

## Metabolic Responses to Temperature Change in a Tropical Freshwater Copepod (*Mesocyclops brasiliensis*) and Their Adaptive Significance

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**Summary.** Metabolic rates of *Mesocyclops brasiliensis* from Lake Valencia, Venezuela, were determined at several temperatures spanning the environmental range (22–28° C). The  $QO_2$ 's (oxygen consumption per unit weight) of all *Mesocyclops* stages from Lake Valencia are higher than most but not all  $QO_2$ 's from temperate copepod species that have been studied. The  $QO_2$  is essentially static through naupliar development and shows a sudden jump between N6 and CI, which probably results from the major change in morphology and behavior at this point in the life history.  $QO_2$  declines steadily between CI and adult stages. Acclimated copepodite and adult *Mesocyclops* show a decreasing metabolic rate with increasing temperature (i.e.  $Q_{10} < 1.0$ ) over the temperature range 26–28° C. This is the range of temperatures normally encountered during the daily vertical migration when the lake is thermally stratified (April–November). Since vertical migration would result in a compromise between a fully acclimated and an acute response, a nearly constant metabolic rate or a slight decline in metabolic rate in the warmer water would be expected in field populations. The results thus show that the metabolic rate of *Mesocyclops* is not reduced when it moves into deeper (cooler) water, as would be predicted by certain energy-based hypotheses that have been used to explain vertical migration. In contrast to the low  $Q_{10}$ 's between 26 and 28° C, copepodites and adults have very high  $Q_{10}$  values in the range 22–26° C. This indicates an adaptive decrease in metabolic rate which is thermally programmed to coincide with the cooler temperatures that are encountered during the mixing season (December–March), when a drastic change in ecological conditions occurs in the lake.

Nauplii show evidence of the same seasonal response but without the superimposed plateau at high temperatures, which they would not need because they are weak migrators. Nauplii show a plateau at the lowest temperatures, however, which suggests that a fixed metabolic reduction occurs at the onset of mixing and metabolism is not altered thereafter with declining temperature.

The change in  $QO_2$  with temperature generally supports the hypothesis

that all *Mesocyclops* stages are adapted to hold a high, constant metabolic rate through the diel cycle but experience a seasonal reduction in metabolic rate in response to major ecological changes in the lake at the time of seasonal mixing.

## Introduction

Vertical migration on a daily cycle is widespread in freshwater and marine zooplankton and has been the subject of numerous hypotheses (Hutchinson, 1967; Bainbridge, 1961). Separate hypotheses have focused on single factors as principal causes, but several investigators have suggested that vertical migration is advantageous in more than one respect (e.g. Hutchinson, 1967; Mauchline and Fisher, 1969). The more obvious (but not simple) external influences (light, food, predation, competition) attracted attention first. More recently, internal factors (metabolism) as well have been brought into consideration. In an influential paper, McLaren (1963) included in a model to explain migration the concept that migration might maximize growth efficiency, since migration to lower temperatures during non-feeding periods reduces metabolic rates. Further possibilities and limitations of this concept have been thoroughly examined since that time (McLaren, 1974; Nival et al., 1974; Enright, 1977). Hutchinson (1967) suggests that migration originated as a response to photic sensitivity and has since acquired additional adaptive functions. Consequently, planktonic animals may migrate for reasons other than the supposed "energy-boost" and accrue an incidental but significant increase in the efficiency of energy utilization by the energy-boost phenomenon. This idea is also inherent in McLaren's (1963) original paper.

Swift (1976) concludes that his own work and that of Lock and McLaren (1970) disprove the adaptive value of the "energy-boost" hypothesis. He argues that the energy-boost concept as usually applied neglects the effect of food supply on growth, and that if this factor is taken into account, energetic considerations alone would lead to one of two strategies: (1) no migration, with the animals remaining in the more productive surface waters, or (2) a physiologically-mediated migration with downward movement triggered by a full gut. While Swift's model does account for the interaction between food supply, temperature and growth, it neglects such factors as predation pressure and photodamage, which may also play a role in migration (Hairston, 1976; Zaret and Suffern, 1976; Enright and Honegger, 1977). A fully satisfactory resolution is still lacking, and more empirical information is needed on metabolism in particular to complement the extensive work on external factors.

