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Effect of photoperiod and temperature on induction, intensity and termination of reproductive diapause in Asellus aquaticus (L.) (Crustacea Isopoda)

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SEZIONE III

(Botanica, zoologia, fisiologia e patologia)

Ecologia. — *Effect of photoperiod and temperature on induction, intensity and termination of reproductive diapause in* Asellus aquaticus (L.) (Crustacea Isopoda) (*). Nota (**) di GIOVANNA TADINI-VITAGLIANO, FLORA VALENTINO e LUCIANA MIGLIORE, presentata dal Socio G. MONTALENTI.

RIASSUNTO. — *Asellus aquaticus* entra in diapausa riproduttiva (r.d.) prima del l'arrivo delle gelate invernali. Solo gli individui che hanno vissuto per un periodo di tempo a fotoperiodo maggiore di 12/12 sono sensibili al fotoperiodo inferiore a 12/12. Alle temperature rilevabili in autunno in natura la r.d. dura due mesi ma si protrae, come quiescenza termica fino a Marzo. Alle temperature di allevamento (alte) e in condizioni di luce continua o buio continuo la diapausa dura 5–6 mesi; può essere terminata al suo insorgere da un forte shock di temperatura a salire. Dopo molte settimane di diapausa l'importanza dell'ampiezza dello shock decresce. Si esclude che l'insorgere, la durata e la terminazione della r.d. siano controllate da un calendario endogeno e si propone una ipotesi alternativa a quella del calendario.

INTRODUCTION

The aim of this note is to confirm or exclude the presence of an endogenous calendar in *A.a.* Some of our previous experiments seemed to indicate and others to exclude an endogenous calendar in this species. We have therefore carried out experiments to: *a*) confirm that reproductive diapause (r.d.) is induced by photoperiod and is not obligatory [1]; *b*) interrupt r.d. by photoperiod and temperature variations (previous attempts gave negative results) [2]; *c*) reinduce r.d. Previous studies have shown that: geographical races systematically subjected to frosts enter r.d. [3, 4]; the intensity (duration) of r.d. is related (also in the laboratory at 18 °C) to the duration of the frosts in nature; diapause is induced also in the laboratory at 18 °C [6].

MATERIAL AND METHODS

Asellus aquaticus L. (Isopod Crustacean) from Utrecht (Holland) was chosen since it: *a*) has a very high percent of individuals responding synchronically to induction of r.d.; *b*) has a longevity of 12 months [5] which

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Abbreviations: *A.a.* = *Asellus aquaticus*; r.d. = reproductive diapause; LL = uninterrupted light; DD = uninterrupted dark; LD = light/dark ratio.

is sufficient to permit individuals to effect several births, enter r.d. (in October) and resume sexual activity in March. Therefore in March there are only individuals from 6 to 12 months old in which it is possible to try reinduction of r. d. We used samples caught in nature and shipped by air from Holland monthly from 1974 to 1979 and also individuals born in the laboratory.

Experimental temperature and light. Thermostatic chambers at 16°, 18° and 24 °C were used. The photoperiod was either natural (Rome latitude) or artificial: LL, LD 18/6, LD 16/8, LD 8/16, DD; fluorescent tubes " F 72 PGl 7 CW Power groove Cool G.E. white " were used in the artificial photoperiod chambers.

Containers, water, food. Individuals were raised in 25×25×10 cm bowls containing 1000 ml of mesosaprobic water filtered with Whatmann paper. Rotting organic material was given as food. 25 ♀♀ and 25 ♂♂ were bred per bowl.

Results and discussion

1. *Induction of r.d.*

1.1. *Organisms that lived in nature under a shorter photoperiod than LD 12/12.* Fig. 1, (2–3–4), shows the attempts to reinduce diapause in individuals with a common physiological background—*i.e.* having lived for several months in winter photoperiods. In none of these individuals is r.d. induced by short photoperiod. These results are in agreement with what has been demonstrated by Solbreck [7]: the percentage of *Neacoryphus bicrucis* individuals entering r.d. after transfer from LD 12/12 to LD 10/14 is really low (27.8 %), whereas it is very high (95.8 %) after transfer from LD 16/8 to LD 10/14.

1.2. *Organisms that lived in nature under a photoperiod longer than LD 12/12.* A short photoperiod induces r.d. in those individuals which have lived under spring or summer photoperiods (Fig. 1, (5)–(6)). This conditions seems to make the individuals sensitive (receptive) to a photoperiod shorter than LD 12/12, as happens in nature in autumn. This hypothesis has been suggested by other researchers [7, 8, 9, 10].

