The effect of extrinsic and intrinsic factors on oxygen consumption by the southern rock lobster, *Jasus edwardsii*

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**Abstract**

The oxygen consumption rate of the southern rock lobster, *Jasus edwardsii*, was evaluated in response to body weight, temperature, activity, handling, diurnal rhythm, feeding and oxygen saturation level. There was a positive relationship between standard oxygen consumption ($M_{O_2}$) and both body weight and water temperature. The relationship between total oxygen consumption and wet whole body weight was described by the equation: \( \log M_{O_2} = 0.595 \log W - 0.396 \) \((r^2 = 0.83)\). The relationship between weight-specific oxygen consumption and temperature was described by the equation: \( \log M_{O_2} = 0.047T - 2.25 \) \((r^2 = 0.94)\). Activity had a significant influence on the oxygen consumption rate, causing a three-fold increase above the standard rate at the temperature of acclimation (13°C). However, at temperatures approaching the upper and lower extremes, lobsters had a decreased ability to increase their oxygen consumption rates during activity. Lobsters took 4.5–5 h to return to standard oxygen consumption rates after a period of emersion and handling. A strong diurnal rhythm to oxygen consumption was recorded. *J. edwardsii* displayed a classic postprandial increase in oxygen consumption. A peak (1.72 times standard $M_{O_2}$) occurred 10–13 h after feeding with an increase above standard $M_{O_2}$ being maintained for 42 h. In its rested state *J. edwardsii* was an oxygen regulator down to a critical oxygen tension of 58 Torr, whilst activity resulted in the critical oxygen tension increasing to 93 Torr. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** *Jasus edwardsii*; Body weight; Diurnal rhythm; Feeding; Handling; Hypoxia; Oxygen consumption; Temperature

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1. Introduction

The southern rock lobster, *Jasus edwardsii*, is the basis of a AUS$150 million fishing industry in southern Australia. Over the last 10–15 years the industry has focused increasingly on the live export of the lobsters with up to 90% of the catch now being exported. To optimise the quality of the water for holding lobsters it is necessary to understand their physiological requirements. Spiny lobsters rely on the uptake of oxygen from water to drive their metabolic processes. It is essential that water flow and aeration are sufficient to provide adequate oxygen for the number of lobsters being held (Beard and McGregor, 1991).

There are many factors (both extrinsic and intrinsic) that affect the rate of oxygen consumption of crustaceans (Cockcroft and Wooldridge, 1985). Considering the economic importance of the palinurids studies on their respiratory physiology have been limited. Winget (1969) reported on the effects of dissolved oxygen levels, body weight, temperature and activity on oxygen consumption of *Panulirus interruptus*. Buesa (1979) investigated the effects of body weight, dissolved oxygen levels, salinity and temperature on oxygen consumption by *P. argus* and the effect of body weight on oxygen consumption by *P. guttatus*. Zoutendyk (1989) studied the effects of temperature and body weight on oxygen consumption by *J. lalandii*. Some information is available on oxygen consumption by *J. edwardsii* through a study by Waldron (1991).

A full understanding of the effects of intrinsic and extrinsic factors on oxygen consumption during post-capture processes is essential if the health of lobsters is to be optimised. This study investigates the oxygen consumption response of *J. edwardsii* to temperature, body weight, activity, feeding, handling, daylight/darkness and dissolved oxygen levels.

2. Materials and methods

2.1. Lobsters

Lobsters were obtained from commercial holding facilities and from the Tasmanian Department of Primary Industries, Taroona. They were maintained in 600 l recirculating seawater tanks for a minimum of 2 weeks prior to experimentation. A maximum of thirty lobsters was kept in each tank. Each tank contained 14–16 concrete building blocks, which served as refuges for the lobsters. The water temperature was maintained at 13±1°C, pH 8.0–8.3 and salinity at 35±1%. Only lobsters judged to be in intermoult, using the moult index of Turnbull (1989), were used for experiments. Lobsters were fed twice weekly with either squid (*Nototodarus gouldii*) or blue mussels (*Mytilus edulis planulatus*) but were deprived of food for 3 days prior to experiments. Light was controlled to provide 12-h light and 12-h dark photoperiods.

2.2. Measurement of oxygen consumption rates

Three intermittent flow respirometers (volume = 18.3 l) were used in the experiments.
Water flow through the respirometers was programmed for the particular sized lobster and water temperature being studied. The normal cycle was 20 min closed (measurement period) and 10 min open (re-oxygenate period). Under normal circumstances the oxygen tension of the chambers did not fall below 125 Torr (80% saturation) at the end of the measuring period.

