

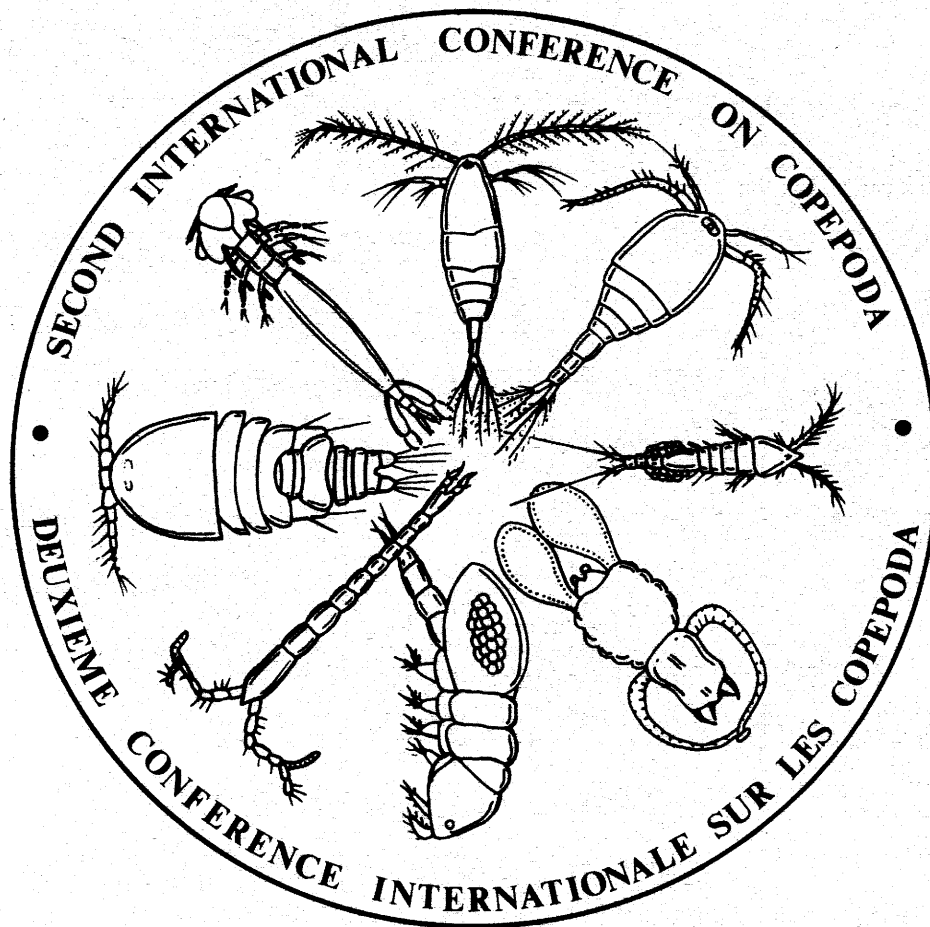
CONSTRAINTS ON THE EVOLUTION OF COPEPOD BODY SIZE

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CONSTRAINTS ON THE EVOLUTION OF COPEPOD BODY SIZE

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Abstract: Using a model based on the theory of adaptation, Myers and Runge (1983; this volume) hypothesize that a seasonal increase in mortality rates causes the well known inverse relationship between temperature and body size observed for multivoltine planktonic copepods. The model in its present form would be invalid, however, if genetic variability to change the development time-temperature relationship does not exist; in other words, if, for individual growth rates observed in the field, body size is physiologically or thermodynamically constrained to be smaller at higher temperatures. Seasonal variation in food supply may also influence body size, but does not fundamentally alter predictions of the theory of adaptation unless individual growth rates in natural populations decrease with seasonal increases in temperature. Testing of the theory of adaptation and its alternatives would clarify our understanding of the coupling between temperature, growth, and mortality in planktonic copepods and perhaps in ectotherms generally.

INTRODUCTION

Except in boreal regions, planktonic copepods usually pass through two or more generations annually. It is a general observation that body length of adult copepods is inversely related to the temperature during development, so that, in temperate climates with a seasonal temperature variation, each generation of the annual cycle is successively smaller (e.g. Deevey, 1960; McLaren, 1963).

