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ENERGETICALLY DEFINING THE THERMAL LIMITS OF THE SNOW CRAB

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Summary

The snow crab, *Chionoecetes opilio*, is a cold-water species found naturally at temperatures below 5°C. Its physiology and energetics were examined to understand the metabolic limitations that restrict the snow crab to these temperatures. The species is not confined to cold water because of a limited respiratory system. Routine oxygen demand can be met even at lethal temperatures of 18°C (56 mg O_2 kg^{-1} h^{-1}, with a Q_{10} of 2·2). Blood lactate levels remain below 1·5 mmol l^{-1} and actually decline slightly with temperature.

Energy budgets, which were constructed from an examination of oxygen uptake, activity and food consumption in morphometrically mature male animals between 0 and 18°C, indicate that the snow crab is energetically restricted to cold water. Rising metabolic costs overtake caloric intake around 7°C. This is probably due to digestive metabolism which is temperature-sensitive. Food consumption increases up to 6°C but then falls. Crabs stop feeding above 12°C. Although the growth equation is positive between 1 and 7°C, it becomes slightly negative below 1°C. This observation is unexpected since snow crabs are commonly found between 0 and 1°C. Slight temperature changes in the natural environment may, therefore, regulate growth and reproduction in this species.

Introduction

Because of the economic importance of the snow crab *Chionoecetes opilio* (O. Fabricius), we were presented with the opportunity of examining the physiology of a crustacean living in a restricted temperature habitat. The snow crab is one of the most important commercial crabs in the world, and heavy exploitation of males

Key words: energetics, respiration, physiology, snow crab, *Chionoecetes*, Crustacea, Decapoda, temperature.

occurs in Atlantic Canada, Alaska and in the Sea of Japan (Bailey & Elner, 1989). Yet, apart from a short note by McLeese & Watson (1968), the respiratory physiology has received little attention.

Oxygen uptake is of interest because *C. opilio* is a deep-water species restricted in the wild to temperatures below 5 °C (Williams, 1984). In the laboratory, snow crabs begin dying at 12–15 °C (McLeese, 1968), temperatures which are relatively cold for many other crustaceans. Few physiological studies have been conducted on cold-water decapods, partly because of the difficulty of collecting such animals and the problems with maintaining low water temperatures for protracted periods. Knowledge of the physiology of *C. opilio* would also aid in understanding its ecology, since population dynamics have been highly erratic (Elner & Bailey, 1986).

We were interested in testing whether specific physiological limitations confine snow crabs to cold water. Our initial hypothesis was that oxygen uptake was inadequate at higher temperatures. This hypothesis was developed because oxygen uptake capabilities in crustaceans are limited by a number of anatomical features. The open circulatory system may be inefficient owing to the lack of fine control mechanisms and the possible presence of stagnant spaces in the sinuses (McMahon & Wilkens, 1983). Also, oxygen-carrying capacity of the blood is poor compared with many vertebrates and invertebrates since haemocyanin concentrations are low and variable (Mangum, 1980, 1983). Chitin lines crustacean gills and may offer an effective barrier to oxygen diffusion, with diffusive resistance possibly 5–10 times as great as for fish (Taylor, 1982). The respiratory system of a cold-water decapod, such as the snow crab, which is designed to meet the low metabolic needs at 0–1 °C, may, therefore, be incapable of supplying sufficient oxygen to meet the increased metabolic costs at higher temperatures.

We acknowledge that our original hypothesis could be incorrect since the perception of the decapod respiratory system has changed, especially as a result of research conducted over the last decade. The classical concept of haemolymph moving slowly through sinuses at low pressures is inaccurate. The heart of the spiny lobster *Panulirus interruptus* produces systolic pressures of 4–6·1 kPa (Belman, 1975) and cardiac output in crustaceans is high (McMahon & Wilkens, 1983). Since the crustacean circulatory system is open, the haemolymph volume is large. The high circulation rate in decapods and large volume of haemolymph in effect counteract the low carrying capacity of the blood. Further, decapods have large gill areas ranging between 4 and 8 $cm^2 g^{-1}$ (McMahon & Wilkens, 1983) and this is thought to compensate for the restricted diffusibility of the chitin layer (Taylor, 1982).

Recognizing that metabolic factors other than oxygen uptake may exclude snow crabs from warmer water, we also examined the effects of temperature on spontaneous activity, food consumption, and blood lactate and ammonia levels. These data then allowed us to calculate energy budgets for the adult male snow crab and to examine changes in energy partitioning in a crustacean over a wide range of temperatures.

Materials and methods

Experimental animals

Male snow crabs were obtained off eastern Cape Breton Island (46°40′ N, 60°10′ W) from commercial traps on 15 August 1986 and transported to Halifax, Nova Scotia. The males were placed in a tank at 11 °C for 3 days until the experimental system was operating.

Healthy, 'morphometrically mature' males, according to the criteria of Conan & Comeau (1986), between 85 and 95 mm carapace width (250 and 370 g) and with all their legs were selected for the experiments. Twenty were then transferred to the experimental system and held at 2·5–4·5 °C for 4 weeks before experiments began. The same 20 males were used throughout the experimental series which lasted a year. This was necessary since the snow crab fishery is remote from the laboratory and, except for scientific cruises, crabs are commonly moribund when landed by the fishermen. The fishery is not undertaken in the winter so it is impossible to obtain specimens during this period. Potential problems with repeated sampling in this study were mitigated by acclimating animals for at least 3 weeks at each temperature and by staggering the temperature series as much as possible. Nevertheless, the highest temperatures (15–18 °C) were examined last since these temperatures are lethal to snow crabs (McLeese, 1968).

Experimental system

Owing to the difficulties of obtaining accurate cold water temperatures for protracted periods, a chilled seawater system was specially designed and built for the experiments. The system consisted of three covered 1·35 m × 0·71 m × 0·15 m seatables containing 115–145 l of water and heavily insulated with polyurethane foam, two titanium heat-exchange coils each sitting in a 35 % ethylene glycol bath and chilled by separate refrigeration units (1500 W and 560 W), a 30 W electric pump, and Tygon tubing insulated with foam cylinders. One tank was used to videotape crab activity, one to measure oxygen uptake, and one for blood sampling. The 20 experimental males were randomly assigned to the experimental chambers: four to the 'activity tank', eight to the 'oxygen uptake tank', and eight to the 'blood assay tank'.

Sea water was pumped from the chambers in the oxygen uptake seatable through the heat exchange coils at 10–15 l min^{-1} to the activity tank and returned to the oxygen uptake tank by gravity. Fresh inflowing sea water entered the recirculation lines and was maintained at approximately 1 l min^{-1} throughout the experiments. The bottom blood assay tank received overflow water (1 l min^{-1}) from the oxygen uptake tank; its temperature ranged from 0·2 to 1·2 °C higher than the other two tanks.

