

SEASONAL RESPIRATION IN THE MARSH PERIWINKLE, *LITTORINA IRRORATA*

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Intertidal invertebrates inhabit an environment which varies on a diurnal, tidal and seasonal basis. It is not surprising that the relationship between their metabolism and the environment may be complex. Adaptations to the intertidal environment by some invertebrates include a standard metabolic rate that is insensitive to a wide range of temperatures and an active metabolic rate that is temperature-independent, or thermo-neutral, within a zone centered about the ambient field or acclimation temperature (summarized by Newell, 1969, 1973, 1976). The relationship between metabolism and environmental variables may be obscured by other adaptations, such as the presence of diurnal or tidal metabolic rhythms (Sandeén, Stephens and Brown, 1954; Sandison, 1966; Shirley and Findley, 1978). Seasonal acclimatization and acclimation temperature may also greatly affect metabolic rate and range of the temperature-insensitive zone (Pye and Newell, 1973). Many metabolic studies of invertebrates have failed to consider these possible complexities of invertebrate metabolism or have not been of a long enough duration to investigate seasonal changes.

The marsh periwinkle, *Littorina irrorata* (Say, 1822), is widely distributed from New York to Texas (Bequaert, 1943) and is the most important gastropod in terms of biomass in the salt marshes of the Gulf of Mexico (Day, Smith, Wagner, and Stowe, 1973; Subrahmanyam, Kruczynski and Drake, 1976; Hamilton, 1976). Its well-studied life history (Bingham, 1972a, b; Alexander, 1976; Odum and Smalley, 1959; Shirley and Findley, 1978) and the concurrent investigation of its biochemical composition and body component indexes (Bistransin, 1976) are useful in understanding the snail's metabolic patterns. The snail is supratidal in habit, normally found on *Spartina* stems above the air-water interface. Although a number of respiration studies of intertidal gastropods have been reported (Bertness and Schneider, 1976; Coleman, 1976; Huebner, 1973; McMahon and Russell-Hunter, 1977; Newell and Pye, 1970a, b, 1971; Sandison, 1966, 1967), relatively few have been performed with supratidal marine snails. A trait of *L. irrorata* also meriting investigation is its ability to attach to a stem by means of a mucous holdfast and withdraw into its shell, supposedly to avoid unfavorable conditions. The effect of formation of mucous holdfasts on the metabolism of the snail has not previously been examined.

The investigation, therefore, focused on three main areas: first, the possibility of diurnal metabolic rate rhythms; secondly, seasonal changes in metabolic rate-

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temperature curves; and thirdly, the metabolic rate of snails in conditions which are conducive to mucous holdfast formation.

MATERIALS AND METHODS

Snails were collected at monthly intervals for 15 months beginning in October, 1973, from a *Spartina alterniflora* salt marsh located 3.5 km northwest of Grande Isle, Louisiana. The snails were transported to the laboratory and maintained under salinity, temperature and photoperiodic regimen corresponding to measured field conditions (Table I). Meteorological data were obtained from the U. S. Coast Guard Station on Grande Isle in order to consider the effects of acclimatization temperatures on experimental results. Inasmuch as the snails are supratidal in habit, air temperature was considered to be of greatest importance and temperature means were determined from measurements made at three hour intervals for the duration of the study. Studies were initiated on the day that snails were collected and respiration measurements of the snails were usually completed within three to four days after collection. Individual oxygen consumption rates of 14 snails were measured for each uptake determination with a Gilson Differential Respirometer using standard manometric techniques. The largest snails present in the field (\bar{x} = 152 mg dry tissue wt) were selected for all determinations. The 110 ml reaction vessels and snails were allowed to equilibrate for one hour prior to the initiation of measurements. Measurements were made for approximately one hour and corrected to STP. The reaction vessels were not shaken during the experiment. A paper wick and 0.5 ml of 30% KOH were placed in the sidearm of each vessel.

