

TEMPERATURE SENSITIVITY OF OXYGEN CONSUMPTION  
OF LATITUDINALLY SEPARATED POPULATIONS  
OF UROSALPINX CINEREA  
(PROSOBRANCHIA: MURICIDAE)

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J. Malcolm Shick

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of  
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Master of Arts

J. Malcolm Slick  
Author

Approved, May 1971

Charlotte P. Mangum  
Charlotte P. Mangum, Ph.D.

Robert E. L. Black  
Robert E. L. Black, Ph.D.

Stewart A. Ware  
Stewart A. Ware, Ph.D.

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## Abstract

Although the oyster drill Urosalpinx cinerea is often cited as an example of a species that has formed physiological races among populations experiencing different thermal conditions, temperature effects on the respiratory metabolism of this organism have not been studied. Acclimated metabolism-temperature curves were constructed for four latitudinally separated populations that include two subspecies. Virginia U. cinerea follyensis, and Massachusetts and Maine U. cinerea cinerea, exhibit the classical pattern of latitudinal compensation of oxygen consumption, apparently due to an inverse size-latitude relationship that is contrary to Bergmann's rule. It is suggested that this anomaly may have resulted from the selective development of a smaller maximum size in the northern populations, although transportation of drills by man along the Atlantic coast has probably confused the situation. For reasons not immediately apparent, the Massachusetts animals show rates consistently lower than those of the North Carolina, Virginia, and Maine animals.

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## Introduction

The oyster drill Urosalpinx cinerea (Say) is a predatory marine gastropod that is believed to be native to the middle Atlantic coast of the United States (Wood, 1968); its present range on the Atlantic coast extends from northern Florida to eastern Canada. The southern limit extends well beyond Cape Hatteras, North Carolina ( $35^{\circ}15'N$ ,  $76^{\circ}35'W$ ), long recognized as a significant faunal barrier (Johnson, 1934; Wells and Gray, 1960; Cerame-Vivas and Gray, 1966; Vernberg and Vernberg, 1970), and the northern limit well beyond Cape Cod, Massachusetts ( $41^{\circ}40'N$ ,  $70^{\circ}00'W$ ), another geographic barrier (Allee, 1923; Johnson, 1934; Ekman, 1953).

Urosalpinx cinerea provides a classic and often cited example of a species that has formed physiological and morphological races (Stauber, 1950; Loosanoff and Davis, 1950-51; Carriker, 1955). Individual populations of U. cinerea vary considerably in shell size, proportions and color, and Walter (1910) noted that drills from different localities can readily be distinguished. Baker (1951) described the giant specimens from the Eastern Shore of Virginia as Urosalpinx cinerea var. follyensis; Carriker (1955) considered the Eastern Shore population to be a subspecies (U. cinerea follyensis) and relegated all other Atlantic coast populations to the subspecies U. cinerea cinerea. Further support for the separation of two subspecies came from Owen (1947), who described a meiotic anomaly in male gonadal tissue of the smaller drills that is not present in the larger animals.

Blake and Carriker (1966) found differences in incubation times, growth rates, maximum sizes, and sexual maturation rates between animals from North Carolina and those from the Eastern Shore reared under identical conditions, thus suggesting genotypic differentiation.

Investigations of temperature effects on U. cinerea consist of determination of critical temperatures for oviposition (Federighi, 1931; Haskin, 1935; Stauber, 1943, 1950; Loosanoff and Davis, 1950-51), feeding (Federighi, 1931; Loosanoff and Davis, 1950-51; Hanks, 1957), and movement or righting response (Stauber, 1943, 1950; Loosanoff and Davis, 1950-51) in different populations. It must be recognized that these various observations were made under a wide range of laboratory and field conditions, and that many of the data are conflicting. Other investigations have dealt with temperature effects on survival at different salinities (Stauber, 1943; Manzi, 1970), on the rate of feeding and reproduction at different salinities (Manzi, 1970), and on the rate of development (Stauber, 1943; Ganaros, 1958). Studies of temperature effects on the respiratory metabolism of these organisms are conspicuously absent from the literature, however.

