiodic conditions (8L:16D) that normally induce production of diapause eggs (Marcus, 1980, 1982). Within 1–2 weeks some or all of the females produced diapause eggs. The percentage of subitaneous eggs in each carboy declined, and the percentage of diapause eggs increased as acclimation continued. Animals collected later in the year (*e.g.*, September, experiment 36) responded to the change more quickly than those obtained earlier (*e.g.*, August, experiment 33). For example, after 10 days at 17.0°–19.0°C and 8L:16D, females in experiment 36 produced only 14% subitaneous eggs, whereas after 11 days at the same conditions, females in experiment 33 still produced 75% subitaneous eggs.

Experiment 41 indicates that females producing diapause eggs can switch and produce subitaneous eggs in response to an appropriate change in photoperiod. This change also requires 1–2 weeks.

DISCUSSION

This investigation has shown that the diapause response of *Labidocera aestiva* is reversible. Adult females collected from Vineyard Sound, MA produced clutches of subitaneous and/or diapause eggs during their first 24 h in the laboratory. These clutches indicate the type(s) of eggs such females would normally have produced in the field. The females that produced both types of eggs may be programmed to always produce heterogeneous clutches. On the other hand, mixed clutches probably represent a transition phase indicating that a female is switching from subitaneous to diapause egg production.

The laboratory acclimation experiments clearly show that some, if not all, adult females can switch the type(s) of eggs they produce. In experiments 33, 34, and 36 egg production was not monitored for all individual females. But since all females were observed to produce only subitaneous eggs initially, some or all must have changed their egg production, as evidenced by the appearance of diapause eggs. The same is true of experiment 41 for which the switch occurred in the reverse direction.

Females require 1 to 2 weeks to adjust. The best example of this is experiment 19 since the entire history of the test animals is known. When the photoperiod was changed from 8L:16D to 12L:12D the percentage of subitaneous eggs gradually increased from 14% to 43% over the period of 12 days. These equilibrium values for subitaneous egg production are comparable to the 13.2% and 49.0% obtained by Marcus (1980, 1982) for experimental populations reared continuously at 8L:16D and 12L:12D, respectively. As for some insects (Gibbs, 1975; see Beck, 1980), the induction of diapause in *L. aestiva* may be determined by a cumulative input of short daylength light-dark cycles. If females possess different response thresholds (*i.e.*, they differ with respect to the number of cycles required to effect the change) due to individual genetic variation, then this would explain the gradual change, followed by stabilization, observed in experiment 19 after the photoperiod was changed. The results of experiments 33, 34, and 36 further substantiate the cumulative light-dark cycle hypothesis. The copepods collected in September (experiment 36) must have experienced more short daylength cycles than those collected in August (experiments 33 and 34) and as predicted by the hypothesis they responded more quickly to the antagonistic photoperiodic conditions experienced in the laboratory.

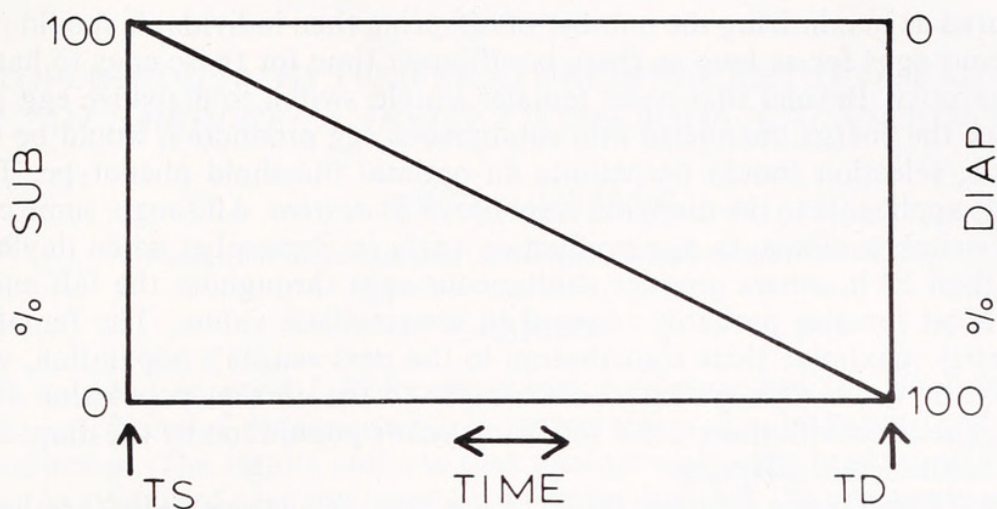


FIGURE 1. Hypothetical model of switch in egg production by individual females. At time_{TS} the female is triggered to convert from 100% subitaneous to 100% diapause egg production. The actual time for conversion will depend on biological aspects of the female. Time_{TD} indicates the switch-point for conversion in the reverse direction.

