

AN ABSTRACT OF THE THESIS OF

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GASTROPOD THAIS EMARGINATA

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Thais emarginata is a gastropod which inhabits the midlittoral zone of the intertidal region. Oxygen consumption of high-level and low-level organisms was determined at various seasons of the year over an experimental temperature range of 5 to 20° C.

No significant difference in respiratory rate between separate populations of high-level and low level organisms was found. Temperature compensation studies performed by testing both field-acclimatized and laboratory acclimated organisms indicated that the low-level organisms adapted to cold temperatures (8-10° C.) responded by having respiratory rates more sensitive to warmer (20° C.) temperatures. High-level organisms adapted to cold temperatures (8-10° C.) responded in the same manner as warm adapted (17° C.) high-level organisms. Both high-level and low-level organisms showed partial temperature compensation.

Respiratory rates measured at different times of the year indicated that respiratory rates were higher during warmer months of the year and also during those months (August and September) in which the organisms were actively feeding. Respiratory rates during this time were also more temperature dependent than at other times during the year.

Respiratory rates tended to be higher before the reproductive season than following reproduction. During the colder months, following reproduction, respiratory rates were generally lower than during warmer months.

It was concluded that T. emarginata is a metabolic regulator. Environmental temperature, feeding activity and reproductive activity are factors which affect respiratory rate of the organism. Individual variability and behavioral modifications are important mechanisms which enable T. emarginata to successfully inhabit the intertidal zone.

Metabolic Adaptations of the Marine Gastropod
Thais emarginata

by

Sister Jean Sweat

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METABOLIC ADAPTATIONS OF THE MARINE GASTROPOD
THAIS EMARGINATA

INTRODUCTION

Objective

Poikilothermic animals were formerly considered to be metabolically dependent upon temperature. It is now becoming evident that these organisms can compensate for temperature changes over a certain temperature range.

The conditions under which an animal is best suited to live depend on its morphological, physiological and behavioral characteristics and their plasticity. Ultimately, the limits of physiological and behavioral adaptation are determined by the genetic constitution of the organism. However, it is the phenotype of the adult which must adapt to changing conditions in order for the species to survive (Warren, 1971).

The objective of this study was to determine the ability of Thais emarginata to adapt to the changing environment of its intertidal habitat. Since the adult organisms of this population are relatively fixed in their position during most of the year, the primary question asked in this study was, "what differences, if any, exist between the metabolic adaptation patterns of organisms from the

low-level extreme of the habitat in contrast to organisms from the high-level extreme of the habitat? "

The process of adaptation involves a physiological response to the environment on the part of the organism. The measurement of some biological rate as a function of environmental stress is a quantitative test for physiological variation under environmental stress (Prosser, 1956). In this study, rates of oxygen consumption were measured to determine responses to temperature of organisms from high-level and low-level areas in the habitat range of Thais emarginata.

Clarification of Terms

Physiological adaptation may be defined as the development of any functional property of an individual which favors continued successful living in an altered environment (Prosser, 1955). Two extreme ways of adapting are alteration of the internal state to environmental change or maintenance of a relatively constant internal state over a considerable range of environmental change. The former mode of adaptation is referred to as physiological conformity and the latter as physiological regulation. Regulating animals tolerate a wider range of environmental variation but a narrower range of internal variation than do conformers.

Acclimation is the process resulting in compensation to a

persistent environmental change in controlled experiments. Compensation resulting from exposure to a set of complex environmental factors, such as seasonal or climatic changes, is called acclimatization (Prosser, 1958). Adaptation which occurs within the range of normal temperatures by a particular organism is called capacity adaptation and adaptation to extreme temperatures is called resistance adaptation (Precht, 1958).

Adaptation of Intertidal Organisms

The process of adaptation in many intertidal organisms has been studied. Some of these studies which are considered relevant to the development of this study of T. emarginata are discussed here.

It has generally been stated (Segal, 1961; Bullock, 1955) that cold acclimated animals show a higher metabolic rate than warm acclimated animals in the range of intermediate temperatures.

Size is a morphological variable which influences respiratory response. It has been shown by Todd and Dehnel (1960) that the size of an organism influences the degree of temperature compensation. In their study all weights of crabs did not have the same resistance to the high experimental temperatures. Smaller animals of two species, Hemigrapsus nudus and H. oregonensis, seemed slightly more tolerant than larger ones.

The stage of development of an organism also has an effect on

its respiration. Dehnel and Segal (1956) concluded that oxygen consumption of adult cockroaches exhibits acclimation effects to temperature. The degree of acclimation was dependent upon both size and stages of development of the organisms. All sizes of nymphs showed a greater degree of acclimation to temperature than all sizes of adults.

The extent of compensatory change in respiration varies greatly, and, in many cases may be correlated with the ecological situations which are commonly used in respiration studies of intertidal organisms. These are microgeographic adaptations of organisms from vertically separated populations and seasonal effects on respiratory rates.

Microgeographic adaptations of populations separated by small vertical distances in the intertidal zone may be more significant for a comparison of physiological functions because of a decrease in the complexity of variables in the situations to be compared. However, it is still impossible to select single environmental variables as the cause of physiological differences. Comparisons of these populations do provide interesting relationships between physiological functions and the environment.

Degree of exposure and desiccation tolerance is an important consideration in the survival of intertidal organisms. Various physiological activities such as heart rate and respiratory rate have

been compared between populations of the same species occupying different zones.

Some organisms in the intertidal region have specific morphological adaptations for survival. The intertidal barnacle, Balanus balanoides, for example, is morphologically adapted for exposure to air by forming a micropylar opening at the opercular valves which allows access of air to the mantle cavity. In contrast to the specific adaptation of B. balanoides, the barnacle, Chthamalus stellatus, which is located lower in the intertidal zone, does not so adapt (Barnes, Finlayson and Piatigorsky, 1963).

Adaptations of two species of limpet were studied by Davies (1969). He found that the upper distribution level of the limpets, Patella vulgata and P. aspera, was determined by effects of desiccation. The upper limit of these limpets in the intertidal zone was determined by loss of water and the time required to regain this water loss when the organism is covered by the tide.

One adaptive measure to prevent desiccation in the high intertidal zone is greater water-holding capacity. Acmaea limatula of high-level and low-level populations have been studied by Segal (1956a). His study has shown that high-level organisms adapt by having a larger water-holding space between the shell and soft parts than do low-level organisms.

Differences in heart rate of low-level and high-level limpets,

Acmaea scabra and A. limatula, have been studied by Segal, Rao and James (1953). They found that the organisms in the lower extent of the intertidal range had a higher heart rate at a given temperature than organisms located higher in the range. Their transplant experiments of high-level and low-level A. limatula have shown that a reversal of activity occurs within a period of four weeks.

Another study of the heart rate of Acmaea limatula revealed that at higher temperatures of the experimental range (4-29° C.) the lower range organisms had a faster heart rate than did higher-level organisms (Segal, 1956b). This suggests that low-level organisms are approaching cold depression at a faster rate than are high-level organisms. After 29 days of reciprocal transplantation the heart rates of organisms of the two populations underwent a complete reversal. These results were interpreted as indications of phenotypic expression of thermal compensation.

High-level and low-level populations of Mytilus californianus show the same adaptive patterns (Moon and Pritchard, 1970). High-level organisms have a higher rate of respiration than low-level organisms when measured at 10° C. Following an exposure period of six to twelve hours the oxygen consumption rate increased the most in the high-level populations. The extent of increase was a function of time of exposure. One consequence of high intertidal existence for M. californianus is an increase in metabolic rate following

submergence and a greater capacity for anaerobiosis.

Changes in respiratory rates have also been studied over periods of time to determine seasonal effects on respiratory rates. Seasonal changes in oxygen uptake have been related to changes in composition and activity of tissues (Barnes, Barnes and Finlayson, 1963), to the nutritional state of the organism (Barnes and Barnes, 1969) and to environmental temperature (Pickens, 1965).

The foregoing reports concerning metabolic adaptation of poikilothermic organisms to their environment indicate that the results of any study involving the measurement of respiratory rates must be critically analyzed along with a knowledge of the history of the organism before respiratory rates are determined. A lack of knowledge of the conditions when animals were collected and conditions in which animals were maintained before respiratory rates were measured leads to much ambiguity in literature reports. For this reason the conditions of collection and maintenance of animals in this study are recorded as carefully as possible.

The question of differences in respiration between high-level and low-level Thais emarginata was studied over a period of time to observe seasonal differences in respiratory rates. Temperature, nutritional state, activity and reproduction were considered as important factors influencing the respiratory rate of this organism at different times during the year.

MATERIALS AND METHODS

Collection and Maintenance

Thais emarginata is a prosobranch gastropod which is abundant on the Pacific coast on exposed rocky shores where the surf is fairly heavy (Ricketts and Calvin, 1966). This organism feeds on barnacles and young mussels (Harger, 1970; Connell, 1970). Hence the boundaries of its habitat correlate closely with that of the barnacle-mussel community.

The location of the collecting site was Seal Rock, approximately ten miles south of Newport on the Oregon coast. This area was chosen because of the abundance of T. emarginata at this location. This site consists of a community with only few young mussels, barnacles and T. emarginata. The main barnacle present is of the genus Balanus.

The mean high and low aerial temperatures (°C.) for the coast at Newport, Oregon during the months of interest in this study are taken from U. S. Environmental Data Service and are given below.

January 1970	10.0	4.1
February 1970	14.4	5.0
March 1970	12.9	3.1
April 1970	11.7	4.3
May 1970	15.1	5.4
June 1970	16.7	8.4
July 1970	17.5	8.8
August 1970	17.6	8.8

September 1970	17.3	7.1
October 1970	14.7	6.5
November 1970	12.0	5.4
December 1970	8.8	1.5
January 1971	8.5	3.0
February 1971	9.9	2.9
March 1971	9.7	2.2
April 1971	11.4	3.5
May 1971	12.8	6.4
June 1971	15.0	7.7
July 1971	16.8	9.9

Snails were collected from both the high and the low extremes of their habitat range. Organisms from the high extreme are designated as high-level organisms and those from the low extreme as low-level organisms. At this collection area these populations^{1/} were separated by a two foot vertical distance and a twelve foot horizontal distance but were continuously distributed throughout the entire range. Snails of high-level and low-level populations were marked to determine the degree of isolation of high and low populations. Results of these experiments are on page 21.