Three separate studies, each with different experimental procedures, were conducted. Studies 1 and 2 were conducted under water saturated conditions. Eight milliliters of artificial sea water (Instant Ocean) of the same salinity as in the field at the time of collection were placed in each reaction vessel. In study 1 the respiration of 14 snails was measured for a one hour period on alternate hours for 36 hours at a 5° C temperature increment $\pm 2.5^\circ$ C of the field temperature at the time of collection. Study 2 consisted of a one hour measurement of respiration of snails during daylight hours at 5° C temperature increments from 5 to 45° C. Fourteen different snails were used for each temperature. In study 3 an attempt was made to induce the snails to form mucous holdfasts by subjecting them to low humidity conditions. Accordingly, no water was added to the vessels and additionally, mantle compartment water was removed by gently pushing the snail as far as possible into its shell after which the snail was dried. A drying tube filled with calcium sulfate was attached to the air intake of the respirometer, and the snails were exposed to the dry air overnight prior to respiration measurements. Measurements in study 3 were made at the same temperature as study 1.

Observations on the condition of the snails and formation of mucous holdfasts were noted after each respiration measurement. After completion of each experiment, the shell of each snail was cracked and the soft parts removed carefully by hand and dried to constant weight at 85° C.

Regression analyses of \log_{10} oxygen consumption per animal against \log_{10} dry tissue weight were determined for each experiment by the least squares method.

Inasmuch as the majority of regression equations were not significant ($P > 0.05$), mean weight specific oxygen consumption rates [$\mu\text{l O}_2/(\text{g}\cdot\text{hr})$] and confidence intervals at the 95% level were calculated for all experiments. In study 1, analysis of variance of the randomized block design was performed to determine differences in respiration rates with respect to time of day. Further partitioning of the variance was tested by orthogonal comparisons. In study 2, Q_{10} values over 5°C temperature intervals were determined, and the significance of each was tested against the null hypothesis that $Q_{10} = 1.0$ using a modified t -test (Snedecor and Cochran, 1971). In study 3, regression equations, mean respiration rates and 95% confidence intervals were calculated separately for those snails that had formed mucous holdfast and those that had not.

One of the principal modifying agents of metabolism is activity, and several methods of coping with animal activity have been attempted to reduce scatter about the regression lines relating log metabolism to log body weight. One of the more recent methods used by Newell and associates (Newell and Northcroft, 1965; Newell and Pye, 1971; Newell and Roy, 1973) has been to separate active rates from standard rates solely on the basis of magnitude without correlation to animal activity. Although this method has been used with success in significantly reducing regression scatter, it ignores the activity-metabolism and individual variation (Barnes and Barnes, 1969; Coleman, 1976). The concept of metabolism increasing directly with activity is obvious. Difficulties in correlating measured activity with metabolism have, however, been encountered by several investigators (McFarland and Pickens, 1965; McLusky, 1973). Additional complications in *L. irrorata*

TABLE I

Average rate of oxygen consumption (Q_{O_2}) of *Littorina irrorata* over 24 hr, expressed as $\mu\text{l O}_2/(\text{g dry wt}\cdot\text{hr})$; $\pm 95\%$ confidence interval (C.I.)

Month	Temperature $^\circ\text{C}$		Orthogonal day/night	\bar{X} dry weight of snails (mg)	Oxygen consumption	
	Field	Expt.			$\bar{X} \pm 95\%$ C.I. Day	$\bar{X} \pm 95\%$ C.I. Night
Oct. 73	24	25	**	121	540.6 \pm 35.0	615.0 \pm 25.4
Dec. 73	19	15	**	148	199.5 \pm 15.0	242.3 \pm 13.6
Jan. 74	12	15	NS	160	245.4 \pm 12.9	241.8 \pm 10.9
Feb. 74	19	25	**	169	530.2 \pm 29.3	622.3 \pm 34.2
Mar. 74	19	25	**	201	561.1 \pm 19.4	673.5 \pm 37.5
Apr. 74	20	25	NS	193	586.6 \pm 28.3	589.4 \pm 38.9
May 74	23	30	**	203	649.4 \pm 20.0	708.3 \pm 27.1
Jun. 74	27	30	**	173	822.2 \pm 37.4	1039.2 \pm 75.8
Jul. 74	26	30	**	163	893.7 \pm 63.3	968.7 \pm 70.2
Aug. 74	27	30	**	175	735.0 \pm 28.7	923.3 \pm 45.5
Sep. 74	26	30	**	121	824.3 \pm 34.5	921.5 \pm 47.4
Oct. 74	21	30	**	127	542.4 \pm 26.9	636.3 \pm 34.5
Nov. 74	19	15	NS	144	236.4 \pm 16.0	220.2 \pm 11.4
Dec. 74	13	15	**	148	238.0 \pm 11.5	264.9 \pm 15.1