Detailed analyses fulfilling the criteria stated by Prosser (1955) for studies on differences in rates of oxygen consumption over a range of temperatures have not been used to a great extent in the study of the evolution of invertebrate species. Studies of physiological races must be made on species with a wide geographic range and a varied evolutionary history. Recent examples include the demonstration of latitudinal divergence of oxygen consumption rates in decapod crustacea by Roberts (1957b), Demeusy (1957), and Vernberg (1959), and in polychaetous annelids by Mangum (1963).

Prosser (1964) recognized the induction of phenotypic variation by environmental variation as the probable first step in allopatric speciation. While such phenotypic adaptations have usually been considered to be reversible through acclimation, Kinne (1962) presented evidence of irreversible nongenetic variation produced by varying the osmotic conditions at which fertilized eggs of the teleost Cyprinodon macularius developed. Schneider (1968) has shown that reversible and irreversible phenotypic adaptations in field populations of the crab Rhithropanopeus harrisi are important components of latitudinal divergence of oxygen consumption, but he also has stated that persistent differences in laboratory reared animals may reflect genotypic divergence.

The objectives of the current study are to examine latitudinally separated populations of Urosalpinx cinerea for evidence of divergence of oxygen consumption rates in animals acclimated to the same temperatures and to characterize the temperature sensitivity of localized populations by means of their acclimated metabolism-temperature curves. Populations taken from three Atlantic coast faunal provinces, delineated by Cape Hatteras and Cape Cod, have been used.

## Materials and methods

### Collection and maintenance of animals

Specimens of Urosalpinx cinerea cinerea used in this study were collected at Beaufort, North Carolina (34°44'N, 76°40'W); Nobska Point, Massachusetts (41°30'N, 70°40'W); and Brunswick, Maine (43°48'N, 70°05'W). Urosalpinx cinerea follyensis was collected at Hog Island Bay (near Wachapreague), Virginia (37°30'N, 75°45'W). The Massachusetts animals are intermediate in size to the extremely small North Carolina and Maine animals and to the giant Virginia drills. Mean dry weights for each population are given in Fig. 1.

Since reproductive state may have a marked influence on respiratory metabolism (Prosser and Brown, 1961), the northern animals were collected later in the summer of 1970 than the southern animals, allowing water temperatures to reach the threshold for egg capsule deposition in all populations. The collection sites were chosen for their relatively uniform salinities to avoid possible effects similar to those reported by Heuts (1947, 1956), who described physiological and morphological races of the stickleback Gasterosteus aculeatus from habitats of different salinities. The salinities at the collection times were approximately 25-31.5 o/oo at Brunswick, 29.5 o/oo at Beaufort, 31.5 o/oo at Wachapreague, and 32.5 o/oo at Nobska Point; all populations are normally exposed to salinities above 30 o/oo in the field (Coast and Geodetic Survey, 1968; Dr. Langley Wood, personal communication).

In the laboratory the drills were maintained at approximately 22°C at a salinity of 30-34 o/oo in 1.5 gal glass aquaria; aerated water and recirculating filters were changed frequently. Although in the field the animals have a wide variety of prey available to them, they were fed only young Crassostrea virginica during laboratory maintenance.

#### Acclimation and experimental procedure

Stickle and Duerr (1970) have shown that the rate of oxygen consumption by Thais lamellosa, a related muricid gastropod, remains constant during 42 days of starvation, but increases after 53 days. The specimens of U. cinerea in the present study were starved for at least one week prior to oxygen consumption determinations, and no group of animals was deprived of food for more than six weeks.

Stickle and Duerr (1970) reported no differences in the oxygen consumption rates of male and female Thais lamellosa collected after spawning, but preliminary experiments in the present investigation indicated that sexual differences in rates may be present in the North Carolina population, though no differences were detected in the Virginia population. Consequently, all animals from the North Carolina, Virginia, and Massachusetts populations were sexed according to the method of Hargis (1957) and only males were used in the experiments. The Maine animals were available in limited numbers, and to assure a minimum acceptable sample size, the sexes were not separated.