All animals used in this study were collected during the months of December, 1970 through September 1971. Animals of comparable sizes (17.32 ± 0.24 mm, shell length measurement) were used in order to standardize the size variable in respiration studies (Todd and Dehnel, 1960).

^{1/} The term population is used here to signify a group of organisms. It is recognized that one cannot conclude that these populations are genetically isolated.

Metabolic rate determinations were made on animals collected and maintained in the laboratory for eight to twenty-four hours and also on animals maintained in the laboratory for ten to twelve days. The former will be referred to as field-acclimatized organisms and the latter as laboratory-acclimated organisms.

Different types of laboratory acclimation schedules were used in this study in order to study the effects of submergence versus submergence and exposure on the organisms. Some organisms were kept submerged in sea water at constant temperature during the period of acclimation. Others were kept in the laboratory under constant temperature with a schedule of sixteen hours submergence in sea water and eight hours exposure in air.

The medium was filtered and ultra-violet irradiated sea water obtained from the Marine Science Center, Newport, Oregon. The sea water was continuously aerated.

The snails were not fed while being maintained in the laboratory. While recognizing the fact that wet weight is a varying quantity, it was observed that the wet weight of the organisms did not decrease during twelve days of acclimation time.

Oxygen Consumption Measurements

A GME Differential Respirometer (Model GRP 14, Gilson, 1963) was used to measure oxygen consumption rates of the snails.

Flasks were prepared with 0.2 ml. of 10% KOH in the side arm to absorb the carbon dioxide given off by the snails during the measurements of oxygen consumption. The amount of oxygen consumed was recorded at 30 minute intervals for a period of two hours. On some occasions one snail occupied a single flask, but, on most trials, three snails were combined in a single flask. Respiration rates were measured at four temperatures, 5, 10, 15 and 20°C. This temperature range was selected because it includes the range of temperatures encountered by this organism in its natural habitat in the collecting area. Aerial temperatures taken at the time of collection ranged from 6°C. in March, 1971 to 20°C in July, 1971.

A preliminary study indicated that three hours were required for oxygen consumption rates of this organism to reach a level with minimal fluctuation. Therefore, a three hour equilibration period was allowed before measuring the respiratory rate at each temperature. Respiratory rates were measured using either an aerial or an aquatic condition within the respirometer flask. Aerial trials were made by placing the snails in flasks which contained a layer of filter paper on the bottom. The filter paper was saturated with sea water to maintain the humidity within the flask. Aquatic trials were made by placing three ml. of sea water in each flask with the snails.

Following each respiration trial the animals were removed from their shells and dried to constant weight at 80°C. Oxygen

consumption was recorded in microliters of oxygen consumed per gram dry weight per hour ($\mu\text{l O}_2/\text{gm/hr}$).

Microgeographical Adaptation Study

Specific procedures for the microgeographical study are as follows. Snails from the high-level populations were marked and transplanted to the low-level area and vice versa during July, 1971. Respiration measurements were made on groups of snails on the day of transplantation and on groups of neighboring snails 15 days later. All measurements in this study were made under aerial conditions. Results of this study are shown in Figures 1 and 2.

High-level and low-level snails were also collected and maintained in the laboratory on acclimation schedules similar to the exposure of high-level and low-level organisms in the field at the time of collection, as follows. It was determined that the low-level organisms inhabit approximately the two foot level during the month of July, the month of testing. The high-level population was collected from a vertical position two feet higher than the low-level population. Laboratory schedules were maintained corresponding to exposure in the field at both population levels. The high-level acclimation 24-hour schedule consisted of five hours submergence in sea water, followed by nine hours in air, five hours in sea water, and then five hours in air. The sea water was maintained at 12°C .

and the aerial environment was maintained at 17°C. The low-level acclimation 24-hour schedule consisted of nine hours submergence in sea water, followed by four hours exposure to air, eight hours submergence in sea water, and then three hours exposure to air. Sea water temperature was maintained at 12°C. and the aerial environment was maintained at 17°C. Snails were acclimated on these 24-hour schedules for a period of ten days. Results of this study are shown in Figures 3 and 4. Organisms labeled, High and Low Control, pre-transfer, are organisms that were collected from their respective high and low-level areas and respiration rates measured before transplantation. Organisms labeled, High and Low Control, post-transfer, are organisms that were collected from their respective high and low-level areas and respiration rates measured 15 days after transplantation. Organisms labeled, High to Low transfer, are those organisms that were collected from the high-level area, marked and placed in the low-level area. These same organisms were collected and their respiratory rates determined 15 days after transplantation. Organisms labeled, Low to High transfer, are those organisms that were collected from the low-level area, marked and placed in the high-level area. These same organisms were collected and their respiratory rates determined 15 days after transplantation.

Temperature Compensation Study

To study the effect of the environmental temperature at the time of collection three groups of organisms were collected on different days within a period of two weeks at aerial field temperatures of 10, 12 and 17°C. Respiratory rates of these three groups of snails were measured on the day following collection. Separate respiratory rates were tested on high-level and low-level organisms. Results of this study are shown in Figures 5 and 6.

Laboratory-acclimated T. emarginata were also used to study temperature compensation. All groups were acclimated by maintaining the organisms totally submerged in sea water. The organisms collected at a field temperature of 10°C. were acclimated at 8°C. in order to create a greater difference, than 10 and 17°C., between the temperatures used for acclimation of these organisms. Those collected at 12°C. were acclimated at 12°C., and those collected at 17°C. were acclimated at 17°C. Respiratory rate measurements in this study were made under aerial conditions. Results of this study are shown in Figures 7 and 8.

Seasonal Adaptation Study

Specific procedures for the seasonal study are as follows. Snails were collected at various times during the year in order to

study seasonal effects on respiratory rate. Seasonal effects on this organism are mainly due to the different occurrence and level of high tides during the year. Hence, the snails are exposed to different temperatures during low tide. Organisms were acclimated in the laboratory for at least ten days prior to respiration measurements. Both of the acclimation schedules previously described were used. One group of snails was kept completely submerged in sea water at a constant temperature. Results of this study are shown in Figures 9-12. The other group was kept at a constant temperature but was maintained on the 24-hour schedule of submergence and exposure (Figures 13-16). The acclimation temperature used was the temperature of the sea water at the time of collection. Oxygen consumption of high-level and low-level populations within both acclimation groups was measured in aerial and aquatic conditions. Table 1 contains a summary of these experiments.

Table 1. Summary of experimental protocol.

Experiment	Description	Date	Organisms as indicated on corresponding Figures	Collection conditions	Treatment of organisms before measuring respiratory rates
1	Microgeographic, field transplantation study ^{a/} (Figures 1 and 2).	July, 71	Low Control, pre-transfer	Low-level area	Rates measured within 24 hours
			High Control, pre-transfer	High-level area	Rates measured within 24 hours
			Low to High transfer	High-level area	Rates measured within 24 hours
			High to Low transfer	Low-level area	Rates measured within 24 hours
			Low Control, post-transfer	Low-level area	Rates measured within 24 hours
			High Control, post-transfer	High-level area	Rates measured within 24 hours
2	Microgeographic, laboratory-simulated transplantation study ^{a/} (Figures 3 and 4)	July, 71	Low Control, pre-transfer	Low-level area	Rates measured within 24 hours
			High Control, pre-transfer	High-level area	Rates measured within 24 hours

Table 1. Summary of experimental protocol (cont.)

Experiment	Description	Date	Organisms as indicated on corresponding Figures	Collection conditions	Treatment of organisms before measuring respiratory rates
			Low to High transfer	High-level area	Acclimated on high level tidal schedule for ten days
			High to Low transfer	High-level area	Acclimated on low level tidal schedule for ten days
			Low Control, post-transfer	Low-level area	Acclimated on low-level tidal schedule for ten days
			High Control, post-transfer	High-level area	Acclimated on the high-level tidal schedule for ten days
3	Temperature Compensation study ^a / (Figures 5 and 6)	Aug. 71	10° C	High and low-level areas	Rates measured within 24 hours

Table 1. Summary of experimental protocol (cont.).

Experiment	Description	Date	Organisms as indicated on corresponding Figures	Collection conditions	Treatment of organisms before measuring respiratory rates
			12° C.	High and low-level areas	Rates measured within 24 hours
			17° C.	High and low-level areas	Rates measured within 24 hours
4	Temperature compensation study ^{a/} (Figures 7 and 8)	Aug. 71	8° C.	High and low-level areas	Acclimated for ten days at 8° C.
			12° C.	High and low-level areas	Acclimated for ten days at 12° C.
			17° C.	High and low-level areas	Acclimated for ten days at 17° C.
5	Seasonal study ^{b/} (Figures 9-12)	Jan. 71	Jan.	High and low-level areas	Acclimated submerged in sea water at 10° C. for ten days

Table 1. Summary of experimental protocol (cont.).

Experiment	Description	Date	Organisms as indicated on corresponding Figures	Collection conditions	Treatment of organisms before measuring respiratory rates
		Mar. 71	March	High and low-level areas	Acclimated submerged in sea water at 10° C. for ten days
		Sept. 71	Sept.	High and low-level areas	Acclimated submerged in sea water at 12° C. for ten days
6	Seasonal study ^{b/} (Figures 13-16)	Mar. 71	March	High and low-level areas	Acclimated on 16-8 schedule at 10° C. for ten days
		June 71	June	High and low-level areas	Acclimated on 16-8 schedule at 12° C. for ten days
		Aug. 71	August	High and low-level areas	Acclimated on 16-8 schedule at 12° C. for ten days

Table 1. Summary of experimental protocol (cont.).

