

# Metabolic adaptation of animals from different latitudes<sup>1</sup>

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**KURZFASSUNG: Stoffwechseladaptation bei Tieren aus verschiedenen Breiten.** In dem Maße, in welchem sich die Verbreitungsgrenzen von Populationen ausweiten, verursachen neue Umweltstresse selektive Beeinflussungen. Es ist daher durchaus denkbar, daß latitudinal getrenntlebende Tier-Populationen sich allmählich in ihren physiologischen Reaktionen zu unterscheiden beginnen. Für einschlägige Studien erwiesen sich Kurzschwanzkrebse der Gattung *Uca* als sehr geeignet, da die Artvertreter sowohl Affinitäten zur gemäßigten Zone als auch zu tropischen Gebieten besitzen und hinsichtlich ihrer Verbreitung eine Überlappungszone entlang der subtropischen Ostküste Zentral-Floridas (USA) besteht. Stoffwechselphysiologische Untersuchungen an *Uca*-Populationen von New York, North Carolina, Florida, Puerto Rico und Jamaika weisen darauf hin, daß tatsächlich eindeutige Unterschiede bestehen. Ganz allgemein reagieren Versuchstiere aus der gemäßigten Zone stoffwechselphysiologisch labiler, während tropische Arten stenothermer sind. Die Untersuchungen wurden durchgeführt über einen Bereich verschiedener konstanter Temperaturen, und zwar sowohl an adulten Tieren und Larven als auch an verschiedenen Geweben (Herz, Muskel, Gehirn, Kieme und Mitteldarmdrüse). Die Beziehungen stoffwechselphysiologischer Reaktionen, welche zwischen Ganztier und Gewebe einerseits und den verschiedenen ontogenetischen Stadien andererseits gefunden wurden, erlauben einige Generalisierungen. Das Akklimatisationsmuster ist nicht bei allen Lebenszyklusstadien dasselbe. Die Gewebe zeigen nicht die gleichen stoffwechselphysiologischen Reaktionen wie das Ganztier. Eine uniforme Beziehung zwischen latitudinaler Verbreitung aller Arten oder Populationen und ihren Reaktionen ist nicht evident.

## INTRODUCTION

As organisms attempt to extend their distributional limits, they are faced with a new complex of environmental stresses. If these new stresses are too extreme and an animal is unable to cope with them, the organism is unable to colonize. However, if the species has the prerequisite adaptive capacity, it may be successful and survive in the new area. At any location in the range of a species, unusual environmental fluctuations, such as hurricanes (WELLS 1961) or heavy rains (GOODBODY 1961), may destroy populations, but normally animals at either end of the distributional limits

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appear most sensitive to changes in environmental factors. An example of this are "winter kills" of fish in Florida following unusually severe winter temperatures (STOREY & GUDGER 1936, MILLER 1940).

The study of the physiological response of organisms to ecological factors is of basic importance in understanding the distribution of animals. Physiologically distinct populations may arise as a result of evolutionary processes operating differentially on latitudinally separated populations of one species. All observed variations in the physiological response of animals from different latitudes may not be genetic; rather these differences may reflect phenotypic expressions induced by different intensities of environmental factors acting in various latitudes. Therefore, it is important to differentiate between genotypic and phenotypic responses. To distinguish between these two responses, some useful information can be obtained by acclimation studies and/or by rearing animals under different environmental conditions.

Historically early significant work in the field of metabolic adaptation was done by FOX & WINGFIELD (1936-1939), SPÄRCK (1936), TAKATSUKI (1928) and THORSON (1936). Since then an ever-increasing interest has been shown in the physiological differences of animal populations that are latitudinally separated (see review by VERNBERG 1962). These studies have taken diverse paths and stress various levels of biological organization: some deal with the response of the whole organism, some with the response of tissues, while still others stress biochemical changes. Because of the complexity of this subject, many of these studies are by necessity of a descriptive nature. In order to understand the mechanism(s) of metabolic adaptation, we must correlate and integrate the results of all these various approaches. Two problems in the field of quantitative biology of metabolism are: 1) to assess adequately the role of physiological variation when different populations of organisms are compared; and, 2) to determine which generalizations and models are valid when the metabolism of latitudinally separated animals is compared.

