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THE NATURE AND ECOLOGICAL SIGNIFICANCE OF METABOLIC CHANGES DURING THE LIFE HISTORY OF COPEPODS[1]

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Abstract. Studies of the relationship between metabolic rate and body weight through development in three species of copepods (two cyclopoids, one calanoid) showed that: (1) for each of the three species, the slope of the regression line relating metabolism to size is not uniform across all twelve developmental stages (six naupliar stages, six copepodid stages), (2) nauplii have a logarithmic metabolism-weight relationship with a slope of ≈ 1.0, indicating little change in QO_2 (oxygen consumed per unit weight) with increasing body size, (3) copepodids have a logarithmic metabolism-weight relationship with a slope $\ll 1.0$, indicating a decline in QO_2 with increasing size, and (4) there is an abrupt increase in QO_2 between the last naupliar stage and the first copepodid stage. These metabolic features of copepods contribute to an explanation of the retention of two very different body forms (nauplius, copepodid) through development in copepods. The smallest nauplii have a relatively low metabolic rate, considering their small size, which suggests that the naupliar form is energy efficient at small body sizes. The nauplii are locked into a steep ($\sim$1:1) increase in metabolism with size, however, which would make the energetic requirements of a mature animal unfeasible. This enforces a transition to a new body form (copepodid) partway through development. The new form has a higher energy consumption than the nauplii just at the point of transition, but shows a declining QO_2 with increasing body size. This allows for a substantial increase in size without a prohibitive increase in energy expenditure. Radical changes in locomotion, behavior, and nutritional requirements probably explain the change in metabolic characteristics with changes in body form.

Key words: copepods; life history strategy; metabolic rate; metabolism; nauplius; respiration; zooplankton.

INTRODUCTION

An inverse relationship between metabolic rate (QO_2: metabolism per unit body weight) and body size has been recognized since the latter part of the nineteenth century (Rubner 1883). Numerous investigators have documented this relationship both within and between species (Weymouth et al. 1944, Brody 1945, Zeuthen 1947, 1953, 1971, Hemmingsen 1950, 1960, Scholander et al. 1953, Winberg 1956, Kleiber 1961, Klekowski and Duncan 1975). Our recent study of the twelve developmental stages of the copepod *Mesocyclops brasilianus* showed that the QO_2 of the last six developmental stages (copepodid [C] 1 through adult) decreased with increasing body size in agreement with the general trend in invertebrates (Epp and Lewis 1979). In contrast, however, the first six developmental stages (nauplius [N] 1 through 6) showed a constant QO_2 despite a large relative change in weight during development through these six stages (more than sevenfold). We postulated that in copepods generally, the change in body form mid-way through development might be accompanied by major metabolic changes, but a generalization of this scope would obviously require support from studies of several species. In the present paper we extend the metabolic

studies to two more species including two different suborders (Calanoida, Cyclopoida). We use the results in support of the hypothesis that an evolutionary-ecological explanation of the radical and previously unexplained shift in body form between the naupliar and copepodid stages in copepods is provided by the metabolism-size relationships for these two body forms.

The relevance of metabolism to life history patterns has been generally neglected. We believe that insight into the interplay between the metabolism-size relationship and life history patterns can be obtained by a detailed examination of metabolism through development in several species that live under similar conditions. The following study of three copepod species (*Notodiaptomus venezolanus, Mesocyclops brasilianus,* and *Thermocyclops hyalinus*) meets these requirements. All three of the species were taken from a tropical environment, although *T. hyalinus* is not restricted to the tropics. The source of the populations is not of primary concern to us here, but work with tropical populations is advantageous in this case because of the reduced complications arising from metabolism-temperature interactions over the environmental thermal range.

MATERIALS AND METHODS

All three of the copepod species were obtained from the plankton of Lake Valencia, Venezuela. Lake Val-

TABLE 1. Slope (*b*) and *Y* intercept (log *a*) for the regression lines relating log weight (nonograms dry weight) to log metabolism (nonolitres per individual per hour) for *Mesocyclops brasilianus, Notodiaptomus venezolanus,* and *Thermocyclops hyalinus.* The linear relationships are in all cases significant at *P* < .001.

