

Geographic Variation in the Respiratory Metabolism and Temperature Coefficient in Tropical and Temperate Forms of the Fiddler Crab, *Uca pugnax*¹

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(Text-figures 1-6)

INTRODUCTION

RECENTLY Rao & Bullock (1953) and Dehnel (1955), in re-evaluating and making rather complete reviews of the literature on climatic adaptation in marine poikilotherms, have brought together convincing evidence in support of the following conclusions: (1) rate functions within a given species are usually similar in individuals from northern and southern regions when measured at their normal environmental temperatures; (2) at any given temperature, activity rates are greater in forms from the northern latitudes; (3) cold-adapted or northern individuals have lower temperature coefficients than related warm-adapted species; (4) larger animals of the same species are generally more sensitive to temperature changes than are smaller ones. The purpose of the present investigation is to examine these concepts on one species having an especially great north-south distribution, for in so doing it would seem that these important basic concepts relating to climatic adaptation in cold-blooded animals could be further clarified.

The fiddler crab, *Uca pugnax*, was considered particularly well suited as the experimental animal, ranging as it does from Cape Cod, Massachusetts, south to Rio de Janeiro, Brazil. This semiterrestrial crab lives in the intertidal zone and is most often found in a muddy rather than a sandy habitat. Two races have been described: the nominate form extending from Massachusetts to east-central Florida, and the southern subspecies (*rapax*) from southern Florida to Brazil. The tropical forms average larger in size

than those from the temperate regions. *Uca pugnax rapax* was studied from material collected in Trinidad, B.W.I., and southern Florida, and *Uca pugnax pugnax* from New York and North Carolina. Comparisons were made not only of the oxygen and temperature coefficients of representative populations throughout most of the range of this species, but also of their tolerance to low temperature.

The experimental work was carried out at the field station of the Department of Tropical Research of the New York Zoological Society, Arima Valley, Trinidad, B.W.I.; the Lerner Marine Laboratory of the American Museum of Natural History, Bimini, Bahamas, B.W.I.; the Duke University Marine Laboratory, Beaufort, North Carolina; and the zoological laboratories of Columbia University, New York. I wish to thank Dr. Charles M. Breder, Jr., director of the Lerner Laboratory, and Dr. Arthur W. Pollister, executive officer of the Department of Zoology, Columbia University, for making facilities available to me as a guest investigator.

I am especially grateful to Dr. William Beebe, director emeritus, and Miss Jocelyn Crane, assistant director, of the Department of Tropical Research of the New York Zoological Society for their support and encouragement of this project. I am likewise much indebted to Dr. F. John Vernberg, Department of Zoology, Duke University, for the loan of apparatus used in these experiments as well as his valuable assistance in many ways during the course of this study. I also wish to thank Mr. David H. McDermott, formerly of the Biology Department of Long Island University, for making some of the respirometers used in this investigation. Identification of much of the critical ani-

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mal material from Florida was made by Miss Crane. Mr. Ludolf Wehekind, hydrologist for the Works and Hydraulics Department, Port-of-Spain, Trinidad, kindly supplied the climatic data for Trinidad.

MATERIALS AND METHODS

In comparing animals from different latitudes, populations were selected having reasonably comparable environmental temperatures at the time of collecting (Text-figure 1). *Uca pugnax* was collected from the vicinity of the following localities on the inclusive dates: Port-of-Spain, Trinidad (10° 40' N), March 29 to April 4; Jamaica Bay, New York (40° 35' N), June 13 to July 12; Beaufort, North Carolina (34° 42' N), July 22 to August 4; and Key Biscayne, Florida (25° 47' N), August 15. Specimens of *Uca leptodactyla* were taken from Bimini, Bahamas (25° 44' N), August 23 to 29. Only males were used. In those crabs from New York, North Carolina and Florida, the males were noted to be displaying (waving the claws) during the collecting periods, implying that they were in breeding condition (Crane, 1943). The one exception was in the New York area where waving was not observed until June 18. The animals were maintained in terraria and fed regularly. It was always sought to collect fresh material weekly; however, in some cases where accessibility was a problem, they were maintained as long as two weeks.

Oxygen consumption was tested in a water-saturated atmosphere at two temperature levels: the upper ranging from 23.3 ± 0.5 to 24.6 ± 0.6° C. and the lower from 14.0 ± 0.1 to 14.9 ± 0.4° C. For large specimens, volumetric respirometers were employed of a type described by Flemister & Flemister (1951), and for the smaller animals a volumetric plastic micro-respirometer designed after that developed by Scholander (1950) was used. In these determinations 30 minutes were allowed for thermal equilibrium, and the test was then run for four and a half hours, the first half hour's reading being discarded. The results are corrected to standard temperature and pressure. The crabs were not acclimated in any way but in all cases were taken directly from room temperature where they had been maintained to the experimental temperature.