The present paper deals only with one aspect of this broad problem, i. e. metabolic adaptations to temperature. This topic is further delineated in that studies involving but one genus of decapod crustaceans, *Uca*, will be emphasized. This paper represents an attempt to review the results of various published studies and unpublished data with the goal in mind of examining aspects of the quantitative metabolism of one genus which extends over a wide geographical range. Metabolic studies involving larval and adult fiddler crabs as well as tissues of these animals will be reviewed.

#### ANIMALS STUDIED

*Uca* is a cosmopolitan genus which inhabits the intertidal zone and regions adjacent to marine waters. The various species show somewhat different habitat preferences. Species of this genus were selected for study for the following three reasons: a) the various species have either temperate zone or tropical zone affinities, and, in addition, there is an area of overlap of some northern and some southern forms along the northeast coast of Florida; b) each species is very abundant and in-

dividuals are not too difficult to collect; c) animals are easily maintained in the laboratory.

The following species have been studied: Temperate zone species: *Uca pugnax*, Massachusetts to northeast Florida; *Uca minax*, Massachusetts to southern Florida; *Uca pugilator*, Massachusetts to southern Florida. Tropical zone species: *Uca rapax*, from northeast Florida to Brazil; *Uca thayeri*, from northeast Florida to Brazil; *Uca mordax*, from the Bahamas to Brazil; *Uca leptodactyla*, from the west coast of Florida to Brazil.

## METABOLIC STUDIES

### Larval stages

In a number of species larval stages tend to respond differently to certain physical factors in degree or manner from the adult stages (COSTLOW, BOOKHOUT & MONROE 1959, MELLANBY 1940). Therefore, to assess the importance of a physical factor to

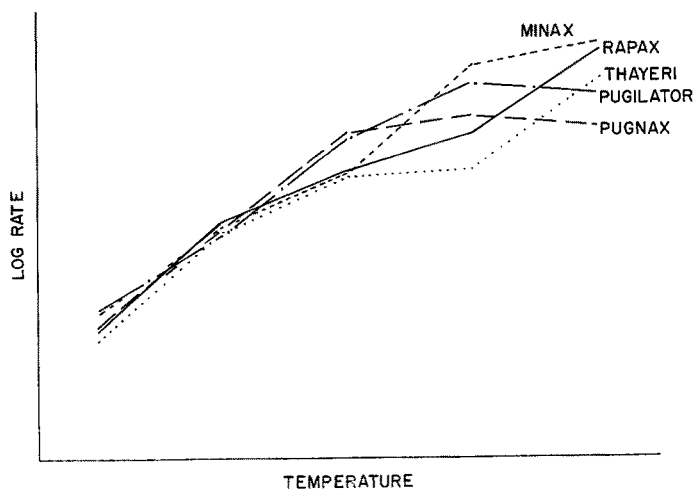


Fig. 1: The comparative metabolic-temperature curves of first stage zoea of various species of temperate zone and tropical zone fiddler crabs

an organism, the effect on all stages in the life cycle should be studied. This section of the paper will review the larval studies on *Uca* (VERNBERG & COSTLOW, in preparation). All stages in the life-cycle of fiddler crabs are free-living; typically, there are five zoeal stages, one megalops, then the crab stage. Data are presented on two tropical zone species, *U. rapax* and *U. thayeri*, and on three temperate zone species. The temperate zone species include populations of *U. minax* from North Carolina, *U. pugnax* from North Carolina and New York, and *U. pugilator* from Florida, North Carolina and Massachusetts.

