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OXYGEN CONSUMPTION AND MOTILE ACTIVITY OF THE BROWN SHRIMP CRANGON CRANGON RELATED TO TEMPERATURE AND BODY SIZE

by

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CONTENTS

I. INTRODUCTION

Several studies of the ecology of North Sea and Wadden Sea populations of *Crangon crangon* have been made. These have shown that a distinct seasonal migratory behaviour occurs that comprises both feeding and spawning migrations (MEYER-WAARDEN, 1935; TIEWS, 1957; BODDEKE, 1975, 1976; VAN DER BAAN, 1975; SPAARGAREN, 1980). Studies on the reproduction of *Crangon* (*cf.* TIEWS, 1970) show that several overlapping brood waves are observed through the warmer part of the year, whereas the number of egg-bearing females is low during winter. From the beginning of April the pelagic larvae settle over the intertidal flats where they feed and have a period of rapid juvenile growth. Peak settlement occurs during May and June, but settling proceeds untill October-November. Thus these intertidal Wadden flats comprise an important, if not undispensable, nursery area for *Crangon* (JANSSEN & KUIPERS, 1980; KUIPERS & DAPPER, 1981). Mean numbers of juvenile shrimps in these areas reach 50 animals per m^2 during the summer months (KUIPERS & DAPPER, 1981). During low water these juveniles, that have a length range from 5 to 35 mm and an average

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length of about 20 mm, remain on the flats where they bury in the sand (JANSSEN & KUIPERS, 1980). Larger immature specimens tend to aggregate in gullies during low tide (HARTSUIKER, 1966), whereas the adults (> 40 mm) inhabit the subtidal permanently.

A preliminary assessment of the role of juvenile *Crangon* in the energy flow of the intertidal area of the Balgzand in the western Wadden Sea was made by JANSSEN (1979) and KUIPERS & DAPPER (1981). In the energy budget estimations of the animals made by VAN LISSA (1977), metabolism values were derived from measurements of the oxygen uptake of the animals by HAGERMAN (1970a). However, HAGERMAN'S data referred to animals of length classes 25 mm and 45 mm and did not include values obtained at temperatures >20° C. In the tidal flat areas of the Wadden Sea during spring and summer over 80% of the *Crangon* population are < 25 mm long and water temperatures >20° C are common; they may reach 30° C in places covered with a film of water at low tide (DE WILDE & BERGHUIS, 1979). More detailed estimates on the respiration of *Crangon* in the tidal zone are needed in further calculations on the energy budget of the system. Therefore, in this study long-term measurements of O_2 uptake were made (between April and September 1978) and discussed in relation to differences in water temperature, body weight, photoperiod and motile activity.

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II. MATERIALS AND METHODS

Experimental animals were collected, at low tide, from an intertidal area close to the Netherlands Institute of Sea Research (NIOZ), Texel. Juveniles (<20 mm) were collected in shallow water, larger specimens (20 to 40 mm) from a gully and larger animals than this were collected from the Marsdiep (*i.e.* sublittorally). Before being used, the animals were allowed to adapt to the experimental temperatures for periods ranging from 3 to 7 days. With temperatures above 20° C long adaptation times are not possible because of the rapid growth of the juveniles and the high mortality of adults. During adaptation the animals were fed mantle tissue of *Mytilus*. The aquaria were provided with a layer of sandy sediment. Cool white tubes over the aquaria were controlled by a seasonal clock which gave the appropriate diurnal rhythm but transitional twilight periods were absent. The aquaria were non-tidal.

Experimental temperatures were 5.8, 10, 15, 20, 25 and 30° C and animals of body length classes 1, 2, 3, 4 and 5 cm were selected. Approximately in step with ambient sea water temperatures, each temperature series lasted approximately a month. At all times a constant salinity of 24‰ was maintained.

Measurements of oxygen consumption were made using a flow-through respirometer (DE WILDE, 1973). Oxygen saturation in the measuring chambers was never allowed to fall below 75%. The measuring chamber (15 cm diameter, 5 cm high) was provided with a 2 cm layer of acid-washed sand. Each series of measurements was completed with a blank without shrimps. The number of animals used in the respirometer at one time was 10, 3, 2, 1 and 1 for the 1, 2, 3, 4 and 5 cm classes respectively. All animals were fed shortly before being put into the respirometer and were not fed again until removed. Usually, each series of measurements included 2 dark and 1 light period. The first few hours of recording were discarded because of the high oxygen uptake values which were attributed to the stresses of handling. At 25° and 30° C, measurements were restricted to 24 h only because of the high mortalities. At 30° C, different animals were needed for the day and the night recordings. The ash-free dry weight of all experimental animals was determined subsequently by drying at 60° C and burning the remains at 600° C for 2 h.