Animals were gradually brought to the appropriate temperature and maintained at that temperature and 30-34 o/oo salinity for at least

two weeks prior to the actual determinations. In achieving the highest temperature ( $32.5^{\circ}\text{C}$ ), animals previously maintained at  $27.5^{\circ}\text{C}$  were raised by a temperature of  $1^{\circ}\text{C}$  every other day for 10 days.

Acclimated rates of oxygen consumption were determined at temperatures of 2.5, 7.5, 12.5, 17.5, 22.5 and  $27.5^{\circ}\text{C}$  for the Virginia and Massachusetts populations; this series, with the addition of  $32.5^{\circ}\text{C}$ , was used for the North Carolina animals, and covers most of the physiological range of temperatures for these organisms. Rate determinations were made on single animals, and a minimum of five animals was used at each temperature. Because of the extremely small size and low number of available animals, rate determinations for the Maine drills were performed on groups of three animals, with two measurements each at 7.5, 12.5, 17.5 and  $22.5^{\circ}\text{C}$ . Each group was used for only one measurement.

Immediately prior to placement in the respirometry vessels, the drills were scrubbed with a stiff brush, dipped in ethanol, and rinsed in seawater to remove shell biota; this seemingly harsh treatment is not injurious, as indicated by the rapid emergence from the shell and attachment to the wall of the vessel by all animals when immersed in seawater. All experiments were performed in Millipore-filtered seawater (33 o/oo) maintained at the appropriate temperature in a constant temperature ( $\pm 0.05^{\circ}\text{C}$ ) bath. Oxygen depletion in darkened, sealed vessels was measured for 1.75 h with a Yellow Springs Instrument Co. Model 5420 self-stirring oxygen probe and Model 54 oxygen meter. At the end of each experiment the animal was removed from its shell, rinsed in distilled water, dried at  $70^{\circ}\text{C}$  for 48 h, and weighed. In each case a measurement of oxygen depletion was made on a vessel

containing only the empty shell of the animal, and the result was subtracted from the experimental value. Oxygen consumption rates were determined from the slope of the line recording oxygen depletion in the respirometry vessel, excluding the initial 15 min interval, during which the animal was allowed to attach to the interior of the vessel. All measurements were obtained at oxygen concentrations greater than 70% air saturation.

Sandeen et al. (1954) have reported diurnal rhythms of oxygen consumption with peaks between 0430-0630 and 1930-2130 hours in Woods Hole, Massachusetts, U. cinerea; all experiments in the present series were performed between 0800 and 1800 hours in an attempt to avoid diurnal effects. Periodic visual observations during the course of the experiments revealed that the animals did not travel appreciably in the vessels but remained fairly quiescent at all temperatures. Despite the absence of locomotion, oxygen consumption rates of individual animals were somewhat variable. The extent to which possible fluctuations of gill ventilation in gastropods may modify oxygen withdrawal is unknown.

#### Statistical methods

Logarithmic regression lines describing the relationship of oxygen consumption and body weight were constructed from data obtained at 12.5°C from the North Carolina and Virginia populations; a minimum of 8 animals from both populations was used, and the weight range is at least one order of magnitude. The  $b-1$  values obtained were used to correct by the method of covariance (Steel and Torrie, 1960) oxygen

consumption rates to the mean dry weight of each population as well as to a standard weight for all populations. The standard weight (66.8 mg) is the mean value for all animals from the North Carolina, Virginia, and Massachusetts populations. The b-1 values for North Carolina U. cinerea cinerea and Virginia U. cinerea follyensis are -0.571 ( $r = 0.831$ ) and -0.565 ( $r = 0.811$ ), respectively. The high correlation coefficients indicate that the individual slopes are homogeneous, and since there is also no significant difference between the slopes ( $P > 0.05$ ), an intermediate b-1 value of -0.568 was used to correct the oxygen consumption rates of Massachusetts and Maine U. cinerea cinerea. These slopes appear to be consistent with those obtained at 25°C for Virginia U. cinerea cinerea and U. cinerea follyensis by Page (1968), who did not calculate the actual b-1 values.

The data of Roberts (1957a), Davies (1966), Sassaman and Mangum (1970), and Green and Hobson (1970) indicate that the variation of b-1 with temperature is not significant, and the b-1 values obtained at 12.5°C in the present study have been used to correct all rates. Corrected rates from the various populations were compared using Student's t test and analysis of variance (F test).