Detailed descriptions of the rearing techniques and methods of determining metabolic rates are described by VERNBERG & COSTLOW (in preparation). All the animals were reared at a temperature of 25° C and a salinity of 30 p. p. t.; this combination resulted in maximum survival and growth of all species. Metabolic rates were measured in microrespirometers after the method of GRUNBAUM et al. (1955).

### *First stage zoea*

There were no striking differences in metabolic rates between tropical and North Carolina temperate zone zoea over a 15° to 30° C temperature range (Fig. 1). However, when the temperature was increased from 30° to 35° C, the respiration rate of the tropical zone species increased slightly more than 50%, while the  $Q_{O_2}$  of the zoea of temperate zone species remained relatively constant. The metabolic rates of *U. pugilator* zoea from Florida were intermediate between the temperate zone and tropical zone species at this temperature. These differences are reflected in  $Q_{10}$  values. The

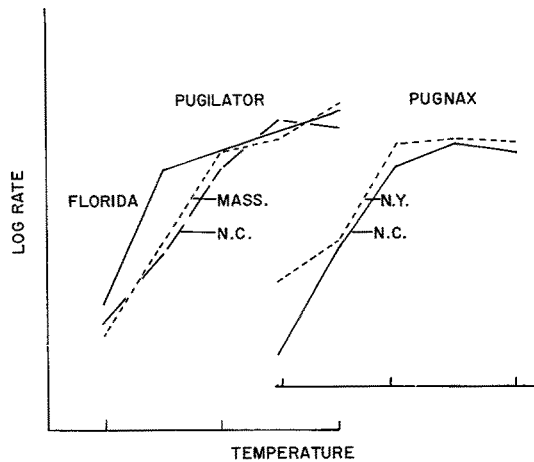


Fig. 2: The comparative metabolic-temperature curves of first stage zoea of latitudinally separated populations of fiddler crabs

$Q_{10}$ 's of the tropical species were between 2.0 and 3.0, while the values of the Florida and temperate zone zoea, when the differences were great enough to calculate, were all less than 2.0.

The most marked differences in the metabolism of latitudinally separated populations were observed in *U. pugnax* at lower temperatures (Fig. 2). The  $Q_{O_2}$  of zoea of crabs from New York was 35% higher than the respiration of zoea of the same species from North Carolina when measured at 15° C. This could quite possibly be correlated with the lower water temperatures found in the New York area. These curves are typical for warm and cold-acclimated animals, i. e., in cold-acclimated or cold-adapted species the curve is displaced laterally to the left of warm-acclimated

or warm-water forms. No generalization could be discerned in comparisons between tropical and temperate zoea at 15° C, and in all species, except *U. pugnax* from New York, the respiration rate increased over 50% when the temperature was raised from 15° to 20° C (Figs. 1 and 2). Perhaps this reflects the relatively warm temperatures to which even the temperate zone zoea would be exposed, since the zoea typically are released during the warmer months.

### *Megalops*

It was not always possible to obtain large numbers of the megalops stage with all species; this was particularly true of *U. pugnax* from North Carolina. Although there was a limited number of *U. pugnax* megalops available, certain trends do seem to be apparent when larvae from New York and North Carolina are compared.

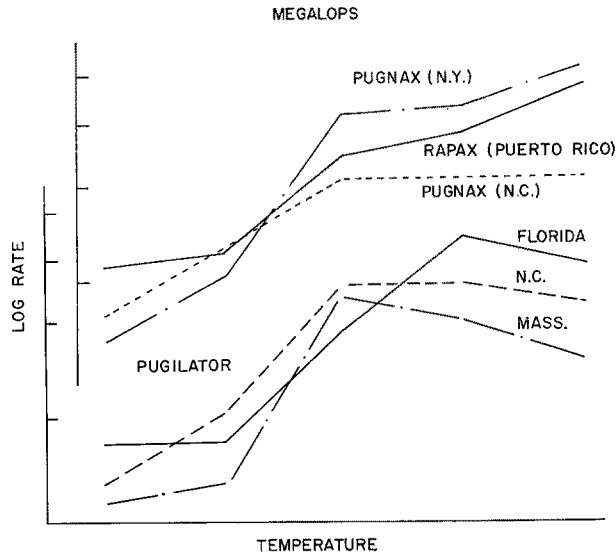


Fig. 3: The comparative metabolic-temperature curves of megalops of various species and populations of fiddler crabs