Certain evidence not derived from energy studies indicates that an energy benefit from migration may be negligible for reasons other than those stressed by Swift. Numerous studies on copepods (Marshall et al., 1935; Gauld and Raymont, 1953; Conover, 1959; Siefken and Armitage, 1968; Moshiri et al., 1969), *Chaoborus* (Swift, 1976) and poikilotherms in general (Bullock, 1955; Vernberg, 1963) indicate the presence of respiratory plateaus that flatten out the metabolic response to temperature change. The metabolic reduction due

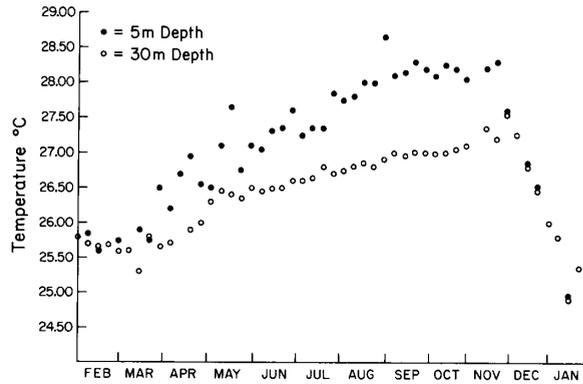


Fig. 1. Thermal characteristics of Lake Valencia, Venezuela, for February 1977 through January 1978

to decreasing temperature cannot exist if these plateaus occur over the temperature range encountered by an organism during migration. The general relationship of such plateaus to temperature ranges in the water column is presently not clear, however.

A corollary of the "energy-boost" hypothesis can be tested even though it is difficult to test the hypothesis directly because of the influence of other factors. If a reduced metabolic rate in deep water offers a significant selective advantage, migrating populations in habitats which offer only a small temperature range should be characterized by a high metabolic sensitivity ( $Q_{10}$ ) in order to benefit from the same relative metabolic advantage as a population with a lower  $Q_{10}$  migrating over a steep thermal gradient. The present study tests this corollary. The experimental animal is the tropical copepod, *Mesocyclops brasiliianus*

Oxygen consumption of *M. brasiliianus* was measured over a narrow temperature range to determine whether the temperature sensitivity of this animal is high within its natural range of temperatures as suggested by the corollary of the "energy-boost" hypothesis or, in contrast to the "energy-boost" hypothesis, if there is a respiratory plateau similar to that observed in many other poikilotherms.

*M. brasiliianus* was first found in Brazil (Kiefer, 1933) and has subsequently been found only in the tropics of South America (Coker, 1944; Cipolli et al., 1973). Cultures used in this study were established with animals from Lake Valencia, Venezuela. In Lake Valencia, the temperature ranges between 25 and 28.5° C (Fig. 1) except at the very surface which can reach higher temperatures during calm weather but is avoided by copepods as is typical of zooplankton generally (Hutchinson, 1967).

Lake Valencia is warm monomictic, i.e., it becomes homothermal each year for an extended period during which complete mixing occurs but is thermally stratified the rest of the year. The mixing season extends from November to March and is clearly visible in Fig. 1 as a convergence of temperatures at 5 and 30 m over that period of the year. The strongest thermal discontinuity is located typically at a depth of about 20–25 m, but secondary discontinuities may occur above this if calm weather allows heat to accumulate unevenly

**Table 1.** Weighted mean depth for the naupliar and copepodite-adult stages of cyclopoid copepods in Lake Valencia at 0800 h showing the tendency of nauplii to stay nearer the surface. Each number is based on 4 different vertical profiles taken a week apart. The months shown fall within the period of stratification

	May	June	July	August	September	October
Depth, Copepodite-Adults (m)	15.1	15.0	16.8	15.5	15.8	17.9
Depth, Nauplii (m)	12.5	12.5	—	13.2	13.3	11.7

in the upper water column. Temporary stratification in the upper water column is a common feature of Lake Valencia and results in a complex pattern of week to week changes in the thermal profiles. The character and causes of these changes are thoroughly described by Lewis (1973) for Lake Lanao, which behaves similarly to Lake Valencia in this respect. The maximum thermal range over the zone inhabited by copepods is about 2.0° C as shown in Fig. 1, and the gradient across any 1 m segment of the water column seldom exceeds 0.5° C.

Weekly data on the distribution of cyclopoid copepods in Lake Valencia show that during the seasonal mixing period, the populations approach a uniform distribution, probably because of passive movement with the powerful currents that develop at this time of year even in the deep water. In addition, the oxygenated conditions throughout the entire water column during the mixing period make the deep water habitable. During the stratification season, the numbers of copepods very near the bottom are low, especially as anoxia develops. During the daytime, the center of mass for the nauplii lies above that of the larger and faster swimming copepodite-adult stages (Table 1). The data in Table 1 show the position of these two groups about 1.5 to 2.5 h after sunrise. The copepodite-adult group continues to descend as the sun rises, so the divergence of the two groups increases towards midday (A. Infante, in preparation). At night all stages move up, but the upward movement of the nauplii is less because they are nearer the surface during the day (Table 1). This is a classical nocturnal migration pattern (Hutchinson, 1967). Similar migrations in other tropical lakes with thermal gradients of only a few degrees Celcius have also been reported (e.g. Ruttner, 1943; Rzoska, 1968; Begg, 1976; Zaret and Suffern, 1976; Lewis, 1977). The major points of interest here are that the nauplii are exposed to a higher mean temperature because they lie above the more advanced stages, and that the nauplii experience a smaller daily thermal range because the vertical distance they travel is not so great as for the older stages.