## Results

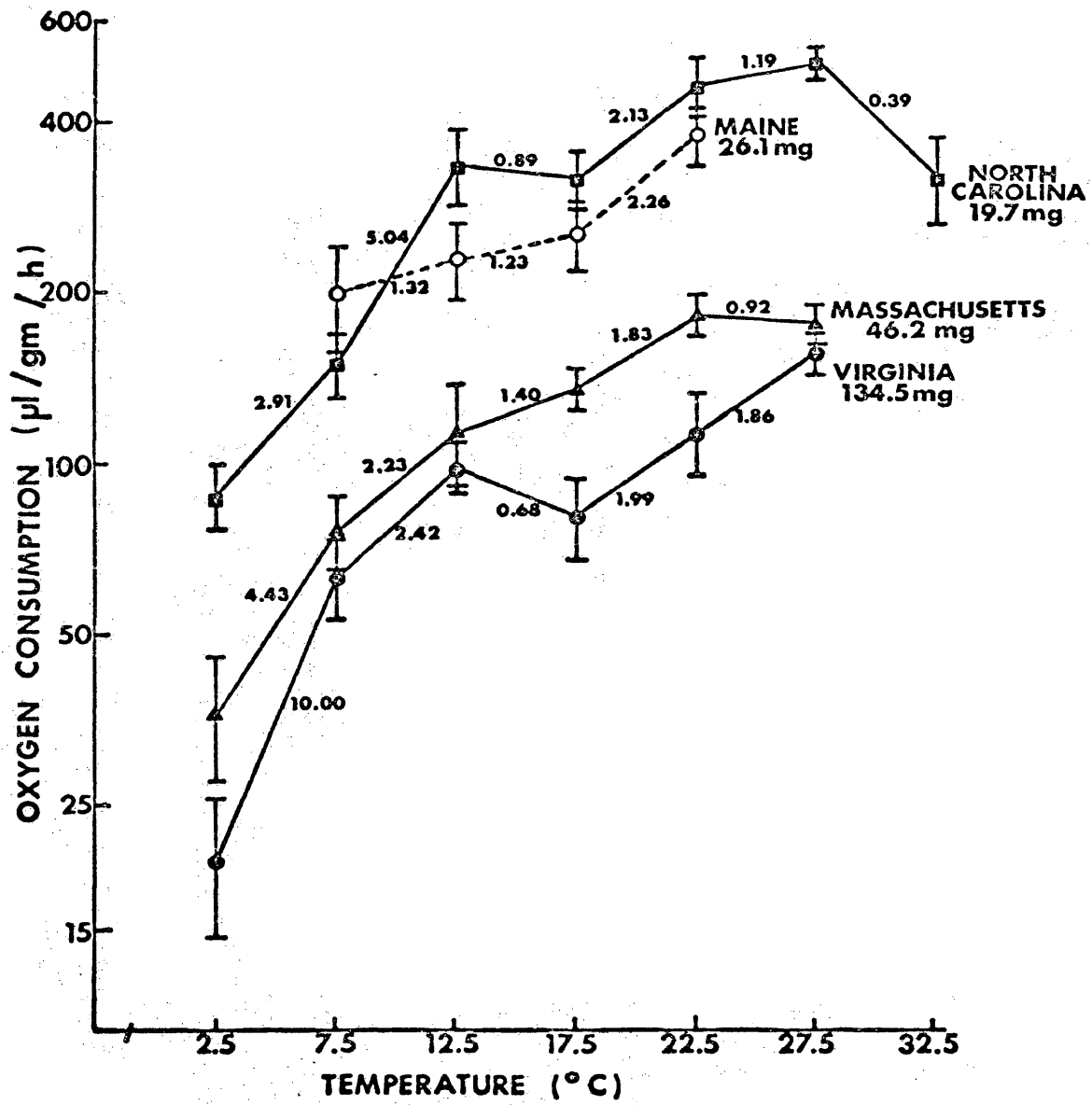
### Survival at temperature extremes

The experimental temperatures include most of the range of tolerance of the various populations. Only the North Carolina drills survived the two-week acclimation period at 32.5°C; mortality in that group exceeded 50%, and the surviving animals showed little movement and a greatly impaired ability to attach to the substrate. The Maine animals did not survive at 27.5°C, and mortality in the Massachusetts drills approached 30% after two weeks at that temperature. Oxygen consumption rates at 32.5°C for the North Carolina animals and at 27.5°C for the Massachusetts animals are reported below, but they are viewed with caution, since they were taken from a highly select group of animals under conditions of extreme physiological stress. The lowest temperature (2.5°C) did not result in significant mortality in any of the experimental groups.

### Acclimated rates of oxygen consumption

Oxygen consumption rates corrected to the mean dry weight of each population are given in Fig. 1. The curve for the Maine animals is only loosely compared with the other three curves, due to the differences in experimental procedure described above. The rates in both the North Carolina and Virginia drills decline slightly between 12.5 and 17.5°C, but neither decrease is statistically significant.

Figure 1. Oxygen consumption rates ( $\pm$  S. E.) of North Carolina, Massachusetts, and Maine Urosalpinx cinerea cinerea, and Virginia U. cinerea follyensis, corrected to mean dry weight of each population.  $Q_{10}$  values are given for each temperature interval.



$Q_{10}$  values (Fig. 1) exhibit some variability. While the majority of the values conforms generally to the van't Hoff  $Q_{10}$  rule, Virginia and Massachusetts animals show great temperature sensitivity in the 2.5 to 7.5°C interval. The lower temperature approximates the winter water temperatures recorded in those areas (Coast and Geodetic Survey, 1968). The North Carolina animals do not show great sensitivity in this range, but do so in the 7.5 to 12.5°C range. While somewhat colder water temperatures occur rarely during Beaufort, N. C., winters, 7.5°C more closely approximates the mean temperatures in the habitat for the mid-winter months (Mangum, 1964). All four populations have very low  $Q_{10}$  values for the 12.5 to 17.5°C interval; additionally, low  $Q_{10}$  values occur in the 7.5 to 12.5°C range for the Maine animals, and in the 22.5 to 27.5 and 27.5 to 32.5°C intervals for the North Carolina animals. The general pattern of all of the curves (except of the Maine animals, for which no value at 2.5°C was obtained) is great temperature sensitivity at the lower temperatures, low to intermediate  $Q_{10}$  values in the middle ranges, and slightly increased  $Q_{10}$  values toward the upper extreme. The obvious exceptions to this generalization ( $Q_{10}$  values less than 1.0 in the highest intervals for the North Carolina and Massachusetts animals) are probably explained by poor physiological condition of those animals at the high temperatures.

Virginia, Massachusetts, and Maine U. cinerea show oxygen consumption rates (Fig. 1) that conform to Krogh's (1916) prediction that populations from colder climates will show higher rate functions than populations from warmer climates measured at a common temperature. The North Carolina population, however, does not conform to the rule. With the exception of the North Carolina and Maine populations, all populations

exhibit significantly different rates at most experimental temperatures when compared using Student's t tests (Table 1).

When the effects of body size are eliminated from the data (Fig. 2), a different pattern emerges. While the shapes of the individual curves and the  $Q_{10}$  values (Table 2) remain essentially unchanged, the classical pattern of temperature compensation disappears. Student's t tests (Table 3) reveal significant differences in rates at a variety of temperatures only in comparisons involving Massachusetts animals. Comparisons of every pair of curves were made by pooling data for each population without respect to temperature, and analysis of variance yielded no significant differences among the North Carolina, Virginia and Maine populations ( $P > 0.05$ ). The curve of the Massachusetts population is significantly lower than those of all other populations ( $P < 0.01$ ), even when the questionable value at  $27.5^{\circ}\text{C}$  is discarded. With the exception of this population, therefore, the apparent latitudinal divergence of oxygen consumption is an indirect effect of size rather than of metabolic compensation per se. The position of the North Carolina curve in Fig. 1 is also explained by the high rate of oxygen consumption of these very small animals.