Species		Intercept (log *a*)	Slope (*b*)	SE of slope	Sample size (*n*)
Stage	Temperature				
Mesocyclops brasilianus					
Nauplii	24°C	−1.83	0.89	0.14	12
	26°C	−2.09	1.06	0.21	9
	28°C	−1.86	1.01	0.14	9
All temperatures (pooled)		−2.11	1.08	0.10	30
Copepodids and adults					
	22°C	−0.87	0.56	0.10	15
	24°C	−0.77	0.58	0.05	19
	26°C	−0.66	0.59	0.06	23
	28°C	−0.61	0.53	0.06	31
All temperatures (pooled)		−0.69	0.56	0.04	88
Notodiaptomus venezolanus 24°C					
Nauplii		−2.27	1.09	0.10	9
Copepodids and adults		−1.13	0.75	0.09	14
Thermocyclops hyalinus 28°C					
Nauplii		−1.56	0.87	0.15	12
Copepodids and adults		0.11	0.26	0.10	39

encia is a large, perennially warm, eutrophic lake of moderate depth (maximum 38 m). The lake is described by Lewis and Weibezahn (1976).

Cultures were established at the University of Colorado, Boulder, for use in these experiments. The copepods were cultured in artificial lake water of the same chemical composition as that of the lake (Lewis and Weibezahn 1976). *Mesocyclops* was cultured at several temperatures (22°, 24°, 26°, and 28°C) as part of a parallel investigation of the temperature-metabolism relationship in tropical copepods (Epp and Lewis 1979). *Notodiaptomus* was cultured at a single temperature (24°C) as was *Thermocyclops* (28°C). Respiration measurements were made only after a 4-wk (minimum) temperature acclimation.

All copepods were fed a mixed algal diet. *Chlorella* sp. predominated in the *Mesocyclops* culture, *Chlorella pyrenoidosa* in the *Notodiaptomus* culture, and *Haematococcus pluvialis* in the *Thermocyclops* culture.

A Cartesian diver microrespirometer was used to measure the oxygen consumption of individual nauplii and copepodids (including adults). Details of the Cartesian diver technique have been presented elsewhere (Epp and Lewis 1979).

Following an equilibration period of 45 min, diver readings were taken at hourly intervals for 2–4 h. An average respiration rate was then determined by subtracting the initial reading from the final reading rather than by averaging the intermediate values. Following each experiment, the length of the test animal was determined with a filar type of ocular micrometer at 125×. Length was converted to weight by means of

length-weight equations for the different species and body forms. The equations were derived empirically from geometric models. The ratio of dry weight to wet weight was assumed to be 0.11 (Sitaramaiah 1967). These equations were very similar to the length-weight relationships presented by Bottrell et al. (1976).

RESULTS

When the logarithm of basal metabolism in animals is plotted against the logarithm of body weight, the relationship is essentially linear for either inter- or intraspecific comparisons (Klekowski and Duncan 1975). The relationship can be expressed by the logarithmic equation log $Y = b$ log $X +$ log a (Brody 1945). In this paper, Y will be oxygen consumption in nanolitres per individual per hour and X will be the dry weight in nanograms. The value b is the slope of the regression line, and thus represents the change in metabolism resulting from a unit change in body weight. The fitting is done separately for each species and each developmental category (nauplii and copepodid-adults, Table 1).

Respiration data on *Mesocyclops* have been reported and discussed in detail elsewhere (Epp and Lewis 1979), and thus will be presented here only in abbreviated form as necessary to support the interspecific comparisons. Analysis of covariance on the *Mesocyclops* data showed that the metabolism-size relationships differ in slope across temperatures for mixed developmental categories, but are indistinguishable across temperatures within either of the two developmental categories. A pooled slope covering the entire temperature range thus can be computed for *Me-*

TABLE 2. Statistical comparisons of metabolism in the two major developmental categories of two copepod species. For each species, the null hypotheses are: (a) equal variances for metabolism exist across developmental categories, and (b) equal slopes of log metabolism on log body weight exist across developmental categories. NS = not significant at $P = .05$.

Species	F	df	P
Thermocyclops hyalinus			
Variances (nauplii vs. copepodid-adults)	2.13	37,10	NS
Slopes (nauplii vs. copepodid-adults)	6.65	1,47	<.015
Notodiaptomus venezolanus			
Variances (nauplii vs. copepodid-adults)	4.66	7,12	NS
Slopes (nauplii vs. copepodid-adults)	5.05	1,19	<.03

socyclops nauplii and another pooled slope can be computed for the copepodid-adults (Table 1). These pooled slopes then can be used for comparison of the metabolism-size relationship in *Mesocyclops* with those of the other two species.