Experiment	Description	Date	Organisms as indicated on corresponding Figures	Collection conditions	Treatment of organisms before measuring respiratory rates
		Sept. 71	Sept.	High and low-level areas	Acclimated on 16-8 schedule at 12° C. for ten days

a/ Respiration measured under aerial conditions.

b/ Respiration measured under aerial and aquatic conditions.

RESULTS

A series of marking experiments was conducted in an attempt to identify separate high-level and low-level populations of T. emarginata. Snails were painted with an oil-base paint, and their movements followed for two to three months.

Sixty snails of both high-level and low-level areas were marked during June, 1970. Two days later 70% were recovered within a two-foot radius of their original positions. Six days later 35% were recovered within the same area. Two weeks later approximately 20% were recovered within the two-foot radius. Those organisms not recovered were simply not found. Only two were found beyond the two-foot radius.

Sixty-five snails of high-level and low-level areas were marked during July, 1970. Sixty percent of these were recovered two days later within the two-foot radius. Thirty percent were recovered 20 days later and 10% were recovered 40 days later. Snails marked and recovered during June and July, 1970, were found an average distance of 18.0 ± 3 inches from their original position.

One-hundred snails of the high-level and low-level areas were marked during June, 1971. Similar recovery results were obtained for these organisms with the exception that, during August, some

organisms had migrated one to two meters higher in the intertidal zone.

Thus, limited movements of Thais emarginata throughout the months of October through July indicate that these high and low-level populations are isolated during this time. However, upward migration of these organisms during the months of August and September breaks down the isolation of these populations.

Results of all respiratory rate experiments are recorded in the Figures and accompanying Tables on the following pages.

Significant differences were determined using the following formula,

$$t = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{\frac{n_1 S_1^2 + n_2 S_2^2}{n_1 + n_2}}} \sqrt{\frac{n_1 n_2 (n_1 + n_2 - 2)}{n_1 + n_2}}$$

(Hoel, p. 227).

\bar{X}_1 and \bar{X}_2 are the mean respiratory rate values for two sets of data to be compared. n_1 and n_2 are the number of tests used. S_1^2 and S_2^2 are the variances for both rates compared. These values are found, or can be computed from values, in Tables 8 through 21.

In order to facilitate reading of graphs, confidence bars are indicated within each graph. These confidence bars were created by measuring the shortest distance between significantly different values on the graph. So values on the graph above each confidence bar which are separated by a distance equal to, or greater than, the

length of the confidence bar are to be considered significantly different at the 5% level. The length of each confidence bar is unrelated to differences in scale on the graph. In cases where no confidence bars are indicated below values, it is to be concluded that no significant differences exist between those values.

Temperature coefficients (Q_{10} values) indicate the ratio of the rate of activity at the given temperature to the rate at a temperature 10° C. lower. Q_{10} values were obtained from the following formula,

$$Q_{10} = \left(\frac{k_2}{k_1} \right)^{10/(t_2 - t_1)}$$

(Giese, p. 248).

k_2 and k_1 are rate measurements and t_2 and t_1 are the temperatures in °C. at the respective rate measurements.

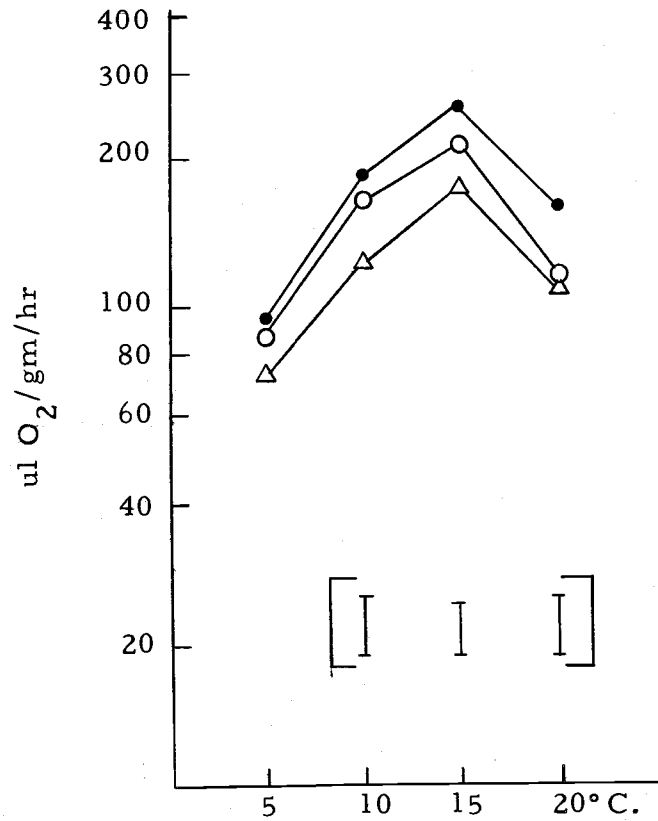


Figure 1. Field transplant experiment of *T. emarginata*.

- Low Control, pre-transfer
- △ Low to High transfer
- High Control, post-transfer

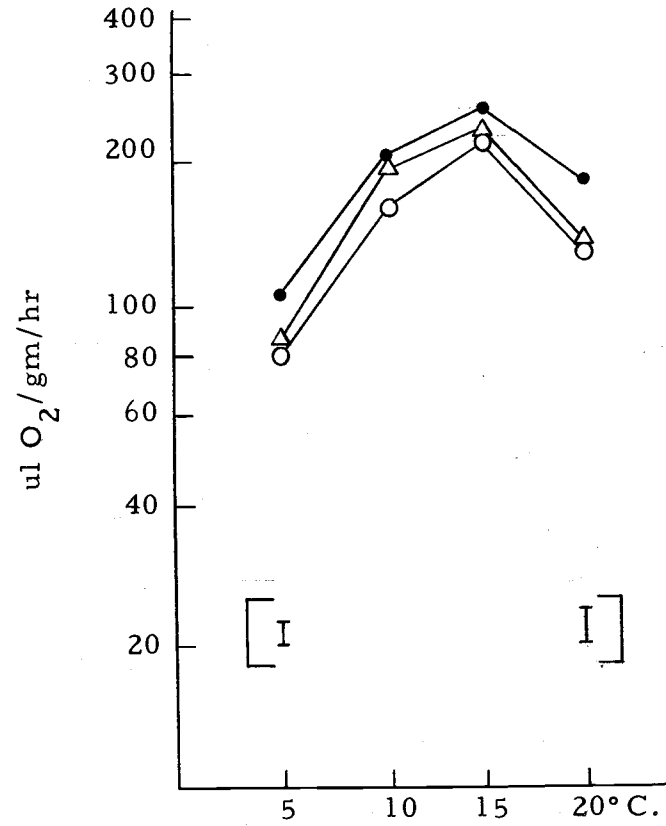


Figure 2. Field transplant experiment of *T. emarginata*.

- High Control, pre-transfer
- △ High to Low transfer
- Low Control, post-transfer

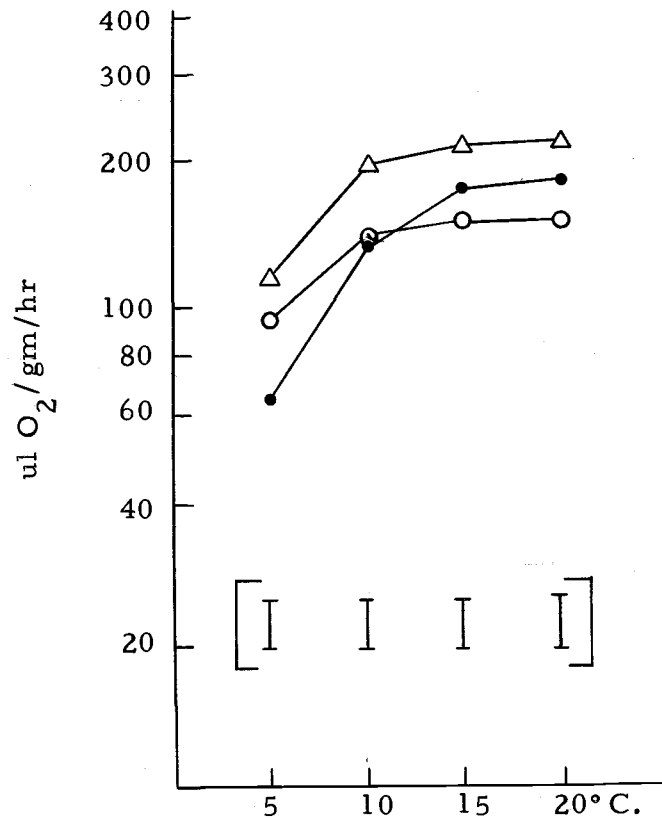


Figure 3. Laboratory simulated transplant experiments of *T. emarginata*.

- Low Control, pre-transfer
- △ High Control, post-transfer
- Low to High transfer

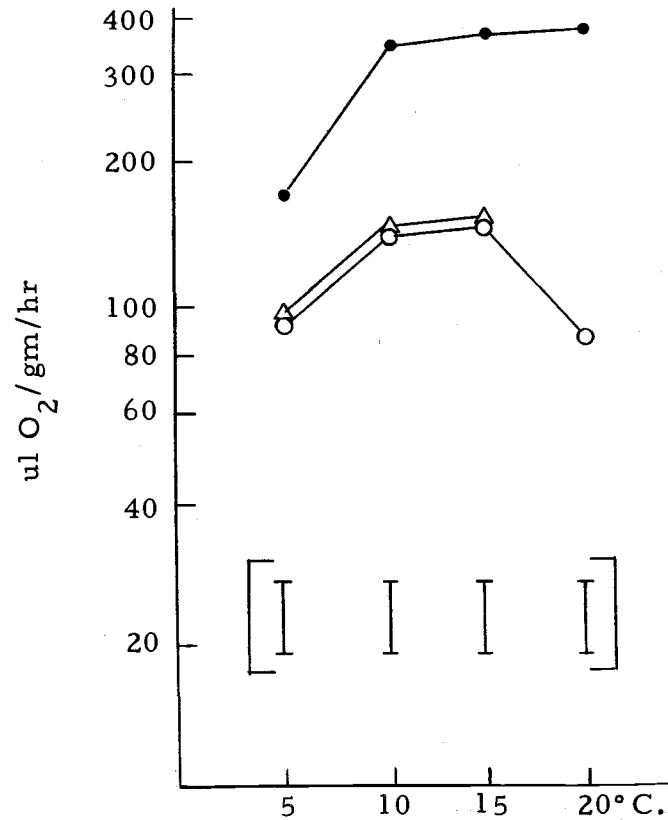


Figure 4. Laboratory simulated transplant experiments of *T. emarginata*.