A submerged powerhead pump (Aquaclear-Powerhead 201) was used to ensure there was both good water mixing within the chamber and sufficient water flow past the membrane of the oxygen electrode. Dall (1986) outlined the inherent problems associated with measuring standard oxygen consumption when crustaceans are placed into smooth walled respirometers. Therefore, attachment points were built into the respirometers so that lobsters had a grasping surface and could remain quiescent; in the wild, lobsters normally remain immobile in caves and crevices during daylight hours (Lewis, 1981).

The chambers were submerged in a water bath, which maintained the water temperature within 0.2°C of the designated temperature. Oxygen tensions were recorded with WTW (Wissenschaftlich-Technische Werkstatten) oxygen sensors (EO 96) and meters (OXI 96) connected to the datalogger. Oxygen consumption ($M_{O_2}$, measured in mg O$_2$/g/h) was determined from the equation:

$$M_{O_2} = \frac{(P_{O_2,i} - P_{O_2,f})V60}{Wt}$$

where $P_{O_2,i}$ is the initial oxygen tension in the respirometer (mg/l), $P_{O_2,f}$ is the oxygen tension after the measuring period (mg/l), $V$ is the volume of water in the respirometer adjusting for lobster volume (l), $W$ is the whole wet weight of the lobster (g) and $t$ is the time of the measuring period (min).

Tests with a blank chamber showed that there was no need to correct for respirometer oxygen consumption. Lobsters were acclimated to the experimental chambers for 36 h prior to the commencement of experiments. In view of the relationship between body weight and oxygen consumption, a restricted weight range (600–900 g) was used except in the body weight and diurnal rhythm studies.

2.3. Standard and active oxygen consumption

Standard oxygen consumption is defined as the minimum oxygen consumption for an unfed, resting fish (Fry, 1971). During the daytime lobsters usually remained motionless in the chambers unless disturbed by movement in the room. The standard oxygen consumption rate of a particular animal was determined when three consecutive measurements of oxygen consumption were similar.

Active oxygen consumption was determined by taking lobsters from the respirometers (air temperature of 13°C) and forcing them to be active by constantly handling them in air over a period of 5 min. The lobsters were replaced into the respirometers and the active oxygen consumption measured, usually over a 15-min period (temperature dependent). This is essentially a measurement of post-exercise oxygen consumption, but it is argued that the results can be used as active rates and compared with the active rates
determined for other species. Active oxygen consumption is basically a measure of the maximal level of oxygen consumption (Bennett, 1978). Maximum oxygen consumption values of *J. edwardsii* after exercise and handling in water were similar to those after a period of air exposure and handling (Waldron, 1991). The author argued that the oxygen consumption rates measured was an accurate determination of the maximum oxygen consumption rate of *J. edwardsii*.

In this study it was decided to use 5 min of air exposure and handling to determine active oxygen consumption, as it was also indicative of the post-capture processes to which the lobsters are subjected. Active rates are usually determined on animals that are fully acclimated to each experimental temperature (Rutledge and Pritchard, 1981). However, lobsters are undergoing a series of acute temperature fluctuations during post-capture processes. Therefore, data on the effect of acute temperature fluctuations were considered to be more pertinent in this study.

### 2.4. Temperature

The effects of acute temperature changes on the oxygen consumption of lobsters were investigated (*N*= 12). Lobsters were acclimated to the respirometers at 13°C before the temperature was raised or lowered to the required temperature at a rate of 2°C/h. Lobsters were maintained at each temperature overnight before the standard and active oxygen consumption rates were established as above.

Log transformed linear regressions of oxygen consumption versus temperature (*T*) were expressed by the general equation: \( \log_{10} M_{O_2} = a + bT \), where \( M_{O_2} \) is the weight-specific oxygen consumption (mg O\(_2\)/g/h) and \( T \) is the temperature (°C).

The aerobic scope for activity was calculated as the difference between standard and active oxygen consumption (Fry, 1947). Aerobic expansibility is a measure of the ratio of the two oxygen consumption levels (active/standard). \( Q_{10} \) values were determined using the following equation:

\[
Q_{10} = \left( \frac{M_2}{M_1} \right)^{\frac{10}{T_2 - T_1}}
\]

where \( M_1 \) and \( M_2 \) are the oxygen consumption at temperatures \( T_1 \) and \( T_2 \), respectively.