Assessments of whole animal activity were made at the same time as the oxygen consumption recordings. Some were made of the animals in the respirometer and others in a similar observation chamber (Fig. 1). In the centre of the Perspex observation chamber (diameter 17 cm) was mounted a 5 × 5 × 5 cm cube whose sides were covered with light

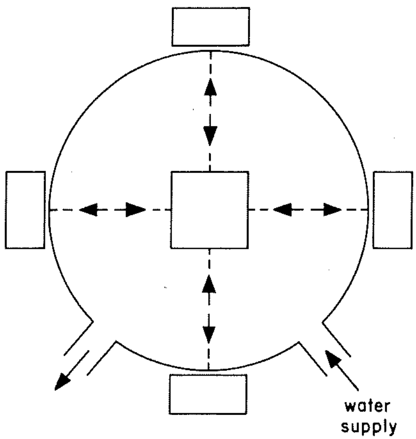

Fig. 1. Cylindrical observation chamber for the registration of motile activity in *Crangon crangon*, seen from above, with the infra-red devices and central reflection cube.

reflecting material. Horizontal beams of infra-red light (I.R.), emitted by 4 I.R. devices (AEG 54 U1) positioned at the sides of the chamber, skimmed the sediment surface and were reflected off the central cube. Beam interruptions were detected and recorded in a Esterline Argus event recorder. When the activity in the respirometer was monitored, only one I.R. device was used. Similar methods of motile activity recording are described by HALCROW & BOYD (1967); HAGERMAN (1970b), GIBSON (1973). Because only a proportion of the total motile activity is recorded, the method provides only relative data (GIBSON, 1973) but suitable for providing the comparative data required here for the series of temperature experiments.

III. RESULTS AND INTERPRETATION

1. OXYGEN CONSUMPTION RELATED TO BODY WEIGHT

Fig. 2 illustrates the relationship between O_2 consumption and the ash-free dry weight (ADW) of *Crangon* as determined for the 6 selected

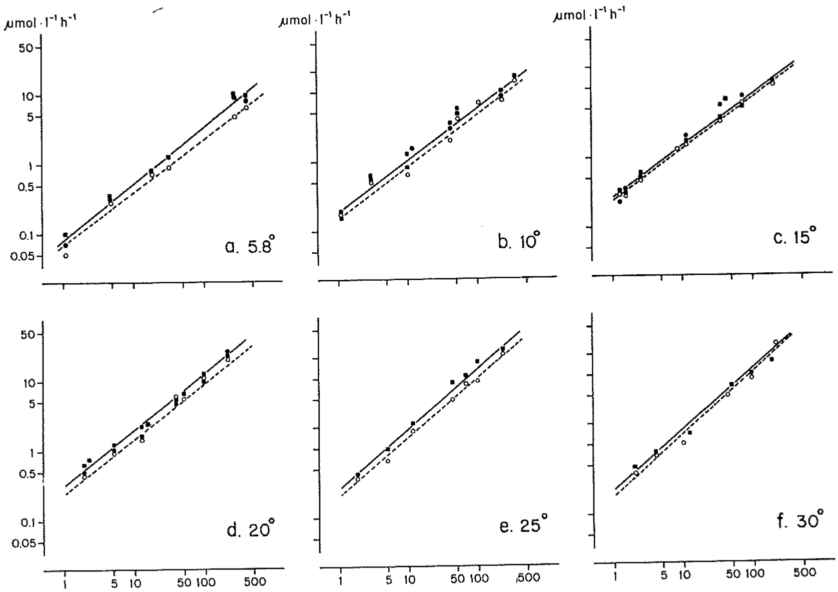

Fig. 2. Relationship between oxygen consumption (μmol · l $^{-1}$ · h $^{-1}$) and body weight (mg ADW) of *Crangon crangon* at the experimental temperatures of 5.8, 10, 15, 20, 25 and 30° C; observations during the first night (■), the following day (○) and the second night (●); values of moulting animals (*) marked. Regression lines calculated for day (broken lines) and night (full lines).

temperatures. In each case the double logarithmic plots are positively linear, as they are for the data of many other poikilotherms (NEWELL, 1970). The day and night data were treated separately in each case and revealed that a small but obvious and consistently higher O_2 consumption occurred during darkness. The relevant regression data are presented in Table I.

TABLE I

Values of *a* and *b* of the linear regressions found in Fig. 2 between the logarithms of oxygen consumption (R; μmol·l^{-1}·h^{-1}) and weight (W; mg ADW) according to the formula $R = a\,W^b$. Night and day values for 6 temperatures with number of observations (n) and correlation coefficient (r).

