Oxygen consumption of *Callianassa kraussi* Stebbing (Thalassinidea, Decapoda, Crustacea) in relation to various environmental conditions

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Oxygen consumption experiments were performed on the thalassinid prawn, *Callianassa kraussi* Stebbing, using an open flow system coupled to a Radiometer electrode and a continuous recorder. The effect of starvation, sex, body size, salinity, temperature, seasons and reduced oxygen tensions on the respiratory rates of the prawns were investigated. Of these factors, body size, temperature and seasons appeared to have the greatest effect. The results obtained showed oxyqen consumption of *C. kraussi* increasing with mass by the mean power of 0,72, a mean Q_{10} value of 2,80, a higher metabolism (at a given temperature) in winter than in summer and a similar respiration rate (at a given temperature) at salinities of 35 and 17 ‰.

Suurstofverbruik-proefnemings is op die garnaal *Callianassa kraussi* Stebbing uitgevoer, deur gebruik te maak van 'n oopvloeistelsel gekoppel aan 'n Radiometer-elektrode en 'n deurlopende registreertoestel. Die uitwerking van uithongering, geslag, liggaamsmassa, soutgehalte, temperatuur, jaargetye en verminderde suurstofspanning op die asemhalingssnelhede van die garnale is ondersoek. Van die bogenoemde faktore het liggaamsmassa, temperatuur en jaargetye blykbaar die grootste uitwerking gehad. Die resultate het die volgende getoon: suurstofverbruik van *C. kraussi* wat met massa toegeneem het met 'n gemiddelde mag van 0,72; 'n gemiddelde Q_{10}-waarde van 2,80; 'n hoër metabolisme (by 'n gegewe temperatuur) in die winter as in die somer en soortgelyke suurstofverbruik (by 'n gegewe temperatuur) by soutgehaltes van 35 en 17 ‰.

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The thalassinid prawn *Callianassa kraussi* Stebbing has a wide distribution in southern Africa (Day 1967) and is common in most of the estuaries of this region (Day 1981b). As part of an ecological study of the dominant macrobenthos in the Swartkops (33°51'S / 25°38'E), aspects of the respiratory physiology of *C. kraussi* were studied. These results are represented in this paper and cover the effects of body mass, salinity, temperature, seasons and reduced oxygen tension on the respiration rates of this species.

Notable studies on *C. kraussi* dealt with growth and reproduction (Forbes 1973, 1977, 1978; Hanekom 1980), osmotic regulation (Forbes 1974) and responses to respiratory stress (Lourens 1970). Respiration works were, however, performed on other thalassinid prawn species (Montuori 1913; Hill 1967; Thompson & Pritchard 1969; Miller, Pritchard & Rutledge 1976; Torres, Gluck & Childress 1977; Felder 1979) and most of these covered the respiratory and physiological responses of the different species to hypoxic conditions. Many of the factors dealt with in this paper were ignored.

Methods

Each set of experiments began 18–26 h after fresh estuarine water and prawns had been collected from the Swartkops estuary and they lasted a further 2–4 days. The water used was passed through a 60 μm Gelman filter. Prawns (20–40 individuals) were kept in two 60 l holding tanks at temperature regimes of *c.* 14–16°C (in winter) and *c.* 18–21°C (in summer) and at salinities which matched those of the experiments. No attempt was made to feed the prawns.

An open flow respirometer was used to determine oxygen consumption (Figure 1). It was placed in an air-

