Patterns of temperature adaptation in North American Atlantic coastal actinians

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Abstract

Although acutely measured rate processes in coelenterates show close correlation with the Van't Hoff Q_{10} rule and the distribution of many coelenterate groups is correlated with temperature, little is known about coelenterate temperature adaptation. Analysis of lethal temperatures shows that the southern distribution of 3 species of North Atlantic actinians is correlated with their upper lethal temperature. Oxygen consumption data from acute measurements indicate conformity to the Q_{10} rule. Oxygen consumption data from animals pre-exposed to various temperatures indicate that oxygen consumption is capable of acclimation to temperature. *Metridium senile* from Massachusetts shows positive acclimation, typical of a poikilotherm partially regulating its metabolic rate in response to temperature change. Two species from Virginia, *Haliplanella luciae* and *Diadumene leucolena*, appear to show a reverse pattern. Their response includes encystment and negative adjustment of metabolic rate, showing evasion rather than regulation in response to environmental change. Temperature has a marked effect on parameters of the activity pattern of *Diadumene leucolena*, but the temperature sensitivity of activity is not correlated with that of oxygen consumption.

Introduction

The coelenterates are of particular interest in the study of temperature adaptation for several reasons. Due to their phylogenetic position, they may offer significant information on evolutionary aspects of the phenomenon. Perhaps more importantly, the distribution of many coelenterate species is remarkably correlated with temperature (Mayor, 1912, 1914). The effect of temperature on coelenterate rate functions has generally been characterized from acute measurements, and the question of acclimation has not been adequately considered.

The general conformity of numerous poikilothermic rate processes to the Van't Hoff Q_{10} rule has been demonstrated by a host of investigators. Many rate processes in the coelenterates exemplify virtually exact conformity to this rule (temperature coefficients of approximately 1.8 to 2.2). This degree of conformity for acutely measured oxygen consumption rates has been described in the scyphozoan *Cassiopea xamachana* (McClendon, 1917) and in *Hydra littoralis* (Lenhoff and Loomis, 1957). Acute measurements of scyphozoan bell pulsation rates show similar con-

formity in *Cassiopea* (Harvey, 1911) and *Rhizostoma pulmo* (Vernon, 1895), as do those in the hydromedusa *Gonionemus* (Wolf, 1928). The rate of luminescent impulse transmission in the colonial anthozoan *Renilla* (Parker, 1920), the frequency of rhythmic potentials in *Hydra pseudoligactis* (Sellers and Roberts, 1964), and the rates of columnar muscle relaxation and contraction in *Metridium senile* (Hall and Pantin, 1937) all show Van't Hoff temperature sensitivity.

In investigating the effect of temperature on the bell pulsation rate of *Aurelia aurita*, Mayor (1914) discovered that acute measurements for animals acclimatized to the conditions prevailing at the Tortugas, Florida, USA, are temperature sensitive in approximate agreement with the Q_{10} rule up to 29 °C, above which the rate decreases. On the other hand, acute measurements of *A. aurita* from Halifax, Nova Scotia, show a plateau of maximum activity over a 21 °C range, in which the rate is practically independent of temperature. It is not clear whether the observed geographic difference is due to ecotypic differentiation or temperature acclimation.

Some evidence indicates that the effect of temperature on the growth of colonial hydroids is not readily explained by simple application of the Q_{10} rule. Individual hydranth development of *Campanularia flexuosa* is faster at higher temperatures, but new hydranths begin to develop faster at lower temperatures (Crowell and Rusk, 1950; Crowell, 1957). A similar phenomenon occurs in the polyp stage of the freshwater hydroid *Craspedacusta sowerbi* (McCary, 1959).

Hall and Pantin (1937) and Pantin and Vianna Dias (1952) have shown that the thermal responses of the decay of facilitation in the nervous system of *Metridium senile* from Plymouth, England, (habitat temperature 7° to 15 °C), and *Bunodactis* from Guanabara Bay, Brazil, (habitat temperature 20° to 30 °C) are essentially identical, although muscle contraction rates and lethal temperatures differ.