Measurements of oxygen consumption on *Thermocyclops hyalinus* and *Notodiaptomus venezolanus* were obtained by similar procedures to those used for *Mesocyclops* except that only one temperature was used (Table 1). For *Thermocyclops*, the data on nauplii were compared with the data on copepodid-adults to determine if the variances were homogeneous (F test, Snedecor and Cochran 1976). Variances were not significantly different between the two developmental categories (Table 2). The test was also applied to *Notodiaptomus* with the same result. The similarity of variances justified a standard analysis of covariance to test for differences in slope between the developmental stages (Snedecor and Cochran 1976).

The covariance test showed that for each of the two species the slopes differed significantly across developmental categories (nauplii vs. copepodid-adults, Table 2).

Fig. 1 shows the line of best fit for each of the three species and both developmental categories. The pooled slopes and intercepts were used for *Mesocyclops*. Data for the other two copepod species were converted to a temperature of 26°C by means of Winberg's standard correction coefficients (Klekowski and Duncan 1975). This will adjust the intercepts to a common temperature but will not affect the slopes, as the slopes are assumed constant across the environmental temperature range on the basis of the *Mesocyclops* study.

There is a significant jump in metabolism between the last naupliar stage and the first copepodid stage in all three species as indicated by the upward shift in the regression lines across this transition (Fig. 1). In the naupliar stages of both *Notodiaptomus* and *Mesocyclops*, body weight and metabolism increase at about the same rate ($b \approx 1.0$). In *Thermocyclops*, naupliar metabolism does not change quite as fast as body weight ($b = 0.87$), but the relationship is not far from unity. In the copepodid-adult stages of all three species, metabolism increases more slowly than body

weight ($b < 1.0$). The degree of divergence varies considerably between species, however (Table 1).

DISCUSSION

With a few minor exceptions, the life history of copepod species is divided into thirteen stages, including the egg, six nauplar stages, and six copepodid stages (the last of which is the adult). During development from egg to adult, the biomass of the individual changes approximately fiftyfold. The reproductive strategy of the copepods thus is based on production of eggs that are small by comparison with the adult. Allan (1976) has shown how the extended growth period, modest intrinsic rate of increase, and sexuality of the Copepoda combine to suggest a K strategy contrasting with the greater opportunism of the smaller and mostly parthenogenetic Rotifera and Cladocera.

Extended development with an attendant radical change in size in the Copepoda is likely to necessitate major shifts in overall ecological strategy during the life cycle. This explains why the less desirable of the two very different body forms has not been eliminated by natural selection during the evolution of the Copepoda. The faithful retention of two very different
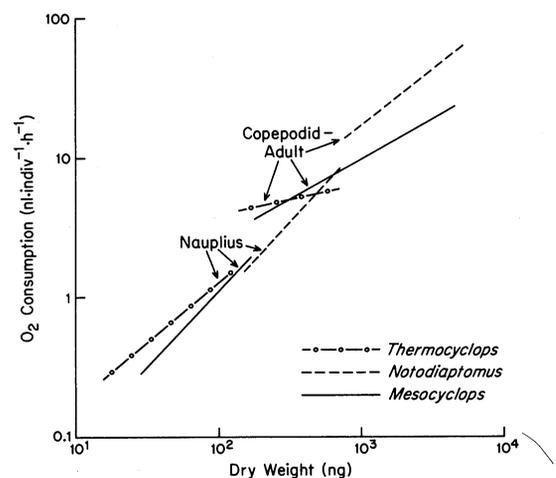

FIG. 1. Oxygen consumption as a function of body weight in *Thermocyclops hyalinus*, *Notodiaptomus venezolanus*, and *Mesocyclops brasilianus*.
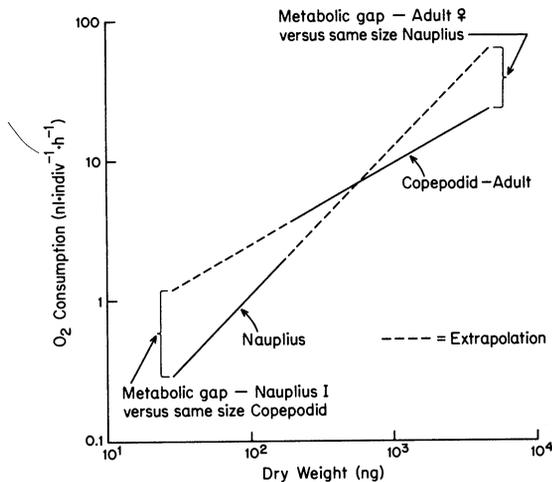
FIG. 2. Metabolism-size regression lines for *Mesocyclops brasilianus*. Broken portions of the lines represent extrapolation of the data to show the metabolic rates of hypothetical copepodids of N1 size and hypothetical nauplii of adult size. Extrapolation for the other two species would be similar.

