

duction of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3^-$ fixation, and oxygen exchange methods. *Limnol. Oceanogr.* **26**: 717–730.

TURNER, M. A., D. W. SCHINDLER, AND R. W. GRAHAM. 1983. Photosynthesis-irradiance relationships of epilithic algae measured in the laboratory

and in situ, p. 72–87. *In* R. G. Wetzel [ed.], *Periphyton of freshwater ecosystems*. Junk.

Submitted: 30 April 1991

Accepted: 3 December 1991

Revised: 30 December 1991

Limnol. Oceanogr., 37(4), 1992, 878–881

© 1992, by the American Society of Limnology and Oceanography, Inc.

A food-independent maturation threshold and size at maturity in *Daphnia magna*

Abstract—Age and size at maturity are among the key traits of life-history evolution in *Daphnia*. Growth data from one clone of *Daphnia magna* show that there is a threshold size above which maturation is initiated. This threshold mechanism regulates body length at maturity at the cost of age at maturity. A model explains how the threshold accounts for large variation in age and size at maturity.

Maturation in *Daphnia* is poorly understood even though age and size at maturity are the two most commonly measured life-history traits in *Daphnia* (e.g. Lynch 1980; Urabe 1988). Many investigators have proposed that a size threshold (e.g. Taylor 1985; Ketola and Vuorinen 1989; Lynch 1989), an age threshold (Sinko and Streifer 1969; Paloheimo et al. 1982), or a combination of an age and a size threshold triggers maturation (Tillmann and Lampert 1984). However, analyses of causes and consequences of such thresholds are lacking, although a threshold independent of the environment has been used to model *Daphnia* life history (e.g. McCauley et al. 1990; Hallam et al. 1990). Here I present a simple model supported by experimental data that analyzes the consequences of an environment-independent maturation threshold in *Daphnia magna*.

Acknowledgments

I thank S. C. Stearns, T. Kawecki, V. Perrot, H. Zandt, A. van Noordwijk, B. Hellriegel, and two anonymous referees for comments on earlier versions of the manuscript and for improving the language.

The work was supported by Swiss Nationalfond grant 3.643.0.87.

The process of egg production takes two instars in *Daphnia* (Zaffagnini 1987). Thus, proliferation of the first eggs starts in the preadolescent instar. A female that lays her first clutch in the fifth instar started to produce this clutch at the beginning of the third instar. McCauley et al. (1990) observed that a small commitment to reproduction is visible at the end of the preadolescent instar, i.e. when vitellogenesis starts (Zaffagnini 1987). If the initiation of egg production is closely coupled with the decision to lay these eggs two instars later, then initiation of egg production signals the actual start of maturation. If a size threshold determines this process, then growth during the subsequent two instars causes variation in size at maturity (=size of primiparous instar). This variation reflects the conditions after the threshold has passed. Under good growth conditions, size at maturity will be much greater than the threshold while with poor growth, size at maturity will exceed the threshold only slightly. A threshold size two instars before eggs are laid was used by McCauley et al. (1990) and Gurney et al. (1990) to model *Daphnia* life history.

Figure 1 shows ranges of possible body length for the primiparous, adolescent, and preadolescent instar as a function of food quantity under the assumption of a size threshold that must be passed before the preadolescent instar. A female that is a bit smaller than the threshold size passes the threshold after molting once more and enters the preadolescent instar. Maturation is then initiated and production of the first clutch is started. She molts twice more be-

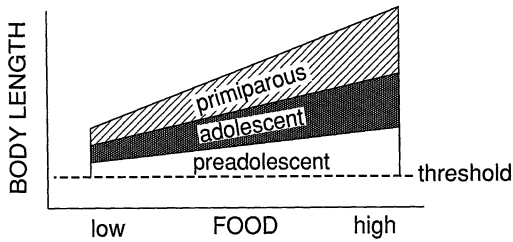


Fig. 1. Body length ranges of the primiparous (first eggs are laid) and two preceding instars in relation to the environment. The preadolescent instar is the first instar above the assumed maturation threshold. Growth per instar is a positive function of the quality of the environment. The range of the preadolescent instar body lengths occurs because some females enter the preadolescent instar considerably after passing the threshold, others only slightly after passing it.