Experiments

The following data were collected between 0 and 18 °C: (a) spontaneous activity; (b) oxygen uptake rates (unacclimated and acclimated routine, after feeding, after

disturbance, and consecutive recordings for 2 days); (c) food consumption; (d) blood lactate and ammonia concentrations. The temperature sequence was 3, 0, 6, 3, 9, 3, 12, 15, 4, 18°C. The daily temperature variation was usually less than 0·3°C. Except for the unacclimated oxygen uptake rates and some lactate and ammonia measurements (see below), all data were collected after at least 21 days acclimation at each temperature.

A 16h:8h light:dark cycle was used throughout the experiments. The tanks were illuminated with a 75 W blue light plus two 40 W red lights during the light period and two 40 W red lights during the dark period. The light intensity falling on the activity tank during the 'day' was $60\,\mathrm{lm\,m^{-2}}$, on the oxygen uptake tank $2\,\mathrm{lm\,m^{-2}}$, and on the blood assay tank $1\,\mathrm{lm\,m^{-2}}$. During the 'night', the light intensity was under $1\,\mathrm{lm\,m^{-2}}$ for all three tanks.

Activity measurements

A low light intensity, black and white videocamera (RCA TC2011N) with a wide-angle lens was mounted on the ceiling to film spontaneous activity of the four crabs in the activity tank. A continuous 16-h light period was recorded at each temperature on a time-lapse videorecorder (Panasonic AG-6010). A numbered grid, 120 mm × 120 mm, was painted on the bottom of the activity tank and a black 4 mm mesh glued down to improve traction for crab movement. To identify crabs on the videorecordings, individual symbols made from orange and black reflective tape were attached to each carapace with cyano-acrylate glue (Krazy Glue Inc., Chicago, IL, USA).

Four 1-h segments on the videorecordings were randomly selected at each temperature and crab movement was recorded by counting the number of grid squares the crab passed through. Movement was scored if the centre of the carapace crossed the line separating squares. Motion laterally between grid squares was recorded separately from diagonal movement. Movements along rows or columns in the grid were translated to distance by multiplying by 120 mm (the length of the grid square), whereas diagonal motion was multiplied by 170 mm (the diagonal distance of a 120 mm × 120 mm square).

Time spent moving was also recorded and speeds calculated. Because a lag occurred before the observer could verify that movement had stopped, a mean lag interval of 11 s was subtracted from all time measurements. The mean lag interval was calculated from 20 measurements on videorecordings that were carefully reanalysed (lag S.D. = 0·4 s). If the adjusted time fell below 5 s, speed measurements were removed from the analysis since very short time intervals resulted in speed estimates which were abnormally high.

Oxygen uptake rates

The eight crabs from the oxygen uptake tank lived continuously in individual polyethylene chambers (300 mm × 300 mm × 130 mm, Tupperware Home Parties Inc., Markham, Ontario), weighted with a ceramic tile, each holding 10·9 l of

water (S.D. = 0·11, $N = 12$). Since the crabs lived in these 'oxygen uptake chambers', no settling time was necessary before measurements could be started.

To record oxygen uptake, flow through the chambers was halted by carefully removing the outflow tube and plugging the hole with a rubber stopper. An Orion oxygen probe with a magnetic stir holder (model 97-08, Orion Research Inc., Cambridge, MA, USA) was gently placed down through the top inflow hole. Underneath the tank, a square of polystyrene insulation was removed and a magnetic stirrer strapped in place (Fig. 1). With this design, oxygen uptake could be recorded without moving the oxygen uptake chamber or disturbing the crab.

Oxygen consumption was recorded on chart paper and each oxygen uptake recording lasted around an hour. By this time, dissolved oxygen had fallen to about 70–80 % of air saturation levels. Each crab was recorded individually and measurements on each animal were replicated three times. Sea water flowed through the containers for 10–30 min before a new replicate was started. The probe was restandardized before each recording in sea water at the experimental temperature which had been saturated with bubbled air.

Oxygen uptake was recorded on undisturbed crabs 1 day after each temperature

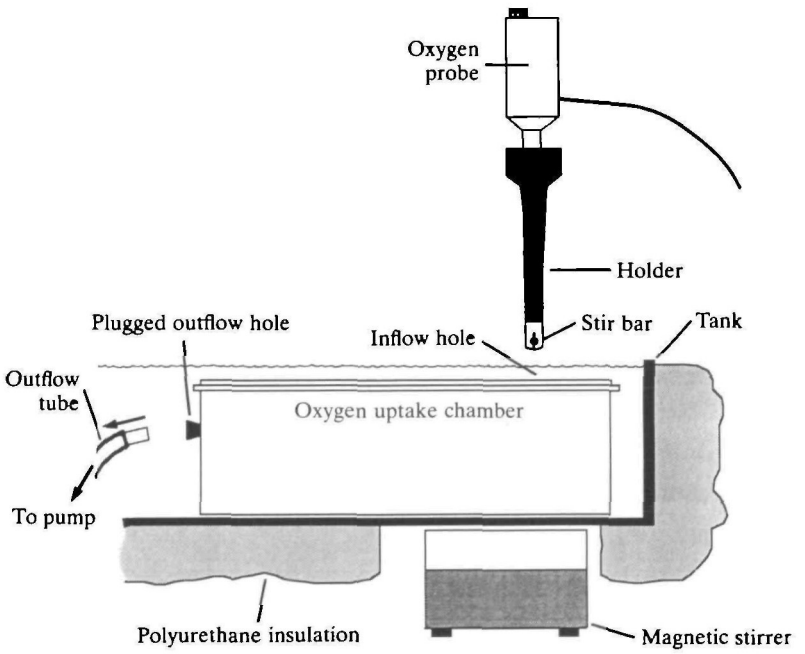

Fig. 1. A schematic diagram of the equipment used to conduct oxygen uptake measurements. The crabs lived in individual polyethylene chambers which rested in heavily insulated tanks. Before measurements were taken, the outflow tube was removed and the outflow hole gently plugged with a rubber stopper. An oxygen probe with a stir bar holder was placed down through a top inflow hole and a magnetic stirrer was strapped underneath the tank. This allowed oxygen uptake to be recorded without disturbing the crabs.

change (unacclimated series) and again after 3 weeks of exposure to each test temperature (acclimated series). Oxygen uptake was also measured after the acclimation period on disturbed crabs and recently fed crabs. Disturbance was provoked by prodding and shaking the crab for 5–10 min before each replicate. The maximum slope of the oxygen consumption curve was then analysed.

For the feeding uptake rates, food was added 6–12 h beforehand and removed with forceps shortly before the first replicate. The foods used (squid mantle, whole shrimp) were chosen since they did not disintegrate during feeding and the remains could easily be removed before recordings began without causing undue contamination of the oxygen uptake chambers. Flow through the chambers between recordings ensured clean water was present when oxygen uptake was measured.

The oxygen consumption rise caused by feeding was calculated by first subtracting resting metabolic rates (see statistical analysis section below) from post-feeding oxygen uptake rates and then dividing by the number of kilocalories consumed per kilogram of crab. In the other oxygen uptake recordings crabs were fasted for at least 2·5 days before measurements.

Consecutive recordings were also taken for a 2-day period at each temperature on two randomly chosen, acclimated animals (one fed and one usually unfed). Three measurements were made before food was added. The chambers were then visually checked before each recording to determine the amount eaten. Once at least one animal had eaten to satiation, the remaining food was removed from both chambers and frozen.

