Rev. Biol. Trop., 18(1, 2): 115-127, 1971

Influence of temperature upon the respiration rate of pre-zoeal and zoeal stages of Pachygrapsus crassipes Randall*.

by

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(Received for publication June 4, 1970)

The life of *Pachygrapsus crassipes* occurs entirely in the intertidal rocky areas. Conditions of life in these zones are quite different from those occurring in the open ocean. When the tide is in, the inhabitants are bathed by sea water but during tidal ebb they are uncovered and exposed to the rigors of the aerial climate. Consequently, throughout their evolution, the vicissitudes of existence associated with this environment have led them to a high degree of specialization (NICOL, 11).

Temperature is an important ecological factor for adults, as well as for larvae of marine organisms, since it determines abundance, life cycle and distribution. Another important aspect of temperature is its effect on respiration. Generally, the metabolic rate of crustaceans is related to temperature. It is well known (FLORKIN, 5) that poikilothermal animals survive only within definite temperature ranges and that, generally speaking, a change of external temperature results in a change of oxygen consumption. Within the temperature range that can be tolerated by a poikilotherm, the rate of metabolism increases with increasing temperature up to some critical value (critical thermal maximum) beyond which deleterious effects become evident and the rate falls off sharply.

Although a great amount of work has been done in the past 20 years on the temperature-metabolism relationship, it has been concerned primarily with adult individuals. Of great interest are the complete series of papers on the physiological variations between tropical and temperate zone species of fiddler

* Part of a Dissertation presented to the Faculty of the Graduate School of California State College at Fullerton, in partial fulfillment of the requirements for the degree of Master of Science.

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crabs, especially those by VERNBERG (17, 18), VERNBERG and TASHIAN (20), VERNBERG and VERNBERG (21, 22), VERNBERG and COSTLOW (19), TASHIAN (16), and DEMEUSY (3), as well as those by DEHNEL (2), EDWARDS and IRVING (4) and GRAINGER (6).

Physiological studies relating to *P. crassipes* are limited to a few papers, mainly those by HIATT (8), HYMAN (9), HART (7) and ROBERTS (13, 14). Of these, Roberts (14) is the only one concerned with metabolism and temperature. The latter study experimentally demostrated and examined adult phenotypic compensations for temperature acclimation.

Pachygrapsus crassipes can be considered as an amphibious species which represents an important step toward the terrestrial habitat. Terrestrial physiological adaptations are concerned primarily with metabolism. Hence, the study of these adaptations is of great importance toward understanding the mechanisms involved in becoming a terrestrial species. This paper was prepared as part of a long term project to be continued in the future with amphibious as well as fresh water species of Central America.

MATERIAL AND METHODS

Gravid *P. crassipes* females were collected in the same stations as indicated in the first paper of this series (VILLALOBOS, 23). Pre-zoeal and zoeal stages were treated as indicated in the same paper.

Oxygen consumption was determined by means of the Scholander microvolumetric respirometer. In the volumetric system, the pressure is maintained constant, and the volume changes are read directly (SCHOLANDER *et al.*, 15). The apparatus consists of manometers (Fig. 1) formed by a block (A) and a plug (B). There is a hole (the rod chamber) in the center of the block to accomodate the rod (C). The rod chamber is connected to the horizontal respirometer vial (D) and to one side of the manometer. The opposite side of the manometer is connected to the vertical compensating thermobarometer (E). The vials are attached to the manometer block by means of molded tygon stoppers. The prongs of the absorption plate (F) pass through the hole of the lucite button of the stoppers.

A glass aquarium (Fig. 2, A) containing a ten-compartment rack (B) in which the manometers are placed, was used as a water bath. This rack was connected to a speed reducer motor (C) which was also connected to a Mark SH-11 shaker (D) at a speed of 200 rpm. A 115 Thermomix II heating unit (E) was used to control the temperature in the water bath. Because this unit works only above room temperature, a water cooling pump was necessary to reduce the temperature.

In order to determine the oxygen consumption the manometers were filled to the mark with standard Brodie's manometer fluid. Because of their small size, 20 pre-zoeal or larval individuals were used for each determination. They were placed in the respiration vials with filtered sea water with a salinity of 30 parts per thousand. For the pre-zoea, determinations were made at 8, 13, 18, 23, 28,

31, 36, and 40 C, for the larvae, determinations were made at 5, 10, 15, 20, 26, 31, 36, and 38 C. Determinations were made in the middle of the day or in the early afternoon to eliminate the possible influence of diurnal rhythm in metabolic activity. Each respirometer was allowed 15 minutes for equilibration before the first reading was taken, except for the lowest temperatures, for which 30 minutes were necessary. The results are expressed as mm^3 oxygen consumption per hour and per body weight.