- High Control, pre-transfer
- △ Low Control, post transfer
- High to Low transfer

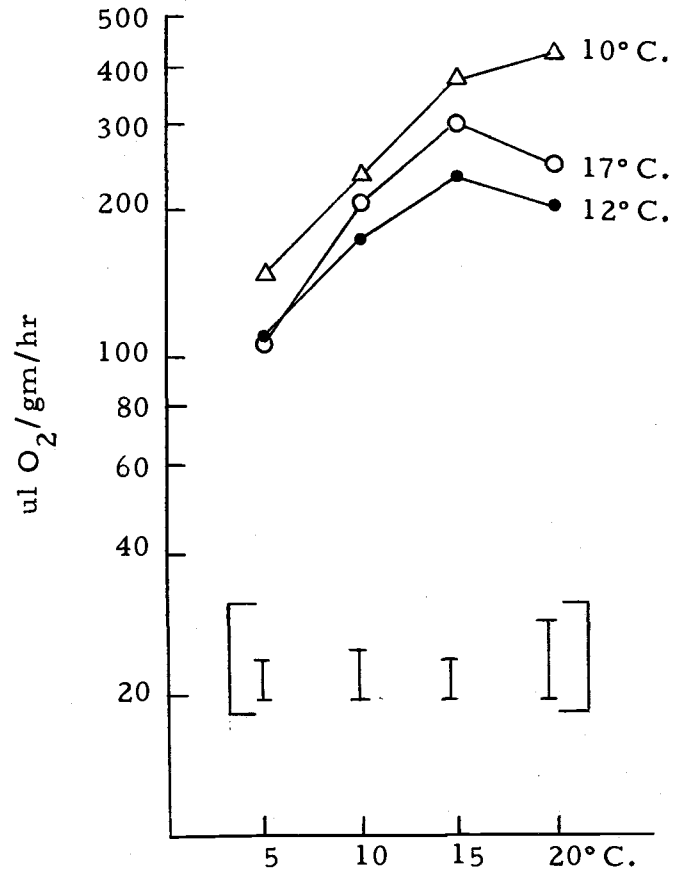


Figure 5. Temperature compensation study of low-level *T. emarginata*. Organisms were collected at the indicated environmental temperatures.

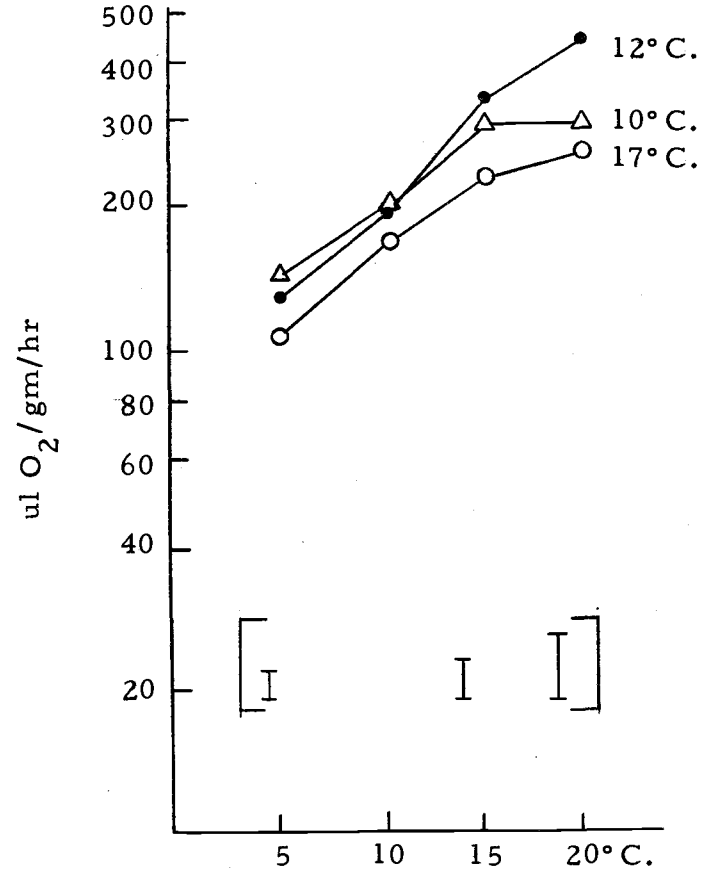


Figure 6. Temperature compensation study of high-level *T. emarginata*. Organisms were collected at the indicated environmental temperatures.

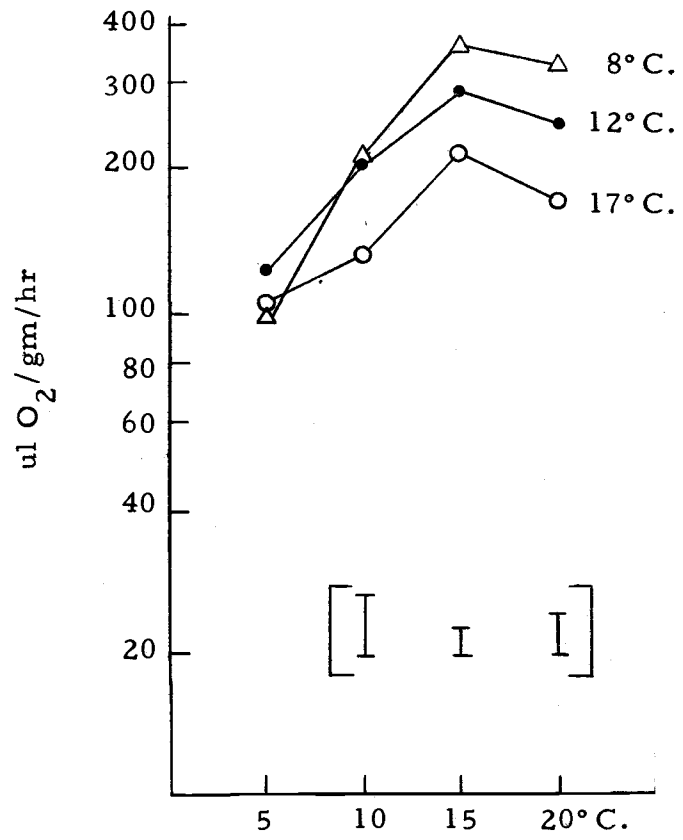


Figure 7. Temperature compensation study of low-level *T. emarginata*. Organisms were acclimated at the indicated temperatures.

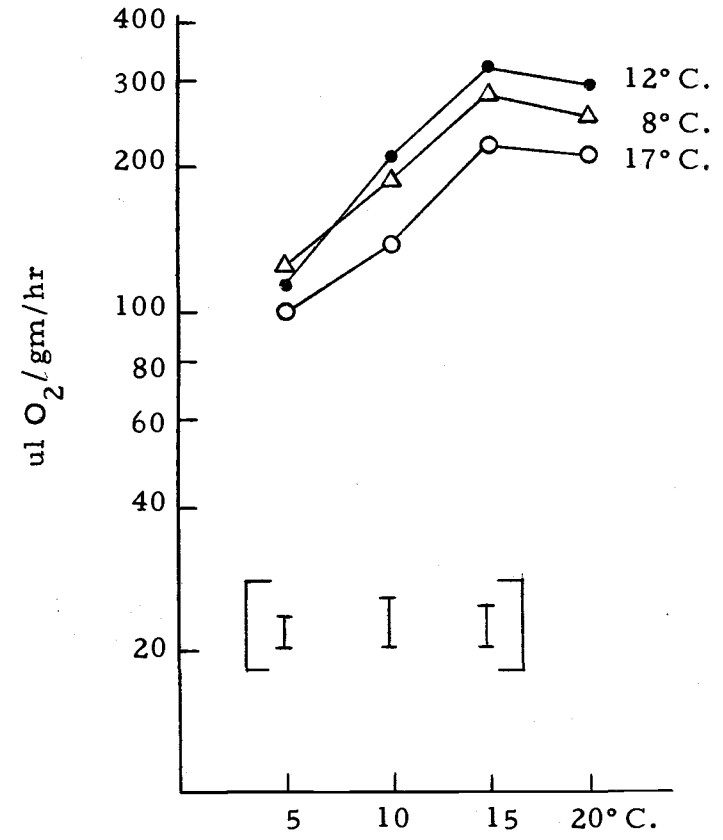


Figure 8. Temperature compensation study of high-level *T. emarginata*. Organisms were acclimated at the indicated temperatures.

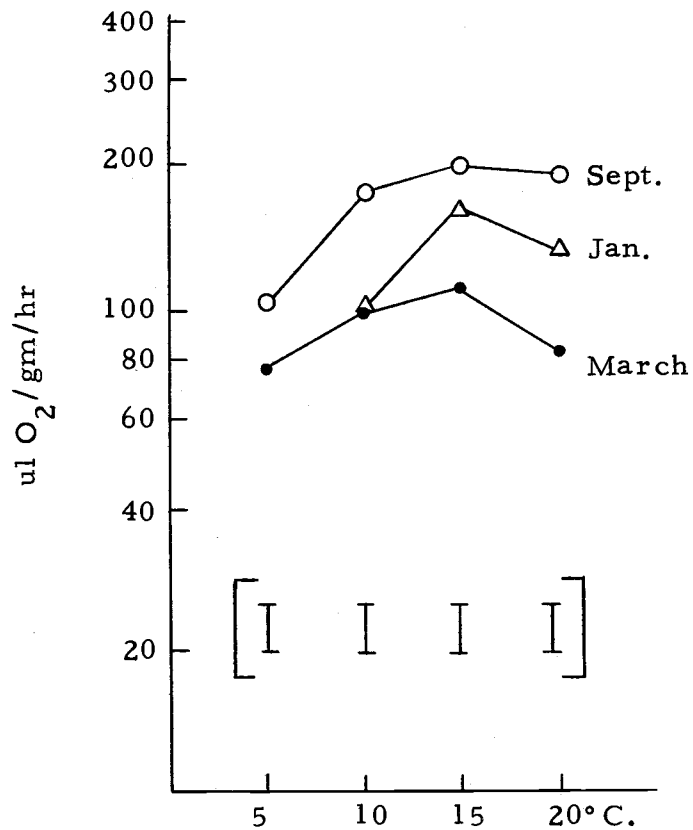


Figure 9. Seasonal study of high-level *T. emarginata*. Organisms were acclimated submerged in sea water and measured under aquatic conditions.