When the oxygen coefficient or Q_{O_2} [total O_2 consumption (cc.)/wet body weight/(gms.)/time (hrs.)] was plotted against the observed weight a curve was obtained of the type:

$$Y = aX^b$$

where Y represents the Q_{O_2} , X the observed weight, and a and b are the regression coeffi-

cients of the intercept and slope. These data were plotted double logarithmically. The constants a and b were determined from the following formulae (deviation from the means of X and Y are represented by x and y , and the number of determinations by N):

$$b = \frac{\Sigma(\log X \cdot \log Y) - N(\Sigma \log x \cdot \Sigma \log y)}{\Sigma \log^2 X - N \log^2 x}$$

$$\log a = \log y - b(\log x)$$

Further statistical data: the standard deviation from regression or standard error of the estimate ($S_{y \cdot x}$ or $S_{\log y \cdot \log x}$) and the coefficient of correlation (r) were calculated from the equations:

$$S_{y \cdot x} = \sqrt{\frac{\Sigma \log^2 y - b(\Sigma \log x \cdot \log y)}{N - 2}}$$

$$r = \sqrt{\frac{b(\Sigma \log x \cdot \log y)}{\Sigma \log^2 y}}$$

In determining the tolerance to low temperatures the crabs from all localities but New York were placed in water-saturated containers (pre-cooled to the experimental temperature) and then immersed in a constant temperature water bath kept at 5° C. The time of entry was recorded and the animals then periodically examined to determine the lethal point. The specimens from New York were kept in moist bowls in a constant temperature (5° C.) cold room and examined daily.

The climatological figures for New York, North Carolina and Florida were taken from the records for New York, Hatteras and Miami Beach in the Climatological Data (U. S. Dept. of Commerce) for 1954-55. The data for Trinidad are from the St. Clair Experimental Station, Port-of-Spain.

RESULTS AND DISCUSSION

Respiratory Metabolism and Latitude

The comparative data on respiration rates are summarized in Table 1. At the upper temperature testing levels (23.3–24.6° C.) *Uca pugnax* from Trinidad showed the highest oxygen consumption. This becomes even more significant when we realize that not only do the Trinidad forms average larger in size, but also that they were not in breeding condition. At the lower temperatures (14.0–14.9° C.) the rates were relatively similar for all populations. Since the warmer testing temperatures were reasonably close to the environmental temperatures during the collecting periods (Text-figure 1), it can be seen that at their normal habitat temperatures

TABLE 1. SUMMARY OF METABOLISM DATA FOR *Uca pugnax*

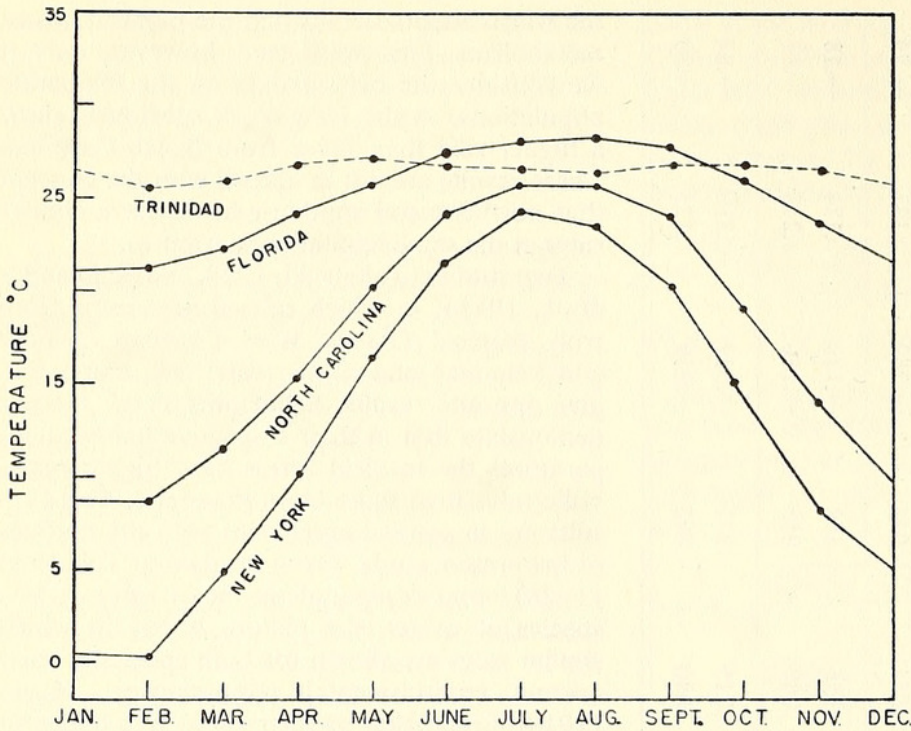
Locality	Temperature °C.	Size of Sample	Wet Body Weight (gms.)		Qo ₂ (cc./gm./hr.)		Statistical Analysis				
			Range	Mean	Range	Mean	a	b	S _{y·s}	r	
New York	23.8 ±0.7	33	.10-4.26	2.09	.070-.575	.154	.140	-.321	.189	-.68	
	14.1 ±0.2	31	.02-4.12	1.54	.038-.269	.107	.091	-.167	.246	-.45	
North Carolina	23.3 ±0.5	41	.09-5.58	2.41	.035-.344	.114	.109	-.305	.162	-.74	
	14.0 ±0.1	33	.07-4.71	1.93	.019-.144	.051	.045	-.269	.131	-.79	
Florida	24.4 ±0.2	24	.50-3.17	1.94	.073-.274	.156	.158	-.148	.174	-.18	
	14.9 ±0.4	23	.19-2.69	1.45	.022-.140	.060	.055	-.110	.213	-.17	
Trinidad	24.6 ±0.6	41	.09-8.51	3.20	.060-.553	.215	.217	-.329	.130	-.84	
	14.6 ±0.2	21	.10-8.32	3.51	.028-.245	.080	.082	-.359	.115	-.89	

