

METABOLIC UNIFORMITY OVER THE ENVIRONMENTAL TEMPERATURE RANGE IN BRACHIONUS PLICATILIS (ROTIFERA)

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Abstract

Organisms inhabiting small water bodies frequently encounter radical, short-term fluctuations in temperature. The population of *Brachionus plicatilis* that was used in this study encounters temperature changes as great as 12°C in 24 hours. In this paper we describe the metabolic response to temperature change in this eurythermal rotifer population. Metabolism was determined over the environmental range (15°C to 32°C) in intervals of 2°C. Utilization of such narrow temperature intervals allowed us to approximate the instantaneous Q_{10} , which we define as the Q_{10} over an infinitely small temperature interval.

Our results show the existence of a plateau in the curve of respiration against temperature ($Q_{10} = 1$) over the range 20-28°C. The plateau is bounded on either side by temperature ranges over which metabolism is temperature sensitive (Q_{10} values from 3.4 to 4.8). It is significant that the plateau occurs over the environmental temperature range for the major portion of the growing season. This population is thus programmed to hold a constant (preferred?) metabolic rate in spite of diel temperature fluctuations when the environment is otherwise favorable.

Introduction

Although the effects of temperature on metabolism have been investigated intensively in many animal groups, the ecological implications of the temperature-metabolism relationship are often difficult to assess. This is especially true of aquatic invertebrates. Part of the problem stems from the fact that metabolic studies are frequently performed with little regard for the environmental temperature range. Studies of Q_{10} in particular typically lack sufficient resolution within the environmental range to provide significant insight into metabolism under field conditions.

In some recent studies of copepod metabolism (Epp & Lewis, 1979a), we have examined Q_{10} over narrow temperature intervals within the environmental range in an attempt to avoid this shortcoming. In the present study, we have taken the same approach to metabolism in a eurythermal population of *Brachionus plicatilis*.

Our work on the tropical copepod *Mesocyclops brasiliensis* documented the existence of a respiratory plateau within the environmental temperature range. Over this plateau, temperature changes have essentially no effect on metabolic rate. This plateau covers the thermal range encountered by the copepods during diel vertical migration. We have argued that the plateau is adaptively significant in maintaining a preferred level of metabolism in spite of the diel fluctuations in temperatures that result from migration. For our present work, we hypothesize that rotifer populations may also show a thermally-independent metabolic rate *within the environmental temperature range* and that this may function as a buffer to maintain a preferred metabolic rate. We have chosen for our study a population that is exposed to rather extreme temperature fluctuations (> 12° per day). If rotifers benefit by maintaining a constant metabolic rate in spite of fluctuating temperatures, then rotifers that are subjected to pronounced short-term thermal variation should show the most obvious respiratory plateau.

Materials and methods

All experimental animals were derived from a single resting egg. The egg was collected from the sediment of a small meromictic pond near Gaynor Lake in Boulder

County, Colorado (Pennak, 1949). The pond is typically frozen solid until early spring and usually dries by early summer. Throughout the ice-free period, a stable stratification exists. Water of high salinity is typical of the bottom layer, and water of a lower salinity is typical of the surface layer. During the study period, the specific conductivity of the bottom ranged from 25,000 to 47,500 $\mu\text{mho/cm}$ (25°C) while that near the surface ranged from 11,000 to 45,000 $\mu\text{mho/cm}$ (25°). Solar heat is trapped in the bottom layer where temperatures exceed 20°C early in the ice-free period. Bottom temperatures are at times 12°C higher than those at the surface. Because the pond is shallow (max. depth = 20 cm), its thermal buffering capacity is minimal. Consequently, there are sizable short-term temperature fluctuations which parallel atmospheric thermal changes. This is especially true of the water near the surface, where a change of 12°C was recorded over a five-day interval during the study period. Bottom temperature remains slightly in excess of 30°C for several weeks in the early summer.

The pond has supported large populations of *B. plicatilis* annually for at least the last five years. These populations are subjected to radical short-term temperature fluctuation as the result of the rapid heat loss and gain at the surface. Additionally, we have indirect evidence for vertical migration. Migration of only 12 cm can result in a temperature change of 10° or more.

All experimental animals were cultured in full strength sea water (35‰) and were fed *Dunaliella salina*. Subsamples from the main culture were maintained at the desired experimental temperature for a minimum of one generation prior to the respiratory measurements. Metabolic rates of individual rotifers were determined with a Cartesian diver micro-respirometer following the precautions described in Epp & Lewis (1979b).