### 2.5. Lobster weight

Standard and active oxygen consumptions of lobsters over a large body weight range (*N*= 47, 186–2180 g) were determined. Log\(_{10}\) transformed linear regressions of the standard and active oxygen consumption versus weight (*W*) were expressed by the general equation: \( \log_{10} M_{O_2} = a + b \log_{10} W \), where \( M_{O_2} \) is the total oxygen consumption (mg O\(_2\)/h), \( a \) is the intercept on the y-axis, \( b \) is the slope of the regression and \( W \) is the wet weight (g) of the lobster. The data were examined to determine if sex of the lobsters influenced oxygen consumption (female, *N*= 16, 190–2140 g; male, *N*= 31, 186–2180 g).
2.6. Diurnal rhythm

Oxygen consumption of lobsters ($N = 22$, 380–2140 g) was recorded over a minimum of 48 h to establish if a diurnal rhythm was present. This allowed the establishment of routine oxygen consumption, which is the oxygen consumption of fasting lobsters over 24 h including that resulting from spontaneous activity (Becker and Fishelson, 1986). Night-time oxygen consumption was calculated on all readings taken in the dark (between 6 p.m. and 6 a.m.). Standard oxygen consumption was used as oxygen consumption during daylight hours as some disturbance (resulting in increased oxygen consumption) during the day was unavoidable. A video camera and infrared light (Javelin Electronics OS-45/IR-121N) were used to examine lobster activity during the night.

2.7. Handling and recovery

Lobsters ($N = 10$) were removed from the respirometer and emersed for 30 min. During this period the lobsters were confined to an open foam box except for periods of handling. Continual handling for the first 5 min of emersion was followed by short periods of handling every 5 min. Lobsters showed a strong escape behaviour (tail flicking) during the initial period of disturbance. The response diminished as the emersion time increased and the tail flicking response was usually not evident after 30 min of emersion. The lobsters were returned to the respirometers and their recovery monitored. A 30-min period was selected as this is a typical maximum emersion time lobsters are subjected to during post-capture practices. For example, the period of time between when the water is drained from a tank on a boat and when the lobsters are placed into a holding tank in the processing shed.

2.8. Feeding

The effect of feeding on oxygen consumption was determined by introducing squid pieces (wet weight $\approx 3\%$ of lobster wet weight) to each chamber. All lobsters ($N = 11$) used in the experiments were fed at the same time of day so that any effects of diurnal rhythm on oxygen consumption could be taken into account. Experiments where lobsters did not eat all of the squid within 1 h were discontinued.

2.9. Dissolved oxygen level

The relationship between the dissolved oxygen level ($P_{O_2}$) and standard oxygen consumption was determined by closing the water flow off and following the response of settled lobsters ($N = 15$) to self-induced hypoxia. High dissolved oxygen levels were obtained by bubbling oxygen through the water. The relationship between active oxygen consumption and $P_{O_2}$ was determined by exposing lobsters that had been emersed and handled for 5 min ($N = 12$) to water with known oxygen levels. Oxygen consumption was measured over a 20-min period after returning lobsters to the respirometers. It was
determined at six $P_{O_2}$ levels (24, 55, 86, 118, 149 and 180 Torr) and the dissolved oxygen levels were kept within 8 Torr of those designated levels. Therefore, a reading at 118 Torr represents the average oxygen consumption over the 110–126 Torr range.

The dissolved oxygen tension where $M_{O_2}$ becomes dependent is termed the critical oxygen tension ($P_c$). $P_c$ was determined by calculating regression lines for the two distinctly different parts of the relationship between oxygen consumption and $P_{O_2}$, the horizontal high $P_{O_2}$ segment and the sharply sloped low $P_{O_2}$ segment. $P_c$ was designated as the intersection point of the two lines (Cochran and Burnett, 1996).

2.10. Statistical analyses

Linear regressions were obtained by the least squares method and were tested for significance by analysis of variance of the regression. Covariance analysis was used to test for differences of oxygen consumption with sex and activity, using lobster weight as the covariate. Student’s $t$-tests (paired where necessary) were used to evaluate differences in the standard and active oxygen consumption rates at each experimental temperature. Paired Student’s $t$-tests were used to evaluate when postprandial and post-handling oxygen consumption had returned to standard levels. Where appropriate a Student’s $t$-test for samples with unequal variances was used. Paired $t$-tests were also used to evaluate if there was a daily rhythm to oxygen consumption by comparing the average night-time rate to the standard rate. Student’s $t$-tests were used to determine which data points were included in each regression when evaluating $P_c$. Values which were significantly lower than that recorded at 149 Torr were included in the lower line. All analyses were performed on the SPSS statistical package with the $\alpha$ set at 0.05. All means are expressed as mean±S.E.