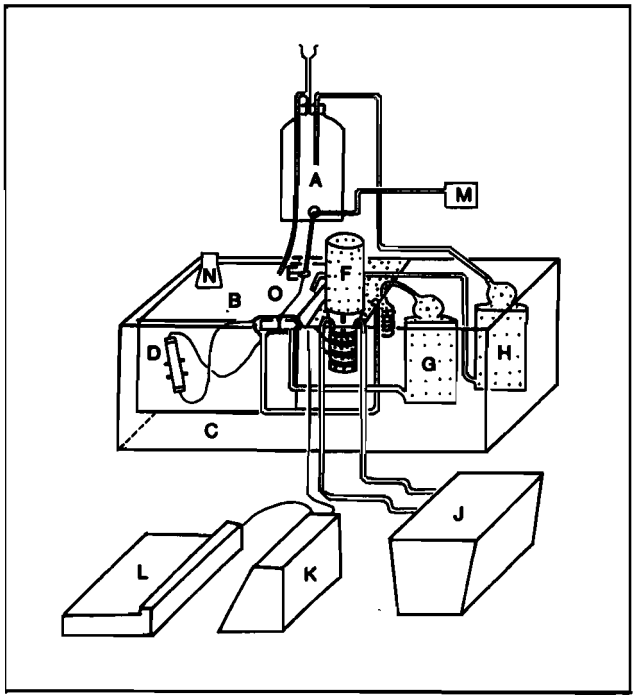

Figure 1 The apparatus used in measuring the oxygen consumption of *C. kraussi* (A = glass aspirator as reservoir, B = sea water tank, C = water bath filled with 15% ethanol solution, D = respiratory chamber, E = gang valves, F = thermostat controlled heating unit, G and H = two Eheim filter and pump units, I = oxygen electrode, J = Fryka cooling unit, K = Radiometer analyser, L = continuous recorder, M = diaphragm pump, N = acclimation flask).

conditioned room and the sides of the water bath (C) and waterjacket of the oxygen electrode (I) were insulated with polystyrene foam. Temperature differences between the various components of the system were less than 0,5°C, while the leakage deflection of the Radiometer analyser (K) was less than 5 mm Hg. To achieve the latter, a thick (5 mm) glass walled experimental tank (B) was used, the Eheim pump (G) was seated in a glass beaker and the metal screws below its impeller were replaced by plastic ones.

Air saturated estuarine water was siphoned from the reservoir (A) by means of a nylon tube (O), which has a low diffusion coefficient (see Yasuda 1966), through a respiratory chamber (D), out via a Radiometer oxygen electrode (L) and into a measuring cylinder.

The flow rate of water through the system was controlled by a series of valves (E) and the oxygen concentration in the respiration chamber remained above the 65–70% level during each experimental run. The respiration chamber was selected from a series of thick walled, cylindrical glass tubes (internal diameters and lengths of 5, 10 or 15 mm and 100, 120 and 130 mm respectively), closed at each end with a pierced rubber stopper . The chamber chosen allowed the monitored prawn to move freely, but not actively swim. It was darkened, secured in a near vertical position and the lower 3–4 cm filled with 2–3 mm sterilized glass balls to ensure thorough mixing of the water before it reached the oxygen electrode. This electrode was pressure sensitive and was first calibrated statically. It was then reset once it was connected to the system and a control run lasting 30–60 min was performed before each experimental run. Each prawn monitored was first placed in a temperature acclimation flask for at least 2 h, before being transferred to the respiration chamber. Measuring started only once the prawn had calmed down and the recordings were of short duration (2–4 h). The hourly respiration rate was calculated from the most even 60-min trace.

Starvation

The hourly oxygen consumption rates at 20°C and 35 ‰ of five *C. kraussi* were determined after 1, 3, 5 and 7 days of starvation and the values for each day were compared using a one way analysis of variance (Snedecor & Cochran 1973).

Sexes

The respiration rates at 20°C and 35 ‰ of five pairs of male and female prawns of similar mass were determined and compared using a paired *t* test .

Salinity and temperature

The respiration rates of *C. kraussi* were determined at various salinities and temperatures, which covered the ranges normally encountered within the estuary (Hanekom 1980). Approximately 15 prawns of both sexes and comprising three size classes (*c.* 5,5–6,0; 7,5–8,0 and 9,0–9,5 mm carapace length) were used in each of these experiments and a mass metabolism equation ($\log M = \log a + b \log W$, where M = respiration rate in $\mu l\ O_2.h^{-1}$, W = dry mass in mg and a and b = constants) was constructed for each set of experimental conditions. The regression lines for these equations were compared in a manner described by Snedecor & Cochran (1973). The Q_{10} values (Schmidt-Nielsen 1975) and the type of seasonal acclimation (Prosser 1973) was determined from the oxygen consumption rates (calculated from the mass metabolism equations) for a standard 300 mg dry mass prawn at various temperatures.