body forms (nauplius, copepodid) indicates a balance between the selective pressures that favor the naupliar form for the smaller sizes and the copepodid form for the larger size. We believe that our metabolic data illustrate a portion of the mechanism by which this balance is maintained.

The metabolic data suggest three generalizations that apply to copepod metabolism: (1) the metabolism of the nauplii increases at about the same rate as does body weight, (2) the metabolic rate shifts significantly upward between the last nauplius and the first copepodid stage, and (3) the metabolism of the copepodids increases more slowly than does body weight. Stages with a common body form, such as the six naupliar stages, probably share a common metabolism-size relationship simply because a common morphology reflects common feeding, locomotor, and general behavioral mechanisms. A given morphology fixes the metabolism-size relationship within rather narrow limits given the implications of a change in size for attrition rate on one hand and for resource gathering efficiency on the other. Attrition, mainly from predation, tends to force metabolic rate up to speed growth and reduce time to maturity, while resource limitation tends to hold metabolism down to match resource supply.

Metabolic explanation of the change in body form

The metabolic advantage of the naupliar form at small sizes is illustrated in Fig. 2. The extrapolation indicates that an animal the size of a first-stage nauplius (N1), but with the metabolic characteristics of a copepodid would have a metabolic rate well above that of the nauplius and of other metazoans of similar size. This suggests that the copepodid body form is ecolog-

ically unfeasible at low body sizes because of its high relative energy requirements in the lowest weight range. This in turn may be traced to the metabolic demands of movement, feeding, and other activity in an animal with copepodid morphology.

Nauplii and copepodids are demonstrably different in behavior and vulnerability to predation. Cyclopoid nauplii remain nearly motionless in the water most of the time and move by means of short hops. Their mean swimming speed thus is much lower than that of the copepodids, which spend a greater proportion of the time in the hop phase (Gerritsen 1979). Field studies have shown that the nauplii are not so vulnerable as copepodids to ambush predators (*Chaoborus*: Lewis 1977, 1979). Laboratory studies indicate that this is explained by the nearly motionless behavior of the nauplii and their escape leaps (Gerritsen and Strickler 1977, Gerritsen 1979). Although much remains to be learned of the specific differences in naupliar and copepodid survival and feeding strategies, it is already clear that the two morphologies may face very different ecological challenges, even in the same environment.

We have shown by extrapolation of Fig. 2 why the copepodid form would not be metabolically feasible at naupliar sizes. It remains to be shown why the naupliar form does not persist throughout development. It would seem that the naupliar form, which operates at a lower energy level than the copepodid form at small sizes and even at the point of transition from N6 to C1, would be retained through the largest sizes. The advantage of the copepodid form is evident from further examination of Fig. 2. The slope for the naupliar form is high because the naupliar form does not become less demanding on energy per unit weight as size increases. This means that at some critical size, the absolute metabolic demands on the individual will become prohibitively high. Fig. 2 shows by extrapolation of the naupliar metabolism line that an adult with naupliar metabolic characteristics would have a metabolic rate of 15.6 μl $O_2 \cdot mg^{-1} \cdot h^{-1}$ (93 nl $\cdot$ indiv$^{-1} \cdot h^{-1}$), which is 3.5 times higher than that of the copepodid form (4.5 $\mu lO_2 \cdot mg^{-1} \cdot h^{-1}$; 27 nl $\cdot$ indiv$^{-1} \cdot h^{-1}$). The slope for the copepodid form is well below 1.0, so that the larger individuals do not function at such a high metabolic rate as the smaller ones.

The actual mechanism responsible for the reduction in metabolic rate with increasing body size and the necessity for this reduction are uncertain; however a metabolic rate reduction with increasing size is an almost universal phenomenon in metazoans (Kleiber 1961), and therefore is probably required over any considerable size range by some very general physiological and ecological laws. The reduction in copepodid metabolism with size is paralleled by other trends, including a reduction in the relative filtration and feeding rates with increasing size (Mullin and Brooks 1970a, b, Paffenhofer 1971).