3. Results

3.1. Effect of temperature on oxygen consumption

Active oxygen consumption was significantly higher ($P<0.01$) than standard oxygen consumption at each temperature (Fig. 1). Standard oxygen consumption ($M_{O_2}$) increased exponentially with temperature ($T$) and is described by the equation: $\log M_{O_2} = 0.047T - 2.25$ ($r^2=0.94$, DF, $MS=0.012$, $F=674$, $P<0.0001$).

Active oxygen consumption increased greatly between 5 and 13°C. At 17 and 21°C active oxygen consumption rates increased, but they were not significantly higher (DF, $MS=0.0003$, $F=3.07$, $P=0.06$) than at 13°C. The response is described by the equation: $M_{O_2} = -3.3 \times 10^{-4}T^2 + 0.013T - 0.044$ ($r^2=0.89$, DF, $MS=0.02$, $F=201$, $P<0.0001$).

The quadratic model suggests a decline in oxygen consumption beyond 21°C, but more data points are required to confirm the presumption.

The aerobic scope for activity increased as temperature increased from 5°C, with a maximum SFA recorded at 13°C (Fig. 1). The increase in the scope for activity over that
Fig. 1. The effect of temperature on oxygen consumption (mean±S.E.) (mg O₂/g/h) of the southern rock lobster, *Jasus edwardsii* (*N*=12). Standard (Δ) and active (O) oxygen consumption rates both increased with temperature. The aerobic scope for activity (mg O₂/g/h) at each temperature is also shown (□).

range was largely due to the increase in active oxygen consumption. At higher temperatures (17 and 21°C) the scope for activity decreased due to the declining rate of increase of active $M_{O_2}$, associated with the exponential increase in standard $M_{O_2}$.

Aerobic expansibility (Table 1) was highest at 9 and 13°C (2.79 and 3.00, respectively) and was lowest at the extremes of the temperature range being 1.52 at 5°C and 1.68 at 21°C.

The $Q_{10}$ of the standard oxygen consumption decreased as the temperature increased (Table 1) ranging from 4.3 ($Q_{10(5-9)}$) to 2.3 ($Q_{10(17-21)}$). The $Q_{10}$ for the active lobsters showed a very different pattern. Between 5 and 9°C active oxygen consumption

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Aerobic expansibility$^b$</th>
<th>Temperature range (°C)</th>
<th>$Q_{10}^c$</th>
<th>Standard $M_{O_2}$</th>
<th>Active $M_{O_2}$</th>
</tr>
</thead>
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<tr>
<td>5</td>
<td>1.52</td>
<td>5–9</td>
<td>4.3</td>
<td>19.4</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>2.79</td>
<td>9–13</td>
<td>3.0</td>
<td>3.6</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>3.00</td>
<td>13–17</td>
<td>2.6</td>
<td>1.1</td>
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<tr>
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<td>2.13</td>
<td>17–21</td>
<td>2.3</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>1.68</td>
<td></td>
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<td></td>
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</tr>
</tbody>
</table>

Average – 5–21 3.0 6.4

$^a$The $Q_{10}$ values of standard and active oxygen consumptions for each temperature range are shown along with the average $Q_{10}$ values over the whole temperature range.

$^b$Aerobic expansibility = active $M_{O_2}$/standard $M_{O_2}$.
increased markedly which resulted in a $Q_{10(5-9)}$ of 19.4. $Q_{10}$ values above 13°C are close to unity.

### 3.2. Effect of body size on oxygen consumption

The sex of the lobsters did not have a significant effect on either the standard (SS = 0.003, $F = 1.00$, $P = 0.32$) or active (SS = 0.004, $F = 0.58$, $P = 0.45$) oxygen consumptions (Fig. 2). Therefore, the data for both sexes have been pooled. A log–log plot of weight specific oxygen consumption (mg O$_2$/g/h) over wet body weight is shown in Fig. 2. The standard and active rates of oxygen consumption ($M_{O_2}$, mg O$_2$/g/h) decreased with increasing lobster wet weight ($W$, g). The regression equations describing the relationships are:

- **Standard oxygen consumption**: $\log_{10}M_{O_2} = -0.405 \log_{10}W - 0.396$ ($r^2 = 0.69$, $DF_{1,45}$, MS = 0.37, $F = 99.9$, $P < 0.0001$).
- **Active oxygen consumption**: $\log_{10}M_{O_2} = -0.312 \log_{10}W - 0.238$ ($r^2 = 0.41$, $DF_{1,45}$, MS = 0.22, $F = 30.5$, $P < 0.0001$).