the warm-adapted crabs had the higher rates of metabolism. This holds true, however, only if we consider the overall data on the temperate populations, as the New York specimens show a higher rate than those from North Carolina. These results are not in accord with the concept that northern and southern forms have similar rates at the same habitat temperatures.

Two studies (Takatsuki, 1928, and Scholander *et al.*, 1953), in which related organisms from truly tropical (Palau, West Caroline Islands? and Panama) and colder waters are compared, give opposite results. Scholander *et al.* (1953) demonstrate that at their respective habitat temperatures the tropical forms have higher metabolic rates than those from the arctic. These results are in general agreement with the findings of the present study. From the data of Takatsuki (1928), who compared the heart rates of two species of oyster, the picture is one in which similar rates are shown for both species at their normal environmental temperatures. Mayer (1914) found that at their respective temperatures the pulsation rates of the medusa, *Aurellia aurita*, from Nova Scotia and Florida, were similar. If we compare the Florida and New York data on *Uca pugnax*, the rates are also quite similar. Material from the middle of the range (North Carolina), however, shows a lower metabolism than either of the other two localities.

It should be kept in mind that previous workers have dealt almost entirely with aquatic organisms. The fact that the fiddler crab is semiterrestrial may have some bearing on the results. In the study on climatic adaptation in truly terrestrial animals (insects and spiders) by Scholander *et al.* (1953), the correlation with their other findings is not pronounced.

If winter animals from the temperate regions were tested, these relations would undoubtedly be modified. Edwards & Irving (1943), in their seasonal study of the sand crab, *Emerita*, found the winter oxygen consumption greater than that of the summer by 50 to 100% at temperatures below 20° C. Roberts (1952) reported that the thermal acclimation of the semiterrestrial crab, *Pachygrapsus crassipes*, from southern California, reflected short term fluctuations in intertidal temperatures during the winter rather than any seasonal trends. He also found that the metabolism of crabs from different localities was adjusted to their respective habitat temperatures, for after 6 weeks of acclimation to 16° C. the original metabolic differences were doubtfully significant. Vernberg (1955), in comparing warm- and cold-acclimated (7 and 27° C.) *Uca pugilator*, showed that the summer warm-acclimated forms



TEXT-FIG. 1. Mean monthly temperatures for the collecting localities.

had a lower Q_{O_2} than the warm-acclimated winter crabs. The cold-acclimated forms showed the opposite picture.