2. *Termination of r.d.*

2.1. *By light shock.* Individuals which entered r.d. in the laboratory, when transferred to a LL chamber or LD 16/8, mated by February/March (Fig. 2), like the organisms remaining in nature. This experiment shows that in *A.a.* long photoperiod and/or continuous light do not terminate r.d., unlike in many Arthropods in which diapause can be terminated by transferring the organisms from a short to a long photoperiod [6, 11, 12, 13].

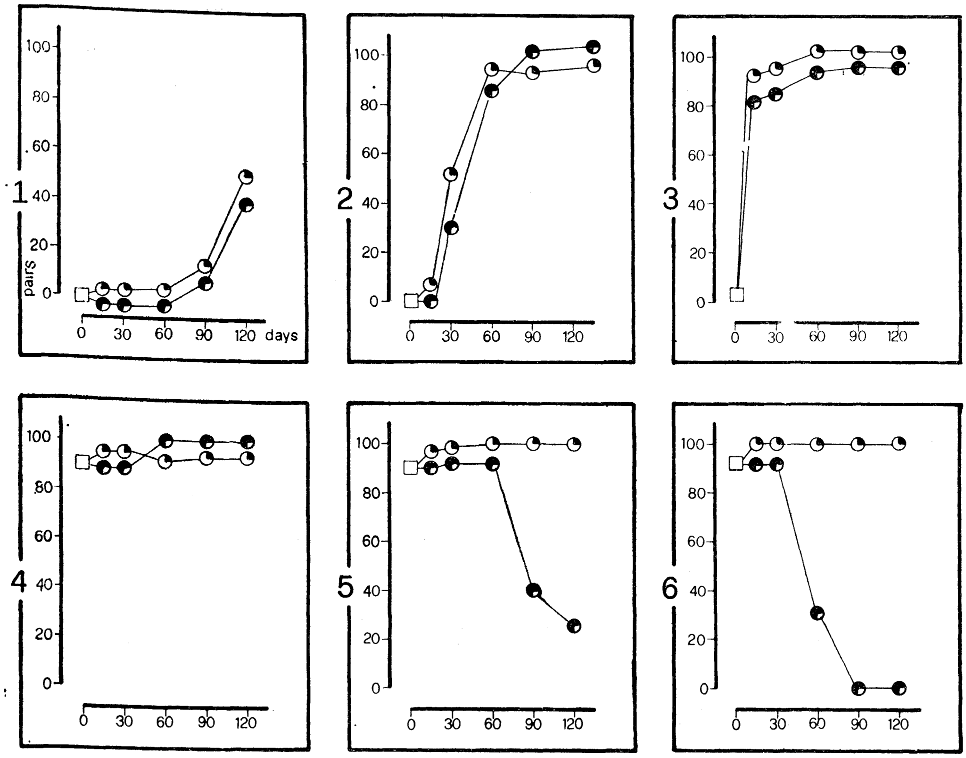

Fig. 1. – Percent pairs after light and temperature shock – from natural temperature (at time of catch) to 16 °C and from natural photoperiod to artificial one.

◔ LD 16/8 — 1500 ♀♀ 1500 ♂♂ ; ◐ LD 8/16 — 1500 ♀♀ 1500 ♂♂

□ Photoperiod and temperature at the moment of the catch:

		LD	t °C			LD	t °C
1 –	Oct.	10/14	11	4 –	Mar.	12/12	6
2 –	Nov.	9/15	7	5 –	Apr.	14/10	9
3 –	Dec.	7/17	4	5 –	May.	15/9	13
3 –	Jan.	8/16	4	5 –	Jun.	16/8	16
3 –	Feb.	10/14	4	6 –	Jul.	15/9	18
				6 –	Aug.	14/10	18

In all the experiments mortality is 15 % after 1 month of breeding and 50% after 6 months.

2.2. *By temperature shock.* Individuals caught in October did not mate until January-February in spite of a high breeding temperature (Fig. 1, (1)). As to those caught in November (Fig. 1, (2)), on the 90th day 100% mating was reached also under a short photoperiod. Almost all individuals caught in December-February (Fig. 1, (3)) mated within 5 days of transfer to thermostatic chambers under both photoperiods. All individuals caught when already in r.d. in nature (October), when subjected to very strong temperature shock (Fig. 2) terminated r.d. These experiments find confirmation in the literature [11,13].