Table 1. Results of Student's t tests performed on mean oxygen consumption rates corrected to mean dry weight of each population. Figures indicate the levels at which differences are significant. NS =  $P > 0.05$ .

Comparisons	Temperature ( $^{\circ}$ C)					
	2.5	7.5	12.5	17.5	22.5	27.5
North Carolina vs. Virginia	0.001	0.01	0.001	0.001	0.001	0.001
North Carolina vs. Massachusetts	0.01	0.01	0.001	0.01	0.001	0.001
North Carolina vs. Maine	—	NS	NS	NS	NS	—
Virginia vs. Massachusetts	NS	NS	NS	0.02	0.02	NS
Virginia vs. Maine	—	0.01	0.001	0.01	0.001	—
Massachusetts vs. Maine	—	0.01	NS	0.01	NS	—

Figure 2. Oxygen consumption rates ( $\pm$  S. E.) of North Carolina, Massachusetts, and Maine Urosalpinx cinerea cinerea, and Virginia U. cinerea follyensis, corrected to a common weight. (■) North Carolina; (●) Virginia; (▲) Massachusetts; (○) Maine.

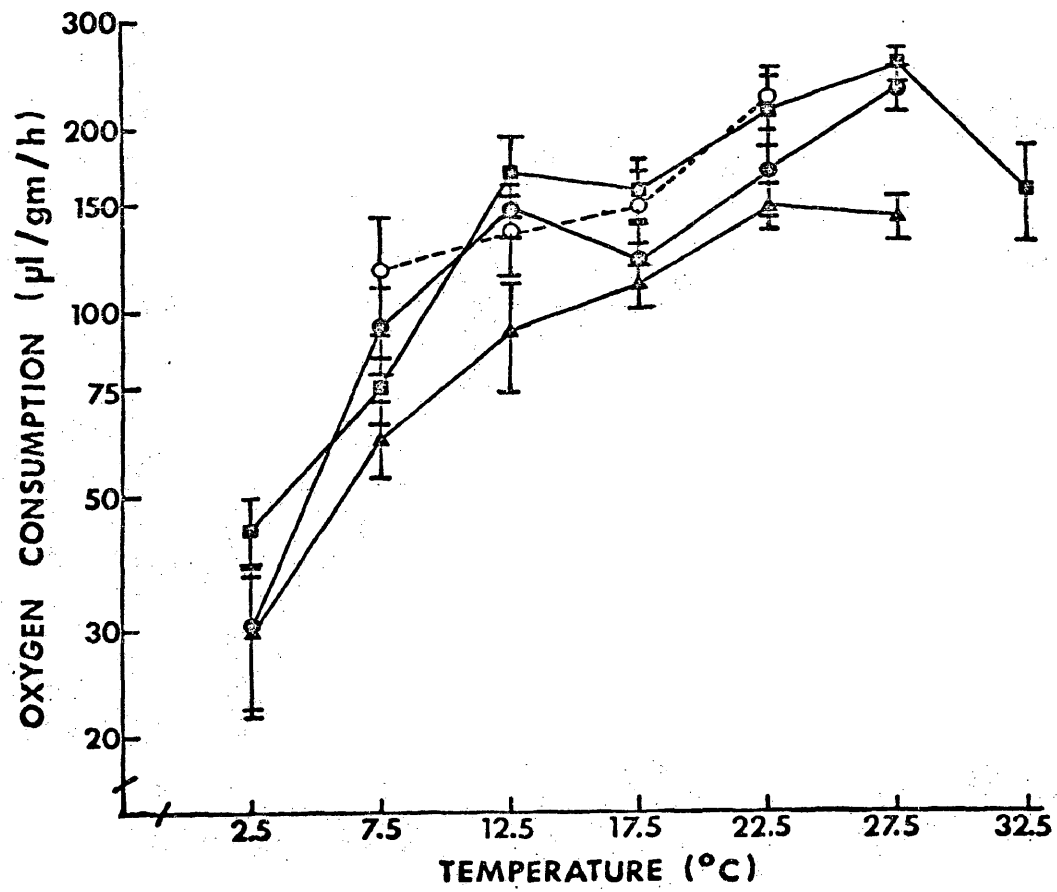


Table 2.  $Q_{10}$  values for temperature intervals of curves for populations corrected to a common weight.