## Materials and Methods

*M. brasiliensis* from Lake Valencia was cultured in artificial lake water of the same chemical composition as that of Lake Valencia (Lewis and Weibezahn, 1976). The copepods were housed in 1.5-liter aquaria which were in turn placed in controlled-temperature water baths. Respiration measurements were made following acclimation to controlled temperatures of 22, 24, 26 and 28° C for adults and copepodites and 24, 26, and 28° C for nauplii. *Chlorella sp.* was used as the primary food source, although no great effort was used to exclude other algae. The algae were cultured in modified Chu medium (Rhode, 1948) under continuous illumination.

One week prior to the respiration measurements, groups of experimental animals were transferred to 100-ml test tubes and placed in a controlled-temperature water bath maintained at the same temperature as the corresponding copepod culture ( $\pm 0.01^\circ\text{C}$ ). A portion of the *Chlorella* culture was added to the tubes at the time of the copepod transfer. This was an adequate food supply, since all of the animals had full digestive tracts just prior to the respiration measurements.

Experimental trials at each of the four temperatures lasted approximately four weeks and were

repeated once during the 12-month study period. The total number of animals used in the study was 118. Respiration measurements were made between 1,200 and 1,400 h, which corresponded to the mid-point of the experimental light cycle (12L:12L). This fixed timing reduced the influence of rhythms, which can be expected to affect the respiration rates of zooplankton (Duval and Geen, 1975).

A Cartesian diver micro-respirometer was used to measure the oxygen consumption of individual nauplii, copepodites and adult copepods. The Cartesian diver technique has been thoroughly described in the literature (Holter, 1943, 1961; Zeuthen, 1943, 1964; Frydenberg and Zeuthen, 1960; Glick, 1949; Klekowski, 1971a, b, 1975). Only the open-neck variety of diver was used. A small amount of mineral oil was used to seal the respiration chamber from the flotation medium (Holter, 1943). Straight-necked divers with gas volumes of 1–3  $\mu\text{l}$  were used for the six naupliar stages, and the copepodites and adults were placed in standard divers (Glick, 1949; Fig. 116A). Divers with gas volumes of 5–8  $\mu\text{l}$  were used for the smaller copepodites (usually instars 1 through 4) and the larger copepodites and adults were placed in divers with gas volumes of 10–14  $\mu\text{l}$ . In all cases the animals could move, although movement was somewhat restricted by the size of the diver. Such measurements were considered to represent "routine metabolism" according to Prosser (1973).

Copepodites and adult animals in the 100-ml subcultures were sorted until the desired number of animals was obtained (generally 5 animals per day). Nauplii were obtained by placing individual female copepods with egg sacs into the 100-ml tubes. All animals were washed just prior to the experiments with culture medium that had been filtered through a membrane filter (pore size, 0.8  $\mu\text{m}$ ). The divers were filled with this same filtered medium.

Following an equilibration period of 45 min, diver readings were taken at hourly intervals for 2 to 4 h. Any substantial drop in  $\text{O}_2$  consumption (greater than 30%) terminated the experiment and the last reading was discarded. An average respiration rate was then determined by subtracting the initial reading from the final reading rather than averaging the intermediate values. The results were expressed as  $\mu\text{l O}_2 \times 10^{-4} \text{ animal}^{-1} \text{ h}^{-1}$  at standard temperature and pressure.

Following each experiment, the length of each animal was determined with a filar type ocular micrometer at  $125\times$ . The animals were suspended in only a small amount of water during these measurements so that they rested on their sides. Such determinations were more reproducible than those made in larger volumes of water because of the curvature of the animals viewed from the dorsal surface. Individuals were stored in Lugol's solution for later identification of sex and stage. Volumes of the animals were determined from models and these were subsequently converted to dry weight using a conversion value of 11% dry: wet weight (Sitaramaiah, 1967). The resulting length: dry weight equations are:

Nauplii	$\log X = 2.145 \log L - 2.946$
Copepodites and Males	$\log X = 2.833 \log L - 5.054$
Females	$\log X = 3.412 \log L - 6.574$

where X is dry weight in ng and L is the length in  $\mu\text{m}$ . These equations compare closely with the generalized copepod equation of Bottrell et al. (1977).

Throughout the presentation and evaluation of results, we will assume that data taken under carefully controlled laboratory conditions as specified above are in fact indicative of metabolic responses under natural conditions. Unquestionably the animals are much more confined in the diver than in the field, but this restriction is inevitable. What is important here is that every attempt was made to make the conditions constant for the four different temperature groups. Thus any differences in respiration rate between groups can be considered to be caused by temperature itself.