fore this clutch is passed into the brood chamber. Her body length at maturity is determined by her length as she passed the threshold and by her growth during the next two instars. If her length in the pre-preadolescent instar was only slightly below the threshold, she considerably exceeds the threshold with the next molt. If her length was further below the threshold she only slightly passes the threshold. The better the growth, the larger the length increase during the two postthreshold instars and the larger the range of possible length at maturity. A maturation threshold independent of environmental conditions requires compensation when growth is poor. Possible compensation mechanisms could be an increase in the number of preadult instars or an elongation of instar duration. Experimental studies of *Daphnia* suggest that in poor feeding conditions, growth is compensated by an increased number of preadult instars (Porter et al. 1983; Urabe 1988).

To test the hypothesis of a size threshold between the preadolescent and the pre-preadolescent instar, I raised 78 females from one clone of *D. magna* Straus in 13 food levels with six replicates in each food condition. Daily food supply varied from 2×10^2 to $2^{13} \times 10^2$ cells $\text{ml}^{-1} \text{d}^{-1}$ of *Ankistrodesmus gracilis*, achieved by doubling the concentration from one level to the next. All females were kept alone in 100-ml beakers at 18°C and 16:8 L/D. Instars were counted until the first eggs were laid and

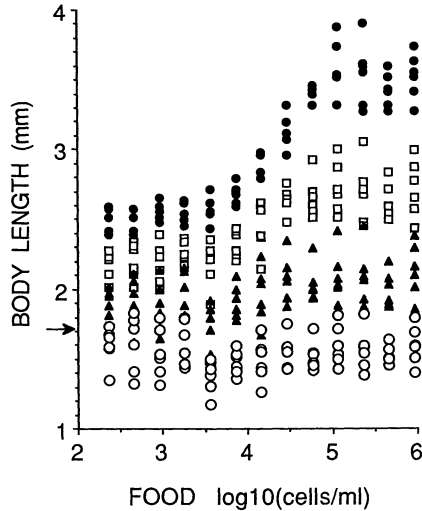


Fig. 2. Body length of the primiparous (●), adolescent (□), preadolescent (▲), and pre-preadolescent instar (○) as a function of food level. For each instar all six replicates per food level are shown. Arrow marks threshold size.

their duration and body lengths were measured. Body length was measured along the longest axis from the top of the head to the base of the tail spine. The 78 females used for the experiment were randomly taken as newborns from 24 lines, represented by one female each, of one clone, which had been kept for two generations at standard conditions (see above), except food, which was $2^9 \times 10^2$ cells $\text{ml}^{-1} \text{d}^{-1}$ for all.

Figure 2 shows the length of the primiparous and the three previous instars. As predicted by the model, mean and variation of length at maturity increase with food level. The borderline between the primiparous and the adolescent instar as well as those between the adolescent and the preadolescent instar has a positive slope, while the line separating the preadolescent from the pre-preadolescent instar seems to be independent of the food level (Fig. 2). I consider this line to be the maturation threshold because egg production starts above it. The data agree with the model (Fig. 1). Statistical analysis of thresholds can be done with a PROBIT analysis. The slope parameter from a PROBIT analysis is an estimate for the sharpness of a threshold. Table 1 shows that this parameter is the highest for the pair

Table 1. Slope and threshold estimates of a PROBIT analysis for maturation threshold size. The slope parameter is an estimate for sharpness of the threshold: the steeper the slope, the sharper the threshold. Data for all instar lengths were divided into size classes of 0.05 mm and log-transformed. Estimates were back-transformed. PROBIT analysis was done for the three instar pairs before the primiparous: pre-pre-pre-adolescent/pre-pre-adolescent—pppA/ppA; pre-pre-adolescent/pre-adolescent—ppA/pA; pre-adolescent/adolescent—pA/A.

