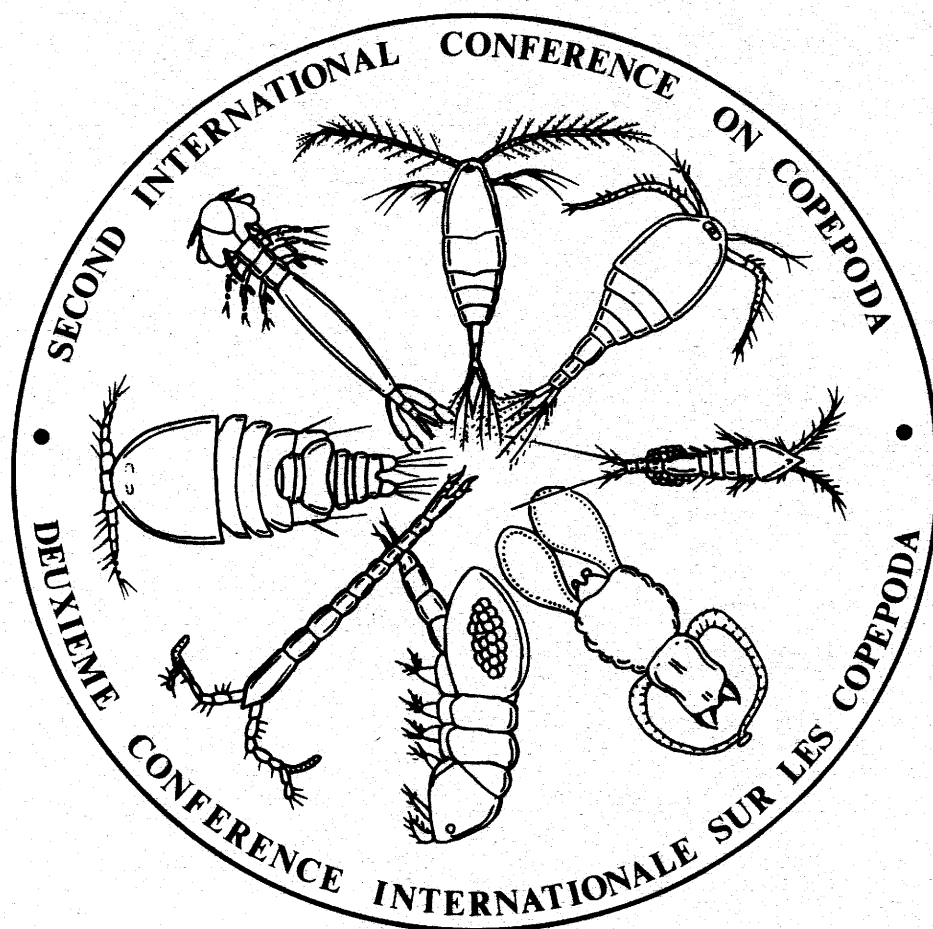


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# TEMPERATURE-DEPENDENT CHANGES IN COPEPOD ADULT SIZE: AN EVOLUTIONARY THEORY

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**Abstract:** Adult size generally decreases with increasing temperature for copepods. It is shown that if growth rates increase with temperature then the hypothesis of adaptation implies that mortality rates must increase as fast or faster than growth rates increase with temperature. Evidence is presented for such an increase.

## INTRODUCTION

Within populations of copepods, adult size typically increases as the seasonal environmental temperature decreases (Deevey, 1960; McLaren, 1963). An apparent exception is reported for an harpacticoid copepod by Evans and Diaz (1978), but that report lacks cohort data and possibly the larger early summer adults could have matured at winter temperatures. The hypothesis that this is an adaptive response to a changing environment is examined here using inverse optimization techniques (Myers and Doyle, 1983; Myers and Runge, 1983) to make quantitative predictions of the environmental conditions under which an increase in size at maturation is adaptive. An alternative hypothesis is that such changes in adult size are not evolutionary adaptations, but are the result of physiological, biochemical or thermodynamic constraints. It has been suggested (Ray, 1960) that such a constraint may be the limitation imposed by requiring enzymes to function over a wide temperature range, even through examples of temperature dependent expression of enzymes are well known. The hypothesis of constraint is examined by Runge and Myers in this volume.

It is possible that the dichotomy between "constraint" and adaptation is more apparent than real. That is, there may exist additive genetic variation in the population that in time would allow maturation at the same size over a range of temperatures. However, the detrimental pleiotropic effects from such a change (e.g. a reduction in growth rate) may prevent such genetic variation from responding to natural selection.

Since growth rates and egg production rates generally increase with size for copepods (e.g. Corkett and McLaren, 1978) it is not true that natural selection acts such that adult body size is "optimized" at the size that energy available for growth and reproduction per unit time is maximized. Thus, changes in mortality must be included in any calculation of fitness and a dynamic optimization approach is needed, and is used here, to determine fitness (Myers and Doyle, 1983).

The fundamental empirical observation used here is that individual growth generally increases with temperature (within the temperature range in which the animal occurs) in the field or under laboratory conditions if adequate food supply is available (reviewed in Hartnoll, 1982). If growth rate increases, and

yet adult size remains the same (or decreases), then it is shown in the appendix that mortality rate must increase at a greater rate than the increase in growth rate. (The result in the appendix is for a special case, e.g. constant mortality; more general results will be discussed elsewhere).