## Results

The relationship between metabolism and body weight can be expressed by the equation  $Y = aX^b$ , which in logarithmic form is  $\log Y = b \log X + \log a$

**Table 2.** Slopes (b) and Y intercepts (log a) for the regression line relating log weight (ng, dry) to log metabolism ( $\mu\text{l O}_2 \times 10^{-4} \text{ individual}^{-1} \text{ h}^{-1}$ ) at different temperatures. The linear relationships are in all cases significant at  $P < 0.001$

Stage/temperature		Intercept (log a)	Slope (b)	Std. error slope	Number N
Nauplii	24°	-0.83	0.89	0.14	12
	26°	-1.09	1.06	0.21	9
	28°	-0.86	1.01	0.14	9
Copepodites and adults	22°	0.13	0.56	0.10	15
	24°	0.23	0.58	0.05	19
	26°	0.34	0.59	0.06	23
	28°	0.39	0.53	0.06	31

**Table 3.** Oxygen consumption of *Mesocyclops brasiliensis* at different acclimation temperatures. Values for specific stages have been calculated on the basis of mean lengths of the stages in lake samples

Stage	Mean length $\mu\text{m}$	Oxygen consumption ( $\mu\text{l} \times 10^{-4} \text{ animal}^{-1} \text{ h}^{-1}$ )			
		22°	24°	26°	28°
N 1	110		2.8	2.7	3.9
N 2	132		3.9	4.1	5.8
N 3	157		5.5	6.1	8.4
N 4	188		7.8	9.1	12.4
N 5	222		10.7	13.3	17.8
N 6	255		13.9	18.3	24.0
C I	379	24.6	34.4	46.6	38.3
C II	446	31.8	44.9	61.2	48.9
C III	522	40.9	58.1	79.6	61.9
C IV	615	53.0	76.1	104.6	79.2
C V ♂	527	54.6	78.5	108.1	81.6
C V ♀	800	99.0	145.3	202.8	143.1
ad ♂	637	56.0	80.6	111.0	83.5
ad ♀	1,006	153.4	228.6	320.5	216.5

(Brody, 1945). Zeuthen (1947, 1971), Hemmingsen (1950, 1960), Winberg (1950), Kleiber (1961), Klekowski and Duncan (1975) and others have employed different symbols to express the same relationship. In this paper, Y represents oxygen consumption in  $\mu\text{l} \times 10^{-4} \text{ individual}^{-1} \text{ h}^{-1}$  and X is the dry weight in nanograms (ng,  $\text{g} \times 10^{-9}$ ). The results were fitted to the equation by the method of least squares. Fitting was done separately for the different stages and the results are summarized in Table 2.

In Table 3, the mean lengths of the various stages, as determined from field samples, are converted to oxygen consumption using the appropriate length: weight and weight: metabolism equations. The range of values is quite high (2.7 to  $321 \times 10^{-4} \mu\text{l animal}^{-1} \text{ h}^{-1}$ , from nauplius to adult), as would be expected due to the large weight change during development. A similar range (approximately 6 to  $400 \mu\text{l} \times 10^{-4} \text{ animal}^{-1} \text{ h}^{-1}$  from nauplius to adult) has been recorded for the copepod *Macrocyclops albidus* at 21° C by Klekowski

**Table 4.** Respiratory rates ( $QO_2$ ) for *Mesocyclops brasiliensis* compiled from Table 3 by use of average dry weights for each developmental stage

Stage	$QO_2$ ( $\mu\text{l mg}^{-1}\text{h}^{-1}$ )			
	22°	24°	26°	28°
N 1		10.3	9.9	14.3
N 2		9.9	10.1	14.3
N 3		9.5	10.4	14.4
N 4		9.1	10.6	14.4
N 5		8.7	10.9	14.5
N 6		8.4	11.0	14.5
C I	13.8	19.2	26.1	21.5
C II	11.2	15.9	21.6	17.3
C III	9.3	13.2	18.0	14.0
C IV	7.5	10.8	14.9	11.6
C V ♂	7.3	10.6	14.5	11.0
C V ♀	4.6	6.8	9.5	6.7
ad ♂	7.2	10.4	14.3	10.8
ad ♀	3.3	4.9	6.8	4.6

**Table 5.** Comparison of the oxygen consumption *Mesocyclops brasiliensis* with that of several species of temperate copepods as reported in the literature. In the final column, the data for *M. brasiliensis* have been converted to 22.5° C by means of the  $Q_{10}$  values in Table 9. Data for the other copepod species have been converted to 22.5° C by means of Winberg's correction coefficients (1950) or by means of the published  $Q_{10}$  values. All  $QO_2$  values are given as  $\mu\text{l O}_2$  per mg dry weight per hour