What are the underlying reasons for seasonal variations in body size? According to the theory of adaptation discussed by Myers and Runge (1983; this volume), the final body size of copepods growing at a higher rate at warmer temperatures should be larger than that of counterparts developing at cooler temperatures, all other factors being the same. That the opposite relationship is generally observed in nature implies that mortality rates must be increasing with temperature at a rate equal to or faster than growth rate, for the observed body size to be adaptive (Myers and Runge, 1983; this volume).

In this paper, we examine two other explanations of seasonal variation in copepod body size. First, the physiological constraint hypothesis states that genetic variability for changes in final body size as a function of temperature may be nonexistent, due to physiological or thermodynamic limitations on growth and development. Second, the food limitation hypothesis states that seasonal changes in food availability generally limit copepod growth rates, resulting in smaller body sizes at higher temperatures. These explanations are discussed in the context of the evolutionary model, as they do not necessarily exclude an adaptive interpretation.

Copepods attain a terminal body size (certainly in length; we will assume in weight also, although there is evidence that this is not strictly the case) upon reaching sexual maturity. Thus, final size is the consequence of the developmental rate, which controls how fast the copepod molts through its

developmental stages, and the growth rate, which controls how much weight or body length is incremented at each molt.

PHYSIOLOGICAL CONSTRAINTS

If growth rates and development rates have different functional relationships with temperature, adult body size will be smaller or larger at warmer developmental temperatures, depending on which of the two processes increases more as temperature increases. In planktonic copepods, growth rates generally have smaller temperature coefficients than development rates, hence body size are smaller. This has been discussed by McLaren (1963) and by Miller et al. (1977; see their fig. 8) who put the situation succinctly: "If an animal is forced through its fixed quota of molts quickly by high temperature, it simply has no chance to grow large".

This physiological relationship may be adaptive (as discussed by Myers and Runge in this volume) or it may be due to a physiological constraint. This distinction is usually not made explicit in analyses of body size, even though very difficult biological conclusions are implied by the two alternatives. By "constraint" we mean a fundamental physiological, biochemical, or thermodynamic barrier that limits the possible shapes of the development rate-temperature relationship. In quantitative genetic terms this implies that there is no additive variation for a shift in this relationship to allow body size to be larger at higher temperatures. Without genetic variation, it would be impossible to select a population with body sizes larger at higher temperatures in conditions of excess food.

The nature of the development time-temperature relationship is of particular importance in the evolutionary model. In predicting mortality rates needed to make the observed life-history characteristics adaptive, the age at sexual maturity is allowed to vary freely to determine the body size that gives the maximum fitness under a given mortality regime. If for any temperature copepod development time is constrained to be a certain value, then the model we presented for Acartia clausi (Myers and Runge, 1983) would be invalid.

Experimental evidence suggests that development of copepods may be the consequence of a series of biochemical reactions which are entirely rate-regulated by temperature in the presence of excess food. Landry (1975a) found that development rates of Acartia clausi fed excess food are predictable from egg development times of the species. This result corroborated a conclusion made earlier by Corkett and McLaren (1970), based on their studies of species of Pseudocalanus, Eurytemora, Temora, and Acartia. Furthermore, Landry (1975b) showed that the relationship of relative egg development times to temperature is the same for 9 species of marine, planktonic copepods. These data suggest that a similar process is controlling the shape of the development time-temperature function.

The question of interest here is the extent to which the temperature relationship of development is genetically variable. Sharpe and Mitchele (1977) presented a model of poikilotherm development determined by activation and inactivation of control enzyme systems, coupled with thermodynamic characteristics of the enzyme reaction rates. Their analysis allows for considerable variation in both shape and translation of the rate-temperature curve, depending on the extent of inactivation of enzyme systems, for which there is potentially additive genetic variation. Clarke (1983) presents the evidence for considerable temperature compensation in the development characteristics of different copepod species, although seasonal variation within a population is not specifically discussed. Perhaps the strongest evidence against a physiological constraint operating generally in ectotherms is that multivoltine insects

generally mature of a larger size at higher temperatures (reviewed in Myers, 1983), an observation that is consistent with the hypothesis of adaptation but not with the hypothesis of constraint.