Temp. (°C)	*Night/day*	*a*	*b*	*n*	*r*
5.8	night	0.08	0.81	10	0.99
	day	0.07	0.75	6	0.99
10	night	0.17	0.74	13	0.99
	day	0.13	0.74	8	0.96
15	night	0.26	0.74	13	0.98
	day	0.23	0.74	8	0.99
20	night	0.32	0.79	13	0.99
	day	0.27	0.79	7	0.99
25	night	0.26	0.87	7	0.98
	day	0.21	0.84	7	0.99
30	night	0.22	0.87	6	0.98
	day	0.18	0.89	6	0.98

Amongst the juvenile shrimps some animals of each sample moulted during the experiment. This normally occurred at night and the violent movements which accompany exuviation cause such animals to have enhanced O_2 consumption levels for about an hour.

2. OXYGEN CONSUMPTION RELATED TO TEMPERATURE

Fig. 3a shows the log O_2 consumption data of 4 "standard" animals of 2, 10, 50 and 200 mg (ADW) plotted against temperature. The 95% confidence limits, calculated from the regression data are included. Fig. 3b also includes such data from 3 "standard" animals of 10, 50 and 200 mg (ADW) but plotted linearly and including also the lowest recorded values obtained at each temperature. The lowest O_2 consumption values are taken here to represent those of completely quiescent animals which had been buried in the sand for some time and occurred during daytime in all cases. According to JOB (1955) such values represent the standard metabolism of such animals. DYER & UGLOW (1977, 1978) however, found still lower ventilation rates in immobile *Crangon* on the sand surface. They assume this to be caused by increased energy costs associated with securing a ventilatory flow in the buried position. Therefore, our standard metabolic rates may represent overestimates to some extent.

Fig. 3 shows that O_2 consumption increases directly with temperature until a maximum is reached. The maximum value is also dependent upon body weight. At higher temperatures mean O_2 consumption is decreased except in the case of the standard metabolism values which, over the temperature range used, continued to increase.

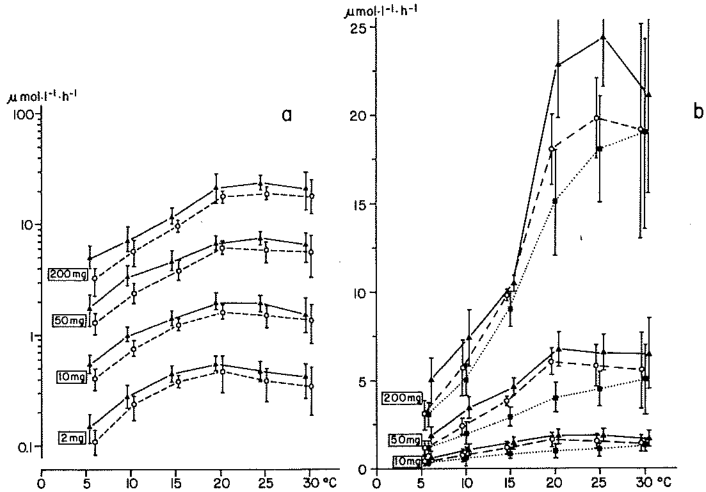

Fig. 3. a. Relationship between oxygen consumption and temperature for 4 "standard shrimps" of 2, 10, 50 and 200 mg ADW; uptake at night (full lines) and during the day (broken lines) on a logarithmic scale with 95% confidence limits. b. The same on a linear scale for 3 "standard shrimps", and the so-called standard metabolism (×) included.

The significance of the inclinations of the curves in Fig. 3 and of the differences between the regression lines in Fig. 2 were tested statistically (Draper & Smith, 1967). In summary, the relationships of the oxygen consumption of *Crangon* to temperature and body weight can be described by the equation:

$$\log O_2 = a + bT + c \log W + dT \log W - eT^2$$

where O_2 is oxygen consumption in $\mu mol \cdot l^{-1} \cdot h^{-1}$, T is temperature in centigrade, W is the ash-free dry weight in mg, a, b, c, d and e are constants; $T \log W$ represents an interaction term. The constants a to e

were calculated, for the day and night data separately, and were all found to be highly significant ($p < 0.001$); they amounted to -1.29, 0.074, 0.69, 0.0078 and 0.016 for the day, and to -1.49, 0.098, 0.68, 0.0080 and 0.0020 for the night, respectively.