Respiratory Metabolism and Size

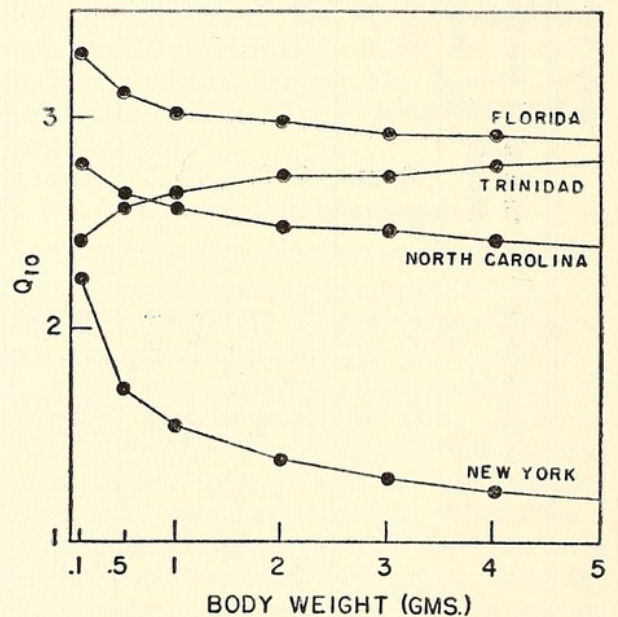
The coefficient of correlation of Q_{O_2} to weight was significant in all but the animals from Florida. Although there was no correlation between slope of regression and latitude at the upper testing temperatures, the slopes at the colder temperatures reflected a flattening with increasing latitude. Between the normal ranges in habitat temperature, Roberts (1952) found that in *Pachygrapsus crassipes* the coefficient of regression (weight to specific respiration) remained at $-.336$. This slope compares favorably with the mean of the significant regression coefficients ($-.318$) in the present study at the warmer testing temperatures.

Temperature Coefficient and Latitude

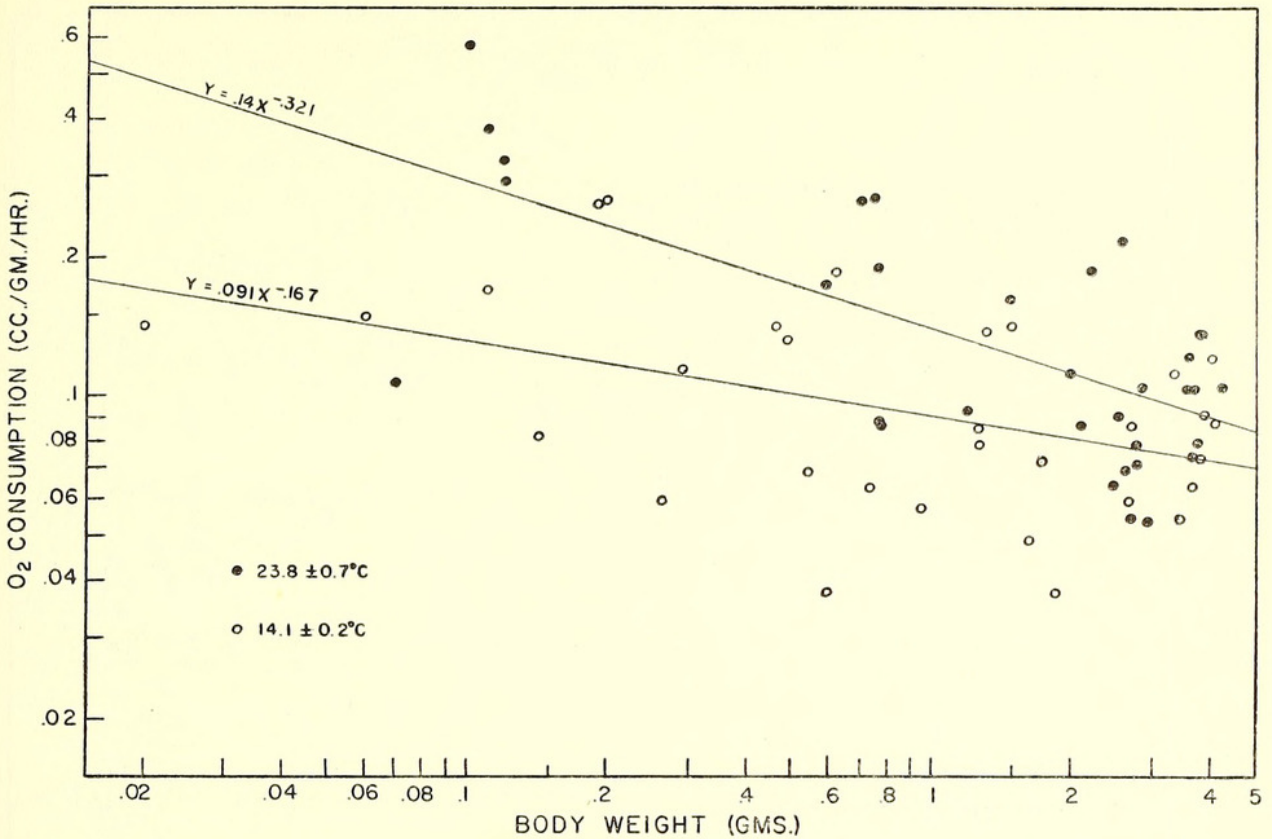
The temperature coefficients of *Uca pugnax* between the two temperature levels tested show a decrease with increasing latitude (Text-figure 2). The Q_{10} 's were calculated directly from the slopes in Text-figures 3-6. Since the temperature coefficients reflect size differences, comparisons were made within weight levels (2-5 gms.) that showed the least change.