Newell and Northcroft (1967) report thermal independence of oxygen consumption (Q_{10} values of

1.0) for acute measurements of the "basal metabolic rate" of *Actinia equina* over an 18 °C range, although acute measurements of total oxygen consumption agree with expected thermal sensitivity in poikilotherms. HOCHACHKA and MANGUM (unpublished) detected low Q_{10} values for acetate metabolism in an Alaskan hydromedusa, *Phialidium islandicum*, over the range 5° to 14 °C, although acutely measured bell pulsation rates follow the Van't Hoff rule.

Materials and methods

Aspects of the temperature adaptation of three actinian species of the Atlantic coast of North America were studied. The nomenclature of HAND (1955), who reviews the taxonomy of these 3 species, has been adopted.

Diadumene leucolena (VERRILL) was collected from the York River estuary at Gloucester Point (37°15′ N, 76°30′ W) and at the mouth of Indian Field Creek (37°16′ N, 76°33′ W). Animals used in oxygen consumption and spontaneous activity experiments were collected during the summer and fall months of 1968; those used in lethal temperature studies were collected in the winter and spring of 1969/1970. *Haliplanella luciae* (VERRILL) was collected at the mouth of Indian Field Creek. All *H. luciae* used in oxygen consumption measurements were obtained in the fall and winter of 1969; those used in lethal temperature studies were collected in the winter and spring of 1969/1970. *Metridium senile* (L.) was either collected at Hadley Harbor, Massachusetts, (41°31′ N, 70°40′ W) or furnished by the Supply Department of the Marine Biological Laboratory at Woods Hole during the summer of 1969 and spring of 1970.

Ecological distribution

Observations on distribution were made at 1 station north of Cape Cod (Barnstable Town Dock), and 4 stations south of Cape Cod (Sengekontacket Pond and Oak Bluffs, Martha's Vineyard; the Wicomico River in Virginia; and in the York River estuary of Virginia).

The vertical distribution of *Haliplanella luciae*, *Diadumene leucolena*, and *Metridium senile* was studied at the Town Dock, Barnstable, Massachusetts. Individual rocks were collected at the mouth of Maraspin Creek. The surface area and depth from which the rock was taken were recorded, and the number of anemones on the upper and lower surfaces of each rock was counted. The vertical distribution of *H. luciae* and *D. leucolena* was similarly studied at the mouth of Indian Field Creek, at its junction with the York River in Virginia. Individual shells were sampled, the collection depth and surface area recorded, and the number of each species counted. In both areas the upper limit of the barnacle line was used as the reference point for depth calculations.

Oxygen consumption

Oxygen consumption measurements were made on *Diadumene leucolena* and *Haliplanella luciae* previously maintained at each of 4 experimental temperatures. Acute measurements were made at each of 3 temperatures on cold-maintained (10 °C) animals. Acute measurements were made at 4 temperatures on warm-maintained (20 °C) *Metridium senile*, and at 3 temperatures on cold-maintained (10 °C) animals. A single set of measurements was made at 22.5 °C on *M. senile* which had been maintained at this temperature. The

Table 1. *Thermal history and size range of animals used in oxygen consumption experiments*

Species	Pre-exposure temperature (°C)	Experimental temperature (°C)	N	Weight range (g)
Diadumene leucolena	10.0	10.0	6	0.04—0.26
	17.5	17.5	21	0.01—0.29
	22.5	22.5	10	0.05—0.16
	27.5	27.5	21	0.01—0.26
	10.0	17.5	5	0.07—0.18
	10.0	22.5	5	0.06—0.11
	10.0	27.5	8	0.03—0.46
Haliplanella luciae	10.0	10.0	7	0.054—0.119
	17.5	17.5	8	0.027—0.086
	22.5	22.5	11	0.023—0.265
	27.5	27.5	4	0.012—0.052
	10.0	17.5	7	0.045—0.111
	10.0	22.5	9	0.078—0.158
	10.0	27.5	6	0.017—0.124
Metridium senile	10.0	10.0	10	0.47—3.56
	10.0	17.5	10	0.22—4.95
	10.0	22.5	10	0.35—4.10
	20.0	10.0	11	0.14—9.51
	20.0	17.5	10	0.28—4.07
	20.0	22.5	10	0.17—8.71
	20.0	27.5	11	0.16—17.09
	22.5	22.5	8	0.08—5.25

thermal history and size range of the animals are given in Table 1.