The principal conclusion from the appendix is thus that mortality rates must change in concert with growth rates for populations of copepods if size at maturation remained the same at all temperatures. Specifically, if two populations are alike except for mortality rates and growth rates, then the ratio of the growth rates, (the greater over the lesser) is less than the ratio of the mortality rates. Although the reasoning for this is not readily evident in the mathematics of the appendix, the proposition is basically true because an increase in energy available for growth and reproduction results in roughly a multiplicative increase in the ability to produce eggs, whereas an increase in mortality results roughly in an exponential decrease. If size at maturation decreases with increasing temperature, as is observed, then mortality must increase even faster with increasing temperature if the change in size at maturation is adaptive.

The definition of fitness used in the appendix is an approximation because nonstable age-structures, and genotypic and phenotypic variability in the life-history traits both exist and are not explained by the maximization process assumed. There is no a priori reason to believe that either effect will lead to a systematic bias in our results. Tests of the predictions of our theory are partially tests of the adequacy of the model in the appendix to explain the evolution of size in copepods.

An important complication relevant to our analysis is that age at senescence decreases with increased temperature. In the appendix, age at senescence was assumed constant. This complication was taken into account in the analysis of the copepod Acartia clausi discussed in Myers and Runge (1983). The predicted and observed slope of mortality vs. temperature (.0151; s.e. = .00197 and .0144; s.e. = .00644 respectively) are approximately equal to the observed slope of the growth rate temperature relationship (.0143; s.e. = .00122). Thus, at least for A. clausi, this complication changes the theoretical prediction of the model slightly. Growth rate and mortality rate are still coupled with temperature, but the differences between the slopes of growth rate and mortality rate with temperature are less.

We have not discussed changes in size-specific mortality. Although such changes certainly exist, this is essentially a specialized version of the proposed coupling between temperature and mortality that is difficult to evaluate with the data presently available.

The hypothesis of adaptation can be rejected if the observed seasonal mortalities contradict the predicted "adaptational" mortalities. Although mortality generally increases with temperature, whether it increases sufficiently to make observed sizes at maturation adaptive is an empirical question that can only be answered with meticulous field measurements of life-history characteristics and natural mortality rates. Landry's (1978) research on the population dynamics of A. clausi may be the most comprehensive in this regard; the adaptational hypothesis was sufficient to account for this data (Myers and Runge, 1983).

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## APPENDIX

### Proposition

Consider an animal whose growth in dry weight ( $w(t)$ ) and reproductive schedules  $m(t)$  by age  $t$  are given by

$$\frac{dw}{dt} = (1-\mu(t))\alpha w(t) \quad (A1)$$

$$m(t) = C_e \mu(t)\alpha w(t) \quad (A2)$$

where  $u(t)$  is the proportion of energy available for growth and reproduction,  $\alpha w(t)$ , that goes into reproduction. Restrict the control variable  $\mu(t)$  such that  $0 \leq \mu(t) \leq 1$ . The growth rate,  $\alpha$ , and egg energy content,  $C_e$ , are assumed constant. If the population growth rate is zero, the appropriate measure of fitness is

$$\int_0^T \exp(-\mu t) m(t) dt, \quad (A3)$$

(Charlesworth, 1980), where  $\exp(-\mu t)$  is the probability of surviving to age  $t$  and  $T$  is the age of senescence, i.e. the age at which survival and egg production drastically decreases. **For an animal that matures at the same size at two different growth, fitness can be maximized in both cases only if mortality increases at a greater rate than growth ( $\alpha$ ).**

### Proof

The control problem specified by A1-A3 can be solved via Pontryagin's Maximum Principle (Pontryagin et al., 1962). For a given  $\alpha$  and  $\mu$  the functional A3 is maximized if  $\mu(t)$  changes from 0 to 1 at time given by

$$\tau = T - (1/\mu) \ln\left(\frac{\alpha}{\alpha - \mu}\right), \quad (A4)$$

i.e.  $\tau$  is the optimal age at maturation and  $w(\tau)$  is the adult weight. Since a directly analogous problem was solved by Macevicz and Oster (1976) the details of the above derivation will not be given here. Consider a second growth rate  $\alpha'$  such that  $\alpha' = \alpha \delta$ , where  $\delta$  is greater than one. For  $\alpha'$  the new optimal age at maturation,  $\tau'$  can be determined using A4 for any new mortality rate  $\mu'$ . For an animal to mature at the same size at two different growth rates  $\alpha \tau$  must equal  $\alpha' \tau'$ . Using this requirement and A4 we can write an implicit equation for  $\mu'$

$$(1-\delta)T = (1/\mu)\ln\left(\frac{\infty}{\infty-\mu}\right) - (\delta/u')\ln\left(\frac{\infty}{\infty-\mu/\delta}\right). \quad (\text{A5})$$

I wish to show that

$$\mu' > u\delta', \text{ if } \delta' > 1. \quad (\text{A6})$$

Note that if  $\delta'$  is greater than one then the left hand side of A5 is negative. Note also that if  $\mu'$  is less than or equal to  $\mu\delta'$ , then the right hand side of A5 is positive. Thus, condition A6 must be true and the proposition is proved.