Reduced oxygen tension

To determine the range of oxygen tensions to which *C. kraussi* in the intertidal zone was exposed, water samples were taken from prawn burrows in the mid-tide region during high and low tide. A 30 cm long, hollow stainless steel needle having 70 µm holes near its end was fitted to a 10 ml glass syringe. The syringe and needle were flushed out with 40% formaldehyde solution to displace any air present. The needle was pushed vertically down the burrow opening. A water sample was drawn into the syringe, where the residue of formaldehyde left behind would kill the micro-organisms present in the water (Pamatmat 1968).

The filled syringes were sealed, transported back to the laboratory in a cool-box and oxygen analyses were done within four hours of sampling , using a Radiometer electrode. Respiration experiments were performed on five *C. kraussi* experiencing 20°C, 35 ‰ and a range of external oxygen tensions from 140–27 mm Hg. The oxygen levels were reduced by bubbling nitrogen through the water reservoir (A). The results recorded at each oxygen level were compared using a one way analysis of variance.

Results

C. kraussi was seldom inactive during the experimental run. It usually beat its pleopods or moved slowly up and down the respiratory chamber. The respiration rates monitored were regarded as routine, namely that of an

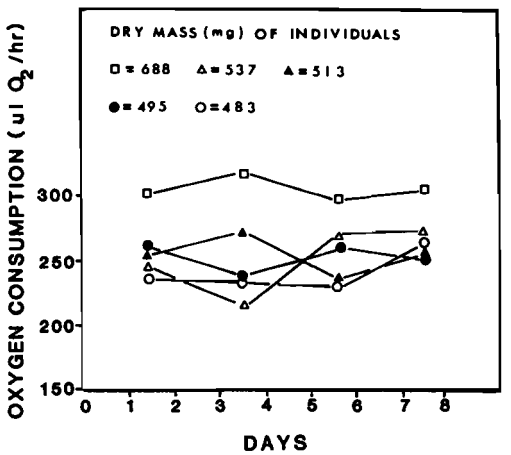

Figure 2 The oxygen consumption of five *C. kraussi* individuals over 8 days of starvation.

organism whose only movements are spontaneous (Wycliffe & Job 1977).

The routine oxygen consumption of five *C. kraussi* monitored after 1, 3, 5 and 7 days of starvation are shown in Figure 2. The respiration rates on the various days were similar ($F = 0{,}18$; $P > 0{,}10$) and no correction factor was applied to the results of the other experiments, which were spread over 3–5 days. Furthermore, no significant difference ($t = -0{,}13$; $P > 0{,}10$) was recorded between the respiration rates of five pairs of male and female prawns of similar mass (Table 1).

Oxygen consumption rates of prawns of different masses and subject to various combinations of temperatures and salinities are shown in Figures 3–6. The regression equations of these lines are listed in Table 2, while the results of stastical comparisons of the various regression lines are given in Table 3. No significant difference ($P > 0{,}05$) was determined between the respiration rates recorded at the same temperature, but differing salinities of 35 and 17 ‰. At 5 ‰ (20°C), however, the respiration rates increased relative to those at 35 and 17 ‰ (20°C) (Figure 3), resulting in a significant ($P < 0{,}01$) increase in the elevation (or *a* constant) of this regression line (Table 3). In the comparison of the respiration rates of prawns collected from the upper and lower reaches of the Swartkops estuary, two of the five pairs of regression lines differed in elevation on the 95% of significance, while only one of these pairs varied on the 97% level (Table 3, Figure 4). The respiration rates of *C. kraussi* from the upper and lower reaches were therefore taken to be similar.

Oxygen consumption rates of *C. kraussi* at 35 ‰ and at various temperatures and seasons are shown in Figures 5–6. The above regression lines all differed significantly ($P < 0{,}01$) from each other in elevation (or in the *a* constant) (Table 3). This indicated an increase in the oxygen consumption with an increase in temperature, as well as a seasonal shift in the respiration rates. These effects are illustrated in Figure 7.