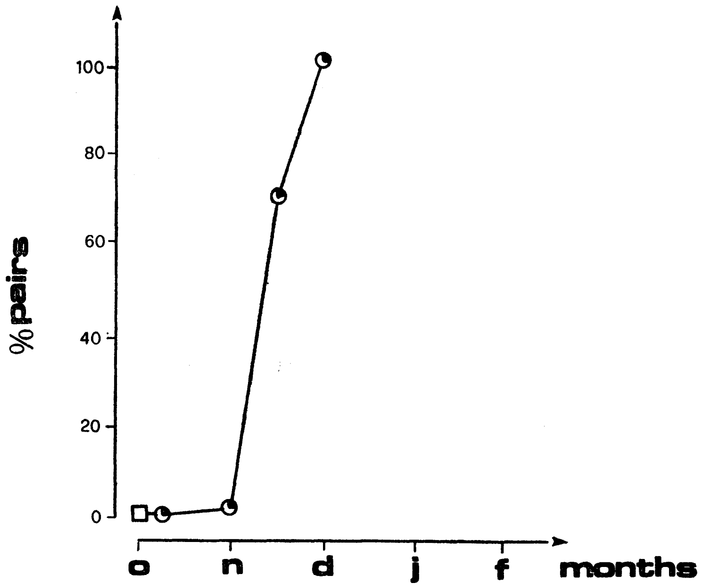

Fig. 2. – Percent pairs after temperature and light shock—from natural temperature (at time of catch) to 24 °C and from natural to artificial photoperiod.

□ natural photoperiod (LD 10/14); ◔ LD 18/16 — 120 ♀♀ 120 ♂♂

Mortality is 15% after 1 month of breeding and 50% after 6 months.

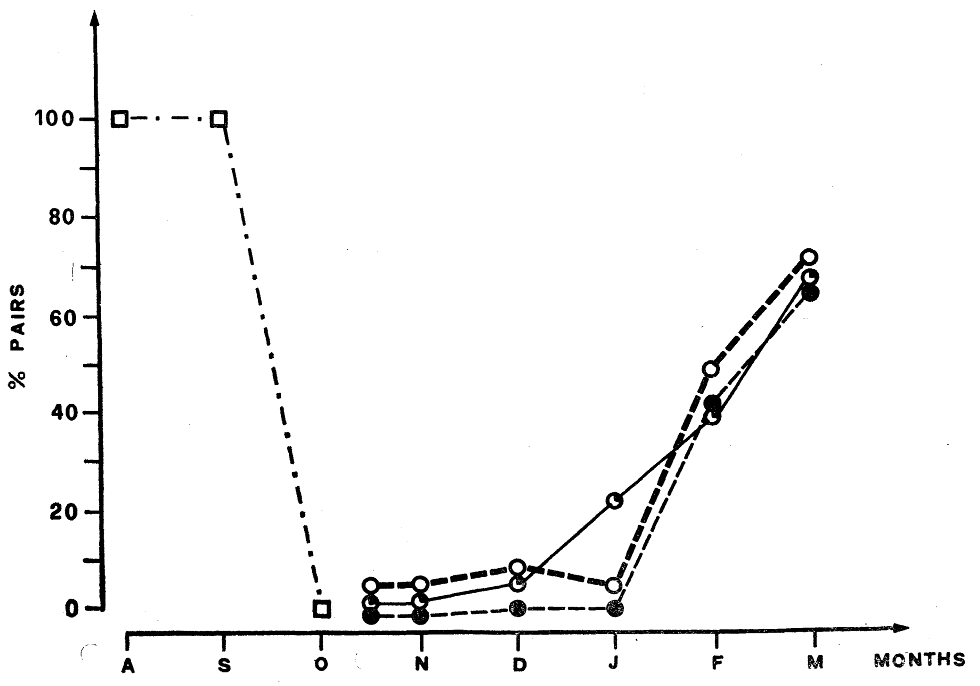

Fig. 3. – Percent pairs after light shock at 18 °C.

□ natural photoperiod; ○ LL — 157 ♀♀ 157♂♂

◔ LD 18/6 — 260 ♀♀ 620 ♂♂ ; ● DD — 648 ♀♀ 648 ♂♂.

Mortality is 15% after 1 month of breeding and 50% after 6 months.

3. *Intensity* (Duration).