Species	Stage	Temperature	$QO_2$	$QO_2$ at 22.5° C
<i>Mesocyclops brasiliensis</i>	N 1-6	26°	10.5	10.5
	C I-III		21.9	13.2
	C IV and V		13.0	7.8
	Adult		10.6	6.3
<i>Macrocyclus adbidus</i> <sup>a</sup>	N 1-3	21°	12.5	13.0
	C I-III		6.7	6.9
	C IV and V		6.8	7.0
	Adult		5.8	6.0
<i>Diaptomus siciloides</i> <sup>b</sup>	Adult	20°	16.0	20.2
<i>D. oregonensis</i>	Adult	20°	13.8	17.4
<i>D. leptopus</i>	Adult	20°	7.8	9.7
<i>D. arcticus</i>	Adult	20°	2.9	3.7
<i>D. oregonensis</i> <sup>c</sup>	Adult	20°	8.2	8.2
<i>Calamoecia lucasi</i> <sup>d</sup>	Adult	20°	14.8	18.7
<i>Boeckella delicata</i>	Adult	20°	6.4	8.4
<i>B. symmetrica</i>	Adult	20°	5.0	6.7

<sup>a</sup> Recalculated from Klekowski and Shushkina (1966), Table 2 and 3

<sup>b</sup> Recalculated from Comita (1964), Table 4

<sup>c</sup> Richman (1964), Table 2

<sup>d</sup> Recalculated from Green (1975), Table 3

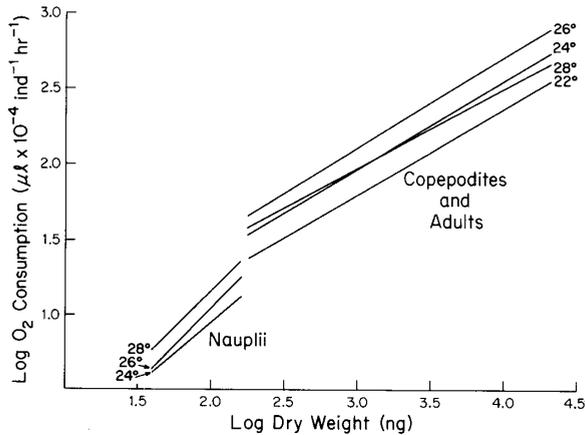


Fig. 2. Oxygen consumption of *Mesocyclops brasiliensis* naupliar and copepodite-adult groups following acclimation to several temperatures

and Shushkina (1966; Figs. 11 and 12). The  $QO_2$  values (metabolism per unit weight) of all stages were computed from the weights and the metabolism data in Table 3. There is a considerable range in the  $QO_2$  values (from 3.3 to 26.1  $\mu\text{l mg}^{-1}\text{h}^{-1}$ , Table 4). Table 4 shows evidence of great metabolic uniformity among the naupliar stages within temperature categories, a significant jump in metabolic rate as N6 changes into CI, and a steady decline in  $QO_2$  with size from the CI to the adult. Mean  $QO_2$  values for various combinations of stages are shown in Table 5 along with selected data for other copepods.

Although Table 4 seems to indicate that temperature has a definite effect on metabolism within either of the two major developmental groups (nauplii, copepodite-adult), it is impossible to judge from the table alone whether the differences are significant. Figure 2, which shows the line of best fit for each of the temperatures, suggests that the  $QO_2$  values at certain temperatures might be so close as to be statistically indistinguishable. Differences in slopes and elevations of the lines in Fig. 2 were tested for significance by analysis of covariance using multiple regression (Snedecor and Cochran, 1976).

The respiration data were first tested for homogeneity across the two developmental categories (nauplii, copepodite-adult) and at all 4 temperatures. The null hypothesis was that *M. brasiliensis* shows uniform slopes of metabolism on size at all temperatures tested. This null hypothesis was rejected (Table 6). Examination of Fig. 3 suggested that the lack of homogeneity might in fact be due solely to the differences between the nauplii and copepodites. Nauplii were thus considered in a separate analysis and the slopes of the metabolism-size relationship then proved to be homogenous for all 3 temperatures (Table 6). The copepodite-adult group also proved to have a homogenous slope for the different temperatures when separated from the nauplii. The metabolism-size relationships thus differ in slope across temperatures for mixed developmental categories but are indistinguishable across temperatures within developmental categories. Nauplii and copepodite-adults are therefore kept separate in further analysis.