The mean oxygen tension recorded for the water samples collected from *C. kraussi* burrows in the mid-tide region during high and low tides were 128 ± 8 ($n = 11$) and 20 ± 6 ($n = 18$) mmHg respectively, while the oxygen

Table 1 The oxygen consumption of five pairs of male and female *C. kraussi*, each pair having a similar mass

Dry mass (mg)		Oxygen consumption ($\mu l.h^{-1}$)		
Male	Female	Male (M)	Female (F)	Difference (M–F)
197	185	101	103	– 2
385	406	179	212	+ 33
465	442	260	238	+ 22
560	573	255	245	–10
645	616	305	308	– 3
				$t = -0{,}13$

Table 2 Values for the constants of the mass metabolism equations ($\log M = \log a + b \log W$) determined for *C. kraussi* at various salinities and temperatures. In the above equation M = oxygen consumption µl O_2 / h, W = dry mass (mg), $a + b$ = constants and in the table U and L = upper and lower reaches respectively, S and W = summer and winter, r = correlation coefficient, n = number of measurements and p = significance of correlation coefficient

Experimental conditions				Parameters of equations				
Salinity ‰	Temp. °C	Region	Season	*a*	*b*	r^2	*n*	*p*
35	30	U	S	0,9890	0,5887	0,87	14	<0,01
35	25	U	S	0,4920	0,7220	0,89	15	<0,01
35	20	U	S	0,3927	0,6745	0,89	17	<0,01
35	15	U	S	0,0125	0,7139	0,89	18	<0,01
35	20	U	W	0,4988	0,6828	0,84	20	<0,01
35	15	U	W	0,1725	0,7227	0,95	15	<0,01
35	10	U	W	0,0398	0,6025	0,80	15	<0,01
17	25	U	S	0,6176	0,6945	0,92	10	<0,01
17	20	U	S	0,1298	0,8003	0,79	18	<0,01
17	15	U	S	–0,4084	0,8873	0,91	14	<0,01
17	15	U	W	0,7961	0,7210	0,90	17	<0,01
5	20	U	S	0,3034	0,8114	0,94	15	<0,01
35	25	L	S	0,5440	0,7147	0,65	15	<0,01
35	20	L	S	0,4449	0,6875	0,83	15	<0,01
35	20	L	W	0,3444	0,7833	0,90	13	<0,01

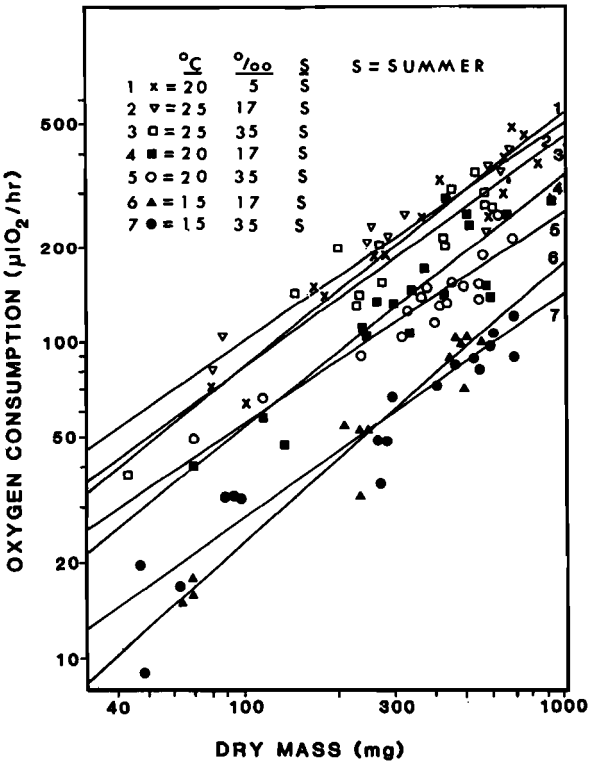

Figure 3 The respiration rate of *C. kraussi* at different salinities (35‰, 17‰ and 5‰) and temperatures (15°C, 20°C and 25°C) during summer.