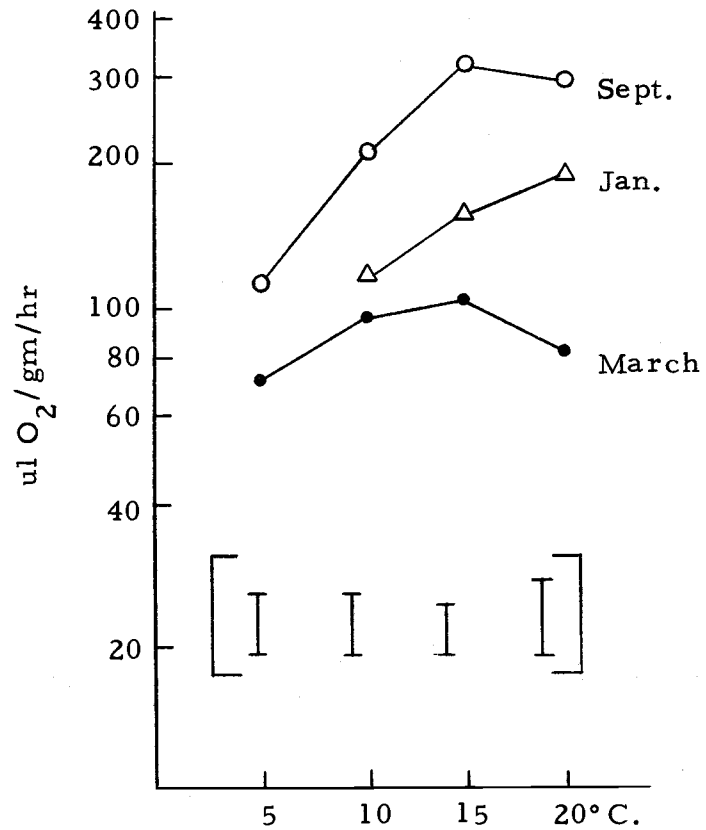


Figure 10. Seasonal study of high-level *T. emarginata*. Organisms were acclimated submerged in sea water and measured under aerial conditions.

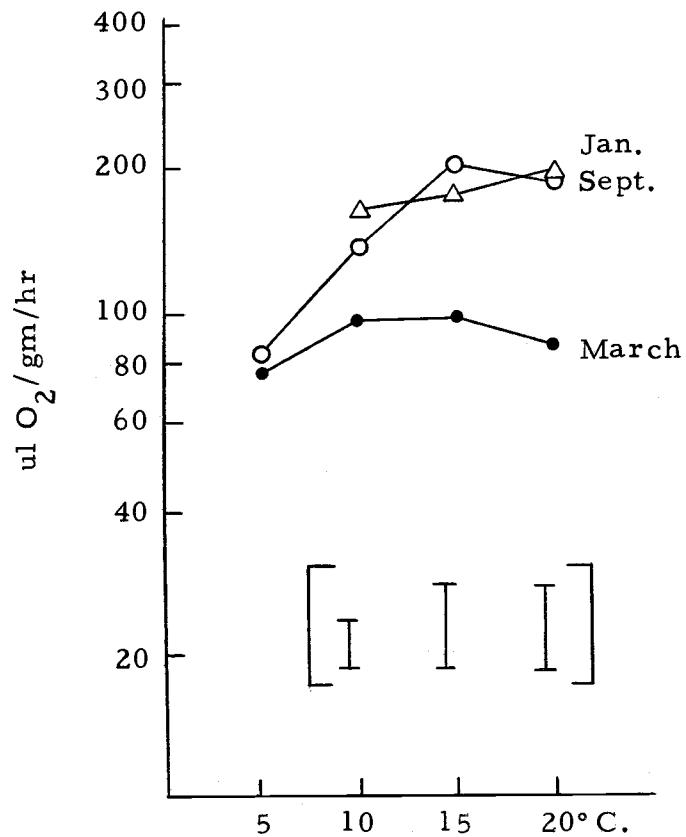


Figure 11. Seasonal study of low-level *T. emarginata*. Organisms were acclimated submerged in sea water and measured under aquatic conditions.

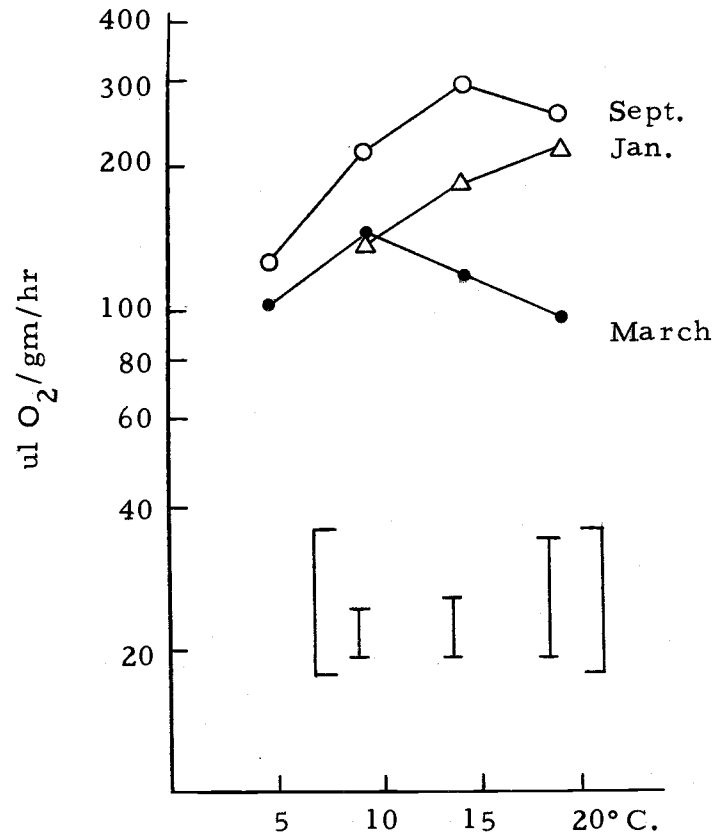


Figure 12. Seasonal study of low-level *T. emarginata*. Organisms were acclimated submerged in sea water and measured under aerial conditions.

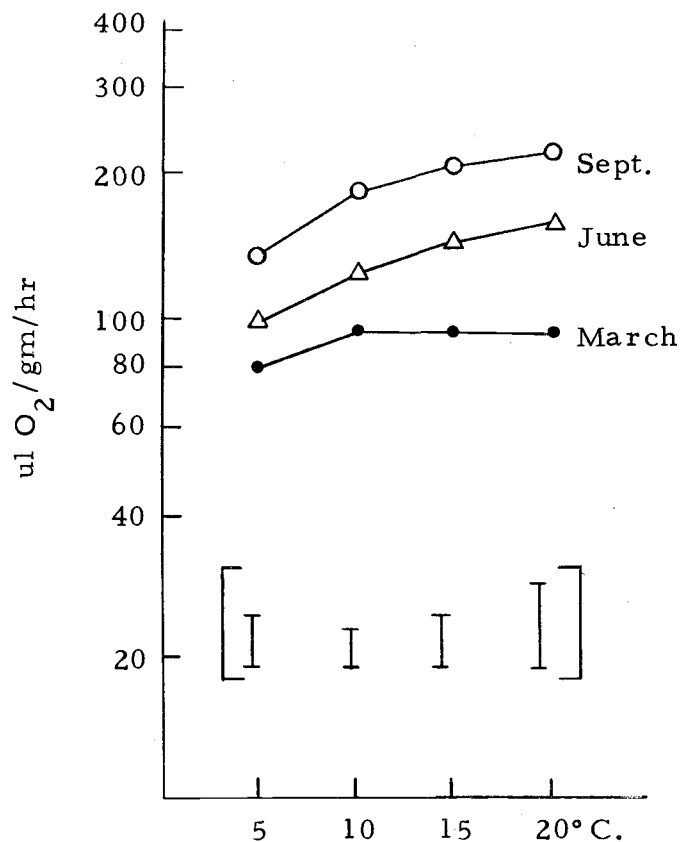


Figure 13. Seasonal study of high-level T. emarginata. Organisms were acclimated on a 16 hr. submergence-8 hr. exposure schedule and measured under aquatic conditions.