** $P < 0.01$.

NS = $P > 0.05$.

are the snail's positive phototropism (Bingham, 1972a) and a lower metabolic rate during light than dark (Shirley and Findley, 1978). Illumination of flasks to monitor activity was therefore avoided during dark conditions in this study. Movement of reaction flasks containing specimens was also avoided to preclude disturbing the specimens and increasing metabolism (Newell, Weiser and Pye, 1974; Aldrich, 1975). Since the snails' activities were not measured, all data were utilized in regression analyses and computations without arbitrarily assigning a basal or active rate. The term "basal" metabolic rate has a number of specific criteria which cannot be readily applied to poikilothermic invertebrates, especially gastropods, because of the plasticity of their oxygen consumption (Lewis, 1971; McMahon and Russell-Hunter, 1977; Russell-Hunter, 1964; Sandison, 1967). The data are hopefully indicative of natural metabolic patterns in study 1 and indicative of routine or normally active snails in the respiration-rate temperature study. McMahon and Russell-Hunter (1977) used a similar approach in their work with littoral snails.

The percentage of caloric content respired per day per snail was determined by month for the year 1974. The total volume of oxygen consumed per gram dry weight of snail per day at the average air temperature of each month was calculated, with adjustment for the increased night consumption for appropriate months. Oxygen consumption was converted to caloric values by means of an oxycaloric coefficient of 4.8 cal/ml O₂ (Crisp, 1971). The oxycaloric value was adjusted to that of the mean weight of snails for each month. The total dry weight of carbohydrate, lipid and protein per snail for each month from the same population sample used for the respiration investigation was obtained from the work of Bistransin (1976) and used to determine the total caloric value for the mean weight snail per month. Division of the caloric value of respiration per day by the total caloric content resulted in the percentage of total calories respired per day.

RESULTS

One of the principal parameters which might be expected to influence metabolism is the acclimatization temperature. The average air temperature for each month, determined from measurements made at 3 hr intervals for the entire year, is listed on Table I.

Regression analyses of log₁₀ oxygen consumption *versus* log₁₀ dry tissue weight were significant ($P < 0.05$) in only 72 of 256 regression equations in study 1. Oxygen consumption, expressed as $\mu\text{l O}_2/(\text{g dry wt} \cdot \text{hr})$ (Table I) was therefore not normalized from regression equations, but rather adjusted to per gram dry tissue wt. No pattern was found in the occurrence of significant regression equations according to time of day or year. The nine months with weight ranges of snails greater than 67 mg, with two exceptions, had the greatest number of significant regression equations.

Highly significant differences in respiration rates with respect to time of day were found by ANOVA in all months except February, 1974. Further partitioning of variance by orthogonal analysis demonstrated that highly significant increased

TABLE II
Monthly Q_{O_2} values of Littorina irrorata expressed in $\mu\text{l } O_2/(\text{g dry wt} \cdot \text{hr}) \pm 95\%$ confidence interval.