Comparison between species

The transition in body form occurs at a much higher weight in the calanoid species than in the cyclopoids (Fig. 1). This confirms that a change in slope from nauplius to copepodid is in fact a by-product of the change in body form and its behavioral and ecological correlates, and not of size alone. Exactly why the naupliar form can exist at a larger size in the calanoid than in the cyclopoid copepods is difficult to discern. The nauplii of the calanoids are quite distinct morphologically from those of the cyclopoids. Behavioral differences related to variations in morphology probably exist, but have not been well studied. The feasibility of the steep increase in the naupliar metabolism in any particular species of copepod is of course determined by a complex of ecological factors, and in the case of *Notodiaptomus* these factors allow the steep increase in metabolism typical of the nauplii to extend to higher weights than in the cyclopoids.

The slopes of both the naupliar and copepodid-adult regression lines are lower for *Thermocyclops* than for the other two species. The maximum sizes of the nauplii and the adults are also lower for *Thermocyclops* than for the other two species. In Lake Valencia, where these three species coexist, *Thermocyclops* is dominant. *Thermocyclops hyalinus* also has a much broader distribution than the other two species. The success of *Thermocyclops* in Lake Valencia and in a broad range of other environments may be related to the unusually low slope for the metabolism-size relationship.

Relevance to general metabolic trends in the metazoa

Up to this point, our discussion has dealt with the adaptive significance of metabolic changes during the life history of the Copepoda. The metabolic data also can be evaluated in the context of metabolism-size changes for invertebrates generally. Recognition of the log-log relationship between metabolism and size has led to the familiar mouse-elephant (Benedict 1938), silkworm-beech tree (Hemmingsen 1950), and bacterium-mammal (Zeuthen 1953) metabolism-size curves in which the value of b has been given as 0.70–0.75 (Zeuthen 1971). Slightly higher values (0.80–0.86) are typical for the Crustacea (Weymouth et al. 1944, Hemmingsen 1950, Scholander et al. 1953, Winberg 1956).

More detailed examination of the metabolism-size relationship at the interspecific level suggests that there may be several distinct kinds of relationships when the entire range of organisms is viewed as a whole (Zeuthen 1953). The first relationship applies to unicellular organisms in which the slope is ≈ 0.75. Small multicellular organisms show a shift in the regression line to a slope approaching 1.0. Organisms weighing >40 mg (wet weight) have a relationship similar to that of the unicellular organisms, i.e. the slope

returns to 0.75 (Zeuthen 1953). Possible physiological causes for the interspecific trends are unknown, although various speculations have been offered (Hemmingsen 1960, Kleiber 1961). Zeuthen (1953) also contends that the same interspecific relationships occur during development in the Metazoa. All five species that were studied by Zeuthen had a developmental period during which metabolic increases were directly proportional to increases in body weight ($b \approx 1.0$). This was followed by a period of decrease in metabolic rate with increasing body size ($b < 1.0$). Zeuthen interprets this deterministically in terms of developmental recapitulation. It is more likely that these rate changes during development have some definite adaptive significance, but Zeuthen's study is nevertheless quite important, as it demonstrates that the metabolism-size relationship is frequently not static throughout development.

Our data for both *Notodiaptomus* and *Mesocyclops* show the same metabolism-size trends with development as the animals studied by Zeuthen (1953). The b-values for the nauplii (1.09 and 1.08) are near unity (and would thus represent very small metazoans according to Zeuthen's recapitulation theory). The b-values of the copepodid-adult groups (0.75 and 0.56) would then represent the relationship that is typical of larger metazoans. While the slopes for the nauplii and the copepodids of *Thermocyclops* are less than the corresponding slopes for the same stages the other two species, the same trend from nauplius to copepodid is evident. Correspondence of our copepod data with the results from Zeuthen's study suggest that the metabolism-size relationship in the Copepoda may in fact be very generally applicable. Partial exemption from the reduction in metabolism with increasing body size may be generally necessary within species which rely on an extended postembryonic growth period so that the duration of mortality risk prior to first reproduction can be minimized. In the Copepoda, this relief comes by way of the naupliar body form, for which metabolic increases are nearly proportional to increases in body weight. Elucidation of the factors that make the reduction of metabolism with increasing size necessary in the copepodids and the factors that allow the nauplii to escape this metabolic reduction might well provide some general insight into the sizes, morphologies, and life history strategies of the invertebrates.

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