The animals were placed singly in respirometry chambers and allowed to attach ("set") prior to exposure to the desired temperature. After the exposure period (a minimum of 3 days in all experiments) the chamber was filled with York River seawater (18.6 to 21.8⁰/₀₀ S) or Woods Hole seawater (32⁰/₀₀ S), similar to that occurring at the collection site and used during the exposure period. The chamber was then sealed by inserting a Yellow Springs Instrument Co. Model 5420 oxygen probe (MANGUM and SASSAMAN, 1969). In the case of acute measurements, filtered water at the experimental temperature rather than the exposure temperature was added immediately before monitoring of oxygen depletion. A continuous recording was made

of the change in oxygen concentration with the Yellow Springs Instrument Co. Model 54 oxygen meter for at least 2 h. All experiments were made in darkened chambers on starved animals with the experimental temperature maintained in a constant temperature bath ($\pm$ 0.05 °C). In each case, a measurement was made on the empty chamber to determine electrode oxygen consumption, the result of which was subtracted from the experimental value. At the end of each experiment the anemone was stimulated to full contraction, blotted and weighed.

Oxygen consumption rates were calculated from the slope of the line recording oxygen depletion in the experimental chamber, excluding the first 15 min interval, during which the animal and the chamber equilibrated to the experimental temperature. All rates were taken at oxygen concentrations above 70% air saturation. A weight regression analysis was performed on the data from all experimental groups with a weight range of more than one order of magnitude, and including at least 10 animals. Homogeneity of regression coefficients was tested using covariance analysis. A regression coefficient of -0.33 was used to adjust all oxygen consumption measurements to common weights. Data from *Diadumene leucolena* and *Haliplanella luciae* were adjusted to 100 mg and those from *Metridium senile* were adjusted to 1.00 g. Comparisons between adjusted rates for different experimental groups were made using Student's t test and analysis of variance (F test).

Spontaneous activity patterns

Activity patterns of the column of intact *Diadumene leucolena* were recorded by inserting a thin stainless steel wire hook through the tentacular ring and recording movements in the dark on a slowly moving kymograph drum (Batham and Pantin, 1950a). Recordings were made at experimental temperatures of 10°, 17.5°, and 27.5 °C on 5 animals previously maintained at 10 °C. The period between contractions, amplitude of writing pen deflection, and time of half relaxation from peak contraction were calculated from the kymograph records. The height of column contraction was calibrated empirically.

The mean period and mean column height change were used to calculate total activity, expressed as mm contraction/min, at each experimental temperature. Similarly, the rate of column relaxation, expressed as mm/min, was calculated from the mean height change and the mean time of half-relaxation.

Lethal temperatures

Upper lethal temperatures were determined on *Diadumene leucolena, Haliplanella luciae,* and *Metridium senile* maintained at 10° and 22.5 °C. The animals were allowed to set in small finger bowls and were

maintained at this temperature until use, generally for over a month. The water was then poured off and the bowl was refilled with seawater of the experimental temperature. The experimental temperature was maintained in a constant temperature water bath for a fixed duration. The animals were then replaced in water at the pre-experimental temperature, and survival was checked several days later. Any animal not showing muscular response to stimulation of the column or tentacles was considered dead.

In addition, 10 cold-maintained (10 °C) individuals of each species were placed in an incubator at 20 °C. The temperature of the incubator was raised 2 C° per day, and subsequent mortality noted.