Food consumption

Continuous feeding records were kept for animals in the activity and oxygen uptake tanks. Crabs were usually fed weekly with frozen squid mantle (*Illex illecebrosus*), a diet supplemented with whole frozen shrimp (*Pandalus borealis*) and frozen mussel (*Mytilus edulis*) flesh. During part of the 0 °C data collection, the crabs were fed once every 2 weeks because of low food consumption. Enough food was added (3–17 g wet mass) to satiate the crabs totally and uneaten pieces were removed 1 day later. The food remains were stored at −17 °C until analysis, at which point they were dried at approximately 95 °C for 24 h and weighed.

Protein, lipid and carbohydrate compositions for the above foods are listed in Watt (1968). The caloric content was calculated by multiplying protein content by $4{\cdot}7\,\text{kcal}\,\text{g}^{-1}$, lipid by $9{\cdot}0\,\text{kcal}\,\text{g}^{-1}$ and carbohydrate by $4{\cdot}0\,\text{kcal}\,\text{g}^{-1}$ (O'Dor & Wells, 1987). The calculated value for shrimp will be slightly biased since the composition listed in Watt (1968) is for the portion eaten by humans.

Blood analysis

Resting levels of haemolymph lactate and ammonia were measured from the eight crabs in the blood assay tank. Each crab was quickly removed from the water, turned upside down, and the proposed needle insertion point quickly disinfected with 95 % ethyl alcohol. Approximately 0·4–0·6 ml of haemolymph

was extracted through a hypodermic needle inserted between the bottom of the coxa and the basis of the third or fourth walking legs. Three 100 μl samples of haemolymph were then each quickly mixed with 200 μl of ice-cold 8% (w/v) aqueous perchloric acid. The samples were centrifuged for 7–10 min and the supernatants stored at −90°C until analysis.

At 15°C, two crabs in the blood assay tank died during the acclimation period and replacement samples were taken from two animals in the oxygen uptake tank. At 18°C, the mortality rate was so high that samples were taken on the remaining six living crabs only 9 days after the temperature change.

Haemolymph extracts were thawed and partitioned for lactic acid and ammonia analysis. In both tests, two replicates were measured. Lactate was assayed enzymatically (Kit 826-UV, Sigma Chemical Co., St Louis, MO, USA) and ammonia was determined colorimetrically by indophenol formation modified from Verdouw *et al.* (1978).

Statistical analysis

Since repeated sampling was conducted on the same 20 experimental animals, an analysis of covariance (Systat Inc., Evanston, IL, USA) was employed in tests of the whole oxygen consumption data set to examine differences between unacclimated and acclimated crabs as well as individual variability. Slopes were then examined for each individual at each temperature interval. The three oxygen uptake replicates for each crab at each temperature were first averaged, lower means subtracted from the next higher, and slopes for each temperature interval calculated. These data were then analysed by a repeated-measures analysis of variance (Statview software, Apple Computer Inc., Cupertino, CA).

As an estimate of overall trends in oxygen consumption, exponential equations were fitted to the unacclimated and acclimated data sets. The exponential equation can be written as:

$$y = ae^{bt},$$

where a and b are constants, t is temperature in °C, and y is the oxygen uptake. The equation can be linearized with a log transformation:

$$\log_e(y) = \log_e(a) + bt,$$

and hence the constants can be calculated by regression analysis of log-transformed data. Respiratory equations were calculated by fitting regression lines to untransformed data and to log-transformed data. The fit was better on log-transformed data, indicating that the exponential equation was more satisfactory than the linear equation. All measurements from undisturbed animals were included in the calculations of routine rates but the lowest value of the three replicates was used as an estimate of resting uptake rate.

For the oxygen consumption rise after feeding (increase in oxygen uptake per kilocalorie ingested) three outliers well below the general trend were not included in the calculations since these points fell below zero and could not be log-

transformed. All these analyses were carried out using SYSTAT statistical software.

In activity measurements, exponential decrease functions (ae^{-bt}) were fitted. However, zero values occurred in the data set so a log-transformation could not be used to determine constants. In the energetics calculations, a Gaussian curve was fitted to food consumption data. For both these situations, a SYSTAT non-linear iterative statistical program was employed using Quasi-Newton and Simplex fitting procedures.

Results

Oxygen uptake rates

The oxygen consumption slopes between consecutive temperature intervals are listed in Table 1. Although variable, a consistent drop in the slopes occurred between 12 and 15°C for both unacclimated and acclimated crabs. Essentially, oxygen uptake rates at 15°C were not much higher than at 12°C. However, at 18°C uptake rates rose well above the 15°C levels so high positive slopes recurred. Temperatures of 15–18°C were lethal to snow crabs (see mortality section below) so oxygen uptake rates appeared first to level off but then to increase as death approached. Overall, the slopes were statistically different from one another ($P < 0{\cdot}001$ for unacclimated crabs, $P < 0{\cdot}05$ for acclimated crabs) but there were no significant differences between individuals ($P > 0{\cdot}05$).

The response to temperature is illustrated in Fig. 2. Several of the oxygen uptake rates were substantially higher than average, which contributed to the variability in slopes in Table 1. Many factors may have been responsible for these higher oxygen consumption rates, the most likely being spontaneous activity in the oxygen uptake chambers. Crabs could sometimes be observed moving under the translucent covers of the containers when high oxygen consumption rates were being recorded. Analysis of the videorecordings revealed that crabs had long periods of inactivity punctuated by short intervals of movement (see activity section below).

Table 1. *Slopes of oxygen uptake rates between temperature pairs*

	Slope ($mg\,O_2\,kg^{-1}\,h^{-1}\,°C^{-1}$)			
Temperature interval (°C)	Unacclimated crabs	*N*	Acclimated crabs	*N*
0–3	1·27 ± 1·28	8	3·43 ± 5·14	8
3–6	3·12 ± 2·08	8	−0·80 ± 4·04	8
6–9	2·14 ± 1·76	8	4·63 ± 3·76	8
9–12	4·16 ± 1·36	8	1·78 ± 2·02	8
12–15	−0·19 ± 2·66	8	0·49 ± 3·16	8
15–18	4·99 ± 2·42	6	3·96 ± 1·72	2

Values are means ± S.D.