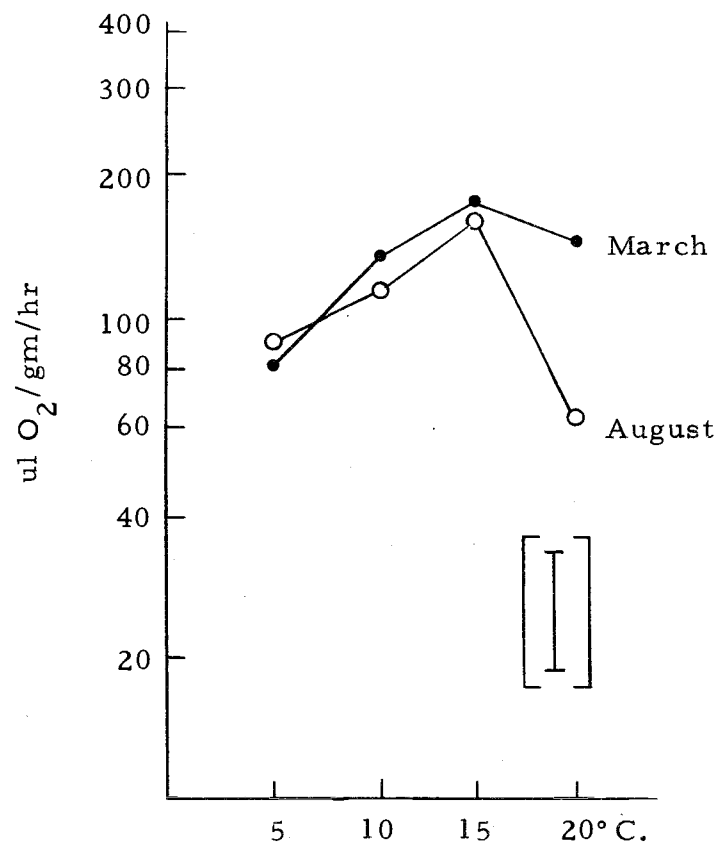


Figure 14. Seasonal study of high-level T. emarginata. Organisms were acclimated on a 16 hr. submergence-8 hr. exposure schedule and measured under aerial conditions.

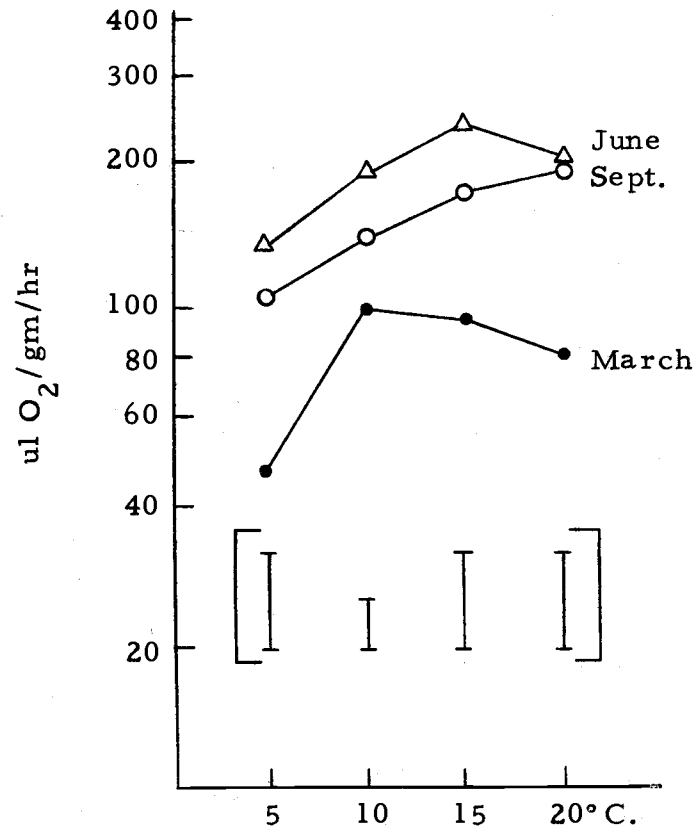


Figure 15. Seasonal study of low-level *T. emarginata*. Organisms were acclimated on a 16 hr. submergence-8 hr. exposure schedule and measured under aquatic conditions.

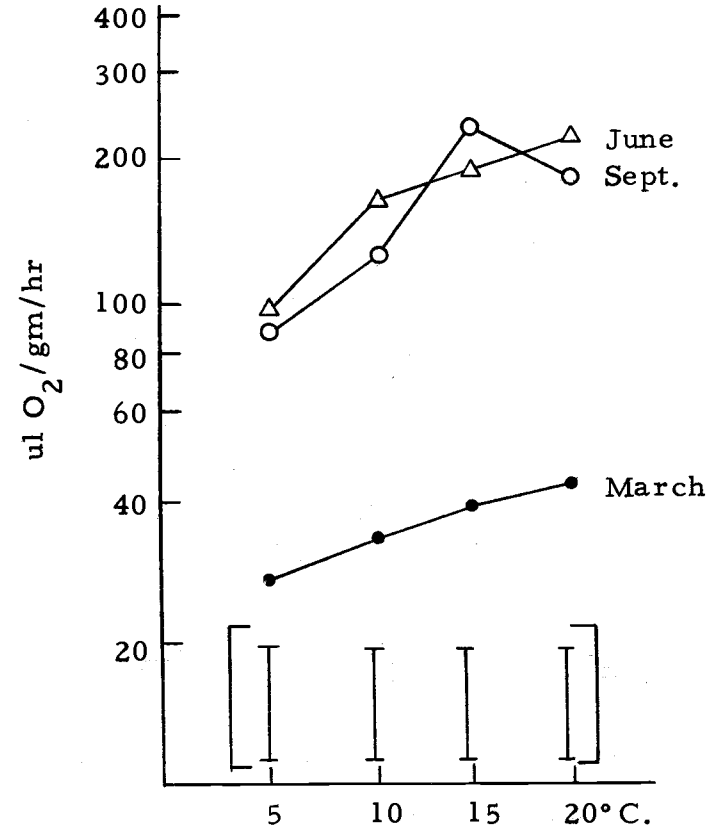


Figure 16. Seasonal study of low-level *T. emarginata*. Organisms were acclimated on a 16 hr. submergence-8 hr. exposure schedule and measured under aerial conditions.

Table 2. Q_{10} values for field transplantation of T. emarginata (Figures 1 and 2).

	5-10°C.	10-15°C.	15-20°C.
Low Control, post-transfer	4.124	1.814	0.339
High to Low transfer	4.104	1.442	0.367
High Control, pre-transfer	3.16	1.79	0.479
High Control, post-transfer	3.591	1.648	0.261
Low to High transfer	2.866	1.982	0.360
Low Control, pre-transfer	3.928	1.789	0.386

Table 3. Q_{10} values for laboratory transplantation of T. emarginata (Figures 3 and 4).

	5-10°C.	10-15°C	15-20°C.
High Control, pre-transfer	4.24	1.02	1.10
High to Low transfer	2.34	1.06	
Low Control, post-transfer	2.37	1.08	0.34
Low Control, pre-transfer	4.12	1.66	1.02
Low to High transfer	2.92	1.16	1.08
High Control, post-transfer	2.16	1.10	1.00

Table 4. Q_{10} values for effects of temperature compensation on field-acclimatized T. emarginata (Figures 5 and 6).

	5-10° C.	10-15° C	15-20° C.
<u>Low</u>			
12° C.	2.52	1.82	0.73
10° C.	2.43	2.59	1.25
17° C.	3.72	1.98	0.68
<u>High</u>			
12° C.	2.16	3.09	1.71
10° C.	1.93	2.31	0.98
17° C.	2.62	1.79	1.23

Table 5. Q_{10} values for effects of temperature compensation on laboratory-acclimated T. emarginata (Figures 7 and 8).

	5-10° C.	10-15° C.	15-20° C.
<u>Low</u>			
12° C.	3.06	1.82	0.73
8° C.	4.36	2.85	0.86
17° C.	1.56	2.75	0.62
<u>High</u>			
12° C.	3.49	2.40	0.77
8° C.	2.28	2.22	0.82
17° C.	1.90	2.52	0.92

Table 6. Q_{10} values for seasonal effects on oxygen consumption of T. emarginata acclimated submerged in sea water (Figures 9-12).

	5-10°C.	10-15°C.	15-20°C.
Low, aerial			
Jan.		1.809	1.364
March	2.064	0.624	0.687
Sept.	3.06	1.82	0.73
Low, aquatic			
Jan.		1.159	1.236
March	1.635	1.034	0.743
Sept.	2.65	2.22	0.81
High, aerial			
Jan.		1.874	1.364
March	1.809	1.168	0.627
Sept.	3.49	2.40	0.77
High, aquatic			
Jan.		1.572	0.672
March	1.710	1.245	0.538
Sept.	2.82	1.21	0.92

Table 7. Q_{10} values for seasonal effects on oxygen consumption of T. emarginata acclimated on a 16 hour submergence-8 hour exposure schedule (Figures 13-16).

	5-10° C.	10-15° C.	15-20° C.
Low, aerial			
March	1.705	1.218	1.234
June	2.842	1.276	1.385
Sept.	2.13	3.49	0.59
Low, aquatic			
March	4.717	0.944	0.683
June	1.993	1.658	0.688
Sept.	1.79	1.51	1.23
High, aerial			
March	2.772	1.666	0.692
August	1.66	1.87	0.16
High, aquatic			
March	1.408	0.996	0.927
June	1.540	1.378	1.089
Sept.	1.76	1.27	1.10

Table 8. Respiratory rates of *T. emarginata* used in microgeographic adaptation study (Figures 1 and 2).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
Low Control, pre-transfer				
5° C.	42	14	94.86	31
10° C.	36	12	188.07	47
15° C.	39	13	252.33	68
20° C.	30	10	157.15	26
High Control, pre-transfer				
5° C.	36	12	107.25	22
10° C.	36	12	191.41	54
15° C.	39	13	258.30	91
20° C.	36	12	178.75	58
Low Control, post-transfer				
5° C.	33	11	78.25	22
10° C.	33	11	158.98	43
15° C.	33	11	214.23	56
20° C.	30	10	124.93	55
High Control, post-transfer				
5° C.	33	11	87.89	30
10° C.	36	12	166.63	53
15° C.	30	10	214.11	67
20° C.	33	11	109.44	55
High to Low transfer				
5° C.	30	10	85.81	24
10° C.	30	10	189.31	59
15° C.	36	12	227.47	75
20° C.	27	9	137.85	48

Table 8. Respiratory rates of T. emarginata used in microgeographic adaptation study (Figures 1 and 2) (cont.).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
Low to High transfer				
5° C.	36	12	73.72	29
10° C.	30	10	124.85	64
15° C.	33	11	175.88	98
20° C.	18	6	109.04	34