Results

Ecological distribution

The vertical distribution of *Haliplanella luciae, Diadumene leucolena,* and *Metridium senile* at Barnstable Town Dock is shown in Fig. 1 A. *D. leucolena* and *M. senile* occur in densities too low to reflect the effect of depth, but the range of their occurrence is shown in Fig. 1 A. Maximum densities of *H. luciae* are shown as a function of depth. The shapes of curves relating mean density to depth and the relationship between them is similar to those for maximum densities in Fig. 1 A.
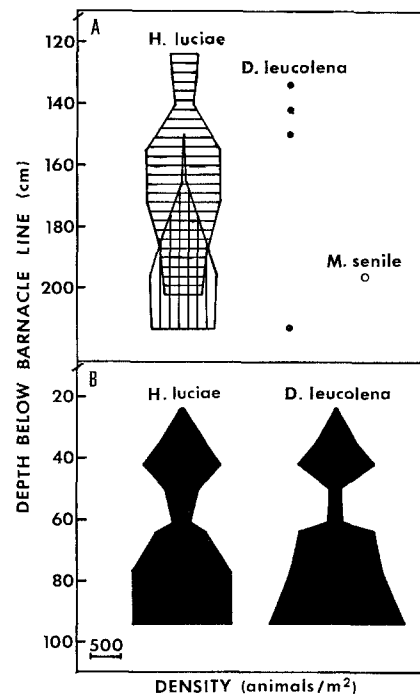

Fig. 1. (A) Vertical distribution of 3 actinian species at Barnstable Town Dock, Massachusetts, USA. Vertical hatching: animals on upper surfaces of rocks; horizontal hatching: animals on lower surfaces of rocks; (B) vertical distribution of 2 actinian species at Indian Field Creek, Virginia, USA

The vertical range for *Haliplanella luciae* and *Diadumene leucolena* is similar, although the former species occurs in considerably greater densities. It is also evident that maximum densities of *H. luciae* occur on the lower surfaces of rocks at a shallower depth than on upper surfaces.

The vertical distribution of *Haliplanella luciae* and *Diadumene leucolena* at the mouth of Indian Field Creek is shown in Fig. 1B. The shapes of the 2 curves are extremely similar, as are the absolute numbers of each species at each depth. Of a total of 1199 anemones counted, 597 were *H. luciae* and 602 were *D. leucolena*. At other locations, *D. leucolena* extends considerably below the depth shown in Fig. 1B. This species was collected in the Wicomico River at depths of approximately 5 m, on oyster beds.

Table 2. *Weight regression parameters for oxygen consumption*

Species	Pre-exposure temperature (°C)	Experimental temperature (°C)	N	$b-1$	r
Diadumene	27.5	27.5	21	−0.26	.62
leucolena	17.5	17.5	21	−0.40	.83
Haliplanella luciae	22.5	22.5	11	−0.51	.67
Metridium	20.0	27.5	11	−0.46	.83
senile	20.0	22.5	10	−0.17	.76
	20.0	17.5	10	−0.34	.52
	20.0	10.0	11	−0.30	.62
	10.0	22.5	10	−0.32	.69
	10.0	17.5	10	−0.42	.65

Oxygen consumption

In 218 continuous recordings of oxygen consumption, no evidence of different levels of metabolism corresponding to active and resting phases of activity was detected. The sensitivity of the technique should be adequate to detect different levels, since it has been used successfully for other animals (MANGUM and SASSAMAN, 1969; HOFFMANN and MANGUM, in press). This finding is contradictory to the report of NEWELL and NORTHCROFT (1967), but it agrees with the continuous activity characterizing actinian behavior (BATHAM and PANTIN, 1950a).

Weight regression parameters are given in Table 2. The pooled regression coefficient $(b-1)$ for all experimental groups listed in Table 2 is −0.348. This value is similar to the regression coefficient for *Cassiopea xamachana* reported by McCLENDON (1917). The regression coefficients for different experimental groups are homogeneous, as indicated by covariance analysis.