Month	Temperature ° C									
	5	10	15	20	25	30	35	40	45	
Oct. 73	238 ± 31	324 ± 42	311 ± 45	440 ± 74	578 ± 95	913 ± 80	936 ± 144	1134 ± 117		
Dec. 73		304 ± 62	245 ± 31	451 ± 33	638 ± 53	1274 ± 473	1283 ± 190	1204 ± 156		
Jan. 74	140 ± 29	165 ± 36	203 ± 32	470 ± 52	881 ± 59	1086 ± 58	1340 ± 122	1466 ± 258	144 ± 33	
Feb. 74	171 ± 14	227 ± 33	287 ± 33	308 ± 36	537 ± 101	565 ± 45	751 ± 88	1040 ± 140	134 ± 77	
Mar. 74	116 ± 26	185 ± 47	291 ± 29	434 ± 43	279 ± 44	604 ± 75	740 ± 90	1030 ± 78	55 ± 39	
Apr. 74	139 ± 18	274 ± 30	289 ± 28	418 ± 34	531 ± 91	640 ± 69	780 ± 97	1014 ± 114	102 ± 19	
May 74	182 ± 32	224 ± 38	289 ± 37	411 ± 50	509 ± 126	673 ± 58	1138 ± 105	1167 ± 150	895 ± 404	
Jun. 74	66 ± 21	211 ± 49	293 ± 60	413 ± 86	487 ± 55	795 ± 141	1087 ± 136	1059 ± 95	301 ± 213	
Jul. 74	109 ± 35	291 ± 47	312 ± 49	487 ± 45	495 ± 105	960 ± 227	1343 ± 160	1377 ± 314	126 ± 61	
Aug. 74	104 ± 21	133 ± 26	346 ± 47	419 ± 41	376 ± 85	604 ± 112	949 ± 134	1195 ± 170	995 ± 186	
Sep. 74	237 ± 37	215 ± 25	484 ± 42	311 ± 60	505 ± 106	865 ± 151	1250 ± 154	1351 ± 202	157 ± 72	
Oct. 74	169 ± 41	252 ± 31	312 ± 38	388 ± 41	547 ± 82	1097 ± 316	939 ± 109	1059 ± 271		
Nov. 74	228 ± 98	442 ± 52	206 ± 35	1323 ± 153	1242 ± 91	834 ± 64	1245 ± 239	1432 ± 95	953 ± 185	
Dec. 74	157 ± 36	323 ± 38	230 ± 33	778 ± 114	803 ± 87	1228 ± 142	1583 ± 188	1619 ± 355		

TABLE III

Monthly Q_{10} values of *Littorina irrorata* at 5° C temperature increments. ND indicates no data available.

Month	Temperature ° C							
	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45
Oct. 73		0.9	2.0	1.7	2.5	1.1	1.5	ND
Dec. 73	1.6	0.6	3.4	2.0	4.0	1.0	0.9	ND
Jan. 74	1.4	1.5	5.3	3.5	1.5	1.5	1.2	<0.1
Feb. 74	1.8	1.6	1.2	3.0	1.1	1.8	1.9	<0.1
Mar. 74	2.5	2.5	2.2	0.4	4.7	1.5	1.9	<0.1
Apr. 74	3.9	1.1	2.1	1.6	1.5	1.5	1.7	<0.1
May 74	1.5	1.7	2.0	1.5	1.7	2.9	1.1	0.6
Jun. 74	10.4	1.9	2.0	1.4	2.7	1.9	0.9	0.1
Jul. 74	7.1	1.2	2.4	1.0	3.8	2.0	1.1	<0.1
Aug. 74	1.6	6.8	1.5	0.8	2.6	2.5	1.6	0.7
Sept. 74	0.8	5.1	0.4	2.6	2.9	2.1	1.2	<0.1
Oct. 74	2.2	1.5	1.5	2.0	4.0	0.7	1.3	ND
Nov. 74	3.8	0.2	41.2	0.6	0.6	2.2	1.3	0.4
Dec. 74	4.3	0.5	11.4	1.1	2.3	1.7	1.0	ND

respiration rates occurred at night in 11 of the 14 months. No relationships between respiration rates and tidal cycle were evident.