Rao & Bullock (1953) have compiled good evidence in favor of decreasing Q_{10} 's with increasing latitude and comment that results to the contrary (Scholander *et al.*, 1953) possibly were due to comparing different tropical and arctic species and to the scatter resulting from size

differences. Where the same species are taken into account (Mayer, 1914; Moore, 1949; Rao, 1953; and Dehnel, 1955) the weight of evidence is strongly in agreement with the idea that northern or cold-adapted poikilotherms are less sensitive to temperature changes than are warm-adapted animals. If we compare the rates between 15 and 25° C. from the data of Takatsuki (1928), we find a Q_{10} of about 1.5 for the temperate species of oyster and 2.6 for the tropical species. No weights are given.



TEXT-FIG. 2. The relation of temperature coefficient to size in four populations of *Uca pugnax*. See Table 2 for temperature levels.



TEXT-FIG. 3. The relation of oxygen consumption to size in *Uca pugnax pugnax* from New York at two temperature levels.

From the metabolism data of Scholander *et al.* (1953, Fig. 10) of *Uca mordax* from Panama we find a Q_{10} of about 2.5 between 15 and 25° C. (1.1–2.4 gms., 8 determinations). In the present investigation, *Uca leptodactyla* from Bimini showed a temperature coefficient of 2.3 when measured between 14.8 and 24.6° C. (.2–.6 gms., 18 determinations) and *Uca speciosa* from Key Biscayne, Florida, a Q_{10} of 2.6 between 14.8 and 24.5° C. (.3–1.4 gms., 7 determinations). All of these species of *Uca* range from southern Florida or the Bahamas south to Brazil with the exception of *Uca speciosa*, which is limited to the West Indies. The temperature coefficients of the tropical subspecies of *Uca pugnax* seem to be in general agreement with those of other tropical species within the family at similar temperature and weight levels.