Whereas the zoea from these two populations differed markedly at 15° C but not at higher temperatures, the megalops had a similar response at 15° C, but at 35° C, the larvae from New York had a  $Q_{O_2}$  which was 41% higher than that of the North Carolina populations (Fig. 3).

The metabolic rate of the megalops stage from the three *U. pugilator* populations (Massachusetts, North Carolina and Florida) also differed somewhat from the response of the zoeal stages. The North Carolina larvae had consistently, but not always significantly, higher  $Q_{O_2}$  values than did the megalops from Massachusetts. The maximum  $Q_{O_2}$  values were obtained at different temperatures for each population. The

highest respiration rate of larvae from Massachusetts was reached at 25° C, for those from North Carolina the highest rates were at 25° and 30° C, and the megalops from Florida reached a maximum  $Q_{O_2}$  at 30° C. Florida megalops also had the highest values of the three populations at 15° C.

The megalops stage of *U. rapax* responded very much the same as did the zoeal stage at the higher temperatures; the highest respiration for both was obtained at 35° C. At 15° and 20° C, however, the pattern shifted. The  $Q_{O_2}$  of the zoea increased 70% when the temperature was raised to 20° C, but in the megalops stage the respiration rate was still depressed at 20° C and increased only 9% over that measured at 15° C.

### Young crabs

After the megalops metamorphosed into the young crab stage, a new pattern of metabolic response emerged among the three populations of *U. pugilator* (Fig. 4). Crabs from the Florida population had the lowest metabolic rate, the ones from Mas-

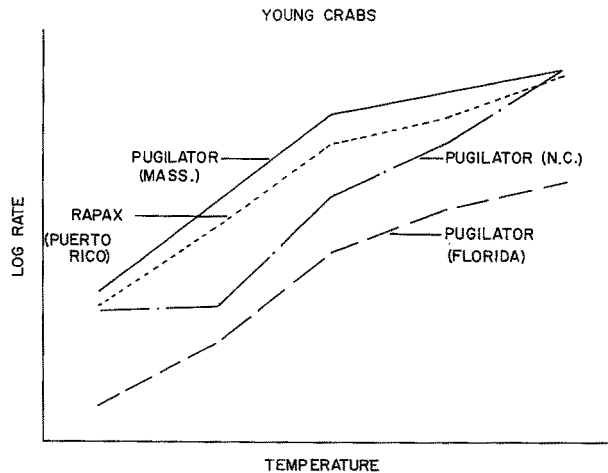


Fig. 4: The comparative metabolic-temperature curves of young crabs of various populations and species of fiddler crabs

sachusetts the highest rate. In all three populations the maximum  $Q_{O_2}$  was obtained at 30° C. Comparable data are not available for *U. pugnax*. The young crabs of *U. rapax* responded very much in the same manner as the megalops stage.

### Adults

A series of metabolic-temperature (M-T) curves is presented in Figure 5 showing the pattern of acclimation in adult *Uca* as reported by DEMEUSY (1957) and VERN-