Van't Hoff's equation was used to obtain Q_{10} values of oxygen consumption that express the change in metabolic rate with temperature.

RESULTS

Data on the average respiration rate of prezoea, expressed as mm^3 of oxygen per hour and per milligram, are presented in Table 1., for temperatures ranging from 13 to 40 C. Fig. 3 shows these results graphically. No respiration was recorded at 8 C. Table 2 shows the mean oxygen consumption for all temperatures. The results are shown in Fig. 3.

The average rates of oxygen consumption for larvae at temperatures ranging from 10 to 38 C are presented in table 3 as well as in Fig. 4. Again the author was unable to record respiration at 5 C. It should be indicated that at such low temperatures, larval activity was diminished, with movements being restricted to the heart, pleopods and abdomen. It also should be indicated that at 38 C respiration during the first 15 minutes was observed to be faster but then dropped precipitously. This is interpreted as the critical thermal maximum of the larvae. Table 4 shows the mean oxygen consumption for all temperatures. These results are also shown in Fig. 4.

Tables 5 and 6 show the Q_{10} values of oxygen consumption for the prezoea and the first larval stage, respectively.

DISCUSSION

As was stated previously, within the temperature range that can be tolerated by a poikilotherm, the metabolic rate increases with increasing temperatures up to a critical value (critical thermal maximum), beyond which the rate falls off sharply. The results obtained in this study for both the pre-zoea and first larval stage agree with this general idea. The respiration rate versus temperature (R-T) curve for the pre-zoea (Fig. 3) illustrates that the respiratory activity changes slowly for temperatures within the annual maximum and minimum. Respiratory activity increased rapidly after passing the ambient temperature range until about 30 C, after which the rate decreased. Thus, many poikilotherms have gained, by means of such adaptations, a striking degree of independence from variations of the thermal environment (ROBERTS, 14). Such compensatory adjustments have been frequently found to be permanent and are assumed to have resulted from the formation of favored genotypes (BULLOCK, 1; SCHOLANDER *et al.*, 15). Adult phenotypic compensations were found in *P. crassipes*

TABLE 1

Average respiration rate of pre-zoea expressed as mm³ of oxygen consumed per hour and per milligram at temperatures ranging from 13 to 40 C.

Group	Temperature °C	Body Weight in mg.	mm rod excurs.	F	Average mm^3 0_2/hr/mg
A	13	0.05	0.07	7.08	0.49
B	13	0.05	0.08	7.08	0.56
C	13	0.05	0.08	7.08	0.56
A	18	0.05	0.10	7.08	0.70
B	18	0.05	0.12	7.08	0.85
C	18	0.05	0.12	7.08	0.85
A	23	0.05	0.10	7.08	0.70
B	23	0.05	0.15	7.08	1.06
C	23	0.05	0.15	7.08	1.06
A	28	0.05	0.36	7.08	2.55
B	28	0.05	0.35	7.08	2.48
C	28	0.05	0.34	7.08	2.41
A	31	0.05	0.54	7.08	3.83
B	31	0.05	0.52	7.08	3.69
C	31	0.05	0.50	7.08	3.54
A	36	0.05	0.35	7.08	2.48
B	36	0.05	0.35	7.08	2.48
C	36	0.05	0.30	7.08	2.12
A	40	0.05	0.24	7.08	1.70
B	40	0.05	0.28	7.08	1.98
C	40	0.05	0.29	7.08	2.05

TABLE 2

Mean oxygen consumption of pre-zoea expressed as mm³ of oxygen consumed per hour and per milligram.

Temperature in °C	Mean mm^3 0_2/h/mg	Standard Deviation	Standard Error
13	0.54	0.388	± 0.129
18	0.80	0.071	± 0.023
23	0.94	0.200	± 0.060
28	2.48	0.071	± 0.024
31	3.69	0.159	± 0.053
36	2.36	0.200	± 0.066
40	1.91	0.187	± 0.062

TABLE 3

Average respiration rate of larvae expressed as mm³ of oxygen consumed per hour and per milligram at temperatures ranging from 10 to 38 C.