I suggest that each female in the population possesses a cumulative photoperiodic response threshold (see Fig. 1). For cumulative photophases (light period) greater than (or scotophases [dark period] less than) the threshold, only subitaneous eggs are produced. For cumulative photophases less than (or scotophases greater than) the threshold only diapause eggs are produced. The actual threshold may be considered as a window whose size is a function of the time required to completely convert from one egg type to the other, once the developmental pathway has been triggered. The duration of the transition phase may be affected by photoperiod, but it seems more likely that photoperiod initiates the switch and then the biochemical and physiological states of each female influence the time necessary to complete conversion. When heterogeneous clutches are no longer produced conversion is complete. The light cue may induce changes in several parallel and/or consecutive pathways involving, for example, neurosecretions, hormone production, and other regulatory activities as is the case for insects (Beck, 1980). It is doubtful that such a conversion response could be instantaneous. As part of a previous unpublished study I collected eggs from individual field-collected females after 24 and 48 h in the laboratory. For some of these females heterogeneous clutches were obtained on both days. These observations support the suggestion that the transition phase is not instantaneous, but rather represents an interval during which time subitaneous and diapause eggs are produced. This type of reversible diapause response and transition period is comparable to that of the red spider mite *Metatetranychus ulmi* (Lees, 1953). That females can alter the type(s) of eggs produced in either direction is interesting from a physiological point of view. However, in the natural situation in Vineyard Sound the change should be unidirectional, from subitaneous to diapause egg production as daylength decreases in the fall. During the spring, daylength increases but the animals are not mature at the time when daylengths are short enough to induce diapause egg production (see Marcus, 1980, 1982). In Vineyard Sound diapause egg production should not precede subitaneous egg production, unless adult copepods were to survive the winter.

A problem confronting individuals that can switch egg production is when to change. For insect diapause, Taylor (1980a, b) suggests that if maximum fitness

is measured as maximizing the number of offspring then individuals should produce subitaneous eggs for as long as there is sufficient time for those eggs to hatch and reach maturity. Beyond that point females should switch to diapause egg production, since the energy channeled into subitaneous egg production would be wasted. Therefore, selection should perpetuate an optimal threshold phenotype. This argument is applicable to the diapause response of *L. aestiva*. Although, some copepod females switch to diapause egg production early in September when daylength is greater than 12 h, others produce subitaneous eggs throughout the fall and never switch. Most females probably respond to intermediate values. The females that switch early maximize their contribution to the next season's population, whereas those that do not switch maximize their input to the current population and only make a genetic contribution to the following year's population by the diapause eggs of their subitaneous offspring.

Several factors may promote the heterogeneity of photoperiodic threshold phenotypes in Vineyard Sound. Although photoperiod is the primary environmental factor affecting the induction of diapause, other factors such as temperature and diet may modify its influence (Marcus, 1980, 1982). Unlike photoperiod, the timing and intensity of these parameters vary from year to year. Such fluctuations might lead to slight variations in the optimal phenotype each year. An additional source of variation would be gene flow with more southern populations. If these populations are adapted to their local environmental conditions, they might reflect different optimal threshold phenotypes due to latitudinal differences in the annual photoperiodic regimen. This type of interpopulation differentiation typifies insects that are capable of limited migration (Danilevsky, 1965). Thus if some migration was to occur between populations of *L. aestiva* this could promote heterogeneity. Elucidating the diapause response of populations from different latitudes should help clarify the population biology and evolution of this species.

ACKNOWLEDGMENTS

I thank Ann Bucklin and George Grice for their helpful comments on the manuscript. This work was supported by NSF Grants OCE78-08857 and OCE80-24440.

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<https://doi.org/10.2307/1540968>.

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