Table 9. Respiratory rates of *T. emarginata* used in microgeographic adaptation study (Figures 3 and 4).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
Low Control, pre-transfer				
5° C.	36	12	67.68	18
10° C.	30	10	137.63	28
15° C.	30	10	178.75	50
20° C.	18	6	181.95	40
High Control, pre-transfer				
5° C.	30	10	170.35	64
10° C.	24	8	350.95	64
15° C.	27	9	354.80	130
20° C.	21	7	373.87	172
Low Control, post-transfer				
5° C.	39	13	90.27	15
10° C.	39	13	139.32	28
15° C.	33	11	145.45	34
20° C.	30	10	85.88	35
High Control, post-transfer				
5° C.	36	12	96.99	23
10° C.	39	13	141.75	38
15° C.	30	10	150.21	32
20° C.	30	10	150.29	68
High to Low transfer				
5° C.	39	13	95.05	28
10° C.	33	11	146.25	41
15° C.	30	10	151.49	36

Table 9. Respiratory rates of T. emarginata used in microgeographic adaptation study (Figures 3 and 4) (cont.).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
Low to High transfer				
5° C.	33	11	115.74	35
10° C.	30	10	198.96	73
15° C.	33	11	215.54	92
20° C.	27	9	224.34	79

Table 10. Respiratory rates of *T. emarginata* used in temperature compensation study (Figure 5).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>12° C.</u>				
5° C.	27	9	110.15	19
10° C.	36	12	175.35	48
15° C.	30	10	237.02	80
20° C.	24	8	204.30	68
<u>10° C.</u>				
5° C.	33	11	150.52	40
10° C.	36	12	236.26	53
15° C.	30	10	380.44	53
20° C.	30	10	426.30	124
<u>17° C.</u>				
5° C.	36	12	109.44	26
10° C.	36	12	211.42	39
15° C.	33	11	300.21	38
20° C.	36	12	250.11	81

Table 11. Respiratory rates of *T. emarginata* used in temperature compensation study (Figure 6).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>12° C.</u>				
5° C.	33	11	128.73	21
10° C.	36	12	190.06	35
15° C.	33	11	335.38	43
20° C.	30	10	440.94	58
<u>10° C.</u>				
5° C.	36	12	140.69	41
10° C.	33	11	196.08	45
15° C.	33	11	298.51	60
20° C.	30	10	297.00	48
<u>17° C.</u>				
5° C.	39	13	103.61	20
10° C.	39	13	167.96	37
15° C.	39	13	226.65	55
20° C.	27	9	251.80	57

Table 12. Respiratory rates of *T. emarginata* used in temperature compensation study (Figure 7).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>12° C.</u>				
5° C.	30	10	124.04	28
10° C.	24	8	217.95	51
15° C.	21	7	295.61	82
20° C.	18	6	255.86	54
<u>8° C.</u>				
5° C.	33	11	102.89	14
10° C.	33	11	215.74	35
15° C.	36	12	364.64	76
20° C.	30	10	341.38	81
<u>17° C.</u>				
5° C.	36	12	106.01	21
10° C.	33	11	133.04	30
15° C.	30	10	221.21	60
20° C.	30	10	176.09	67

Table 13. Respiratory rates of *T. emarginata* used in temperature compensation study (Figure 8).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>12° C.</u>				
5° C.	30	10	116.27	23
10° C.	27	9	217.94	27
15° C.	27	9	338.69	46
20° C.	36	12	299.04	104
<u>8° C.</u>				
5° C.	36	12	123.24	25
10° C.	36	12	186.16	38
15° C.	36	12	278.04	65
20° C.	33	11	254.02	114
<u>17° C.</u>				
5° C.	30	10	100.24	18
10° C.	39	13	138.46	48
15° C.	27	9	220.22	72
20° C.	21	7	212.60	77

Table 14. Respiratory rates of T. emarginata used in seasonal study (Figure 9).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	33	11	106.91	28
10° C.	27	9	179.92	42
15° C.	30	10	199.58	70
20° C.	24	8	193.53	52
<u>Jan.</u>				
10° C.	18	18	102.66	26
15° C.	20	20	166.45	48
20° C.	20	20	136.55	66
<u>March</u>				
5° C.	42	14	76.03	32
10° C.	42	14	99.52	36
15° C.	42	14	111.08	42
20° C.	42	14	81.55	45

Table 15. Respiratory rates of T. emarginata used in seasonal study (Figure 10).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	30	10	116.27	23
10° C.	27	9	217.94	27
15° C.	27	9	338.69	46
20° C.	36	12	299.07	104
<u>Jan.</u>				
10° C.	44	44	114.88	36
15° C.	42	42	157.33	44
20° C.	30	30	183.86	38
<u>March</u>				
5° C.	36	12	71.04	28
10° C.	30	10	95.57	50
15° C.	30	10	103.36	41
20° C.	42	14	81.94	54

Table 16. Respiratory rates of T. emarginata used in seasonal study (Figure 11).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	33	11	85.45	19
10° C.	30	10	139.95	64
15° C.	27	9	209.25	101
20° C.	30	10	189.80	105
<u>Jan.</u>				
10° C.	28	28	161.70	59
15° C.	27	27	174.20	66
20° C.	25	25	193.75	73
<u>March</u>				
5° C.	39	13	75.97	29
10° C.	33	11	97.21	41
15° C.	30	10	98.89	31
20° C.	36	12	85.27	16

Table 17. Respiratory rates of T. emarginata used in seasonal study (Figure 12).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	30	10	124.04	28
10° C.	24	8	217.95	51
15° C.	21	7	295.61	82
20° C.	18	6	255.86	54
<u>Jan.</u>				
10° C.	27	27	135.86	45
15° C.	25	25	182.79	58
20° C.	21	21	213.66	74
<u>March</u>				
5° C.	42	14	102.16	25
10° C.	42	14	146.57	38
15° C.	36	12	116.06	41
20° C.	39	13	96.31	32

Table 18. Respiratory rates of T. emarginata used in seasonal study (Figure 13).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	39	13	136.90	35
10° C.	36	12	182.74	32
15° C.	33	11	207.42	45
20° C.	36	12	218.18	103
<u>June</u>				
5° C.	39	13	100.53	29
10° C.	30	10	124.80	33
15° C.	36	12	146.63	54
20° C.	30	10	153.10	50
<u>March</u>				
5° C.	33	11	80.63	25
10° C.	33	11	96.78	19
15° C.	33	11	96.60	20
20° C.	39	13	93.11	30

Table 19. Respiratory rates of T. emarginata used in seasonal study (Figure 14).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>August</u>				
5° C.	33	11	89.42	13
10° C.	33	11	115.81	41
15° C.	24	8	159.68	50
20° C.	33	11	64.36	19
<u>March</u>				
5° C.	21	7	81.46	15
10° C.	24	8	135.68	19
15° C.	30	10	175.25	22
20° C.	30	10	145.82	37

Table 20: Respiratory rates of T. emarginata used in seasonal study (Figure 15).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	27	9	105.32	22
10° C.	27	9	141.93	34
15° C.	27	9	175.29	59
20° C.	21	7	194.69	47
<u>June</u>				
5° C.	36	12	134.60	34
10° C.	36	12	190.10	32
15° C.	33	11	244.96	57
20° C.	30	10	203.53	60
<u>March</u>				
5° C.	33	11	46.81	16
10° C.	30	10	101.68	21
15° C.	27	9	98.85	22
20° C.	36	12	81.80	27

Table 21. Respiratory rates of T. emarginata used in seasonal study (Figure 16).

	No. of snails used	No. of tests used	Mean value ul O ₂ /gm/hr	Standard deviation
<u>Sept.</u>				
5° C.	33	11	87.11	20
10° C.	30	10	127.39	42
15° C.	27	9	238.34	48
20° C.	33	11	183.87	79
<u>June</u>				
5° C.	33	11	98.10	11
10° C.	36	12	165.42	39
15° C.	33	11	187.05	60
20° C.	27	9	220.21	60
<u>March</u>				
5° C.	36	12	26.75	15
10° C.	30	10	34.96	14
15° C.	42	14	38.63	12
20° C.	39	13	42.94	12

DISCUSSION

Variability and Population Properties of *T. emarginata*

The main difficulty encountered in testing differences between high-level and low-level *T. emarginata* was the fact of individual variability in the respiratory response of each organism. Of course a variable respiratory response over a temperature range of 5-20° C. may be a good survival mechanism in an organism inhabiting the intertidal region with a daily fluctuation of temperature and exposure. This fact may indicate inherent plasticity in the physiology of the organism which allows for tolerance of external variation.

Other difficulties associated with confirming differences between high and low-level populations of *T. emarginata* were the lack of knowledge of their breeding habits and also the fact of dramatic upward migration of this organism during the months of August and September. It may be that, even though the high and low-level populations were isolated populations during most of the year, there was enough mixing within the entire population to prevent marked differences in respiratory rates of high and low-level populations.

Upward migration of *T. emarginata* has also been reported by Connell (1970). He attributed the cause of this movement to a

depletion of food in the lower zones. The upper limit of the Thais population is determined by a combination of two factors, the distribution of barnacles upon which they feed and the time available for feeding during high tide.

Microgeographic Adaptations of T. emarginata

Bullock (1955) states that differences in metabolic rates between organisms separated by a vertical distance of less than a meter have been found in intertidal invertebrates. Reference has already been made to some studies of intertidal organisms where physiological differences have been found in high and low-level organisms. This study of T. emarginata indicates no general significant difference between high-level and low-level organisms (Figures 1 and 2).

In the simulated transplantation experiment, the high-level organisms exhibited a considerably higher respiratory rate than the low-level organisms (Figures 3 and 4). After prolonged exposure of the high-level organisms to the low-level tidal schedule, these organisms exhibited the same respiratory rate as the low-level controls, thus showing acclimation to the low-level conditions. The low-level organisms also showed some accommodation of respiratory rate to the high-level conditions. This ability of the organism from one level to accommodate after prolonged exposure to conditions of the

other tidal level indicates that any differences noted in respiratory rates before acclimation are phenotypic expressions of metabolic rate and are indications of the adaptive flexibility of this organism.