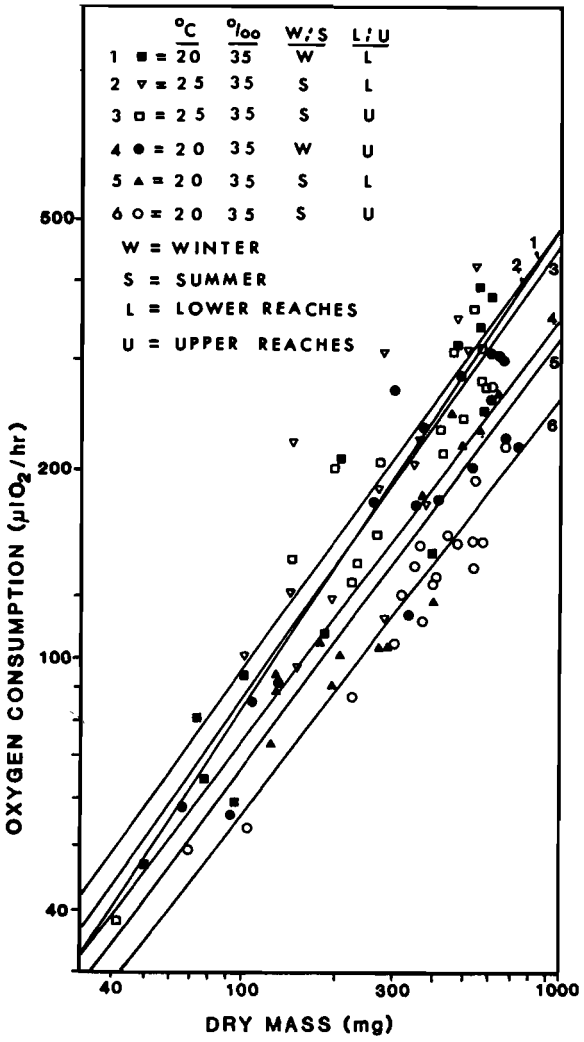

Figure 4 Comparison of the respiration rates of *C. kraussi* from the upper and lower reaches of the Swartkops estuary.

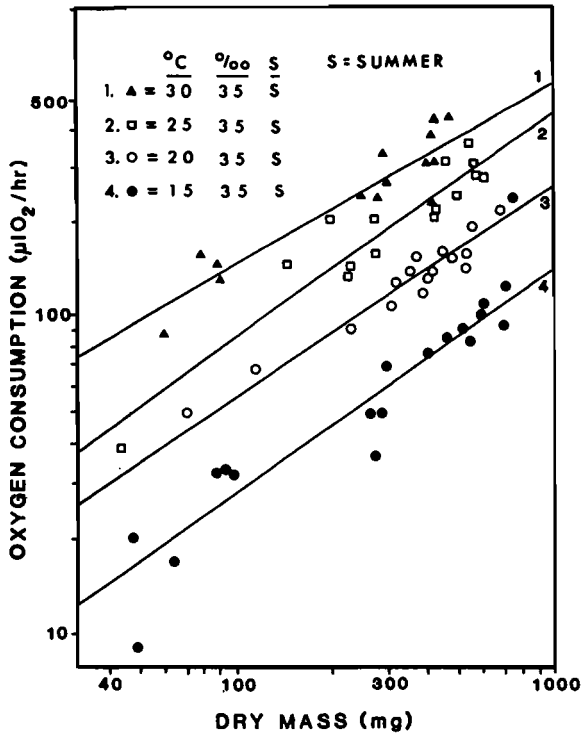

Figure 5 The effect of acute temperature change on the respiration rate of *C. kraussi* during summer.