Weight adjusted oxygen consumption rates as a function of temperature, and the Q_{10} values for each

temperature interval are given in Fig. 2. Acutely determined rates for cold- and warm-maintained animals of all 3 species show rather close agreement with the Van't Hoff Q_{10} rule, with the single exception of *Haliplanella luciae* between 17.5° and 22.5 °C. Q_{10} values for rates from pre-exposed animals are more variable, being considerably greater than Van't Hoff predictions in the 10° to 17.5 °C interval for *H. luciae*
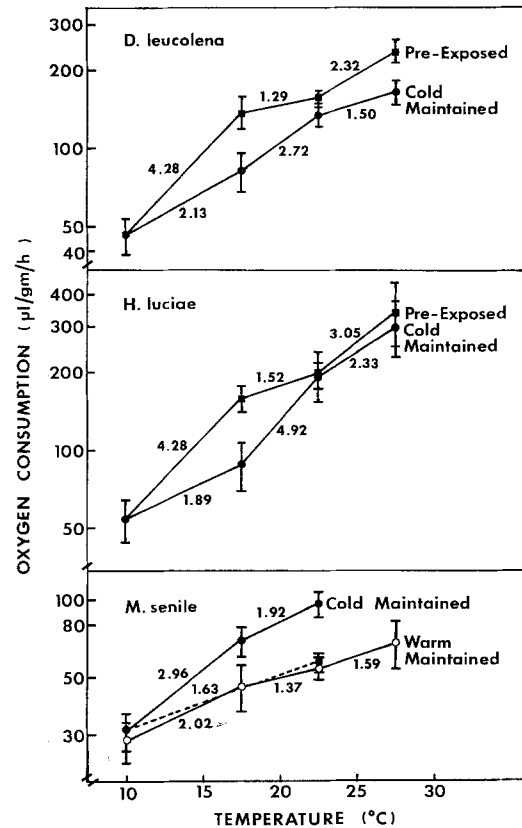

Fig. 2. Oxygen consumption as a function of experimental temperature and thermal history in 3 actinians. (●) Cold-maintained (10 °C) animals; (○) warm-maintained (20 °C) animals; (■) animals pre-exposed to experimental temperature. Vertical bars indicate plus and minus one standard error (s$\bar{x}$). Dotted line: animals pre-exposed to experimental temperature

and *Diadumene leucolena*, and somewhat lower than expected for the 17.5° to 22.5 °C interval. These results indicate that oxygen consumption rate is extremely temperature sensitive in pre-exposed *H. luciae* and *D. leucolena* between 10° and 17.5 °C, but that there is partial metabolic compensation between 17.5° and 22.5 °C.

The oxygen consumption rate of cold-maintained *Metridium senile* is greater at all temperatures (10°, 17.5°, and 22.5 °C) than that of warm-maintained animals (Fig. 2). This difference is significant at

22.5 °C (P < .05), as is the difference between rates of cold-maintained animals measured at this temperature and those pre-exposed to 22.5 °C (P < .05). Further, the pooled value for cold-maintained animals, without regard to experimental temperature, is significantly higher than that for warm-maintained animals (P < .005). This response pattern of *M. senile* is that expected of a poikilotherm showing partial metabolic acclimation to temperature change (Prosser and Brown, 1961).

The oxygen consumption rate of *Diadumene leucolena* maintained at the experimental temperature prior to measurement is greater at all 3 temperatures (17.5°, 22.5°, and 27.5 °C) than that of cold-maintained animals (Fig. 2). The difference is not significant (P > .05) at any one of these 3 temperatures. However, the value for pre-exposed animals, averaged without regard to experimental temperature, is significantly higher (P < .05).

As for *Diadumene leucolena*, the rate of *Haliplanella luciae* pre-exposed to the experimental temperature is greater than that of cold-maintained animals at all 3 temperatures (17.5°, 22.5°, and 27.5 °C). This difference is significant at 17.5 °C (P < .05), but not at 22.5° and 27.5 °C. In contrast to *D. leucolena*, the value for pre-exposed *H. luciae*, averaged without regard to experimental temperature, is not significantly higher than that for cold-maintained animals (P > .05).