High-level and low-level T. emarginata from another area were also compared. In this area the high-level and low-level organisms were separated by a horizontal distance of approximately 100 feet and a vertical distance of two feet, without a continuous distribution of organisms between the high and low-level populations. The results of this study are not included in this paper and did not indicate any differences in high and low-level organisms of this area, even though they probably were separate populations and located sufficiently far enough apart to permit no migration to occur from one population to the other.

From this study one may conclude that populations of T. emarginata separated by small distances within their habitat do not exhibit different respiratory rate responses to temperature changes, even though the populations may be isolated from one another for a long period of time.

Results of the temperature compensation study of T. emarginata are confusing (Figures 5-8). In general, the low-level organisms, that were either collected at 10° C. or acclimated at 8° C. in the laboratory, appear to respond as cold-adapted organisms (Figures 5 and 7). These organisms have a higher respiratory rate

at 15-20°C. than do low-level organisms acclimated or collected at 17°C.

The respiratory rates of organisms collected at three different field temperatures vary at the testing temperatures of 15-20°C. (Figures 5 and 6). Lewis (1971) found that in comparing the respiration of three tropical gastropods the respiratory rate varied with the area where the snails were collected. Rates were higher in those organisms collected from habitats with higher mean maximum temperatures. However, in contrast to the results of Lewis (1971), low-level T. emarginata collected at 10°C. had a higher respiratory rate than those collected at 17°C.

Ulbricht (1969) found, in a study of sea urchins, that Strongylocentrotus purpuratus, which inhabits a higher intertidal level than S. franciscanus, had a greater capacity for temperature compensation of metabolic rate than did S. franciscanus. This study indicates that both high and low-level T. emarginata exhibit the same capacity for temperature compensation, even though the low-level (cold-adapted) organisms exhibit a higher respiratory rate at 15-20°C. than the high-level organisms adapted to the same temperature.

Seasonal Adaptation of T. emarginata

Results of the seasonal adaptation study of T. emarginata generally indicate that there is no difference between the respiratory

rate of high-level and low-level organisms measured under comparable conditions. However, there are interesting observations of seasonal effects that can be shown from this study.

Respiratory rates of high-level and low-level T. emarginata measured under aerial conditions during the month of September are dependent upon temperature changes when measured between 5-15° C. (Figures 9-16). Metabolic rates of high-level and low-level organisms measured under aquatic conditions are less affected by temperature changes. The average Q_{10} values for metabolic rates during September, measured under aerial conditions, are 2.87 for rates measured from 5-10° C. and 2.23 for rates measured from 10-15° C. The comparable Q_{10} values obtained under aquatic conditions are 2.23 and 1.55 respectively. Respiratory rates measured at other times of the year were generally more temperature independent.

Newell (1966) has suggested that many measurements of oxygen consumption of invertebrates have been made by sampling only the respired medium at various intervals and that this may lead to false conclusions concerning the effect of temperature on poikilotherm metabolism. He suggests that instead of a gradual increase in oxygen consumption with time there is an alteration between rapid oxygen consumption when the animal is active and a slower rate corresponding to periods of quiescence. Rapid respiratory rates

vary with temperature in much the same way as reported for direct observations of activity, however, rates of slower animals studied by him do not vary greatly with temperature over the range of 7.5-20°C. He concluded that the metabolic processes of intertidal invertebrates may be relatively independent of short term temperature fluctuations over the normal environmental temperature range. The range in which this independence occurs is related to the environmental temperatures to which the poikilotherm is subjected.

Newell and Pye (1970) studied the seasonal metabolic rates of acclimatized Littorina littorea and Mytilus edulis and found that active metabolic rates were temperature dependent for all seasons and standard or basal metabolic rates were temperature independent.

A study by Mangum and Sassaman (1969) on the temperature sensitivity of active and resting metabolism in a polychaetous annelid indicated different results. Neither active nor resting metabolism of acclimated worms showed perfect thermal compensation. Instead, Q_{10} values for active and resting metabolism were found to be similar to one another and also similar to values from previous work where a distinction was not made between active and resting metabolism.

Numerous workers have obtained data which yields evidence for the dependence of the "basal" metabolic rate on temperature (Tribe and Bowler, 1968). Another interpretation of Newell's results

for intertidal organisms may be that during quiescence the organisms incur an oxygen debt while relying on anaerobic metabolism to some degree. This oxygen debt is then restored when the organism is again submerged in water. A difficulty in Newell's interpretation is that it may be inaccurate to break up rate-temperature curves into phases since these phases may be interdependent. It is also difficult to know how to accurately describe activity versus nonactivity in many intertidal organisms.

The metabolic rates observed in this study of T. emarginata were more dependent on temperature changes during September. According to Newell's interpretation the September rates may represent active rates, since this is the time of active feeding for this organism. March rates may be more representative of standard rates.

Temperature is also a seasonal variable which must be considered in an interpretation of seasonal data. Average monthly high and low temperatures, shown on page 8, indicate aerial temperatures. However, these may not be the aerial temperatures to which intertidal organisms are exposed. It is possible that organisms were exposed to colder aerial temperatures in March than in January, since, during January, the low tides generally occurred during the afternoon and evening whereas in March the low tides generally occurred in early and mid-morning.

The results for T. emarginata generally correlate with seasonal work done on intertidal crabs. Dehnel (1960) found that Hemigrapsus nudus and H. oregonensis have a higher respiratory rate in summer than in winter over the same temperature range. Respiratory rates of Uca pugnax were also observed to be higher in June, July and August than in December, January and February (Webb and Brown, 1961).

Respiratory rates of Patella aspera and high and low-level populations of P. vulgata were related with intertidal location (Davies, 1966). In January no difference in the respiratory rates of these was found. During July, the respiratory rates of low-level P. vulgata and of P. aspera were higher than in January while the rate of high level P. vulgata was unchanged. These phenomena were interpreted as results of thermal acclimation, since during January Davies found the temperature at low and high tide levels to be very much the same. During July the high-tide organisms were exposed to high temperatures for a longer period of time.

The seasonal studies reported in this paper in Figures 13 and 16 are similar to results obtained on seasonal studies reported in Figures 9-12. The only difference is the respiratory rates measured under aerial conditions for organisms tested during March. This difference must be due to the alteration of submergence at 10° C. and exposure at 10° C. used in the acclimation schedule of one group

of organisms (Figures 13-16), in contrast to an acclimation schedule of complete submergence in sea water at 10°C. for the other group of organisms (Figures 9-12).

Roberts (1957) studied respiratory rates of Pachygrapsus crassipes and found no significant relation to seasonal trends in temperature. He concluded that behavioral modifications of activity and habitat selection were more significant adaptation factors than thermal acclimation of respiration.

A seasonal study should also consider the factor of reproduction. While there were always a number of egg capsules of T. emarginata present in the area of study, a very significant increase in egg capsules was observed during March, 1971. The March metabolic rates were determined from organisms collected after this time. Precht (1958) notes that, during winter months, there is usually a decline in metabolic rate. The low metabolic rate values obtained during March are probably correlated with lower aerial temperatures rather than with reproductive activity since they are post-reproductive rates.

In conclusion it may be stated that T. emarginata is a regulating organism in terms of maintaining a stable respiratory rate in relation to external changes in temperature. There are behavioral modifications which are also effective in maintaining an internal equilibrium in environmental stress situations of the intertidal

habitat. Thais emarginata tends to cluster within rock crevices during times of severe temperature stress.

Temperature and activity are two important factors which affect the respiratory rate of this organism. There is a trend toward higher respiratory rates during months with warmer aerial temperatures during low tides and also during months of greater feeding activity.

Upward migration of these organisms and a lack of knowledge of the breeding habits of this population make it difficult to conclude that high and low-level populations are truly distinct even though mobility of these organisms during most of the year indicates that high and low-level organisms are isolated. Low-level (cold-adapted) organisms have a higher respiratory rate at 15-20° C. than high-level organisms acclimated and tested at the same temperatures. Even though there was a difference in the response of high and low-level (cold-adapted) organisms, there was no difference in the respiratory rate of high and low-level organisms when the respiratory rate was tested over an experimental temperature range of 5-20° C.

The outstanding metabolic adaptation feature of T. emarginata is that, while this organism can regulate its metabolic rate under circumstances of changing environmental conditions, there is also a wide margin of variability in metabolic rate which can be tolerated by the organism. This characteristic helps to insure survival of a population of T. emarginata in the intertidal zone where daily as

well as seasonal, environmental changes in temperature and exposure regularly occur.

SUMMARY

1. Metabolic rate-temperature relationships for Thais emarginata, a marine gastropod, were determined using oxygen consumption rate measurements.
2. Two groups of experiments were performed. In one, organisms from vertically-separated populations were studied to determine microgeographic differences in metabolic rates. Field transplantation and laboratory simulated transplantations were also performed in this group. Metabolic rates of warm-adapted and cold-adapted organisms were also determined in order to study temperature compensation of this organism. In the second, metabolic rates were determined over a range of temperatures using animals collected during several months of the year.
3. Studies of microgeographic metabolic rate results indicate that where low-level and high-level populations of T. emarginata are separated by small distances there is no significant difference between the metabolic rate response of these organisms to temperature change.
4. Results of transplantation studies, generally indicate that no significant difference exists in metabolic rate between high-level and low-level organisms.

5. Results of temperature compensation studies indicated that the low-level (cold-adapted) organisms were more sensitive to warmer temperatures than high-level (cold-adapted) organisms.
6. Both high-level and low-level (warm-adapted) organisms responded with the same degree of cold sensitivity and resistance to warm temperatures.
7. The seasonal metabolic rate results indicate that the rate-temperature measurements are higher and more dependent upon temperature changes during months of feeding activity than during months of little feeding activity.
8. The seasonal metabolic rate results also indicate that the rate-temperature measurements were lowest during the month during which the coldest aerial temperatures were measured and during the time following deposition of egg capsules.
9. Thais emarginata generally regulates its respiratory rate in relation to external changes in temperature.

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