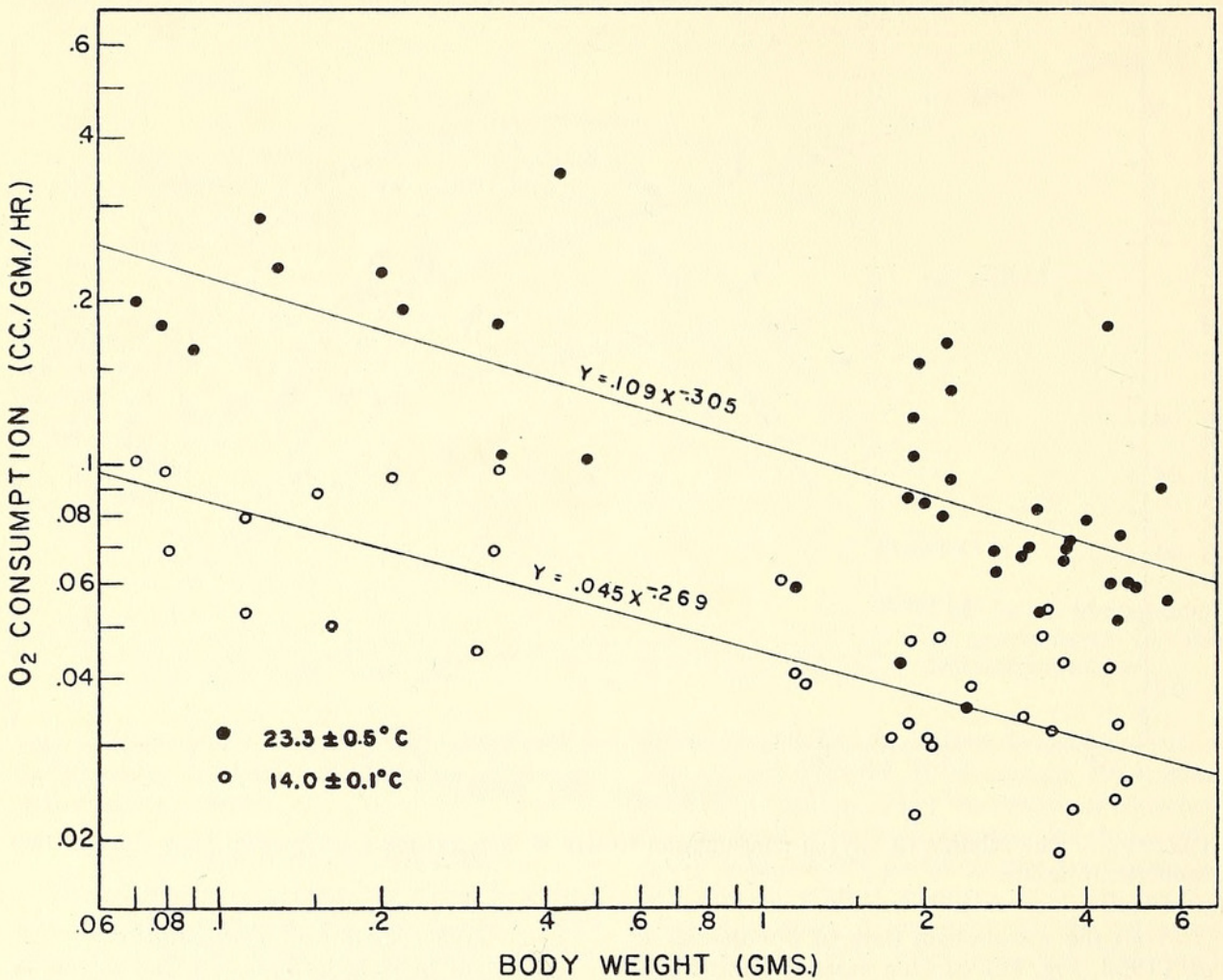
Temperature Coefficient and Size

Three of the weight-temperature coefficient curves (New York, North Carolina and Florida) in Text-figure 2 show decreasing Q_{10} values with increasing weight. In the case of the Trinidad material the opposite is true. We have here, then, in a single species, examples of two trends. Rao & Bullock (1953) believe that the tendency for larger animals to be more sensitive to temperature change is the general rule.

Tolerance to Low Temperature

As might have been expected, the results in this phase of the study revealed an increasing tolerance to low temperatures at the higher latitudes (Table 2). Intrasubspecifically, the southern populations responded in a similar fashion to cold stress. There was, however, a significant gap in the data from Florida and North Carolina, and an even greater one between North Carolina and New York. The only other species of *Uca* tested, *Uca leptodactyla* from Bimini, showed a lower tolerance than *Uca pugnax rapax*. This may have been partially due to the small size (.2–.6 gms.) of the *Uca leptodactyla* tested. There is good correlation between low temperature tolerance and the respective temperature coefficient, the picture being one of increasing temperature tolerance with decreasing sensitivity to temperature change.

The crabs from Trinidad were, in addition, subjected to a series of low temperatures ranging from 2 to 9.5° C. The time between the first death and last recovery was seen to increase proportionately with an increase in temperature. For example, at 2° C. the interval was only 1.5 (1–2.5) minutes; at 5°, 5 (5–10) minutes; at 7°, 45 (15–60) minutes; and at 9.5°, over 150 minutes. This general curve probably does not vary significantly in other species of this family



TEXT-FIG. 4. The relation of oxygen consumption to size in *Uca pugnax pugnax* from North Carolina at two temperature levels.

from tropical regions. In cold-adapted species, however, one would expect the curve to be considerably lower, with some toleration of freezing or sub-freezing temperatures for short periods.