Comparison of respiration rates in study 1 across all months at the same temperature is not possible, because of the different experimental temperatures. For those months with the same experimental temperatures, as February through April, 1974, at 25° C, and May through October, 1974, at 30° C, direct comparisons can be made. An increase in oxygen consumption rate occurred for both day and night readings for the period February through April, with the exception of the day rate in April. The increase in oxygen consumption rates continued for the period May through July, with the exception of the day rate in July. Oxygen consumption rates then declined for the period August through October, with the exception of the day rate in September. A comparison of the rates during the remaining months can be made by using the readings from November and December of 1974 and January of 1973, as all have experimental temperatures of 15° C. The decline continued through November, increased in December and remained at that rate in January. It may be presumed that experimental snails were acclimatized to field temperatures, making some degree of seasonal comparison possible. Increased respiration rates, and presumably activity, increased with increasing temperatures from late winter through midsummer. Oxygen consumption rates started declining, however, prior to a corresponding decline in ambient temperatures. The decline in rate of consumption continued from late summer through the fall months and early winter before starting to increase again.

In study 2, regression equations of \log_{10} respiration rate *versus* \log_{10} snail dry weight were significant in only 44 of 121 metabolic rate-temperature experiments. Monthly Q_{O_2} values, expressed as $\mu\text{l O}_2/(\text{g dry wt} \cdot \text{hr})$ were therefore not norma-

TABLE IV

Monthly Q_{O_2} values of *Littorina irrorata* in vessels with sea water (controls) and in low humidity, expressed at $\mu\text{l O}_2/(\text{g dry wt}\cdot\text{hr}) \pm 95\%$ confidence interval.

Month	Temp. ($^{\circ}\text{C}$)	Controls	Low humidity	
			– mucous holdfast	+ mucous holdfast
Dec. 73	15	257 \pm 46	118 \pm 69	171 \pm 209
Jan. 74	15	244 \pm 29	208 \pm 77	215 \pm 23
Feb. 74	25	538 \pm 101	677 \pm 160	
Mar. 74	25	279 \pm 44	421 \pm 81	400 \pm 758
Apr. 74	25	533 \pm 103	444 \pm 46	455 \pm 73
May 74	30	673 \pm 58	336 \pm 101	249
Jun. 74	30	795 \pm 141	921 \pm 153	
Jul. 74	30	960 \pm 227	841 \pm 167	
Aug. 74	30	604 \pm 112	846 \pm 1037	687 \pm 148
Sep. 74	30	865 \pm 151	879 \pm 132	
Oct. 74	30	544 \pm 81	498 \pm 48	368 \pm 179
Nov. 74	15	206 \pm 35	300 \pm 29	
Dec. 74	15	276 \pm 53	219 \pm 32	192 \pm 155

lized from regression equations (Table II). The lowest temperature at which rates were measured, 5°C , had no significant regression equations. Similarly, the highest temperature, 45°C , had only two significant regression equations. The higher temperatures, 35° and 40°C , had the most significant rate *versus* weight regression equations: 9 and 8, respectively, for the entire study.

Although the snails were inactive at 5°C in all months, with the exceptions of May and September, the rate of consumption was higher during the colder months and lower during the warmer months. The trend was more obvious at 10°C , with highest consumption rates during the colder months. The snails were always in a heat coma at 45°C , although no snails died during the experiment. The O_2 consumption rates at 45°C frequently approximated those at 5°C during certain months. The relatively stable metabolic rate at intermediate temperatures might best be observed by examining Q_{10} values (Table III). For the months March through August, 1974 the Q_{10} values for the temperature range $20\text{--}25^{\circ}\text{C}$ are not significantly different from 1.0, indicating a temperature insensitivity. Values of Q_{10} at $15\text{--}20^{\circ}\text{C}$ and $25\text{--}30^{\circ}\text{C}$ average around 2.0–2.5 over the year, a normal temperature response in poikilotherms.