Instar pair	Slope	Threshold	95% C.I.
pppA/ppA	12.01	1.33	1.29–1.37
ppA/pA	15.25	1.71	1.67–1.74
pA/A	11.94	2.14	2.09–2.19

pre-adolescent/pre-pre-adolescent instar, proposing that the threshold is there rather than earlier or later. The threshold size was 1.71 mm for this clone.

Figure 3a shows the body lengths of all females in their second instar, separated according to instar number at maturity. Clearly, within each food level, the females that will mature in their sixth or seventh instar are smaller than those maturing in their fifth. When one plots the body lengths of the pre-pre-adolescent instar, the picture changes (Fig. 3b). The females that will be primiparous in their fifth instar (closed circles) plot at the same location as in Fig. 3a, because their second instar is the pre-pre-adolescent instar, while those that will be primiparous in their sixth or seventh instar have molted once or twice more. These additional instars, which were more common in poorer food conditions (Fig. 3), compensated for slower growth and for smaller body length in earlier instars. This confirms that, within environments, individuals that are smaller at birth take more instars to mature than those that are larger at birth (Green 1956; Ebert 1991) and that the number of instars at maturity increases when growth is slow (Porter et al. 1983; Urabe 1988). The addition of juvenile instars reduces the variance in length at maturity within food environments.

Age at maturity shows a different picture (Fig. 4). Length at maturity is regulated by flexibility in the number of juvenile instars, but each additional instar costs time, which is important because of the risk of mortality

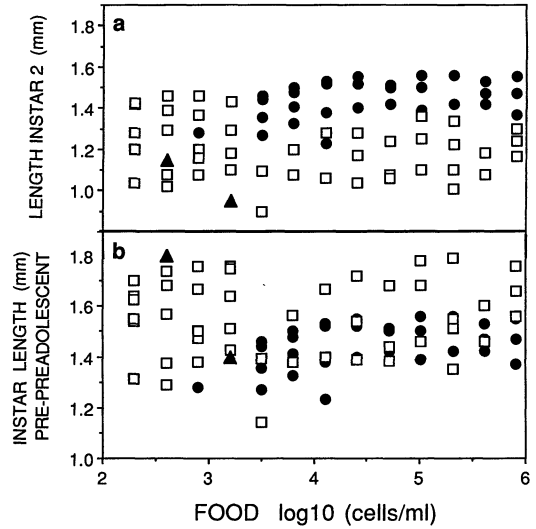


Fig. 3. Body length of (a) the second instar and (b) the pre-pre-adolescent instar, separated according to instar number at maturity. Symbols show the number of instars a particular female had when the first eggs were laid into the brood chamber: ●—five instars; □—six instars; ▲—seven instars. Note that the second instar of those females which matured in the fifth instar in panel a is equal to the pre-pre-adolescent instar in panel b; this is not the case for the other females.

before reproduction and because delayed reproduction decreases the population growth rate. Females with more instars are older at maturity (Fig. 4). Thus, length at maturity is regulated at the expense of age at maturity.

Within food levels, i.e. equal environmental quality, the costs of delayed maturity due to additional instars is to some ex-

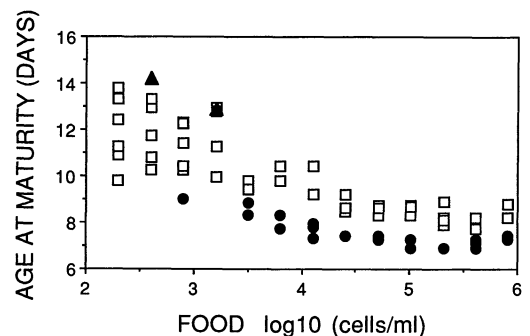


Fig. 4. Age at maturity as a function of food level. Symbols given in legend to Fig. 3.

tent compensated by changes in other fitness components, e.g. additional instars allow reproduction at larger size with higher fecundity. Ebert (1991) showed that daphnids having one instar more at maturity had ~30% more eggs in the first clutch. Furthermore, being the right size at maturity may reduce adult mortality due to size selective predation.