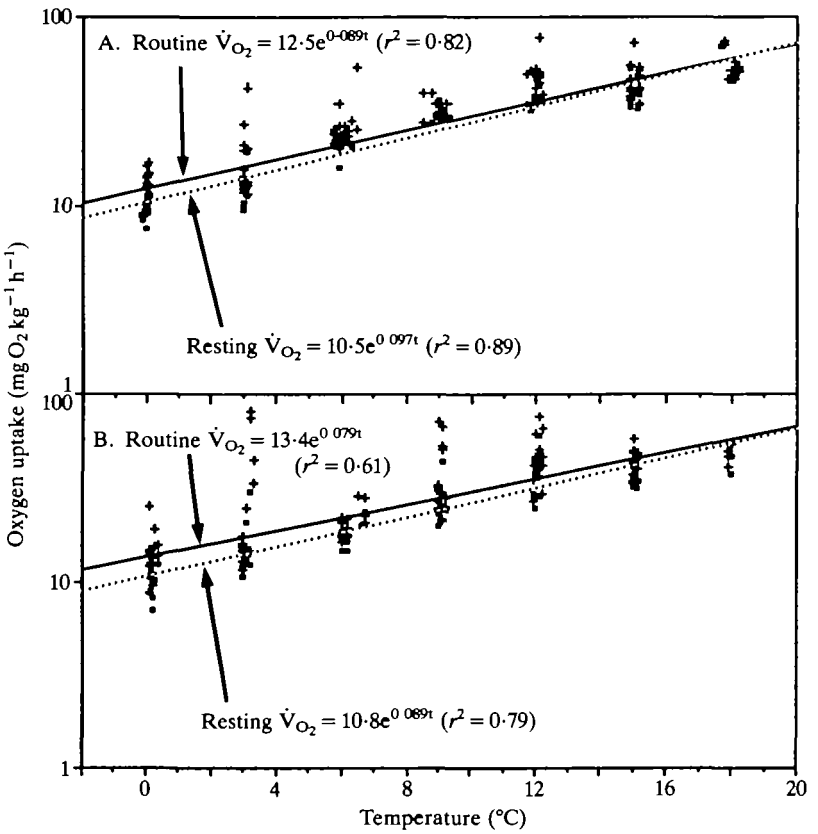

Fig. 2. Routine and resting oxygen consumption in eight male snow crabs either immediately after a temperature change (A) or after 3 weeks acclimation to the test temperature (B). The equation fitted through all three replicates (+) defined the routine respiration rate. The equation fitted through the lowest value for each crab (■) defined the resting metabolism.

As an estimate of overall trends, exponential equations were fitted to the oxygen uptake rates in Fig. 2. Although Table 1 shows that the slopes changed, especially at the higher temperatures, the exponential equations nevertheless fitted the data well, with r^2 values ranging from 0·61 to 0·89. This approach was necessary so that predictive equations could be produced from the empirical data for the energetics analysis (see Discussion).

Based on the equation for unacclimated animals (Fig. 2A, recorded 1 day after each temperature change), 'routine' oxygen consumption (quiescent animals with minimal but uncontrolled amounts of activity) at 0°C was low (12·5 mg kg^{-1} h^{-1}) but rose to 62 mg kg^{-1} h^{-1} at 18°C with a Q_{10} for the respiratory quotient of 2·2 for unacclimated animals. As an estimate of resting metabolism, an exponential equation was fitted to the lowest recorded value of the three replicates for each crab (Fig. 2A), a procedure which removed most of the high oxygen uptake

Table 2. *Analysis of covariance results comparing oxygen uptake rates of unacclimated and acclimated crabs*

Category	*P*
Temperature	***
Crab	***
Acclimation	NS
Interactions	
Temperature and crab	***
Temperature and acclimation	NS
Crab and acclimation	NS
Temperature and crab and acclimation	*

Temperature, effect due to temperature; crab, effect due to individual animals; acclimation, effect due to differences between unacclimated and acclimated rates.
* Significant at $P < 0{\cdot}05$; *** at $P < 0{\cdot}001$; NS, not significant, $P > 0{\cdot}05$.

values. The resulting equation had a lower intercept ($10{\cdot}5\,mg\,kg^{-1}\,h^{-1}$) but rose more rapidly with temperature ($Q_{10} = 2{\cdot}6$). The slower rise in the routine rate was probably due to a decrease in activity with rising temperature (see activity section below).

A slight acclimation response occurred after 3 weeks of exposure to each test temperature (Fig. 2B). The difference in the oxygen uptake rates between unacclimated and acclimated animals was not great but the third-order interaction in the analysis of covariance (Table 2) revealed that the two data sets were changing with temperature at different rates ($P < 0{\cdot}05$). Compared with the unacclimated state, oxygen consumption after the 3-week acclimation period was slightly higher at 0°C, but uptake increased less rapidly with temperature, leading to lower oxygen consumption at the higher temperatures. Thus, there was a slight decrease in the slopes of the curves ('rotation'). Individual differences in consumption rates (Table 2) were also revealed by the analysis of covariance.

Oxygen consumption in disturbed animals is presented in Fig. 3. 'Disturbed' rates were quite variable, ranging from 30 to $130\,mg\,kg^{-1}\,h^{-1}$. The variability was high because crabs were prodded to elevate rates, not systematically exercised. Nevertheless, oxygen uptake could be appreciably higher than resting levels, even at lethal temperatures. Maximum consumption at 0°C reached $80–90\,mg\,kg^{-1}\,h^{-1}$; at other temperatures the highest recorded rates ranged between 110 and $130\,mg\,kg^{-1}\,h^{-1}$. Aside from this difference, disturbed oxygen uptake rates did *not* increase with temperature.

Fig. 4 shows the oxygen consumption increase, R, per kilocalorie of food ingested. These data can be considered as a measure of the maximum additional oxygen required to digest food. The value was low at 0°C, being only $0{\cdot}37\,mg\,O_2\,kcal^{-1}\,h^{-1}$ but rose steeply with temperature ($Q_{10} = 5{\cdot}5$). At 12°C, a maximum of $2{\cdot}3\,mg\,O_2\,h^{-1}$ would be required to digest the same kilocalorie. Above 12°C, feeding ceased. Digestive metabolism was therefore temperature-dependent.

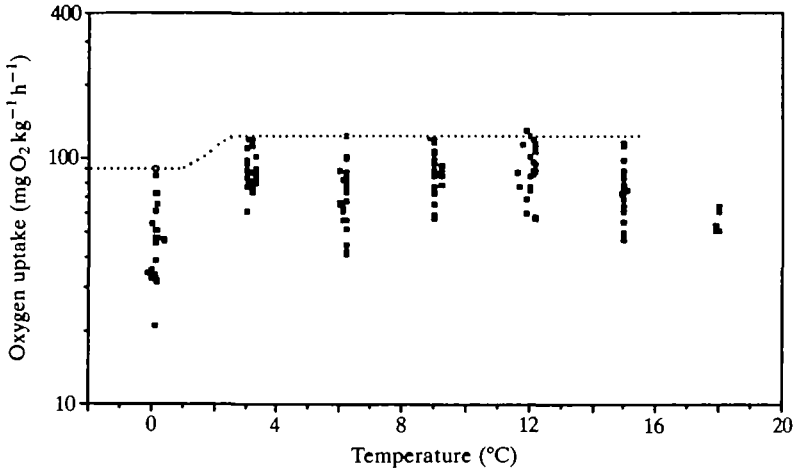

Fig. 3. Oxygen consumption rates of snow crabs disturbed for 5–10 min. All three replicates shown for each of eight crabs. The dotted line indicates maximum consumption which reaches about 120 mg kg^{-1} h^{-1} and remains virtually unchanged between 3 and 15°C.