Results

Sixty-one animals were tested at nine temperatures (15°C through 32°C). The effect of temperature on metabolism was tested for significance by analysis of variance (Sned-

cor & Cochran, 1976). The null hypothesis is that metabolism is uniform across temperature. This hypothesis was rejected ($P < 0.001$) indicating that the temperatures used in this experiment have a significant effect on metabolism. In the next step of the analysis, the method of a posteriori contrasts (Student-Newman-Keuls: Snedecor & Cochran, 1976) was used to determine which metabolic rates were distinct from each other and which are not. The results of the analysis are shown in Table 1. Metabolic rates that are not significantly different are joined by a dotted line. A noticeable respiratory plateau exists over the temperature range 20° to 28°C . Metabolic rates change significantly with temperature below 20°C and above 28°C .

The Q_{10} for any temperature interval can be calculated according to the equation of Prosser (1973). For purposes of comparison, we have computed Q_{10} values for intervals varying in breadth from 2°C to 17°C . Some of these are shown in Figure 1 along with the deduced Q_{10} vs temperature relation for instantaneous Q_{10} based on an infinitely small interval. Q_{10} is assumed equal to 1 when the difference between metabolic rate at different temperatures is not significant (Table 1). Q_{10} is equal to 1 over any temperature interval that is totally within the range 20° to 28°C . Q_{10} values for restricted temperature intervals which are totally or partially outside the range 20° to 28°C are very high (i.e., 3.4 to 4.8). Q_{10} values for broad temperature intervals which also span the range 20° to 28°C are intermediate (i.e., 1.9 to 2.4) and within the range that is considered typical for many metabolic reactions (Prosser, 1973).

Discussion

Our populations of *B. plicatilis* encounter temperatures within the thermal range 20° to 28°C over the major portion of the growing season. Over this thermal range, metabolism is not affected by temperature change. Metabolism is a reflection of the energy-requiring processes within an animal and the respiratory plateau indicates the constancy of these processes over the environmental thermal range. The data thus confirm our general hypothesis

Table 1. Results of the Student-Newman-Keuls multiple range test for the effect of temperature on metabolism. Means that are statistically indistinguishable at $P = 0.05$ are joined by a dotted line.

Temperature, $^\circ\text{C}$	15	18	20	22	24	26	28	30	32
Mean Oxygen Consumption nl/ind/h	1.124	1.732	2.373	2.826	2.706	2.544	2.705	3.765	4.905

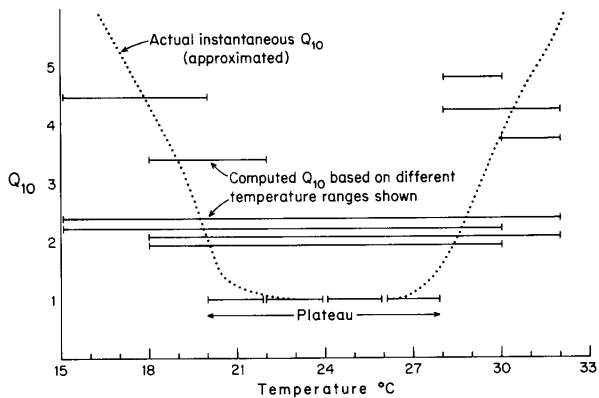


Fig. 1. Q_{10} values of *Brachionus plicatilis* over selected temperature intervals. The constancy of metabolism over the range 20° to 28°C is illustrated by the Q_{10} value of 1 over this thermal range.

that freshwater invertebrates tend to maintain a constant metabolic rate over temperature ranges that are typical of the environment.

Metabolism is affected significantly by temperature change below 20°C and above 28°C. Temperatures below 20°C are encountered only early in the growing season. High Q_{10} over the range 15° to 20°C (Fig. 1) allows metabolism and associated energy-requiring processes to be accelerated up to the preferred level when conditions permit. Stable metabolic rates between 15° and 20°C are either not possible or not desirable. Temperature above 32°C is indicative of the desiccation of the pond. The rapid increase in metabolism with temperature in this thermal range may signal this event and thereby play a role in resting egg production. Alternatively, this may simply be outside the zone of feasible metabolic control.

Q_{10} is frequently determined over relatively large temperature ranges (i.e., > 5°C) with little regard for the environmental range of the animal in question. The present study illustrates how such determinations can lead to erroneous conclusions concerning the effect of temperature on metabolism. In the present case, the Q_{10} is actually 1 over an extended thermal range which coincides with the thermal range encountered most frequently by the animals, but this would not necessarily be evident without documentation of metabolic rates at numerous temperatures within the normal environmental range.

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