Neither *Diadumene leucolena* nor *Haliplanella luciae* shows unequivocal evidence of temperature acclimation at all 3 experimental temperatures. However, the curves for both species suggest that animals pre-exposed to the experimental temperature have a higher oxygen consumption rate than cold maintained animals. This pattern is the reverse of that expected in poikilotherms showing positive acclimation to temperature (Prosser and Brown, 1961) and of that for acutely measured rates from warm and cold-maintained *Metridium senile* (Fig. 2).

Spontaneous activity patterns

Spontaneous activity patterns have been characterized in *Metridium senile* by Batham and Pantin
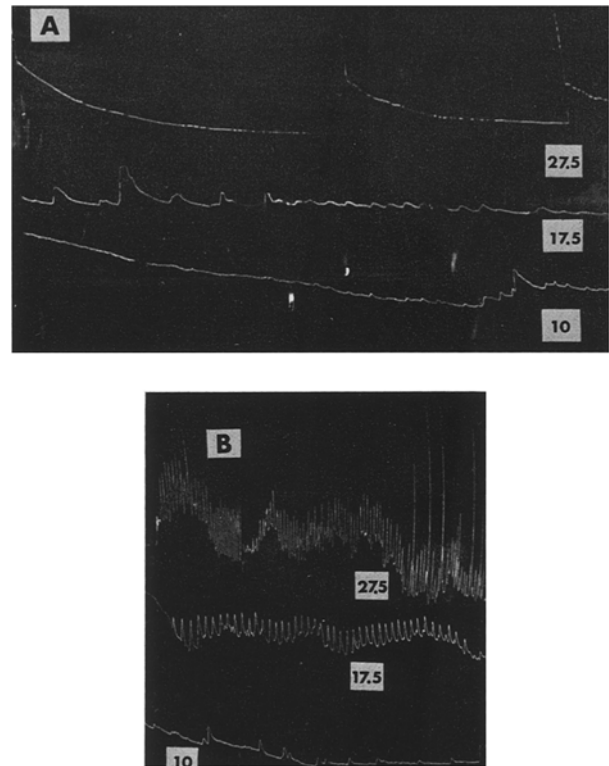

Fig. 3. Effect of temperature on the spontaneous activity of *Diadumene leucolena*. Temperature for each recording in °C. Total recording time: trace A — 8 h; trace B — 5.5 h

(1950a). However, temperature was not included as one of the environmental stimuli affecting these patterns (Batham and Pantin, 1950b). *Diadumene leucolena* is particularly suited for this type of study because of its greatly elongated column.

Temperature has a marked effect on the activity pattern of *Diadumene leucolena* (Fig. 3, Table 3). Fig. 3B shows the degree of rhythmicity which actinians are capable of attaining. This pattern is not the result of stimulation of stretch receptors by the tension in the recording apparatus, since excess stretching of the animal does not cause contraction.

Table 3. *Effect of temperature on activity in Diadumene leucolena*

Temperature (°C)	Total recording time (h)	Mean period between contractions (min)	s$\bar{x}$	Mean height change (mm)	s$\bar{x}$	Mean activity (mm/h)	Q_{10}	Time of ½ relaxation (min)	s$\bar{x}$	Rate of ½ relaxation (mm/h)	Q_{10}
10.0	51.5	13.20	1.33	0.41	0.05	1.86		3.28	0.46	3.75	
							1.23				1.79
17.5	42.9	19.90	2.05	0.72	0.08	2.17		3.72	0.44	5.80	
							1.64				3.87
27.5	54.2	73.02	11.55	4.31	0.47	3.54		5.78[a]	2.30	22.32	

[a] N = 3

Table 4. *Upper lethal temperature of warm- and cold-maintained actinians*

Species	Experimental temperature (°C)	Dosage (min)	Survival of cold-maintained animals (%)	Survival of warm-maintained animals (%)
Metridium senile	22.5	120—240	100	100
	27.5	120—240	0	100
Diadumene leucolena	35	240	100	—
	40	30	100	100
		60	100	100
		120	20	50
		240	0	20
	45	30	0	0
Haliplanella luciae	40	240	100	100
	45	30	100	100
		60	82	80
		120	22	91
		300	0	0
	50	30	22	—
		60	30	—
		120	0	—

Fig. 3 A shows the drastic effect of temperature on the amplitude of contraction and period between contractions. With the sole exception of the animal in Fig. 3 B, increasing temperature causes a consistent increase in the period between contractions. In all experiments, the amplitude of contraction increased with temperature. In all experiments but one, the activity of the animals showed a marked increase with temperature.