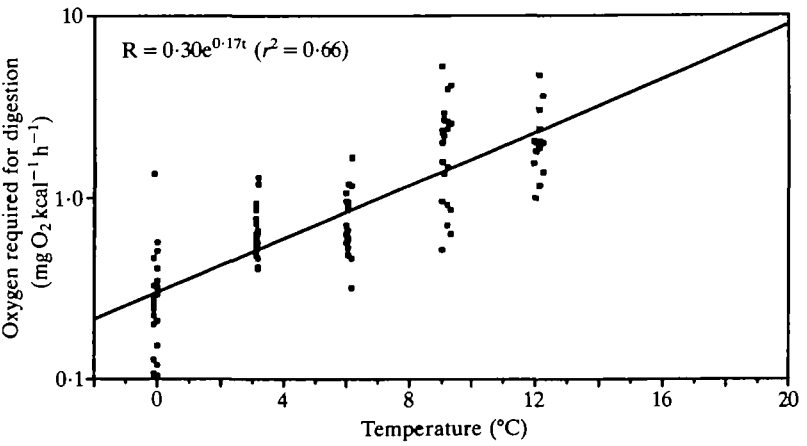

Fig. 4. The oxygen consumption rise after feeding was calculated by subtracting resting oxygen consumption values (Fig. 2B) from post-feeding oxygen uptake rates and then dividing by the number of kilocalories eaten per kilogram of crab for all replicates. Digestive metabolism rises dramatically with temperature, and oxygen consumed to digest a kilocalorie shows a Q_{10} of 5·5 between 0 and 12°C.

Consecutive recordings over a 50 h period revealed how oxygen consumption patterns varied with time, including after meals. An example is presented in Fig. 5. There was no respiratory cycle corresponding to the light and dark periods at any of the temperatures. Around the time of feeding, oxygen consumption

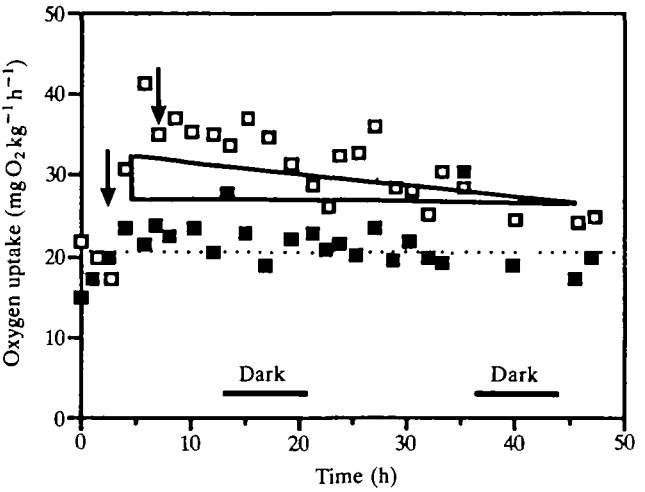

Fig. 5. Example of consecutive recordings of oxygen uptake for a fed (□) and unfed (■) animal at 6°C over a 48 h period. Responses could be more variable than shown, but in all cases respiration rates after feeding fall back to resting levels in about 40 h. At the colder temperatures (0 and 3°C), periodic spikes of high oxygen consumption are found which are probably caused by spontaneous activity. Arrows indicate points at which food was added and removed. A dotted line shows the mean value for the unfed crab. The area of the triangle represents the calculated cost of digestion used in the energetics equations (see text). The height of the triangle was calculated from the increased respiration after feeding (Fig. 4). In this case, the calculated cost appears to underestimate the actual oxygen consumption rise.

increased substantially and rates gradually fell back to resting levels in about 40 h. The response to feeding is similar to McLeese & Watson's (1968) findings.

Activity

Crabs were characteristically sedentary with long periods of inactivity interrupted by short bursts of movement. Many 1-h sequences were examined in which crabs remained motionless for the entire period. Once a crab began to move, it could remain active for 30–45 min, with frequent alternating bouts of rest and activity.

Little aggressive behaviour occurred between crabs and no dominance hierarchy was noted among the four animals. If a crab began walking over a neighbour, the lower crab would flatten against the bottom and remain still until the other had passed over it. Although the experiments lasted a year, only one crab autotomized a leg and this may have been due to an aggressive encounter.

Activity fell with rising temperature (Fig. 6A), a trend which was highly significant ($P < 0{\cdot}001$). Speeds are illustrated in Fig. 6B. Speeds increased gradually with temperature, a trend that was statistically significant ($P < 0{\cdot}05$).

Food consumption

The effects of temperature on food consumption are shown in Fig. 7. Caloric intake rose up to 6°C but then began falling. Crabs stopped feeding above 12°C.

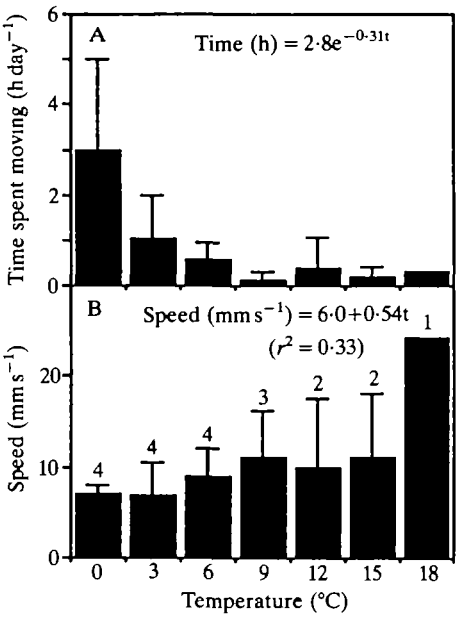

Fig. 6. Time spent moving (A) and speed during movement (B). Data were taken from videorecordings of four animals, except at 18°C when only one crab survived the 3-week acclimation period. Crabs which did not move were discounted for the speed calculations and the numbers of animals used in the calculations are presented above the standard deviation (S.D.) bars. Time spent moving falls significantly ($P < 0{\cdot}001$) but speed during movement increases significantly ($P < 0{\cdot}05$) with temperature.

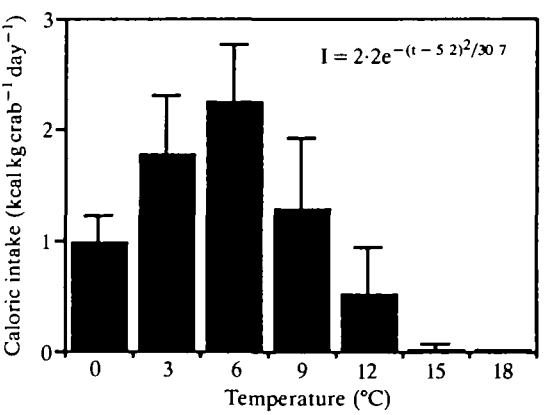

Fig. 7. The mean caloric intake (+S.D.) for snow crabs in the activity and respiration tanks. Food consumption increases as expected but then falls at higher temperatures. $N = 9$, except at 18°C where $N = 6$ because of deaths.