In the next step of the analysis, the difference in elevation of the lines was tested within each of the two developmental categories. The test is an

**Table 6.** Interaction of size and metabolic rate as affected by temperature. Slope of the line indicates increase of metabolism with size, which is being tested for homogeneity across temperature. Elevation of the line indicates metabolism per unit weight, which is being tested for homogeneity across temperatures

	F	d.f.	P
<i>Slope of line</i>			
All stages	11.51	3,110	<0.001
Nauplii only	0.35	2,24	>0.50
Copepodites and adults	0.23	3,80	>0.75
<i>Elevation of line</i>			
Nauplii only	6.17	2,24	<0.01
Copepodites and adults	16.19	3,80	<0.001

**Table 7.** Student-Newman-Keuls analysis for the elevation of metabolism-size relationships shown in Fig. 2. Values are mean ratios of log dry weight (ng) to log oxygen consumption ( $\mu\text{l} \times 10^{-4}$  individual $^{-1} \text{h}^{-1}$ ). Means that are statistically indistinguishable at  $P < 0.05$  are joined by a dotted line

	Nauplii			Copepodite-adult			
	24°	26°	28°	22°	24°	28°	26°
Mean ratio	0.42	----- 0.47	0.57	0.61	0.65	----- 0.65	0.70

analysis of covariance in which the null hypothesis is that the mean metabolic rate, when adjusted for body size, is the same for all temperatures (i.e. the  $QO_2$  is uniform). For both the nauplii and the copepodite-adult groups the null hypothesis is rejected (Table 6), indicating that within both groups the  $QO_2$  is affected by temperature.

In the final step of the analysis, the method of a posteriori contrasts (Student-Newman-Keuls test, Snedecor and Cochran, 1976) is used to determine exactly which of the  $QO_2$  values are distinct and which are not. Once again, the nauplii and copepodite-adults must be considered separately. Table 7 show the results of the analysis. The ratio between the log oxygen consumption and log weight is given for each temperature and the temperatures not showing a significant difference ( $P < 0.05$ ) are joined by a dotted line. For the nauplii, the change from 24 to 26° C does not affect the  $QO_2$ , but the change to 28° C increases the  $QO_2$  significantly. For the copepodite-adults, the  $QO_2$  at 22° C is distinct from all other  $QO_2$ 's at higher temperatures and the  $QO_2$  at 26° C is also distinct from all other  $QO_2$ 's. The  $QO_2$  values at 24 and 28° C are indistinguishable because of a decline in the metabolic rate if the temperature exceeds a certain threshold between 26 and 28° C.

The ratio between log oxygen consumption and log weight (Table 7) can be used to determine the  $Q_{10}$  for the nauplii and copepodite-adult groups over each temperature interval. The mean weight of each developmental category ( $\bar{X}$ ) is first determined for each temperature. The log of this value is used in conjunction with the ratio from Table 7 to determine the log mean oxygen consumption for each temperature ( $\log \bar{Y}$ ). These values can then be used in conjunction with the pooled slopes for the nauplii (1.08) and for the copepodite-adults (0.57) to formulate equations describing the metabolism-weight rela-

**Table 8.** Mean weights ( $\log \bar{X} = \log \text{ng dry wt}$ ) and oxygen consumptions ( $\log \bar{Y} = \log \mu\text{l O}_2 \times 10^{-4} \text{ ind}^{-1} \text{h}^{-1}$ ) used to calculate the intercept ( $\log a$ ) of the weight-metabolism relationships.  $\log \bar{X}$  and  $\log \bar{Y}$  have been used in conjunction with the pooled slopes (b) as justified in Table 6 to calculate  $\log a$

Stage	Temperature	$\log \bar{X}$	$\log \bar{Y}$	$\log a$	Slope (b)
Nauplii	24°	1.85	0.78	-1.22	1.08
	26°	1.89	0.86	-1.64	1.08
	28°	2.03	1.17	-1.02	1.08
Copepodite and adult	22°	3.01	1.82	0.12	0.57
	24°	3.16	2.04	0.25	0.57
	26°	3.04	2.12	0.40	0.57
	28°	3.41	2.23	0.30	0.57

**Table 9.** Acclimation  $Q_{10}$  values for the nauplii and copepodite-adult groups of *Mesocyclops brasiliensis*.  $K_1$  and  $K_2$  are the velocity constants corresponding to  $t_1$  and  $t_2$ . The values for  $a$  from Table 8 were used as measures of  $K_1$  and  $K_2$

$Q_{10} = \left( \frac{K_1}{K_2} \right)^{\frac{10}{t_1 - t_2}}$			
	22-24° <sup>c</sup>	24-26°	26-28°
Nauplii	a	b	5.45
Copepodites and adults	4.30	5.78	0.31

<sup>a</sup> Not tested

<sup>b</sup>  $Q_{10}$  not statistically distinguishable from 1.0

<sup>c</sup> This temperature range is never encountered in the habitat

tionship at each temperature (Table 8). The pooled slopes are appropriate since the slopes within developmental categories have previously been shown to be indistinguishable. The  $Q_{10}$  can be determined for each temperature interval according to the equation of Prosser (1973) by using the constant  $a$ , derived from Table 8 for each temperature, as a measure of oxygen consumption. The equation and results of the computation are shown in Table 9. The  $Q_{10}$  value is omitted (assumed equal to 1.0) where the difference between  $QO_2$  values at different temperatures is not statistically significant (Table 7).