A threshold size which triggers initiation of maturation also has important consequences for the evolutionary ecology of *Daphnia*. An evolutionary change in size at maturity could be achieved by selection on the size of the threshold. If genetic variation exists for threshold size, as shown by Ebert (1991) between populations of *D. magna*, selection could act on it and lift or lower the size range of primiparae.

The results of this study pertain to one clone of *D. magna*. It is not yet clear if the results hold for other clones or species. However, recent studies on *Daphnia pulex* (Lynch 1989) suggest that a maturation threshold independent from feeding conditions can also be found in other species.

Dieter Ebert¹

Institut für Zoologie
Universität Basel
Rheinsprung 9
CH-4051 Basel, Switzerland

References

- EBERT, D. 1991. The effect of size at birth, maturation threshold and genetic differences on the life-history of *Daphnia magna*. *Oecologia* **86**: 243–250.
- GREEN, J. 1956. Growth, size and reproduction in *Daphnia* (Crustacea: Cladocera). *Proc. Zool. Soc. Lond.* **126**: 173–204.
- GURNEY, W. S. C., E. MCCAULEY, W. W. MURDOCH, AND R. M. NISBET. 1990. Physiological ecology of *Daphnia*. 2. Formulation and tests of a dynamic model of growth and reproduction. *Ecology* **71**: 716–732.
- HALLAM, T. G., R. R. LASSITER, J. LI, AND L. A. SUAREZ. 1990. Modelling individuals employing an integrated energy response: Application to *Daphnia*. *Ecology* **71**: 938–954.
- KETOLA, M., AND I. VUORINEN. 1989. Modification of life-history parameters of *Daphnia pulex* Leydig and *D. magna* by the presence of *Chaoborus* sp. *Hydrobiologia* **179**: 149–155.
- LYNCH, M. 1980. The evolution of cladoceran life histories. *Q. Rev. Biol.* **55**: 23–42.
- . 1989. The life history consequences of resource depression in *Daphnia pulex*. *Ecology* **70**: 246–256.
- MCCAULEY, E., W. W. MURDOCH, R. M. NISBET, AND W. S. C. GURNEY. 1990. The physiological ecology of *Daphnia*. 1. The importance of stage stage-specific pattern of growth. *Ecology* **71**: 703–715.
- PALOHEIMO, J. E., S. J. CRABTREE, AND W. D. TAYLOR. 1982. Growth model of *Daphnia*. *Can. J. Fish. Aquat. Sci.* **39**: 598–606.
- PORTER, K. G., J. D. ORCUTT, AND J. GERRITSEN. 1983. Functional response and fitness in a generalist filter feeder, *Daphnia magna* (Cladocera: Crustacea). *Ecology* **64**: 735–742.
- SINKO, J. W., AND W. STREIFER. 1969. Applying models incorporating age-size structure of a population to *Daphnia*. *Ecology* **50**: 608–615.
- TAYLOR, B. E. 1985. Effects of food limitation on growth and reproduction of *Daphnia*. *Ergeb. Limnol.* **21**: 285–296.
- TILLMANN, U., AND W. LAMPERT. 1984. Competitive ability of differently sized *Daphnia* species: An experimental test. *Freshwater Ecol.* **2**: 311–323.
- URABE, J. 1988. Effect of food conditions on the net production of *Daphnia galeata*: Separate assessment of growth and reproduction. *Bull. Plankton Soc. Jpn.* **35**: 159–174.
- ZAFFAGNINI, F. 1987. Reproduction in *Daphnia*. *Mem. Ist. Ital. Idrobiol.* **45**: 245–284.

Submitted: 16 January 1991

Accepted: 7 October 1991

Revised: 18 December 1991

¹ Present address: Oxford University, Department of Zoology, South Parks Road, Oxford, OX1 3PS U.K.