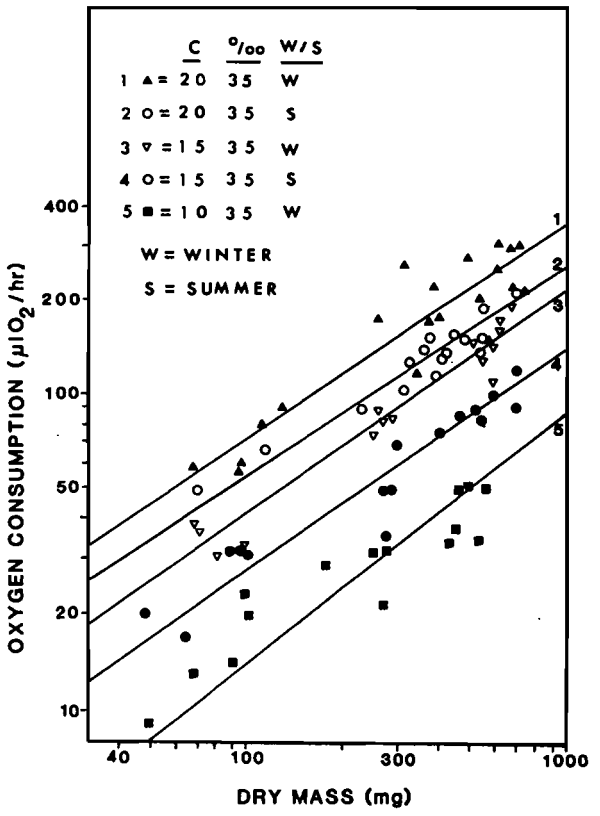

Figure 6 The effect of acute temperature change and seasons on the respiration rate of *C. kraussi*.

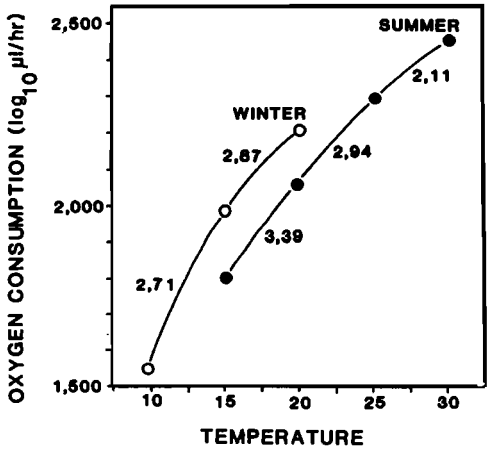

Figure 7 The calculated respiratory rate for a 300-mg prawn at different experimental temperatures during summer and winter. The Q_{10} for each 5°C increase in temperature is shown.

consumption rates of *C. kraussi* over a similar range of oxygen tensions (140–27 mmHg) is shown in Figure 8. No significant decline ($F = 0{,}09$; $P > 0{,}10$) was measured in the respiration rates over this range.

Discussion

The temperature and salinity experiments, in which 14–18 prawns were each monitored for 2–4 h, ran continuously over a 3–4-day period. The effects of diurnal

Table 3 *F* values and degrees of freedom (*df*) recorded in the comparisons of the elevation, residual variance and slopes of the various regression lines describing the respiration of *C. kraussi* under various environmental conditions. Letters U, L, S and W are defined in Table 2. The significance of the differences is shown by asterisks

	Elevation		Residual variance		Slope	
Regression line compared	*F* value	*df*	*F* value	*df*	*F* value	*df*
(A)Comparison of regression lines constructed from the respiratory rates at various salinities						
(U S 25°C) 35‰ : 17‰	3,74	1 : 22	1,09	8 : 13	0,22	1 : 21
(U S 20°C) 35‰ : 17‰	3,81	1 : 33	1,71	16 : 16	1,32	1 : 32
(U S 15°C) 35‰ : 17‰	0,02	1 : 29	1,26	12 : 16	0,36	1 : 28
(U W 15°C) 35‰ : 17‰	3,75	1 : 29	1,67	13 : 15	0,28	1 : 28
(U S 20°C) 17‰ : 5‰	31,16***	1 : 30	2,69	13 : 16	0,27	1 : 29
(B)Comparison of regression lines constructed for the respiratory rates of prawns from the upper and lower reaches						
(S 25°C 35‰) U : L	1,47	1 : 26	2,49	13 ; 13	0,002	1 : 26
(S 25°C 35‰) U : L	10,10***	1 : 30	1,33	13 : 16	0,13	1 :29
(W 20°C 35‰) U : L	5,06*	1 : 30	1,10	11 : 18	0,90	1 : 29
(S 25°C) 17‰ U : 35‰ L	3,74	1 : 22	1,09	8 : 13	0,22	1 : 21
(S 20°C) 17‰ U : 35‰ L	1,09	1 : 30	2,28	13 : 16	0,62	1 : 29
(C) Comparison of regression lines constructed for the respiratory rates of prawns at various temperatures						
(U S 35‰) 30°C : 25°C	44,8***	1 : 25	1,18	12 : 13	2,12	1 : 25
(U S 35‰) 25°C ; 20°C	75,8***	1 : 30	1,35	13 : 16	0,51	1 : 29
(U S 35‰) 20°C : 15°C	87,6***	1 : 32	1,30	15 : 16	0,42	1 : 32
(U W 35‰) 20°C : 15°C	61,2***	1 : 31	2,30	13 : 17	0,20	1 : 30
(U W 35‰) 15°C : 10°C	17,8***	1 : 27	2,32	13 : 13	1,68	1 : 26
(D) Comparison of regression lines constructed for the respiratory rates of prawns for different seasons (summer – winter)						
(U 20°C 35‰) S : W	23,2***	1 : 32	1,31	16 : 18	0,12	1 : 34
(L 20°C 35‰) S : W	12,8***	1 : 25	1,92	11 : 13	0,16	1 : 24
(U 15°C 35‰) S : W	34,1***	1 : 30	2,47	13 : 16	0,01	1 : 29