The duration of r.d. in the absence of time-givers approximates that in nature (Fig. 3). Interpreted in terms of the endogenous calendar these results (maintenance, in the absence of *Zeitgebers*, of proper " timing ") should lead to the conclusion that *A.a.* possesses an endogenous mechanism capable of self-sustained oscillations [14]. But we interpret these data on the basis of the results obtained by Andrewartha [15], Wall [16] and others on the effect of temperature on diapause development in numerous Arthropods.

4. *Mechanism regulating induction, termination and intensity of r.d.* The onset, intensity and termination of embryonic diapause may be assumed to be controlled by an endogenous calendar. The endogeneity of the "calendar" is deduced from: *a*) the beginning of diapause in a precise stage of the biological cycle (*commitment point*) [10,16] and *b*) the " spontaneous " termination in the absence, of a *Zeitgeber*, after times roughly approximating those in nature [8, 11].

After comparing our results with those reported in the literature on the effect of photoperiod and temperature on embryonic and reproductive diapause [7, 13, 16], we exclude that in *A.a.* the periods of sexual activity and r.d. are controlled by an endogenous calendar (no commitment point; timing temperature-dependent). We put forth the hypothesis that the time span between parturition and subsequent fertilization is genetically programmed for a time X and the possibility of contracting or expanding this time interval, consequent to acceleration and deceleration, is also genetically programmed. Following deceleration—mainly due to variation in photoperiod—the rate of transition of the various physiological stages is slackened and the time span in prolonged—*i.e.* r.d. is induced. Following acceleration—mainly due to temperature rise—the phenomenon is inverted and the time span becomes shorter—*i.e.* r.d. is terminated. During diapause—in the absence of shock—the velocity of transition from the various physiological stages is determined by temperature [10]. The time spans required to reach the final stages are those " ordained " by natural selection at the " optimal temperature for diapause development" [15]—*i.e.* at a temperature corresponding to that in nature in autumn [10] when r.d. has its onset. The time span is much longer if temperature shifts away from the optimal values.

5. *Velocity of transition from the various physiological stages of reproduction.*

5.1. *Deceleration/acceleration in the velocity of transition.*

The hypothesis that the transfer from a long photoperiod to a short one induces deceleration and not an arrest of sexual physiology is based on two considerations:

One: embryonic diapause is a moment of slowing down of development and not a true arrest of embryonic (or larval) growth: the longer the organisms have been in this state [7, 8, 15] the sooner will diapause terminate.

We therefore suggest by analogy that also r.d. is a moment of deceleration and not the arrest of sexual activity. In fact the longer *A.a.* has been in diapause the sooner will sexual activity be resumed (cf. Fig. 1, (1)–(3)). This means that individuals are ready to resume sexual activity but remain in sexual quiescence if (as in nature) water temperature is 4 °C.

Two: an organism in embryonic (or larval) diapause resumes development sooner the stronger the shock (temperature rise), since the shock spans two temperatures compatible with embryonic development and/or diapause. The importance of the amplitude of shock has been more than once demonstrated [14] but only Veerman [11] explicitly attributes the immediate recovery of development to this factor. This is in agreement with the comparison of Fig. 1, (1) and Fig. 2.

5.2. *Constant velocity of transition in the laboratory.*

The hypothesis is that in individuals entering r.d. at 18 °C and then transferred to DD or LL (at the same temperature) there is no acceleration in the velocity of transition from the first to the last physiological stage connected with reproduction. In this case the velocity is weak and constant and depends on the last deceleration. Moreover, the high breeding temperature does not facilitate development of r.d. [15, 16].

5.3. *Velocity of transition in nature.*

Once Aselli have undergone deceleration by photoperiod they do not undergo further acceleration until spring, when the temperature gradient is positive. However diapause begins and develops at " optimal " temperatures corresponding to those for which they have been selected. Within two months r.d. is terminated but in the meantime the temperature has reached 4 °C, a temperature which maintains the organisms in thermal quiescence (as for *Chesias legatella* [16] and Chironomids [8]). The coincidence of diapause intensity in the laboratory and in nature is therefore only apparent. That is the individual is not " genetically programmed " to time a 5–6 months diapause but is genetically programmed for an " optimal development " of diapause at those temperatures as a rule present in nature.

In conclusion, the negative photoperiod gradient causes the species to enter r.d., the absolute temperature values to determine the duration of r.d. and the positive temperature gradient to resume sexual activity. So natural selection has ensured that in *A.a.* r.d. sets in at the most opportune time and reproductive activity coincides with the " optimal " period for offspring.

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