3. MOTILE ACTIVITY

Fig. 4 shows the relative mobile activity, expressed as the number of activity counts per hour, plotted as a function of time for 4 "standard" animals of 2, 10, 50 and 200 mg ADW. The values represent the data obtained from the circular observation chamber experiments and those obtained using the measuring chamber of the respirometer. Because of technical problems, recordings at the lowest temperature used are lacking. The number of counts representing the groups of smaller-sized animals probably are underestimates as small animals are sometimes able to avoid the infra red beam. The highest activities were recorded at night with a distinct maximum shortly after the dark period had started. Increased activity commenced some hours before darkness which suggests an endogenous character of this behaviour. The predominance of nocturnal activity in *Crangon* has been shown also by HAVINGA (1929), HAGERMAN (1970b) and TIEWS (1970). Because there was no gradual transition from light to dark in these experiments, the observed peak of maximum activity during the first hour of darkness may be due to the stress of an abrupt change in the light intensity. However, similar experiments carried out under natural light conditions produced similar results (HAGERMAN, 1970b). HAGERMAN (1970b) also noted enhanced activity in the period before sunset. The data in Fig. 5 reveal the persistence of a diurnal activity pattern some 92 hours after the start of the experiment with freshly-collected animals. This finding contrasts with those of HAGERMAN (1970b) which indicated a disappearance of such rhythms after 48 hours.

Temperature has important effects on the motile activity of *Crangon*. Between 10 and 20° C, activity increased in all but the smallest (2 mg ADW) group, which showed a higher activity at 10° than at 15° C. However, with 10° C a larger number of animals was used and overcrowding may have prevented normal behaviour in the small animals. In the range from 20 to 25° C hardly any increase in activity occurred in the small animals whereas in the larger animals activity decreased. This trend is extended at higher temperatures. At 25° C adult shrimps start to suffer mortality and different groups of animals were used during the subsequent 12 h periods of night and day. Generally juvenile shrimps will resist high temperatures much better than large ones. At 30° C mortality prevented the adults to survive the 24 h observation

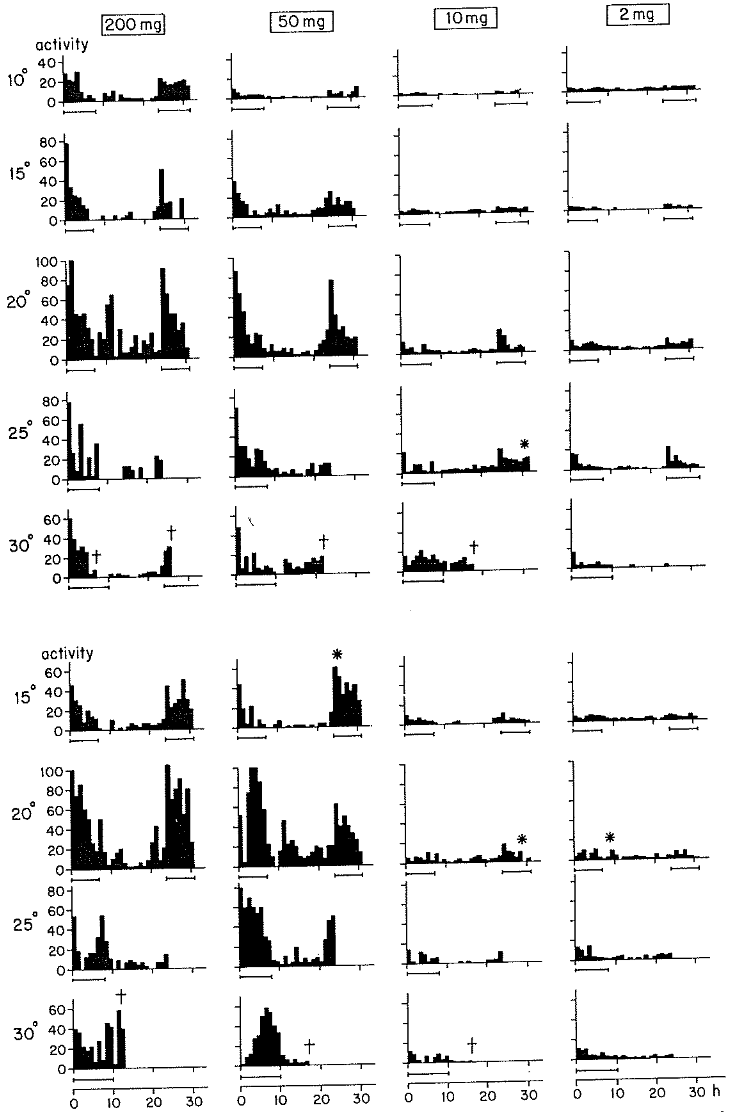

Fig. 4. Histograms showing relative motile activities per animal per hour in *Crangon* of 2, 10, 50, and 200 mg ADW in relation to temperature and light periods of natural length. Data obtained from observation chamber (upper set of histograms) and from respirometer (lower set of histograms). Indicated are dark periods (horizontal bars) and death (†) or moult (*) of the experimental animal.

periods. In the smallest size groups mortalities were negligible at 30° C.