The critical experiment to determine the extent of genetic variability has not been carried out. Conditions required for a proper test of a physiological constraint have been discussed by Myers (1983). There is in addition the possibility that, while additive variation for a shift in the development time-temperature relationship exists, the shift is coupled with detrimental pleiotropic effects and so is not expressed (Myers, 1983). This alternative could also be disproved by the appropriate experiment in quantitative genetic selection.

It is important to note that constraints on maximum and minimum size of a species may be in effect regardless of constraints on the development time-temperature relationship postulated here. For example, Corkett and McLaren (1978) found that, in populations in Pseudocalanus from the Canadian Arctic, Long Island Sound, and Loch Striven, minimum and maximum adult body sizes were similar even though they occurred at very different developmental temperatures. As copepods appear to have fixed cell numbers (McLaren and Marcogliese, 1983), the range of possible body sizes may be related to constraints on nuclear size and DNA content (Cavalier-Smith, 1978).

FOOD LIMITATION

In laboratory experiments, Vidal (1980) and Klein Breteler and Gonzalez (1982) have shown that food shortage can limit final size of copepods, in terms of both weight and length. There is growing evidence that food availability may limit growth and reproduction in natural copepod populations (eg. Landry, 1978; Checkley, 1980; Durbin et al., 1983; Runge, in press). As phytoplankton food and temperature are often negatively correlated in temperate, oceanic environments, food limitation may be as important as temperature in determining seasonal variation in final body size (Deevey, 1960; Frost, 1974; Vidal, 1980; Klein Breteler and Gonzalez, 1982).

While food availability can influence final body size of copepods, we question whether food limitation by itself is ever a sufficient explanation of the inverse body size - temperature relationship. In laboratory experiments under, constant food conditions, body size of copepods was still either negatively related to temperature (Coker, 1938; Corkett and McLaren, 1978; Landry, 1978; Vidal, 1980) or, at best, remained unchanged (Mullin and Brooks, 1970a,b). In most cases, therefore, food limitation apparently would only determine the extent to which body size is lower at higher temperatures. We suggest that food effects be divided into 3 categories, as follows:

(1) Food limitation occurs especially at higher temperatures but individual growth rates in natural populations still generally increase as ambient temperature rises. In this situation, mortality rate is still predicted to increase with temperature, given the inverse body size relationship. For example, while growth of Acartia clausi in Jakles Lagoon appears to have been food limited in the late summer (Landry, 1978), growth rates nevertheless still increased with temperature (Fig. 14: Landry, 1978); hence predicted and observed mortality rates were also higher. Here, food limitation is not an explanation and the probable cause is the constraint hypothesis or the adaptational theory suggested by Myers and Runge (this volume).

(2) Food limitation at higher temperatures is so severe that individual growth rates generally decrease with seasonal increases in temperature. In this case, the prime requirement needed for the application of the theory in Myers and Runge (this volume) is violated and sexual maturity would occur

at smaller sizes at higher temperatures with a temperature-independent mortality regime. It is unlikely that this is a general situation, but it may occur during stratified summertime conditions for larger copepods, like species of Calanus, adapted to exploit phytoplankton blooms (Vidal, 1980).

(3) Food is generally limiting during colder ambient temperatures and body size is greater at higher temperatures, in exception to the general rule. We are not aware of many published examples of this situation. Evans (1981) found no evidence for a simple size-temperature relationship for Temora longicornis and concluded that variability in food supply was the overriding factor determining body size of the species in the North Sea.

CONCLUDING REMARKS

The existence of either physiological constraint or food effects discussed here has important consequences for understanding the ecology or physiology of copepods. If a physiological constraint is involved, then there is something fundamental about the biology of copepods, and perhaps ectotherms in general, that we do not understand. On the other hand, support for the hypothesis of adaptation of Myers and Runge (1983; this volume) implies a general coupling between temperature, growth and mortality and advances the use of life-history theory to estimate mortality rates of natural populations.

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