Respiration rates of snails in vessels containing sea water and snails with and without mucous holdfasts in low humidity for all months are given in Table IV. No apparent relationship between mucous holdfast formation and oxygen consumption rates was evident. No significant difference in respiration rates was found between those with and without mucous holdfasts for snails in low humidity. Although significant differences often occurred between respiration rates of snails in low and high humidity, the relationship varied. During some months the Q_{O_2} values of snails in dry air would be significantly lower than those of snails in high humidity, while in other months the inverse was true. In addition to those mucous hold-

TABLE V

Energy budget for *Littorina irrorata* for the year 1974. Dry weight index is given in g/100 g standard animal, and caloric content is modified from Bistransin (1976).

Month	Temp. (° C)	Dry wt index	Mean dry wt (mg)	Caloric content (calories)	Cal/day respired	Percentage of caloric content respired per day
Jan.	12	5.31	160	554	3.6	0.65
Feb.	19	6.21	169	624	6.5	1.04
Mar.	19	6.08	201	711	10.2	1.43
Apr.	20	6.47	193	810	9.3	1.15
May	23	6.33	203	957	10.9	1.14
Jun.	27	5.71	173	737	16.1	2.18
Jul.	26	4.59	163	696	11.2	1.60
Aug.	27	5.99	175	747	11.7	1.56
Sep.	26	3.93	121	409	8.4	2.04
Oct.	21	4.43	127	407	6.7	1.65
Nov.	19	4.33	144	528	18.3	3.47
Dec.	13	5.47	148	572	5.2	0.92
\bar{x}	21	5.40	165	646	9.8	1.57

fasts whose formation were induced in study 3, the formation of mucous holdfasts also occurred in studies 1 and 2. A record of these mucous holdfasts was kept and most were formed during the winter months at the coldest experimental temperatures. None was formed at temperatures above 15° C, with the exception of two that were formed at 40° C in January, 1974. Of 74 mucous holdfasts that were formed in all determinations in studies 1 and 2, 63 were formed at 5 or 10° C, and 47 of those were formed in January and February of 1974.

Seasonal changes in the respiratory expenditure of energy by *Littorina irrorata* are given in Table V. The average dry weight of the population varied seasonally as the animals accumulated nutrient reserves for spawning, which probably occurred in two episodes: June to July and August to September (Bistransin, 1976). The average dry weight of snails cycled very closely with the average dry weight index of the same population as determined by Bistransin (1976). Caloric content cycled with the dry weight indexes and average dry weight. The average number of calories respired per day over the course of the study was 9.8, and the percentage of caloric content respired per day was 1.57. Both values cycled seasonally. The calories respired per animal per day cycled more closely with average air temperature than did the percentage of caloric content respired per day. This was principally due to concomitant changes in the dry weight index. The high respiratory loss in November is the result of the highest respiration rate of the year occurring at 20 and 25° C during that month.

DISCUSSION

A circadian rhythm of oxygen consumption, with higher rates of consumption during the night, was present in all months of the year. Further investigation of the rhythm of *L. irrorata* under various experimental conditions has demonstrated

that light is the phase-setting factor and that the rhythm can be shifted according to the light regime (Shirley and Findley, 1978). It is probable that the rhythm reflects changes in the activity of the snails, such as foraging, breeding and movements to more optimal conditions. A circadian rhythm of feeding-related activity is not likely, as *L. irrorata* feeds on the exposed marsh floor during low tide (Alexander, 1976; Bingham, 1972a). A tidal rhythm of activity might therefore be expected; however, no activity of *L. irrorata* is synchronous with the tides other than its moving up *Spartina* stems when covered by a rising tide (Bingham, 1972a). The stimulus to move down the stems and initiate feeding is apparently increased temperature, but feeding will proceed only if the marsh floor is exposed (Bingham, 1972a). Moreover, no tidal rhythm of respiration was detected in this study. The absence of tidal rhythms of activity in other supra and upper-littoral littorinid snails has been reported (Zann, 1973). The vagaries of the tide in the marshes of the northern Gulf of Mexico, with the wind often having a greater effect than lunar forces on tidal height, may help explain the lack of a tidal rhythm.