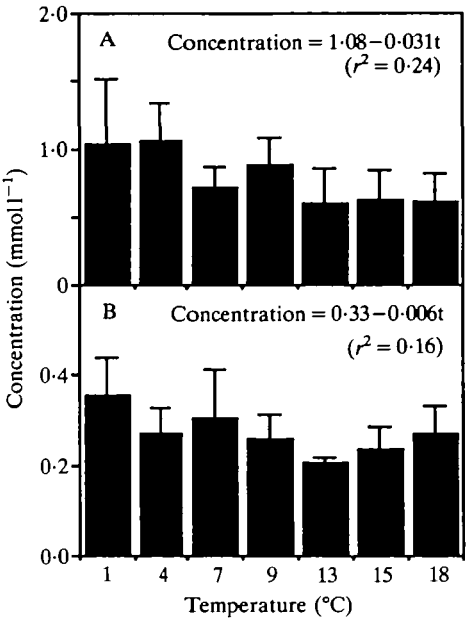

Fig. 8. Haemolymph lactate (A) and ammonia (B) concentrations. All readings are means +S.D., $N = 8$, after 3 weeks of acclimation except at 18°C since only six crabs were still alive when sampled after 9 days. Concentrations are low and decline significantly ($P < 0{\cdot}001$ in both cases) with temperature.

Blood lactate and ammonia levels

Both lactic acid (Fig. 8A) and ammonia concentrations (Fig. 8B) in the haemolymph were low at all temperatures. Lactate levels ranged between 1·2 and 0·6 mmol l^{-1}, and mean ammonia levels did not exceed 0·4 mmol l^{-1}. Both decreased gradually, but significantly, with temperature ($P < 0{\cdot}001$).

Mortality rates

Mortality began at 15°C and three animals were lost over a 1-month period at this temperature. Mortality was much higher at 18°C and only two of 13 animals were alive after 1 month. Analyses of the mortality curves gave death rates of 0·6 % day^{-1} at 15°C and 6·7 % day^{-1} at 18°C.

Discussion

Chionoecetes opilio does not appear to be confined to cold water because of limitations in its respiratory system. If inadequate intake of oxygen were the critical factor, then oxygen consumption should increase asymptotically with temperature, since the gas exchange system would not be capable of extracting any further oxygen. Furthermore, lactate levels would be expected to rise at 15–18°C as the anaerobic pathways begin to supplement the energy requirements not

supplied by aerobic respiration. After strenuous exercise or hypoxia, lactate levels rise considerably in crabs such as *Cancer* (McMahon *et al.* 1979) and *Carcinus* (Taylor *et al.* 1977). Yet, in the snow crab, oxygen consumption increases even at 18°C and disturbed rates reveal that O_2 uptake can be significantly increased above routine rates. Lactate concentrations in the blood of resting individuals remain low and actually decline slightly with temperature.

Oxygen consumption in disturbed animals reached 85 mg kg^{-1} h^{-1} at 0°C and 120–130 mg kg^{-1} h^{-1} at other temperatures. Disturbed oxygen consumption does not increase with temperature above 3°C, which suggests that the limits of the respiratory system have been met and that no more oxygen can be extracted. Oxygen consumption after disturbance appeared to fall off at 18°C since maximum values reached only 60 mg kg^{-1} h^{-1}. However, it is difficult to make conclusions about this drop because disturbed uptake rates are so variable and only two animals were alive after 3 weeks of acclimation at 18°C. This drop may be due, not to limitations of the respiratory system, but to the confounding effects of lethal temperatures on metabolism; caused, for instance, by protracted starvation (Depledge, 1985) or, potentially, by repeated sampling.

Lactate concentrations recorded here are similar to the resting values reported in other studies on crabs which used a standard Sigma enzymatic analysis (McMahon *et al.* 1979; Taylor *et al.* 1977). Graham *et al.* (1983) report that this enzymatic determination for lactate must be modified for haemocyanin-containing bloods, because of the presence of copper, to avoid higher readings than normal. Since this modification was not included in these experiments, the lactate values presented for the snow crab will be overestimates. Snow crabs were also briefly removed from water to obtain blood samples and this disturbance may also have elevated lactate concentration. Nevertheless, our finding that anaerobic metabolism is not important at higher temperatures is reinforced by these overestimated lactic acid levels.

Some authors have stated that deep-water organisms typically have low metabolic rates when compared to their shallow-water counterparts and attribute this as an ecological adaptation to a cold environment with a limited food supply (George, 1979). Although the snow crab is found in this deep, cold environment, its physiology appears to be similar to that of shallow-water decapod crustaceans. Oxygen uptake rates in the snow crab are within the range for shallow-water crabs when compared at similar temperatures (see McMahon & Wilkens, 1983). A similar result was found when the physiology of the deep, oceanic hydrothermal vent crab *Bythograea thermydron* was examined. Oxygen uptake rates increase in this species between 2 and 25°C and resemble consumption rates found in shallow-water crabs (Mickel & Childress, 1982). In *C. opilio*, circulating ammonia and lactic acid levels are also similar to those of other decapods (Binns, 1969; Taylor *et al.* 1977; McMahon *et al.* 1979; Claybrook, 1983).

In contrast, activity in the snow crab appears to differ from that of other crustaceans since snow crabs are most active at 0°C and time spent moving falls as the temperature rises. Although speeds during movement increased with tempera-

ture, the energetics calculations (see below) revealed that this increase in speed did not compensate for the declining movement. Little energy was channelled into spontaneous activity above 4°C. The highest activity therefore occurs close to the species' lower lethal temperature since snow crabs are killed when the water freezes (T. P. Foyle, personal observation). In the crayfish *Astacus astacus* (Kivivuori, 1983), spontaneous activity increases up to 20–25°C but then drops as temperatures reach lethal levels (32–35°C). In acclimated lobsters (*Homarus americanus*) activity increases with temperature up to 25–29°C (McLeese & Wilder, 1958; Reynolds & Casterlin, 1979).

Energy balance

Since many of the parameters needed for energetics calculations were examined in this study, energy budgets were constructed for the snow crab over a wide temperature range.

The basic energy budget equation is:

$$I = M + G + E, \tag{1}$$

where I is intake, M is metabolic cost, G is growth and E is loss through egestion and excretion (principally ammonia in crustaceans). Growth can be divided into somatic (Gs) and reproductive (Gr) components, metabolic costs into maintenance (Ms), activity (Ma), and digestion costs (Md), and egestion/excretion into faecal (Ef) and non-faecal (En) losses. Hence, rearranging to calculate growth, the energetics equation can be written as:

$$(Gr + Gs) = I - (Ef + En) - (Ms + Ma + Md). \tag{2}$$

Food intake, I, was carefully recorded in this study. Egestion and excretory losses, E, were not examined but were estimated from tanner crab *Chionoecetes bairdi* values (Paul & Fuji, 1989). Metabolic costs, M, can be calculated through indirect calorimetry by converting oxygen uptake rates to energy equivalents (kcal). Oxygen consumption rates were multiplied by 3200 kcal $mg\,O_2^{-1}$, a value recommended by Brett & Groves (1979) for carnivorous fish fed a protein or a protein and lipid diet. While Joule is now the accepted unit to express energy, kilocalorie (1 kcal = 4188 J) was retained for comparison with the energetics literature.