Q_{10} values for total activity are somewhat lower than expected from application of the Van't Hoff rule, and do not closely parallel the Q_{10} values from measurements of oxygen consumption (Table 3, Fig. 2). The rate of column relaxation, on the other hand, is very temperature sensitive above 17.5 °C.

Lethal temperatures

The survival of warm- and cold-maintained animals of each species at different experimental temperatures is given in Table 4. In order of increasing upper lethal temperature, the 3 species are: *Metridium senile, Diadumene leucolena, Haliplanella luciae*. The order is the same for the mortality point of animals placed at 20 °C and warmed 2 C° per day.

The upper lethal temperature of *Metridium senile* is related to previous thermal history, whereas the upper lethal temperatures of *Haliplanella luciae* and *Diadumene leucolena* appear less subject to modification by acclimation.

Discussion

Diadumene leucolena ranges northward at least to Cape Cod Bay, as evidenced by its presence at Barns-table Town Dock, but its northern limit is not known. It extends southward past Cape Hatteras to Beaufort, North Carolina (Field, 1949). *Haliplanella luciae*, whose northern limit is near Salem, Massachusetts (Parker, 1919), ranges southward to the Gulf Coast of Florida (Allee, 1923). *Metridium senile* is circumpolar in temperate and cold waters (Hand, 1955), but is not known on the Atlantic coast of North America as far south as Virginia (Wass, 1965).

The 3 species, in order of increasing southernmost distribution, are: *Metridium senile, Diadumene leucolena, Haliplanella luciae*. This order is identical to that of their upper lethal temperatures (Table 4). There is some evidence that the order of northernmost distribution of *H. luciae* and *M. senile* is similarly correlated with that of their lower lethal temperatures (Parker, 1919; Allee, 1923). This correlation between latitudinal distribution and lethal temperature is similar to that in *M. senile* and *Bunodactis*, discussed by Pantin and Vianna Dias (1952).

In areas where the geographic ranges of the 3 species overlap they are sympatric (Barnstable Town Dock and Sengekontacket Pond). *Haliplanella luciae* and *Diadumene leucolena* are sympatric at the mouth of Indian Field Creek, Virginia, and at Beaufort, North Carolina (Field, 1949). The 3 species are ecologically similar, being found on the same type of substrate, and they are often found on the same rock. Their vertical distribution is also similar (Fig. 1). Thus, it is unlikely that physical factors other than temperature are of major importance in limiting the southern distribution of these 3 species.

Acute measurements of metabolic rates agree with the predictions of the Van't Hoff rule and, therefore,

show temperature sensitivity which is quite typical of many coelenterate rate processes. Measurements on animals pre-exposed to the experimental temperature, on the other hand, indicate some deviation from strict conformity to the Q_{10} rule. This deviation occurs within a 12.5 C° temperature range which the animal normally encounters. The mean monthly surface temperatures at the latitude of Virginia range from 5.0° to 27.2 °C, and at the latitude of Woods Hole, Massachusetts from 1.8° to 21.8 °C (COAST and GEODETIC SURVEY, 1960).

Acclimated rates for *Metridium senile* between 10° and 22.5 °C do not show pronounced temperature sensitivity. In addition, this species shows a response pattern to low temperature (10 °C) that is typical of partial metabolic acclimation. It thus appears that *M. senile* is capable of partially regulating its metabolic rate in response to environmental temperature change.