Respiratory rhythms that have been reported for other marine gastropods differ from that of *L. irrorata*. Sandeen *et al.* (1954) reported both diurnal and tidal rhythms in *Littorina littorea* and *Urosalpinx cinereus*. In both species, maximal respiration rates occurred in the hours following sunrise and sunset. The lowest rates occurred during the early morning hours, when the highest rates were found in this study. Sandison (1966) also reported a diurnal rhythm of respiration by *L. saxatilis* in water, *L. littorea* in air and a tidal rhythm of respiration in the latter species while it was in water. Sandison (1966) reported the highest rates for *L. littorea* to be between the hours of 800 to 1200. As he only measured rates for 12 hours of the day, the possibility of increased nocturnal respiration was not examined. Both the investigations by Sandeen *et al.* (1954) and Sandison (1966) measured the rates of groups of snails rather than the rates of individual snails, as was done in this study.

The adaptive significance of the circadian rhythm of respiration with respect to the biology of the snail is uncertain and warrants further investigation. One possible explanation is that increased nocturnal respiration, and presumably activity, may be related to predation. The snail may be more active at night when it is less susceptible to visually oriented predators, such as the blue crab, *Callinectes sapidus* (Hamilton, 1976). Certainly the amplitude of the rhythm is great enough to obscure relationships between oxygen consumption and experimental variables, and should be a consideration in metabolic experiments.

A seasonal comparison of respiration rates may also be made from the data of study 1. The increase in respiration rates at 25° C from February through April and likewise from May through July at 30° C may be due to warm temperature stimulation of metabolism. The subsequent decrease in respiration rates from August through October at 30° C occurs prior to the corresponding decrease in seasonal temperatures. The decrease in oxygen consumption rates, indicative of a seasonal change in metabolism, is perhaps related to changes in photoperiod (Dehnel, 1958). The increase in respiration rate in the winter at 15° C prior to an increase in ambient temperature is suggestive of cold temperature acclimatization.

The oxygen consumption rates of *L. irrorata* in study 2 differ notably from those of temperate species (McMahon and Russell-Hunter, 1977; Sandison, 1967). *Littorina irrorata* is active near its upper lethal temperature, while the temperate species are not. Also, the temperature at which *L. irrorata* enters heat coma is much higher than temperate littorinids (Sandison, 1967; McMahon and Russell-Hunter, 1977). The two-phased reaction of snails entering heat coma observed by Sandison (1967), which consisted of an initial rise in respiratory rate followed by an irregular fall, was not observed in *L. irrorata*. Low Q_{10} values for the entire year are present for the temperature range of 35–40° C. Although activity of the snails was not inhibited at 40° C during any season of the year, the low Q_{10} values suggest that 40° C is near the snails' upper limit of capacity adaptation. Lewis (1971) also found that activity was not inhibited in three species of tropical intertidal gastropods at 37° C. A seasonal increase in the upper limit of thermal tolerance reported for some temperate intertidal molluscs (Newell and Pye, 1970a) was not evident in *L. irrorata*.

One of the more interesting aspects of the respiration rates at various temperatures in study 2 is a plateau in oxygen consumption rates in the temperature range of 20–25° C, clearly demonstrated by the Q_{10} values being not significantly different than 1.0 for the months of March through August. This is perhaps a thermo-neutral zone, or zone of temperature independence, for *L. irrorata* during these months. This narrow zone of metabolic homeostasis occurs near the average annual temperature at the collection site, approximately 20° C. Likewise, the range of the temperature independent zone approximates the average daily temperature range, 6.5° C. Daily temperature variations of 10° C or greater occurred less than 8% of the time. Since oxygen consumption rates were measured only at discrete 5° C increments, the actual temperature independent zone may be several degrees broader than the discernable 5° C zone. The zone may shift seasonally, as suggested by another group of low Q_{10} values present at 5–10° and 10–15° C in October, 1973 through January, 1974. Yet another set of low Q_{10} values is present in the 15–20° C range in August through October, 1974, and in the 10–15° C range in October through December, 1974. The lack of correlation between activity and oxygen consumption in this study may have made temperature independent zones less distinct. Most temperature independent zones reported for marine invertebrates have been restricted to standard metabolic rates (summarized by Newell, 1969, 1973), although other temperature independent zones have been reported for routine metabolic rates of intertidal snails (Bertness and Schneider, 1976).