Since this study used morphometrically mature male snow crabs which do not appear to moult (Conan & Comeau, 1986), growth of body tissue is assumed to be negligible (Gs = 0), a valid assumption if the crabs are well past moult. Virtually all surplus energy would then be channelled to reproductive tissue, Gr. Similarly, since Paul & Fuji (1989) showed that ammonia losses in the tanner crab *C. bairdi* amounted to only 0·2 % of total energy costs, En is disregarded. The energetics equation therefore reduces to:

$$Gr = I - Ef - (Ms + Ma + Md). \tag{3}$$

Equations calculated for the above components can be found in Table 3 and the most complex calculations are described below.

Since the food consumption data appeared to be normally distributed with temperature (Fig. 7), gross intake was estimated by fitting a Gaussian-type equation to these data with the SYSTAT non-linear algorithms. At feeding, oxygen uptake rates increased then gradually declined back to resting values around 40 h later (Fig. 5). The area under this curve represents the cost of digestion, Md. This cost can be approximated by calculating the area of an appropriate-sized triangle, 0·5bw, where b equals the time taken for oxygen consumption rates to fall back to resting levels (40 h) and w equals the initial oxygen consumption increase after feeding. Multiplying 0·5×40 h by the post-feeding oxygen uptake increase (w) in Fig. 4, and converting oxygen consumption to caloric equivalents ($\times 3200$ kcal mg O_2^{-1}), produces:

$$Cd = 0{\cdot}019e^{0{\cdot}17t}\,(\text{unitless}), \tag{4}$$

where Cd, the coefficient of digestion, is the fractional cost of digesting 1 kcal of food. Hence the actual cost in kilocalories, Md, would be Cd multiplied by the gross food intake, I.

Activity costs, Ma, are the most difficult to estimate since oxygen uptake during movement could not be measured directly. We assumed the maximum disturbed oxygen uptake rate approximated the best uptake capabilities for this species, equivalent to *maximum* aerobic activity. The scope for activity was estimated by subtracting resting oxygen consumption at 0°C (10·8 mg kg^{-1} h^{-1}, Fig. 2B) from the maximum disturbed oxygen uptake rate at this temperature (85 mg kg^{-1} h^{-1}, Fig. 3).

We assumed that, at 0°C, crabs consumed oxygen during spontaneous activity at 50 % of the maximum scope [$0{\cdot}50\times(85-10{\cdot}8) = 37$ mg kg^{-1} h^{-1}]. We also assumed that activity costs increased with temperature since speed increased with temperature (Fig. 6B). The speed relationship in Fig. 6B was therefore normalized by dividing by the intercept, 6·0 mm s^{-1} which, when multiplied by 37 mg kg^{-1} h^{-1}, produces the *respiratory* costs of activity at different temperatures:

$$Ra = 37 + 3{\cdot}3t\ (\text{mg}\,O_2\,kg^{-1}\,h^{-1}). \tag{5}$$

The estimated cost of movement, Ma, would be the product of the respiratory cost of activity, Ra, and the *time* spent moving (from Fig. 6A) converted to caloric equivalents ($\times 3200$ kcal mg O_2^{-1}):

$$Ma = (0{\cdot}34 + 0{\cdot}03t)e^{-0{\cdot}31t}\ (\text{kcal}\,kg^{-1}\,day^{-1}). \tag{6}$$

The assumption that routine locomotion consumes 50 % of the maximum scope is probably an overestimate. Nevertheless, except at 0°C, activity, Ma, represents a small fraction of the total cost in *C. opilio* (Fig. 9). In juvenile lobsters, *Homarus americanus* (Koshio, 1985) spontaneous activity costs are also low and range between 5 and 9 % of intake ration. A similar situation occurs in *Octopus*, with active metabolism accounting for only 3 % of total intake (O'Dor & Wells, 1987).

Table 3. *Energetics equations*

Component*	Equation used	Source	Conversion factor	Final equation (kcal kg^{-1} day^{-1})
I, gross energy	Gaussian equation	Fig. 7, see also text	Fitted by non-linear algorithms	$I = 2{\cdot}2e^{-(t-5{\cdot}2)^2/30{\cdot}7}$
Ef, faecal loss	Assimilation efficiency = 89 %	Paul & Fuji (1989)		$Ef = 0{\cdot}11I$
Id, digestible energy	$Id = I-Ef$			$Id = 0{\cdot}89I$
Md, digestion costs (4)	$R = 0{\cdot}30e^{0{\cdot}17t}$	Fig. 4	$\times 0{\cdot}5\times 40\times I\times 3200$ kcal mg O_2^{-1}, see also text	$Md = 0{\cdot}042e^{0{\cdot}17t-[(t-5{\cdot}2)^2/30{\cdot}7]}$
Ms, maintenance costs	$\dot{V}_{O_2} = 10{\cdot}8e^{0{\cdot}089t}$	Fig. 2B	$\times 3200$ kcal mg O_2^{-1}	$Ms = 0{\cdot}83e^{0{\cdot}089t}$
Ma, activity costs (5,6)		Figs 3, 6A,B	See text	$Ma = (0{\cdot}34+0{\cdot}03t)e^{-0{\cdot}31t}$
M, metabolic costs, total (2)				$M = Ms+Ma+Md$
Gr, reproductive growth				$Gr = Id-M$

t in equations equals temperature in degrees centigrade
* Number in brackets refers to equation in text.
See text for an explanation of abbreviations.

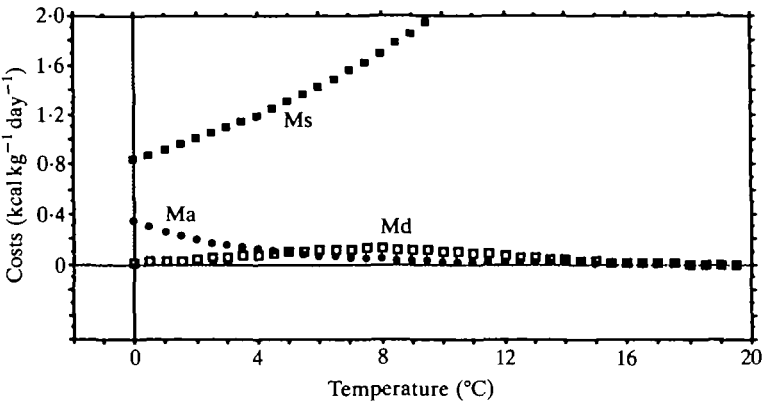

Fig. 9. Plots of the energetics equations for maintenance costs (Ms), activity costs (Ma) and digestive costs (Md). Activity costs are only important at 0°C.

Laboratory studies are often considered to underestimate activity costs in the wild but Mather (1988) has recently shown that wild *Octopus* expend only a small proportion of their total energy for activity.

In the snow crab, most energy is directed towards simple maintenance, Ms (Fig. 9). Paul & Fuji (1989), who recently examined aspects of the bioenergetics of the tanner crab *Chionoectes bairdi* at 5°C, also found that maintenance costs were substantial, accounting for 60 % of the total energy expenditure.