Table 1  
Comparisons of patterns of acclimation in *Uca*

species	stage of life cycle or type of tissue	pattern number (according to PROSSER)	comment	reference
<i>pugilator</i>	adults	II A	populations from Mass. & Fla.	DEMEUSY (1957)
<i>pugilator</i>	young adults	II A	populations from Mass., N.C. & Fla.	VERNBERG & COSTLOW (in preparation)
<i>rapax</i>	adult	I or III B	animals from Jamaica	VERNBERG (1959)
<i>rapax</i>	adult	III A	animals from Fla.	VERNBERG (1959)
<i>pugnax</i>	adult	IV A	animals from N.C.	VERNBERG (1959)
<i>pugnax</i>	adult	II A	populations from N.Y. & N.C.	TASHIAN (1956)
<i>rapax</i>	adult	II A	populations from Fla. & Trinidad	TASHIAN (1956)
<i>pugilator</i>	1st stage zoea	IV D	populations from Fla. & N.C. (or Mass.)	VERNBERG & COSTLOW (in preparation)
<i>pugilator</i>	1st stage zoea	I	populations from N.C. & Mass.	VERNBERG & COSTLOW (in preparation)
<i>pugnax</i>	1st stage zoea	IV A	populations from N.Y. & N.C.	VERNBERG & COSTLOW (in preparation)
5 species of <i>Uca</i>	1st stage zoea	I	three temperate zone species from N.C. and two tropical species	VERNBERG & COSTLOW (in preparation)
<i>pugnax</i>	megalops	III B	populations from N.C. & Mass.	VERNBERG & COSTLOW (in preparation)
<i>pugilator</i>	megalops	doesn't fit any described pattern	populations from Fla. & N.C. (or Mass.)	VERNBERG & COSTLOW (in preparation)
<i>pugnax</i>	gill	IV A	populations from N.C.	VERNBERG (1960)
<i>pugnax</i>	mid-gut gland	III A	populations from N.C.	VERNBERG (1960)
<i>rapax</i>	gill	III A	populations from Jamaica	VERNBERG (1960)
<i>rapax</i>	mid-gut gland	I	populations from Jamaica	VERNBERG (1960)
<i>pugilator</i>	brain	II B	populations from N.C.	VERNBERG & VERNBERG (unpublished)
<i>pugilator</i>	muscle	III B	populations from N.C.	VERNBERG & VERNBERG (unpublished)
<i>pugilator</i>	heart	IV C	populations from N.C.	VERNBERG & VERNBERG (unpublished)

BERG (1959). Populations of *U. pugilator* from Massachusetts consumed oxygen faster than a population sample from Florida. Cold- and warm-acclimated *U. rapax* from Jamaica displayed similar metabolic responses to temperature at lower temperatures; at higher temperatures the cold-acclimated animals had a higher rate. In contrast a more northern population of *U. rapax*, living in a sub-tropical region, had a distinctly

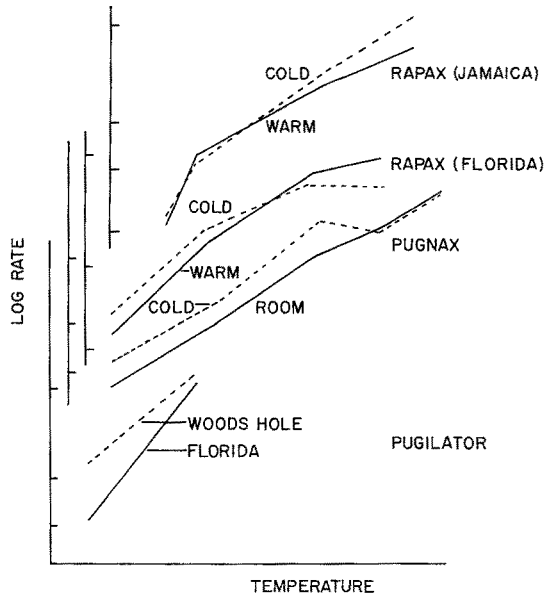


Fig. 5: The comparative metabolic-temperature curves of adult crabs of various populations and species of fiddler crabs

different pattern; at lower temperatures the cold-acclimated forms had higher  $Q_{O_2}$ 's and at higher temperatures the warm-acclimated animals had the higher rate. Thus, physiological diversity can be observed within one species. A temperate zone species, *U. pugnax*, had still another pattern of response; at low and intermediate temperatures the cold-acclimated animals had higher metabolic rates, but at high temperatures the response was similar. The work of TASHIAN (1956) further demonstrated that M-T curves of fiddler crabs from various geographical areas are dissimilar.