( ) = conditions common to both regression lines.
*, **, *** indicate significance at 5, 2,5 or 1% levels respectively.

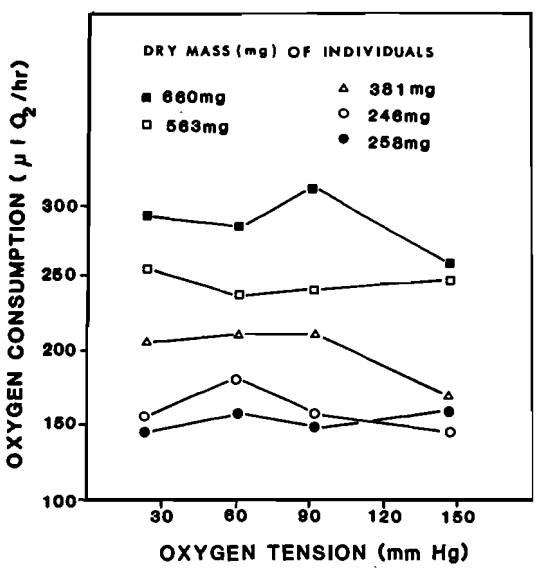

Figure 8 The respiration rate of *C. kraussi* over a range of oxygen tensions, 27–140 mmHg.

fluctuations in the respiration rates of *C. kraussi* would therefore have been incorporated into the mass metabolism equations determined in Table 2. Any such variation would have adversely affected both the correlation coeffients and the *b* values (or slopes) of the above regression equations. The correlation coeffients were, however, all significant ($P < 0,01$), while the *b* values ranged from 0,59–0,89 and had a mean of 0,72 (Table 2). This mean corresponded to the average *b* value of 0,75 determined for poikilotherms by Hemmingsen (1960) in a review study (Davies 1966). These results would suggest that diurnal variations in the respiration rates of *C. kraussi* are relatively small. Hill (1967) recorded no discernable diurnal change in the respiration rates of a similar thalassinid species, *Upogebia africana*.

In the comparison of the oxygen consumption rates of male and female *C. kraussi*, the limited data ($n = 5$ pairs) indicated no significant difference between the two sexes ($t = 0,13$; $P > 0,10$). Hill (1967) and Thompson & Pritchard (1969) made no mention of res-

piratory differences between the sexes of *U. africana, U. pugettensis* and *C. californiensis* and their data showed relatively little variation in oxygen consumption rates between prawns of similar mass. This would suggest similar respiration rates for both sexes. The magnitude of the oxygen consumption values determined for *C. kraussi* (at 35 ‰ and at various temperatures) corresponded well to those derived for other thalassinid prawn species (Table 4) and the experimental data obtained in this survey were taken as acceptable.

The oxygen consumption rates of *C. kraussi* were apparently influenced by both acute and chronic temperature changes. The effects of the former are shown in the Q_{10} values of Figure 7. These Q_{10} values were high and the means for summer and winter over respective temperature ranges of 15–20–25–30°C and 10–15–20°C were similar (*c.* 2,8). This suggested no compensation or seasonal change in the metabolic response of *C. kraussi* to acute temperature variations. Conversely, long term seasonal temperature changes apparently caused a shift in the metabolism of *C. kraussi,* because the respiration rates recorded at a given temperature were higher in winter than in summer (Figure 7). This meant that despite the lower temperatures associated with winter, the respiration rates of *C. kraussi* in the Swartkops estuary during the latter period would approximate those of summer (regression lines 2 and 3 in Figure 6). Hill (1967), on the other hand, recorded low Q_{10} values (*c.* 1,6) over a temperature range of 16–29°C and no seasonal variation in the oxygen consumption rates of *U. africana.* Reasons for the above discrepancies between *C. kraussi* and *U. africana* are not apparent, as both species burrow in the intertidal regions of estuaries and have similar distributional ranges in southern Africa (Day 1981a).