Populations	Temperature ( $^{\circ}\text{C}$ )						
	2.5-7.5	7.5-12.5	12.5-17.5	17.5-22.5	22.5-27.5	27.5-32.5	
North Carolina	2.91	5.03	0.88	1.83	1.40	0.39	
Virginia	10.01	2.42	0.67	1.99	1.86	—	
Massachusetts	4.44	2.23	1.40	1.83	0.92	—	
Maine	—	1.32	1.23	2.26	—	—	

Table 3. Results of Student's t tests performed on mean oxygen consumption rates corrected to a common weight. Figures indicate the levels at which differences are significant. NS =  $P > 0.05$ .

Comparisons	Temperature ( $^{\circ}$ C)						
	2.5	7.5	12.5	17.5	22.5	27.5	
North Carolina vs. Virginia	NS	NS	NS	NS	NS	NS	NS
North Carolina vs. Massachusetts	NS	NS	0.05	0.05	0.02	0.001	0.001
North Carolina vs. Maine	—	NS	NS	NS	NS	—	—
Virginia vs. Massachusetts	NS	NS	0.05	NS	NS	0.01	0.01
Virginia vs. Maine	—	NS	NS	NS	NS	—	—
Massachusetts vs. Maine	—	0.05	NS	NS	0.05	—	—

## Discussion

Populations of Urosalpinx cinerea are relatively eurythermal throughout the zoogeographic range examined in this study. The southern animals (North Carolina and Virginia) show greater survival at high temperatures than do the northern animals (Massachusetts and Maine). This result is rather obviously correlated with the summer habitat temperatures (Mangum, 1964; Coast and Geodetic Survey, 1968).

The shapes of the acclimated curves appear to be consistent with the expectation for a wide-ranging species; the generally low to moderate  $Q_{10}$  values may be a generalized adaptation to different thermal regimes in the absence of restricted gene flow, as suggested by Mangum (1963). The high temperature sensitivity at the lowest temperature interval in the Virginia and Massachusetts animals, and in the North Carolina animals at the next higher interval, is probably correlated with increases in activity and the onset of feeding when water temperatures warm in the spring. This result cannot be interpreted as a reflection of a change from "resting" to "active metabolism" under experimental conditions, however, for visual observations do not confirm such a dramatic change in activity of the animals within the darkened experimental vessels.

The latitudinal pattern of oxygen consumption rates in the Virginia, Massachusetts, and Maine populations (Fig. 1) seems to conform to Krogh's (1916) hypothesis. This compensation is due to size differences of the individuals comprising the various populations, in a pattern opposite

to that of Bergmann's rule and to that reported by Mangum (1963) for maldanid polychaetes. The small size of the Massachusetts drills (relative to Virginia U. cinerea follyensis) and the extremely small size of the Maine animals suggest that higher metabolic rates of the small northern animals may be due to the selective development of latitudinal "size compensation" rather than to metabolic compensation per se. An inverse size-latitude relationship may not be solely related to temperature or respiratory metabolism, for Franz (1971) has demonstrated the effects of the availability and quality of food in the first summer on growth rates and attainment of maximum size in Connecticut drills. With the long duration of very low water temperatures in the northern habitats, and a possible shorter period of water temperatures above feeding thresholds, the rapid attainment of a small maximum size could be a selective advantage. Unfortunately, the lower temperature limits to feeding in the Massachusetts and Maine populations are unknown, and a shorter period of feeding and growth is thus not a certainty. Further, while only small Maine animals were observed in the field (Dr. Langley Wood, personal communication), it is possible that the animals were juveniles and had not attained maximum size. On the other hand, Dehnel (1955) reported higher growth rates in several species of marine gastropods from Alaska than in those from California at the same temperatures, and Franz (1971) found that Connecticut U. cinerea exhibit maximum growth rates by the end of the first growing season and attain 70% of the adult shell height by the end of the second growing season. Therefore, the possibility of the selective development of small size and high growth rates in the northern populations cannot be discounted.