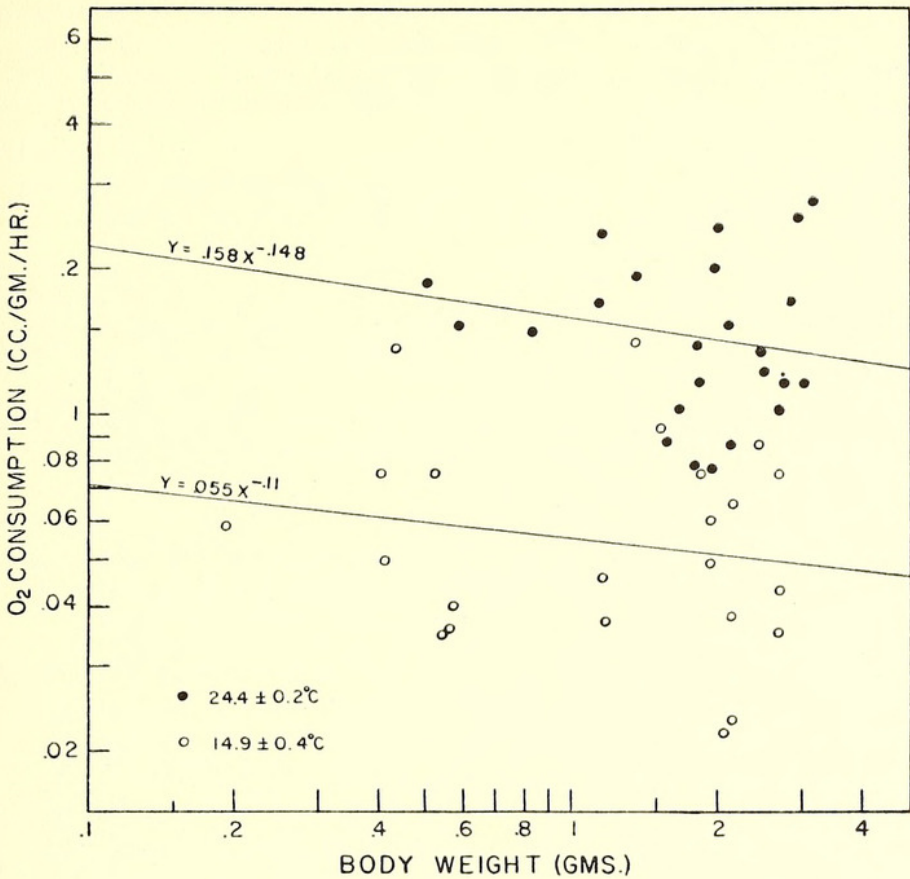
Phylogenetic Significance

The two races of *Uca pugnax* appear to be morphologically sound. In addition, Crane (1943) found that the display patterns of the males from the northern subspecies differ significantly from that of the southern form. With both criteria the separation between the races seems to occur in the region of east-central Florida. Physiologically, in the only values that give a good clinal trend (temperature tolerance and Q_{10}), the break appears to take place north of southern Florida. The forms from Trinidad and Florida have very similar values, indicating homogeneity within the southern race, at least for these characters. In the northern subspecies, however, there is considerable variation.

Although comparative data are sparse, the responses to temperature change in *Uca pugnax*,

which has successfully adapted to wide thermal fluctuations, does not seem to differ significantly with related species of more limited distribution at similar latitudes. This is essentially what was observed in *Rana pipiens* by Moore (1949), who suggests that in view of the variations in embryonic growth rates, temperature tolerance, Q_{10} , etc., in a single species (*Rana pipiens*) of wide distribution, and the lack of variation in these factors in other species of *Rana* with more limited range, this very lack of adaptive embryological factors might be responsible for the inability of these species to radiate adaptivity in space. He later found (Moore, 1952) that a frog (*Rana septentrionalis*) may have a restricted southern distribution even though it possesses adaptations which had been previously shown to be successful in the southern distribution of other species of *Rana*. Obviously factors in addition to physiological ones are responsible for the successful encroachment in time and space of ecological niches.

During its evolution and distribution from



TEXT-FIG. 5. The relation of oxygen consumption to size in *Uca pugnax rapax* from southern Florida at two temperature levels.