Group	Temperature in °C	Body Weight in mg.	mm rod excurs.	F	Average mm³ O_2/hr/mg
A	10	0.048	0.18	7.08	1.32
B	10	0.048	0.13	7.08	0.96
C	10	0.048	0.14	7.08	1.03
D	10	0.048	0.20	7.08	1.46
E	10	0.048	0.15	7.08	1.10
A	15	0.048	0.36	7.08	2.34
B	15	0.048	0.49	7.08	3.61
C	15	0.048	0.33	7.08	2.42
D	15	0.048	0.35	7.08	2.58
E	15	0.048	0.20	7.08	1.48
A	20	0.048	0.58	7.08	4.28
B	20	0.048	0.52	7.08	3.83
C	20	0.048	0.48	7.08	3.64
D	20	0.048	0.65	7.08	6.25
E	20	0.048	0.25	7.08	1.84
A	26	0.048	0.52	7.08	3.83
B	26	0.048	0.30	7.08	2.21
C	26	0.048	0.46	7.08	3.39
D	26	0.048	0.50	7.08	3.69
E	26	0.048	0.14	7.08	1.03
A	31	0.048	0.61	7.08	4.50
B	31	0.048	0.45	7.08	3.31
C	31	0.048	0.58	7.08	4.28
D	31	0.048	0.62	7.08	4.52
E	31	0.048	0.65	7.08	4.79
A	36	0.048	0.43	7.08	3.17
B	36	0.048	0.50	7.08	3.69
C	36	0.048	0.45	7.08	3.31
D	36	0.048	0.39	7.08	2.88
E	36	0.048	0.26	7.08	1.94
A	38	0.048	0.29	7.08	2.13
B	38	0.048	0.30	7.08	2.20
C	38	0.048	0.31	7.08	2.28
D	38	0.048	0.29	7.08	2.13
E	38	0.048	0.32	7.08	2.35

TABLE 4

Mean oxygen consumption of first zoeal stage expressed as mm³ of oxygen per hour and per milligram.

Temperature in °C	Mean mm 0_2/h/mg	Standard Deviation	Standard Error
10	1.17	0.206	± 0.0412
15	2.48	0.240	± 0.048
20	3.97	1.440	± 0.288
26	2.83	1.190	± 0.238
31	4.28	0.570	± 0.114
36	2.99	0.660	± 0.132
38	2.21	0.010	± 0.002

TABLE 5

Q_{10} values of oxygen consumption for pre-zoea of P. crassipes.

Thermal range in °C	Mean mm 0_2/h/mg	Q_{10}
13 — 18	0.54 — 0.80	2.19
18 — 23	0.80 — 0.94	1.37
23 — 28	0.94 — 2.48	6.91

TABLE 6

Q_{10} values of oxigen consumption for the first zoeal stage of P. crassipes.

Thermal range in °C	Mean mm 0_2/h/mg	Q_{10}
10 — 15	1.17 — 2.48	4.49
15 — 20	2.48 — 3.97	2.56
20 — 25	2.97 — 2.83	negative value

by ROBERTS (12). The results obtained in this study show that the pre-zoea of *P. crassipes* do not adjust to temperature changes, which would probably indicate a non-genetic condition; this would favor the Roberts proposition of phenotypic compensations.

The R-T curve for the first larval stage (Fig. 4) also illustrates an increase in oxygen consumption with an increase in temperature. My opinion is that the drop in respiration rate between 20 and 30 C is a consequence of having used just five groups of larvae. An increased number of groups would produce a more or less straight R-T curve between the above mentioned values. A straight line would indicate that variations in respiration rate are sufficiently small to be considered as the result of ontogenetic phenotypic compensations. It should also be noted that the Q_{10} results (Table 6) do not support this idea since they are based only on available data and there is a decrease in the mean oxygen consumption between 20 and 30 C. If the idea of ontogenetic phenotypic compensations is correct, Q_{10} should remain essentially uniform. KINNE (10) has pointed out that the capacity for non-genetic adaptations depends on the genetic background of the organism involved. When present, they should be variable in different ontogenetic stages, such as eggs, larval stages and adults. The same author has also indicated that the velocity of non-genetic adaptations tends to increase with increasing rates of metabolism.

This study confirms the fact that *Pachygrapsus crassipes* shows a higher metabolic rate as a consequence of its semi-terrestrial habitat, and that the higher metabolic rate, the capability of non-genetic adaptations, and the semi-terrestrial habitat all explain the tremendous adaptative capacity of this species.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. Lon McClanahan, California State College, for his advise in using the Scholander respirometer and also for his review of the manuscript. Thanks are also given to Drs. Kenneth McWilliams and David Walkington for their review of the manuscript, and to Dr. Donald B. Bright for his technical assistance.