## Discussion

Two aspects of the metabolic data should be considered in conjunction with the ecology of the species: (1) change in  $QO_2$  with development, and (2) relation of  $QO_2$  to temperature (i.e.  $Q_{10}$ ).

### *Changes in $QO_2$ with Development*

Between N6 and CI developmental stages the copepod changes drastically in morphology. Swimming, feeding, and predator avoidance all change consider-

ably as a result of this morphological change (for a detailed treatment of ecological changes through development for a tropical population, see Lewis, 1979). The movement rate of the nauplii is known to be much lower than that of the copepodites and adults, for instance, which results in a lower naupliar vulnerability to ambush predators (Gerritsen, 1978). We believe that these morphological and behavioral/ecological changes necessitate the jump in  $QO_2$  between N6 and CI, as the weight increase across the N6-CI transition would otherwise lead one to expect a decline in  $QO_2$  from N6 to CI.

#### *Relation of $QO_2$ to Temperature*

The analysis of  $Q_{10}$  in its environmental context is simplified by a separation of copepodites and adults from the nauplii. As the nauplii are very weak migrators, their diel temperature range is very small or negligible, and the principal thermal variations which they encounter are seasonal. The situation is more complex with copepodites and adults as these stages are powerful migrators and experience diel changes in the range 26–28° C during stratification as well as seasonal changes (Table 1; Fig. 1). It is most convenient to analyse the more complex situation of copepodites and adults and then show how the nauplii differ.

During periods when Lake Valencia is stratified, *Mesocyclops* copepodites and adults migrate over a maximum thermal range of 2° C (26.5 to 28.5° C, Fig. 1). Over this range, a significant decrease in oxygen consumption occurs with increasing temperature ( $QO_2$  declines; Tables 3, 4 and 7; Fig. 2), which results in a  $Q_{10}$  less than 1 (26 to 28° C, Table 9). This phenomenon which is sometimes called "thermal overcompensation" is relatively rare within the normal thermal range of a population (Precht et al., 1955).

A decline in  $QO_2$  above 26° C in acclimated *Mesocyclops* indicates that acutely-exposed copepods would show less decline or no significant decline in  $QO_2$  (respiratory plateau) in this temperature range. Copepodites and adults would normally experience something between an acute exposure and an acclimated response to thermal changes between 26 and 28° C in the course of vertical migration (Fig. 1). Our data suggest that under these conditions the metabolic rate would be nearly constant or increase very slightly with descent into the deeper water, which means that natural selection has acted on the metabolic responses to stabilize the metabolic rate through the normal diel thermal cycle associated with migration.

The diel metabolic cycling between lower metabolic rates in deep (cooler) water and higher metabolic rates near the surface as required by the "energy-boost" hypothesis clearly does not apply to the Lake Valencia population of *Mesocyclops brasiliensis*. There are two possible ecological/evolutionary reasons for this. First, the food supply at greater depths may not be inferior in quality to the surface food supply during the stratified periods, as required to render the change in metabolic rate advantageous. Second, there may be serious disadvantages to reduced metabolic rate even when food is of lower quality. Escape from predators or other behavioral traits may require certain minimum metabolic rates, for instance. It is also possible that the copepods may ingest more food than they can effectively convert into structural protoplasm while in the

**Table 10.**  $Q_{10}$  values for temperate-zone copepods as reported in the literature

Species	$Q_{10}$	Source
<i>Diaptomus arcticus</i>	2.0	Comita, 1968
<i>D. siciloides</i>	3.75	Comita, 1964
<i>D. clavipes</i>	2.6 and 3.05	Siefken and Armitage, 1967
<i>D. pallidus</i>	3.3 and 4.95	Siefken and Armitage, 1967
<i>D. siciloides</i>	3.0 and 3.55	Siefken and Armitage, 1967

upper layers, in which case any reduction in metabolism would simply penalize the organism by lowering growth and reproduction rates below their full potential.

Discussion thus far has centered around metabolism in the range 26 to 28° C which is the relevant environmental range during the stratification season. *Mesocyclops* adults and copepodites encounter temperatures below 25.5° C only during the seasonal mixing period (Fig. 1). In contrast to the low  $Q_{10}$  values between 26 and 28° C, the  $Q_{10}$  values for *Mesocyclops* copepodites and adults below 26° C (Table 9) are higher than those reported for copepods from the temperate zone (Table 10). Although the values reported in this paper are based on acclimated animals rather than acutely-exposed animals such as those used in most of the temperate studies, acclimation would only reduce the observed  $Q_{10}$  and thus cannot account for the high  $Q_{10}$  values of our tropical *Mesocyclops* below 26° C.