A system of classification of patterns of acclimation of rate function to temperature was proposed by PROSSER (1958). Briefly the different patterns are as follows: Type I: No adaptation; cold- and warm-acclimated animals have similar responses. Type II: Translation; the M-T curve of cold-acclimated animals is displaced either to the left or to the right of the curve of the warm-acclimated animals. Type III: Rotation; the M-T curves may intersect as a result of a change in the  $Q_{10}$  values. Type IV: Translation and Rotation; in certain cases the intersection of the two M-T curves may be observed only by extrapolation and may occur outside the range of normal temperature tolerance. Four variations of this type were described. See also page 442 of this volume.



Certain generalizations can be made if this system of classification of PROSSER's is applied to the studies on adult and larval *Uca* as well as their tissues (Table 1). The pattern of acclimation in *Uca* is not the same in all stages of the life cycle of the species. Moreover, a uniform relationship between latitudinal distribution of all species and pattern of response is not evident. That is, all the southern populations of different species of *Uca* do not exhibit the same pattern nor do all the northern

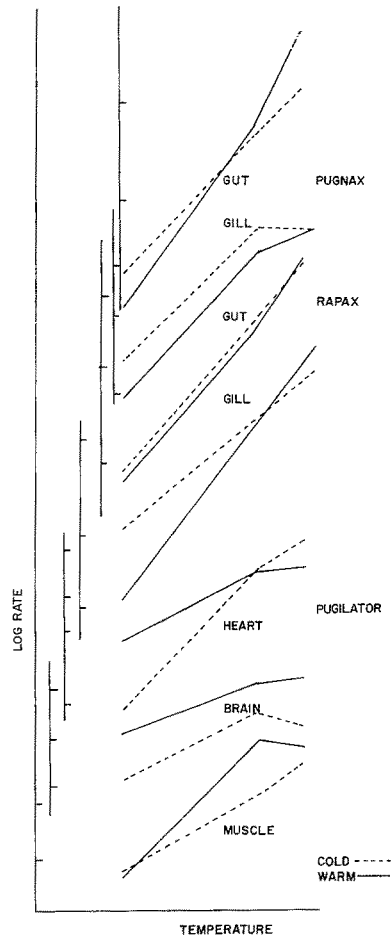


Fig. 6: The comparative metabolic-temperature curves of tissues of various species of tropical and temperate zone fiddler crabs

populations. The pattern has to be determined for each species and cannot be postulated from a generalized relationship. Because different patterns are observed in latitudinally separated populations, inherent physiological differences have apparently taken place during the evolution and distribution of a species.

The description of patterns of acclimation is of significance in that they permit some speculation concerning biochemical mechanisms. PROSSER (1958) has described

the biochemical implications of the different patterns which includes such possibilities as change in enzyme activity, change in activation energy, or shift between alternate enzymatic pathways. Detailed studies of these various biochemical alternatives should greatly improve our understanding of the quantitative biology of metabolism during thermal acclimation. By investigating populations of animals from different latitudes, comparative information on metabolic patterns of response should shed light on the mechanism or mechanisms involved.

**Tissues:** To attempt to understand mechanisms involved in temperature acclimation the question may be asked if the response of the tissues is the same as that of the whole animal. If acclimation to temperature is not a general cellular response representing one pattern, then one suggestion might be that certain regulatory mechanisms coordinate the response exhibited by the whole organism. Although work on tissues of *Uca* is in the preliminary stages, M-T curves of some tissues from warm- and cold-acclimated animals of certain species are available (Fig. 6) (VERNBERG 1960).