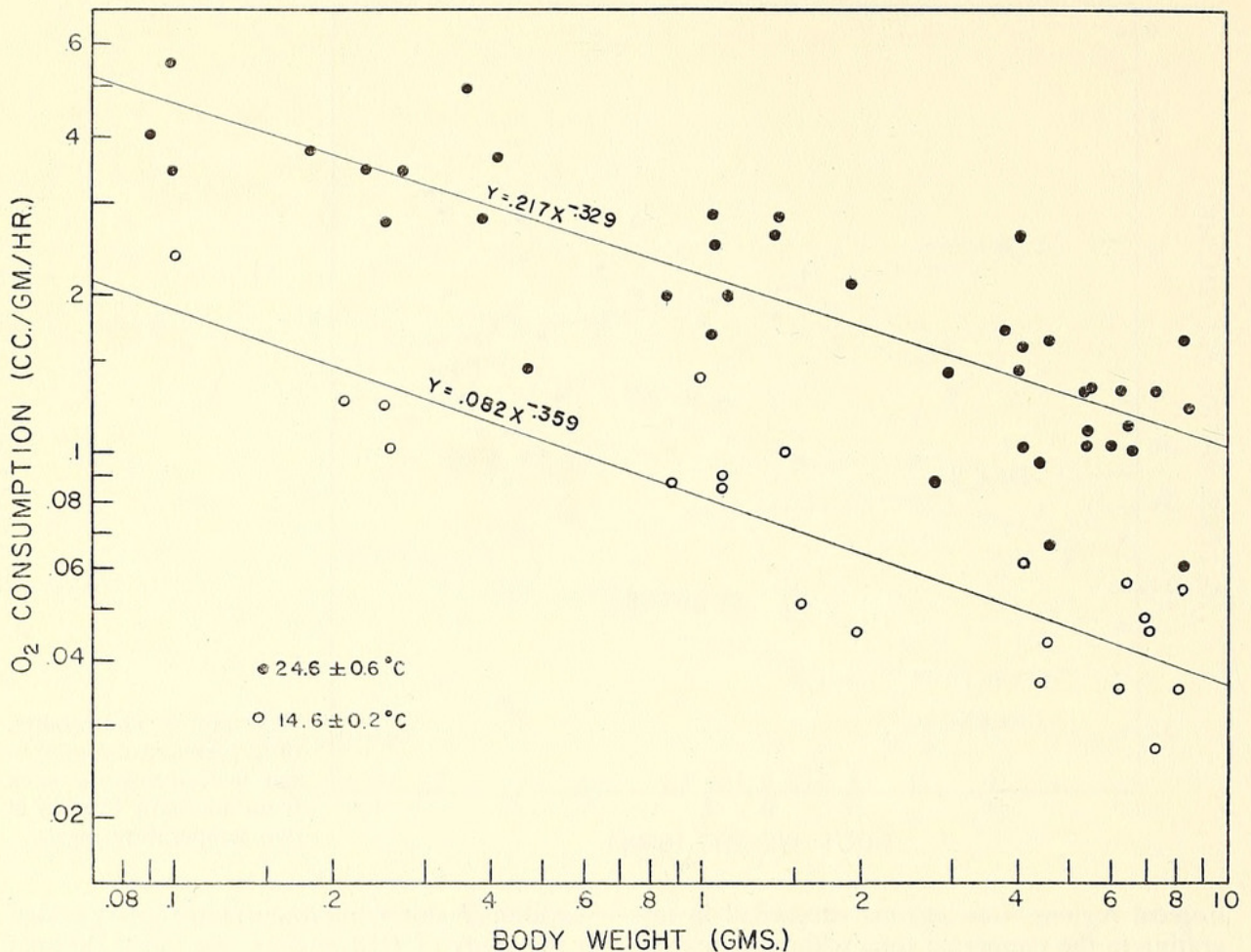
tropical regions, *Uca pugnax* succeeded in migrating to the temperate zone without being accompanied by any great morphological changes. The fact that it was successful physiologically is more important, evolutionally speaking, than any structural features that may have been related to these adaptive processes.

Although non-embryonic factors were tested in the study of *Uca pugnax*, the lower thermal sensitivity of the northern populations as well as the differences in their courtship displays indicate that northern and southern individuals could be separated on the basis of these factors alone. The subspecies of *Uca pugnax*, therefore,

TABLE 2. TOLERANCE OF *Uca pugnax* AND *Uca leptodactyla* TO 5°C

Locality	Annual Temperature °C.			Size of Sample	First Death	Last Recovery
	Monthly Range	Mean	Q ₁₀ *			
<i>Uca pugnax pugnax</i>						
New York	0.3-24.3	12.4	1.21	5	28 days	30 days
North Carolina	8.6-25.8	17.2	2.40	12	150 mins.	240 mins.
<i>Uca pugnax rapax</i>						
Florida	21.1-28.2	24.7	2.89	14	10 mins.	15 mins.
Trinidad	25.6-27.3	26.5	2.80	8	5 mins.	10 mins.
<i>Uca leptodactyla</i>						
Bimini				12	2 mins.	3 mins.

*Taken from Text-figure 2 for weight of 5 gms.



TEXT-FIG. 6. The relation of oxygen consumption to size in *Uca pugnax rapax* from Trinidad, B.W.I., at two temperature levels.

appear to be as sound behavioristically and physiologically as they are morphologically.

Careful studies on the growth rates and breeding cycles throughout the range of *Uca pugnax* would contribute much to the further understanding of its evolution and distribution.

SUMMARY

1. Determinations were made of the respiratory rates in *Uca pugnax* from New York, North Carolina, Florida and Trinidad, B.W.I., at two temperature levels.

2. At their normal habitat temperatures the Trinidad forms showed a higher metabolic rate than those from higher latitudes.

3. Although there was no apparent correlation between slope of regression (Q_{O_2} to size) and latitude at the warmer testing temperatures, the slopes at the colder temperatures reflected a flattening with increasing latitude.

4. A decrease in sensitivity to temperature change from southern to northern populations is shown along with an increase in tolerance to low temperature.

5. Individuals from New York, North Carolina and Florida showed a decrease in temperature coefficient with increasing size, whereas the opposite was true in the Trinidad forms.

6. The phylogenetic significance of thermal adaptation in temperate forms is discussed.

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ADDENDUM

The following important review articles bearing on the present study have come to the author's attention:

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