Scholander et al. (1953) mention the possibility of a reduction in  $Q_{10}$  as an adaptation to temperature fluctuation, but in their extensive survey of animals found no case where animals showed an insensitivity to such changes because of a low  $Q_{10}$ . In a related attempt, Rao and Bullock (1954) considered the hypothesis that animals adapted to warm, thermally stable environments would have a high  $Q_{10}$  and did find numerous examples to support this hypothesis. They point out, however, that the correlation is poor because the data are limited. In support of the Rao and Bullock hypothesis, examples of high  $Q_{10}$  values for animals from warm and thermally stable habitats have been presented by Belehradek (1936), Schlieper (1950), Rao (1953) and Bullock (1955).

The metabolic response of adult and copepodite *Mesocyclops* to changing temperatures supports the hypothesis of Rao and Bullock, but only over temperature ranges other than those encountered during vertical migration. In other words, the metabolic machinery of *Mesocyclops* is highly stable over the diel temperature range but highly sensitive to the seasonal temperature range. We hypothesize that *Mesocyclops* has the capacity to buffer out variations in resource supply over the diel cycle by storage mechanisms, hence natural selection has acted to stabilize the metabolic rate over the diel cycle. Obviously such mechanisms cannot extend across seasonal thermal changes, however, and this accounts for the adjustment of metabolism to temperature over the seasonal thermal gradient. This hypothesis accounts well for the high  $Q_{10}$  over the seasonal thermal range. A significant adjustment of metabolic rate through the seasons would require an exceptionally high  $Q_{10}$  in the tropics because the thermal

change is slight (Fig. 1). High  $Q_{10}$  is in fact characteristic of *Mesocyclops brasilianus* adults and copepodites below 26° C. We would expect the mixing period, when the temperatures are the lowest, to be the most unfavorable time of year for growth because of the drastic decline in phytoplankton abundance in tropical lakes of this type during complete mixing (Talling, 1966; Lewis, 1973, 1978). Field studies of herbivore production rates support this (Lewis, 1979; Lewis and Saunders, in preparation). The *Mesocyclops* adults and copepodites appear to compensate for a seasonal change in available resources by a reduction in metabolic rate. Other seasonally changing factors may also be involved, of course.

Discussion to this point has been based on the copepodites and adults. The nauplii show very different  $Q_{10}$  patterns (Table 9). The key ecological difference is that the nauplii are very weak migrators and are thus adapted solely to seasonal thermal changes in temperature rather than a combination of diel and seasonal changes. A second important difference is that the nauplii are positioned higher in the water column during the day (Table 1) and consequently experience a high mean daytime temperature during the stratification season. The upper part of the water column where the nauplii live will always be very near 28° C (Fig. 1) during stratification. Consequently, when an organism experiences a temperature of 27 or 26° C, it will be indicative of a change in seasons, i.e., the onset of the seasonal mixing. Once the seasonal metabolic adjustment has been made, further changes are not necessary, as indicated by the stability of  $QO_2$  between 24 and 26° C.

We have shown earlier that the metabolism-temperature relationships of the copepodites and adults would result in a reduced metabolic rate at the onset of the mixing season. The high  $Q_{10}$  at 26 to 28° C in the nauplii would have an identical effect because the temperature indicative of mixing would occur in this range. The threshold temperature indicative of mixing must be lower for copepodites and adults because these stages migrate daily through a thermal gradient encompassing more of the 26–28° C range. All stages are present throughout the year but are programmed differently because of differences in behavior and position in the water column. The net effect is the same for both developmental categories: stable metabolism over the diel cycle and a change in metabolism over the seasonal cycle from a higher level during the stratification season to a lower level during the mixing season.

The  $QO_2$ 's of all stages are relatively high in Lake Valencia. Many investigators have shown that the metabolic rates of animals from warm habitats tend to be lower than those from cold habitats over an intermediate temperature range, but that animals from warm habitats have higher metabolic rates at the temperatures normal to their habitats (Roberts, 1953; Scholander et al., 1953; Rao, 1953; Bullock, 1955). The respiratory rates of *Mesocyclops* support this generality, but only weakly (Table 5). The respiratory rate of *Mesocyclops* adults at 26° C is higher than 6 out of 9 temperate copepod species listed in Table 5 at their normal habitat temperatures (column 4). In column 5 of Table 5, the  $QO_2$  values of all copepods have been converted to an intermediate temperature of 22.5° C. At this intermediate temperature, the  $QO_2$  of *Mesocyclops* adults is lower than the values for 7 of the 9 other species of adult copepods.

Generally high  $QO_2$  coupled with a metabolic stability over the diel temperature range and a thermally programmed seasonal reduction in metabolism are the ecologically critical aspects of metabolism in *Mesocyclops brasiliensis* from Lake Valencia. These metabolic features suggest that in tropical copepod species at least, it is energetically efficient to buffer against diel changes in metabolic rate but to change metabolic rate seasonally in response to major environmental change.

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