The ability of littorinid snails to attach themselves to a substrate by means of a mucous holdfast and then withdraw into their shell has been considered a means by which they decrease exposure to unfavorable conditions. The relationship that salinity and relative humidity have on mucous holdfast formation in *L. irrorata* has been investigated (Bingham, 1972b). The effect of temperature on holdfast formation and the effect that holdfast formation has on metabolism has not been reported. Although it would seem that inactive snails attached by a mucous holdfast would have reduced metabolic demands, no significant difference was found between the respiration rates of snails in containers with sea water and those with

and without holdfasts in low humidity. The greater number of mucous holdfasts formed at low temperatures during the winter months suggests that temperature must be considered as an important factor in inducing holdfast formation, as well as relative humidity and salinity. W. A. Murphy (Tulane University, personal communication) has found that snails form holdfasts more rapidly at various relative humidities at 10° C as compared to 20 and 30° C. The terrestrial snail *Otala lactea* is also more likely to become dormant and form epiphragms at low relative humidities and low temperatures than at high relative humidities and high temperatures (Rokitka and Herreid, 1975). Although no metabolic advantages were found for mucous holdfast formation in this study, presumably holdfast formation in *L. irrorata* serves the same functions that were reported by Vermeij (1973) for mucous holdfasts in other littorinid snails: to reduce water loss and contact between soft tissues and substrate; to obviate the need for a large water reservoir; and, to increase the degree of temperature regulation.

In previous productivity studies of *Spartina* marshes, the contribution of *L. irrorata* to community metabolism has been estimated (Day *et al.*, 1973; Odum and Smalley, 1959). Alexander (1976) measured the egestion rate of *L. irrorata* to be 145 g organic matter/(m²·yr). Day, Smith and Gayle (unpublished manuscript) have estimated the standing crop *L. irrorata* in Louisiana salt marshes to be 4.9 g/m². If our respiration data, Alexander's egestion data and the Day, Smith and Gayle's standing crop data are used, and annual energy budget for *L. irrorata* is calculated to be: 182.7 g organic matter/(m²·yr) total food intake, 4.9 g/m² standing crop, 9.8 g/(m²·yr) net organic production, 145 g organic matter/(m²·yr) feces production and 27.9 g organic matter/(m²·yr) lost to respiration.

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SUMMARY

1. Respiration rates of *Littorina irrorata* were measured monthly for the period from October, 1973, through December, 1974. The study consisted of three main parts: first, hourly measurements of respiration rates at ambient field air temperature over a 36 hr time period; secondly, one-hour measurements of respiration rates at 5° C temperature increments from 5° to 45° C during daylight hours; and thirdly, one-hour measurements of respiratory rates under conditions conducive to mucous holdfast formation. Respiration rates were measured with a Gilson respirometer using standard manometric techniques.

2. A diurnal rhythm of respiration was found for 11 of the 14 months. Respiration rates during the night were significantly higher than during the day.

3. Snails were in thermal stress at 5° C and 45° C and their respiration rates were depressed. Respiration rates at 10° C were highest during the colder months, demonstrating inverse cold temperature acclimatization. The Q_{10} for the temperature range 20–25° C were not significantly different from 1.0 for the months March through August, suggesting thermal insensitivity or the presence of a thermo-neutral zone.

4. No apparent relationship between mucous holdfast formation and oxygen consumption was evident. Mucous holdfasts were formed most frequently during the winter months at the coldest experimental temperatures.

5. An annual energy budget of *L. irrorata* is calculated.

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