If acclimated rates of oxygen consumption corrected to a common weight are useful indices of genotypic differences among latitudinally separated populations, it must be stated that U. cinerea cinerea from Beaufort, North Carolina, and Brunswick, Maine, and U. cinerea follyensis from Hog Island Bay, Virginia, are all genotypically similar with respect to this character, although they have been classified as subspecies on the basis of studies of other characters. Despite different temperature thresholds for spawning among various populations (data from several sources summarized by Carriker, 1955), which must result in development under different thermal conditions, there is a similarity of acclimated rates of oxygen consumption among these three populations that is contrary to the suggestion of irreversible non-genetic differences proposed by Schneider (1968).

Although there are no significant differences between many of the individual points on the various curves (Table 3), Massachusetts U. cinerea exhibit consistently lower rates over the entire range of temperatures examined, and analysis of variance indicates that the curve is significantly different from those of all other populations studied. The reasons for this particular divergence are not immediately apparent, but the shape of the curve is basically the same as for the other populations.

The unexpected small size of the northern animals in itself might be taken as an indication of genetic divergence, for Ray (1960) points out that Bergmann's rule can be applied only to populations within a species, or at most, to closely related species within a genus. It is also likely that the predominantly northward transportation of oyster drills in shipments of commercial oysters along the Atlantic coast since

the 18th century has confused the situation, although transportation alone probably cannot account for the observed anomaly. Bergmann's rule does not entail genotypic differentiation, and the offspring of southern animals transplanted to the colder waters of higher latitudes might be expected to show increased adult size, a supposition that is supported by the experiments of Ray (1960). While Carriker (1955) concludes that drill migration is not extensive, he recognizes that the spread of U. cinerea by man may have overwhelmed genetic divergence in localized populations and has resulted in a great extension of the geographic range of this species. This fact might also account for the similarity of the curves in the present study, although the true extent of transportation and its effects are unknown.

All of the populations in the present study are from temperate regions, and although there are differences in annual mean water temperatures at the various latitudes, the intertidal and shallow subtidal habitats of all populations are likely to be characterized by marked temperature fluctuations. Conditions such as these may account for the shapes of the curves obtained for all populations. While specialization for a particular temperature interval would not seem to be an adaptive advantage for a species inhabiting waters of widely different thermal regimes (Mangum, 1963), the  $Q_{10}$  values considerably below 2.0 between 12.5 and 17.5°C in all four populations may be explained as adaptations to rapidly increasing spring and summer water temperatures, a situation previously described by Davies (1966) for two species of the intertidal gastropod Patella.

## Summary

1. The greater survival at high temperatures of animals from southern populations of Urosalpinx cinerea, relative to that of animals from northern populations, is correlated with the summer habitat temperatures.

2. The generally low to moderate  $Q_{10}$  values in all populations studied may be a generalized adaptation to different thermal regimes in the absence of restricted gene flow.

3. The great temperature sensitivity of the North Carolina, Virginia, and Massachusetts animals in the lower temperature ranges is probably correlated with the onset of activity and feeding when water temperatures begin to warm in the spring. There is no evidence that reflects a change from "resting" to "active metabolism" under experimental conditions.

4. Oxygen consumption rates corrected to mean dry weights of the Virginia, Massachusetts, and Maine populations show latitudinal compensation in conformity with Krogh's (1916) prediction.

5. This compensation is apparently due to an inverse size-latitude relationship opposite to Bergmann's rule.

6. When rates are corrected to a common weight, those of the Massachusetts animals are consistently lower than those of the North Carolina, Virginia, and Maine animals.

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VITA

John Malcolm Shick, Jr.

Born on 3 August 1947 in Washington, District of Columbia. Graduated from George Mason Jr.-Sr. High School, Falls Church, Virginia, in June 1965. NSF Undergraduate Research Participant, Virginia Institute of Marine Science, summer 1967. Received B. S. from College of William and Mary, Williamsburg, Virginia, in June 1969. Entered graduate school at William and Mary in September 1969, and has served as a Graduate Teaching Assistant, NSF Graduate Trainee, and College Graduate Fellow. Currently a candidate for the degree of Master of Arts in Biology.