SUMMARY

Physiological studies on the influence of temperature on the respiration rate of pre-zoeal and first zoeal stages of *Pachygrapsus crassipes* demonstrate an increase in oxygen consumption with increasing temperature and suggest the possibility of ontogenetic phenotypic compensations.

RESUMEN

Estudios fisiológicos de la influencia de la temperatura en la respiración de los estados de prezoea y zoea en *Pachygrapsus crassipes* demuestran un aumento en el consumo de oxígeno con aumento en la temperatura y sugieren la posibilidad de compensaciones fenotípicas ontogenéticas.

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Fig. 1 Complete manometer assembly. A: Block; B: Plug; C: Rod; D: Vial; E: Thermobarometer; F: Absorption plate.

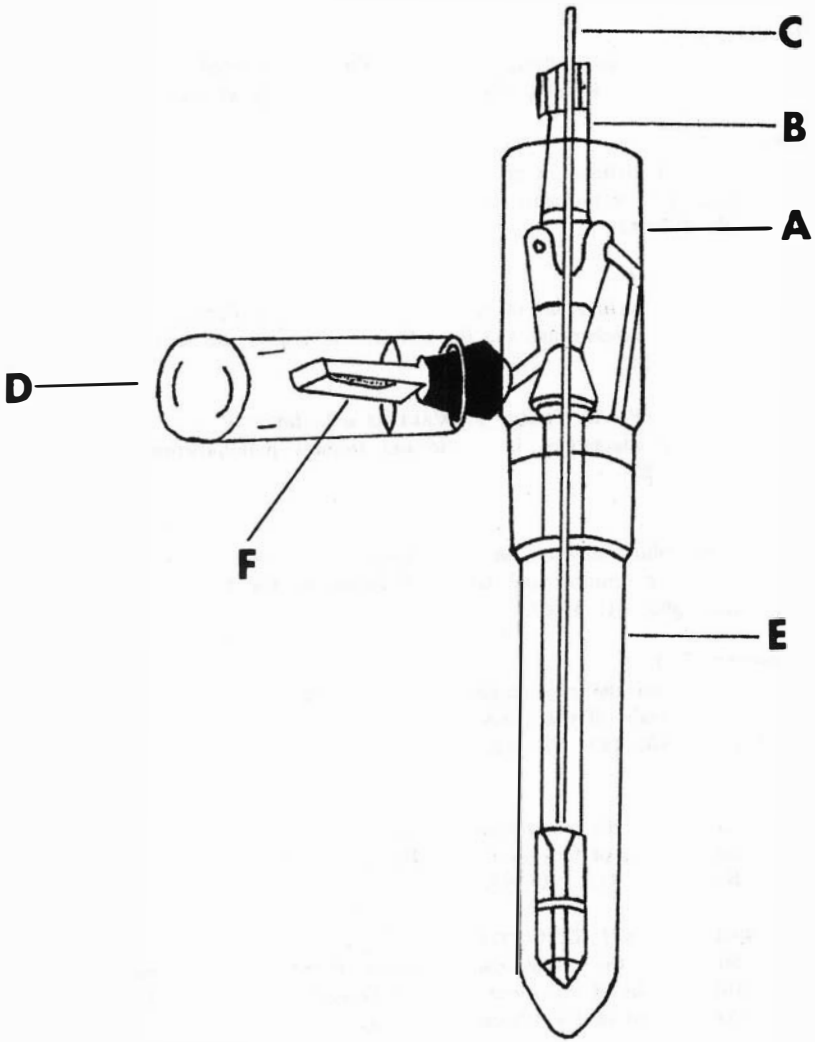
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Fig. 2. Scholander microvolumetric respirometer. A: water bath; B: rack; C: motor; D: Mark SH 11 shaker; E: Thermomix 11.