The energy expended on motile activity can be estimated from the difference in oxygen requirement during the active period at night and during standard metabolism. Actually this represents the energy which is available to the animal to perform its body movements, searching for food, migrations, *etc*. FRY (1955) introduced the concept of the "scope for activity" for this.

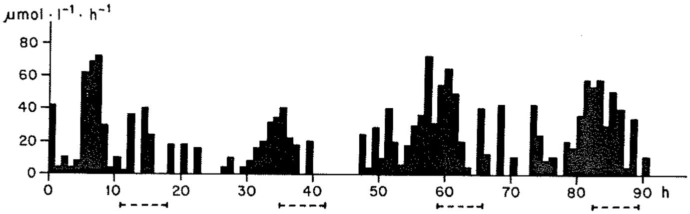

Fig. 5. Hourly activity rhythm as demonstrated by an adult shrimp of 40 mm length kept in darkness immediately after collection; natural periods of darkness indicated (horizontal bars).

Again for 4 "standard" shrimps of 2, 10, 50 and 200 mg ADW the scope for activity is plotted versus temperature (Fig. 6). Moreover the average activity at each temperature, as obtained from the recordings in the observation chamber during the night are given. By comparing

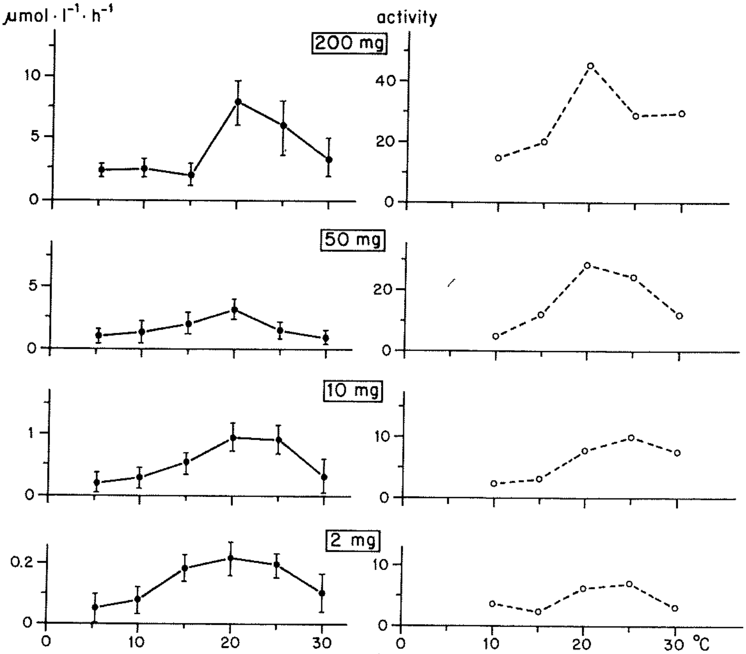

Fig. 6. Scope for activity (left; μmol · l $^{-1}$ · h $^{-1}$) and relative activity (right) in "standard shrimps" of 2, 10, 50 and 200 mg ADW in relation to temperature.

both results at equal temperatures, it appears that both the maximum values of the "scope" and of motile activity in adults occur at about 20° C. In juveniles maximum "scope" is found at a somewhat lower temperature (20°) as compared to that (25°) of maximum activity. According to BRETT (1956) the temperature of the maximum "scope" generally equals the so-called preferential temperature of the species.

IV. SUMMARY

Oxygen uptake of the brown shrimp, *Crangon crangon* (L.), from the Dutch Wadden Sea was measured in relation to body size and temperature. Simultaneously, motile activity was recorded to investigate its metabolic consequences. Data on O_2 uptake were obtained in a flow-through respirometer under almost natural conditions.

At night the overall O_2 demand was found to be enhanced due to increased nocturnal activity. During day time *Crangon* remains buried in the sand. Both standard and active metabolism showed to be strongly temperature dependent. Moreover, the influence of temperature on energy metabolism is related to body weight. Juveniles show a better temperature tolerance than adults, the adults suffering considerable mortalities at high temperatures. In juveniles a maximum "scope for activity" occurs in a wider range than in adults.

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