Although digestive metabolism in *C. opilio* is sensitive to temperature, only a small fraction of the energy is consumed by actual digestive costs (Md; Fig. 9) with a coefficient of digestion, Cd (equation 4) ranging from 2 % at 0°C to 15 % at 12°C. Digestive costs, also known as heat increments, have been much higher in other studies. In juvenile lobsters, heat increments can consume 17–37 % of the calories ingested (Logan & Epifanio, 1978; Capuzzo & Lancaster, 1979) and juvenile *Macrobrachium*, fed proteinaceous diets, lose 16–28 % in digestive costs (Nelson *et al.* 1977*b*). These studies, however, were conducted above 20°C. If snow crabs had continued to eat at higher temperatures, digestive costs at 15°C would have amounted to 24 % of the calories consumed, based on equation 4, a cost that would have increased to nearly 60 % at 20°C.

In Fig. 10, the functions describing digestible energy, Id (=I−Ef), and total metabolic costs, M, are shown. Although metabolic costs continue to increase at higher temperatures, digestible energy rises but then falls. Reproductive growth, Gr, for mature male snow crabs, is the difference between these two functions. Reproductive growth is optimum around 4°C but declines at higher and lower temperatures. There are two break-even points; a lower one around 1°C and an upper one around 7°C.

Snow crabs appear to be *energetically* confined to cold water. Above the 7°C break-even point, metabolic costs overtake intake. At 15°C, the crab is losing 3 kcal kg^{-1} day^{-1}; energy probably supplied by the metabolism of muscle protein

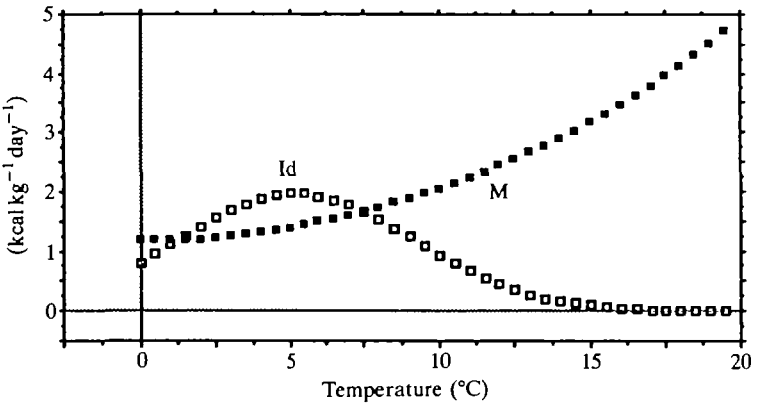

Fig. 10. A comparison of the digestible energy (Id = I−Ef) and the total metabolic costs (M = Ms+Ma+Md). Activity becomes negligible above 5°C but total metabolic costs continue to rise as a result of increasing maintenance costs, Ms (Fig. 9). Costs overtake gains above 7°C owing to declining food consumption. Below 1°C, intake is also insufficient to meet metabolic demands, giving a surprisingly narrow temperature zone for growth (Gr = Id−M).

(Claybrook, 1983). Intake cannot keep pace with the metabolic costs since digestive metabolism appears to be sensitive to temperature. Food consumption increases, as expected, up to 6°C but then falls. The sensitivity of the digestive system to temperature is also seen in the post-feeding oxygen uptake increase (Fig. 4) with its high Q_{10} (5·5).

It is unclear why digestion is so sensitive to temperature. Enzyme inefficiency may become a factor. Nutrient assimilation could become less efficient so movement of food substances into and out of cells and through the circulatory system may become costly at higher temperatures.

An intriguing outcome of the energetics calculations is the low-temperature break-even point which occurs around 1°C. The slight calculated negative growth below this temperature is surprising since snow crabs are commonly found in water between 0 and 1°C. At these temperatures, morphometrically mature crabs may be living at the break-even point and may actually be depleting reserves. This implies that mature non-moulting males (Conan & Comeau, 1986), to be able to channel surplus energy towards reproduction, should experience water temperatures above 1°C through at least part of their reproductive cycle. Slight temperature changes may therefore be important in regulating reproduction in this species. If immature crabs react in a similar way, somatic growth may also be regulated by slight temperature shifts.

These findings may be of considerable use in explaining the erratic recruitment into the snow crab fishery, although bottom temperatures are unknown for most of the fishing areas. Bottom temperatures have been recorded for water off eastern Newfoundland, Canada. Crabs from this area in Newfoundland normally experience colder water temperatures (−1·5° to −0·5°C) than crabs from eastern Cape

Breton, Nova Scotia, which were used in this study (approx. 0–4°C). Taylor & O'Keefe (1986) have, nevertheless, correlated continuously cold bottom temperatures (−1·5°C) with poor recruitment and growth for this snow crab population in eastern Newfoundland.

The energetics calculations may be influenced to some extent by laboratory-induced artifacts. The type of food used in the experiments is different from a natural diet, which consists principally of crustaceans, polychaetes, brittlestars and clams (Miller & O'Keefe, 1981; Brêthes *et al.* 1984). Food consumption might have been higher if food had been presented more frequently. Repeated sampling of the same 20 animals throughout the experiments may have influenced food consumption or oxygen uptake rates. The crabs ate less during the second and third reacclimation periods in water at 3–4°C after being exposed to high temperatures (9 and 15°C). However, the animals were in good condition at the beginning and at the end of the experiments, until killed by high water temperatures. Their robustness is seen in the low mortality rate at lethal temperatures (6·7% mortality per day at 18°C) compared with McLeese's (1968) study (50% mortality per day at 18°C).

To test the energetics calculations, the equations were reanalysed by reweighting the activity equation and by using the routine oxygen uptake rate instead of the resting metabolism and activity costs. The routine rate can be substituted for these two equations since routine metabolism includes an activity component. This is similar to the approach used by Nelson *et al.* (1977*a*) and Logan & Epifanio (1978). The shapes of the curves and the break-even points in the modified analyses were similar to those of the initial energetics calculations, so the equations appear rigorous. For marine organisms, energy budgets are at best estimates. The exponential equations fitted to the oxygen uptake rates approximate the actual data. Excretion and anaerobic metabolism costs are underestimated in this analysis but these errors are probably compensated by overestimated resting metabolism and activity costs.

Virtually all the previous crustacean energetics studies examined young, growing animals and were conducted at a constant temperature. To the best of our knowledge, the present study is the first to calculate energy budgets for a crustacean at different temperatures. The outcome of our calculations for the snow crab is interesting since the balance of gains to losses is highly temperature-dependent. It appears to be energetically unfeasible for snow crabs to live in warmer water since costs overtake gains above 7°C. In the natural temperature range of this species (−1 to 5°C), the ratio of intake to metabolic losses also changes and below 1°C reproductive growth may be absent. Even though the snow crab lives in a narrow temperature band, our calculations indicate that slight temperature changes may be important in regulating reproduction and possibly growth in this species. This bioenergetic approach has not only disproved the original hypothesis of oxygen limitation, but has also provided a new hypothesis about the ecology of an economically important species which can now be tested in the wild.

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