Gill tissue from warm- and cold-acclimated North Carolina animals displayed a similar response (Pattern IV A) as did the whole organism. But a different pattern for mid-gut gland was observed (III B). Neither gill tissue nor mid-gut gland from warm- and cold-acclimated *U. rapax* gave the same response pattern as for the whole organism: gill tissue was pattern III A; mid-gut gland, I; and the whole organism, III B. In preliminary studies of a third species, *U. pugilator*, we have found that the heart, supraesophageal ganglion (the "brain"), and muscle each had a different pattern and all were different from that of the whole animal (Fig. 6). The patterns are IV C, II B, III B, and II A respectively. From these data all tissues apparently do not behave metabolically the same as the whole organism during thermal acclimation.

#### SUMMARY

1. The present paper reviews certain quantitative aspects of the physiological characteristics of animal populations from different latitudes. Special emphasis is placed on decapod crustaceans of the genus *Uca*, the fiddler crabs.
2. Metabolic characteristics, determined over a graded temperature series and under different conditions of thermal acclimation, are given for larvae and adults of tropical and temperate zone species. Patterns of thermal acclimation according to Prosser's system may be different for each stage of development. No consistent pattern appears to be typical of either tropical or temperate zone species or for different latitudinally separated populations of the same species.
3. The patterns of metabolic-temperature response of various tissues ("brain", muscle, gill, heart, and mid-gut gland) are not all the same as the response of the whole organism.

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*Discussion following the paper by VERNBERG & VERNBERG*

KRÜGER: Ich kenne Ihre sehr interessanten und wichtigen Untersuchungen über *Uca* aus dem Biological Bulletin. Ich habe versucht, sie mit der von mir vorgeschlagenen Temperaturfunktion auszuwerten. In einer Reihe von Fällen scheint es mir möglich zu sein, sie mit der neuen Funktion darzustellen. Man würde dann zu Parametern kommen, die den Kurvenverlauf charakterisieren, und könnte dann diese Parameter vielleicht zur Charakterisierung des Klima-Einflusses auswerten. Die Beschäftigung mit den Wachstumsproblemen hat mich leider daran gehindert, diese Auswertung zum Abschluß zu bringen.

VERNBERG: I would like to learn your new technique of plotting mathematic expressions of temperature-rate functions.

WIESER: You have shown that in the small zoea larvae the warm-acclimated animals have a higher metabolism than the cold-acclimated ones, whereas in the young adults the reverse holds true. Could it be that this is so because the larvae have a relatively larger surface and therefore can avail themselves of more oxygen than the adults?

VERNBERG: This is possible. However, it should be noted that the first stage zoea have not been acclimated for as long a period as the megalops and young crabs.

ROBERTS: Is there a possibility that in observing the higher metabolism of warm-adapted (N. Carolina) zoea stages as opposed to cold-adapted (Massachusetts) stages, that this might be due to more frequent molting by the warm-climate animals and reflect molting metabolism?

VERNBERG: At 25° C the rate of molting appears to be similar in northern and southern forms. The animals from the different regions are used in the same stage of molting.

GRAINGER: To what extent have differences in body size (for the same developmental stage) with latitude complicated results?

VERNBERG: Larvae from the north are larger than ones from the south based on nitrogen. However, influence on respiration is not clear. In *Uca pugilator*, southern forms are higher than northern forms, but relationship was reversed in case of *U. pugnax*.

KINNE: Have you attempted to differentiate between non-genetic and genetic components of the adaptations reported? Long-term rearing experiments on individuals from different localities may here prove very useful.

VERNBERG: By rearing studies, we hope to be able to have animals grown at different temperatures so we can determine genotypic limits. Rearing experiments are in progress now.

KINNE: And how about transplantation experiments?

VERNBERG: No transplantation studies have been made. Jamaica animals will not survive at the low temperatures of Beaufort, North Carolina. Evidence from field studies show that Florida species are killed off by cold winters.