The oxygen consumption rates of *C. kraussi* recorded at the same temperatures, but differing salinities of 35 and 17 ‰ were similar ($P > 0,05$). At 5 ‰, however, the rates increased significantly ($P < 0,01$) (Table 3). This was probably related to greater osmoregulatory activity, since *C. kraussi* is an osmoconformer between salinities of 35–20 ‰, but a hyper-osmoregulator in waters of *c.* 15–3 ‰ (Forbes 1974). The above hypothesis was supported by the findings for *U.africana.* The oxygen consumption rates of this species, which is a hyper-osmoregulator between salinities of *c.* 30–4 ‰ (Hill 1971), increased steadily with declines in salinities to reach a maximum at *c.* 8 ‰ (Hill 1967). Despite this response to low salinities, there appeared to be no major long-term shift in the metabolism of the *C. kraussi* from the upper reaches of the Swartkops estuary, because four of the five pairs of the mass metabolism regression lines for prawns from the upper and lower reaches were similar ($P > 0,025$) (Table 3).

The mean oxygen tension (20 ± 6 mmHg) recorded for the water samples collected from intertidal *C. kraussi* burrows during low tide corresponded to that (*c.* 15 mm Hg) determined from *U. pugettensis* burrows (Thompson & Pritchard 1969). Over a range of external oxygen tensions of 140–27 mm Hg, which reached levels similar to that recorded at low tide, no significant change ($P > 0,10$) was determined in the routine (activity of prawn spontaneous) oxygen consumption rates of *C. kraussi* (Figure 8). Hill (1967) and Thompson & Pritchard (1969) recorded similar oxygen independence in the standard (activity minimal) or routine (activity spontaneous) respiration rates of *U. africana, U. pugettensis* and *C. californiensis* above external oxygen levels of about 45, 45 and 15 mm Hg respectively. The above values and those for this survey suggested a wider range of oxygen independent respiration for *Callianassa* species than those of *Upogebia.* Recorded LT_{50} values (time taken for 50% of the individuals to die) in anoxic conditions for *Callianassa* species [*c.* 138 h for *C. californiensis* (Thompson & Pritchard 1969), *c.* 100 h for *C. kraussi* (Lourens 1970) and *c.* 85 h for *C. jamaicene* (Felder 1979)] were also greater than those for *Upogebia* species [*c.* 81 h for *U. pugettensis*, (Thompson & Pritchard 1969) and *c.* 20 h for *U. africana* (Hill unpubl.)]. Pritchard & Eddy (1979) found that in anoxic

Table 4 A comparison of the respiratory rates recorded in this survey with those of other thalassinid prawns

Species	Researcher	Experimental conditions	Oxygen consumption calculated for a 1-g prawn (µl g^{-1} wet mass h^{-1}
C. kraussi	This study	20°C (S)	105
U. africana	Hill (unpubl. data)	20°C*	103
C. kraussi	This study	25°C (S)	169
U. africana	Hill (unpubl. data)	25°C*	230
C. subterranea	Montuori (1913, Thompson & Pritchard 1969)	25°C*	*c.* 132
C. kraussi	This study	10°C (W)	29
C. californiensis	Thompson & Pritchard (1969)	10°C*	*c.* 29
U. pugettensis	Thompson & Pritchard (1969)	10°C*	*c.* 59

W = winter, S = summer, *seasons not stated.

conditions *U. pugettensis* accumulates lactate (an end product of anaerobic glycolysis) in the hemolyph at a much greater rate than *C. californiensis,* despite the similar levels of lactate dehydrogenase in the tissues. These researchers felt that the early levelling off in the rate of lactate accumulation in *C. californiensis,* suggested that this species may be switching to a metabolic pathway other than glycolysis under anoxic conditions. The use of anaerobic metabolism by *C. kraussi* is a factor which should be investigated in the future.

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