Haliplanella luciae and *Diadumene leucolena* show hypersensitivity to temperatures below 17.5 °C. In addition, data from both species show some evidence that the response to low temperature is the reverse of that expected in poikilotherms capable of acclimating to low temperature. We do not interpret this reverse response as unadaptive. The lowered metabolic rate may well be associated with encystment in mucous secretion, which is a common means of evading environmental extremes of oxygen (PIERON, 1908), salinity (SHOUP, 1932), and temperature (CARGO and SCHULTZ, 1967; CONES and HAVEN, 1969) in sessile coelenterates. Encystment occurred commonly in cold-maintained (10 °C) *H. luciae*, although mucous secretions were removed 24 h prior to oxygen consumption measurements and also immediately before all experiments. Natural populations of *H. luciae* at Indian Field Creek show both encysted and non-encysted individuals in the winter months, when the surface temperature is below 10 °C. High intertidal populations generally show a greater degree of encystment than low intertidal and subtidal populations. Therefore, while the method of adaptation to cold temperatures in *Metridium senile* from Woods Hole involves metabolic regulation, the adaptive response of *H. luciae* and *D. leucolena* from Virginia may involve evasion in the form of encystment, mucous secretion, and metabolic slowdown. Although it may initially appear to be small, the degree of acclimation observed in the 3 actinian species studied is comparable to that in several arthropod species (ROBERTS, 1957; TRIBE and BOWLER, 1968) where appropriate statistical tests have been used to determine the significance of the data.

The anomalous relationship between the temperature sensitivity of oxygen consumption rate and that of total activity may at first appear to contradict the hypothesis that *Diadumene leucolena* and *Haliplanella luciae* undergo encystment and metabolic slowdown in

response to low temperature. However, the hydrostatic pressures needed to maintain and produce normal muscular movements in actinians are very slight (BATHAM and PANTIN, 1950c), and it is doubtful that the energy expended in this muscular activity would be reflected in oxygen consumption measurements.

The effect of temperature on the activity pattern of *Diadumene leucolena* is very different from that reported in other coelenterates. Bell pulsation rates in scyphomedusae and hydromedusae show an increase with higher temperature (VERNON, 1895; MAYOR, 1914; McCLENDON, 1917; WEESE and TOWNSEND, 1921; WOLF, 1928). However, the analogous parameter in *D. leucolena*, period between contractions, shows an inverse response. Period increases with temperature (Table 3); therefore, the frequency of contraction decreases with temperature. Spontaneous activity patterns in anthozoans are generally less obviously rhythmic than those in scyphomedusae (BATHAM and PANTIN, 1950a) but the pattern shown in Fig. 3 B is very similar to that in the sessile scyphozoan *Haliclystus auricula* (GWILLIAM, 1960). Unfortunately, the effect of temperature on activity patterns of sessile scyphozoans is not known.

Summary

1. The order of southernmost distribution of 3 Atlantic coast actinians of North America is correlated with experimentally determined upper lethal temperature.

2. The upper lethal temperature of *Metridium senile* is related to previous thermal history, whereas the upper lethal temperatures of *Haliplanella luciae* and *Diadumene leucolena* appear less subject to modification by acclimation.

3. Acute measurements of metabolic rates are in agreement with Van't Hoff predictions and show temperature sensitivity which is quite typical of acutely measured rate processes in coelenterates.

4. Measurements of metabolic rate on animals pre-exposed to the experimental temperature show deviation from strict conformity to the Q_{10} rule. This deviation occurs within a temperature range that the animal normally encounters.

5. *M. senile* from Woods Hole, Massachusetts, shows a metabolic response to temperature change which is typical of poikilothermic acclimation.

6. *H. luciae* and *D. leucolena* from Virginia appear to show a response to 10 °C that involves encystment, mucous secretion, and negative adjustment of metabolic rate.

7. Acute measurements of total activity and column expansion rate in intact *D. leucolena* indicate that temperature sensitivity of these rate functions is not closely correlated with temperature sensitivity of oxygen consumption. This lack of correlation is

understandable in the light of the low energetic demands of actinian behavior.

8. The effect of temperature on the period between contractions in the activity pattern of *D. leucolena* is the opposite of previous findings for the analogous parameter in scyphomedusae and hydromedusae.

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