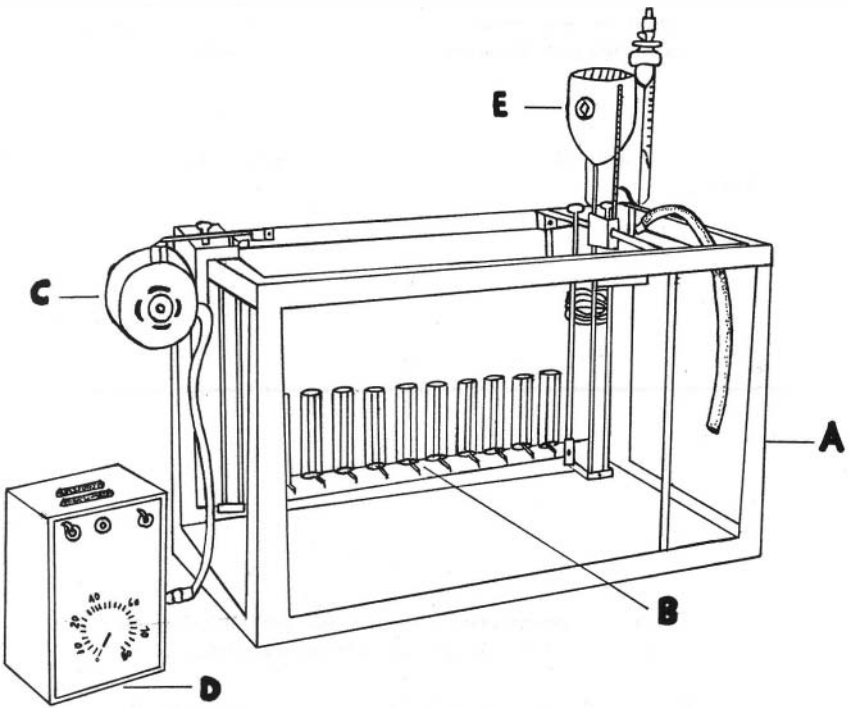

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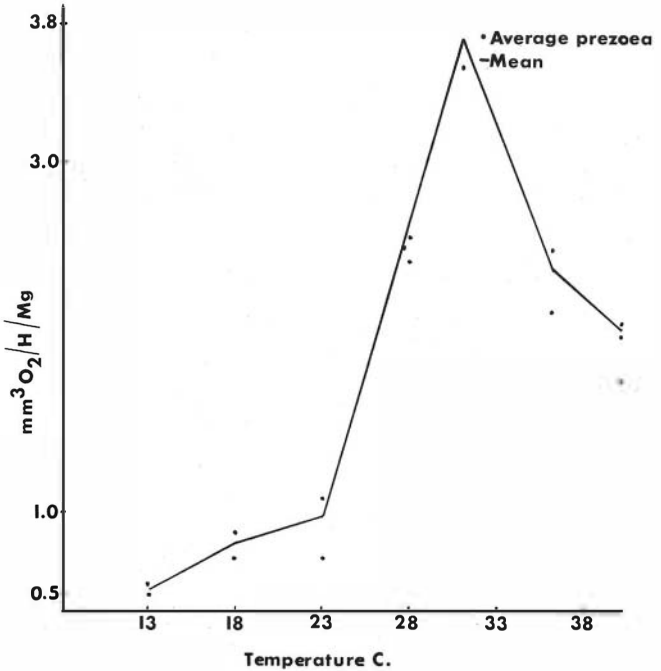
Fig. 3. Oxygen consumption per hour and per milligram for pre-zoea of *P. crassipes* at different temperatures.

Fig. 4. Oxygen consumption per hour and per milligram for the first zoeal stage of *P. crassipes* at different temperatures.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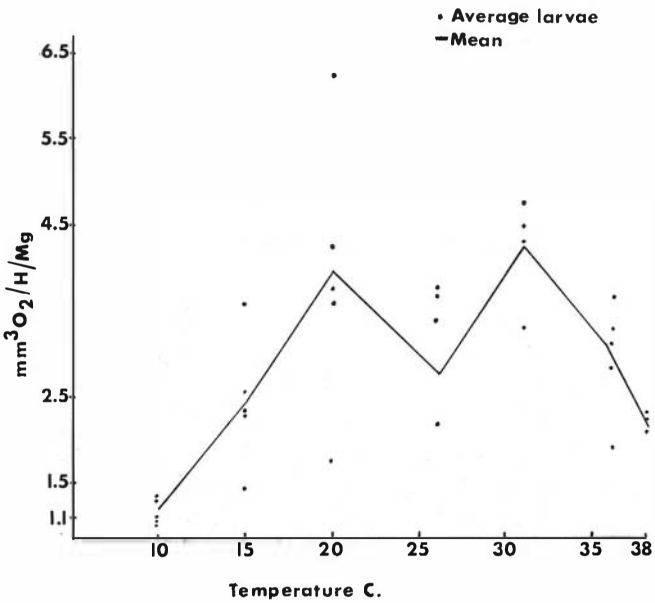
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