There was no significant difference between the slopes of the regressions for standard and active oxygen consumption (SS = 0.01, $F = 1.77$, $P = 0.186$), although there was a significant increase in oxygen consumption with activity (SS = 0.56, $F = 99$, $P < 0.0001$). When the data were plotted as total oxygen consumption (mg O$_2$/h) then both standard and active rates were positively correlated to the wet weight, with slopes of 0.595 and 0.688, respectively. The weight-specific aerobic scope for activity decreased significantly.

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**Fig. 2.** A log–log plot of weight specific oxygen consumption ($M_{O_2}$, measured in mg O$_2$/g/h) against body weight (g) (range = 186–2180 g) of the southern rock lobster, *Jasus edwardsii*. Standard (O) and active (□) oxygen consumption rates of males (clear symbols) and females (black symbols) are shown.
(DF$_{1,45}$, MS = 0.002, $F = 13.7$, $P = 0.0006$) with weight, and for a 700 g lobster was approximately 0.05 mg O$_2$/g/h. As indicated by the similarity between the $b$ values, there was no significant difference (DF$_{1,45}$, MS = 0.055, $F = 0.20$, $P = 0.65$) in aerobic expansibility with weight. The mean aerobic expansibility was 2.72 ± 0.08 (±S.E.) with a range between 2 and 4.

3.3. Effect of diurnal rhythm on oxygen consumption

Lobster weight did not have a significant affect (DF$_{1,20}$, MS = 193.1, $F = 0.77$, $P = 0.78$) on the night-time increase in oxygen consumption. Lobsters consumed significantly (DF$_{45}$, $t = 7.916$, $P < 0.001$) more oxygen at night, with consumption up to four times the daytime rates being recorded. Average night-time consumption was 48.3 ± 6.1% higher than standard oxygen consumption. Using standard oxygen consumption as a measure of oxygen consumption during the entire 12-h daylight period, and the recorded night-time rates, routine oxygen consumption was calculated to be 24.2% higher than the standard rate. Video recordings demonstrated that lobsters were very active at night, continuously moving (walking) around the respirometer, whilst during daylight hours they were generally immobile. The oxygen consumption of a 728-g lobster over a 48-h period is shown in Fig. 3 to demonstrate the general diurnal response.

3.4. Effect of emersion and handling on oxygen consumption

Handling and emersion caused a significant ($t = 6.75$, $P < 0.001$) increase in oxygen consumption.

![Fig. 3. Oxygen consumption (mg O$_2$/g/h) of an undisturbed 728 g southern rock lobster (Jasus edwardsii) over a 48-h period. Each symbol represents oxygen consumption over a 20-min measuring period. The lobster was in complete darkness between 6 p.m. and 6 a.m. The line is drawn for ease of viewing.](image)
3.5. Effect of feeding on oxygen consumption

Oxygen consumption increased after feeding, reaching a maximum 10–13 h after feeding (Fig. 5). The maximum oxygen consumption was 1.72 times the preprandial level. From this maximum level, oxygen consumption slowly declined until it was not significantly different ($t = 1.67$, $P = 0.13$) from the pre-emersion level at 4.5–5.0 h.

3.6. Effect of dissolved oxygen levels on oxygen consumption

Settled lobsters were able to maintain a constant rate of $M_{O_2}$ as the dissolved oxygen level of the water decreased (Fig. 6). Standard $M_{O_2}$ was maintained down to a critical oxygen tension ($P_c$) of 58 Torr. Below the $P_c$, $M_{O_2}$ decreased linearly with the dissolved
Fig. 5. Oxygen consumption (mg O$_2$/g/h ± S.E.) of the southern rock lobster, *Jasus edwardsii*, over a 48-h period (N = 11). The lobsters were fed squid, *Nototodarus gouldii*, (3% of the lobsters body weight) at 9:00 a.m. on the first day. Preprandial (□) and postprandial (●) oxygen consumption rates are shown. Each symbol represents the average oxygen consumption over 1 h (i.e., two measuring periods). For ease of viewing lines are drawn between succeeding data points. The asterisk indicates when postprandial oxygen consumption is not significantly different to the preprandial level.

Fig. 6. The relationship between dissolved oxygen tension (Torr) and oxygen consumption (mean ± S.E.) (mg O$_2$/g/h) of settled (O) (N = 15) and active (▲) (N = 12) southern rock lobsters, *Jasus edwardsii*. The aerobic scope for activity (mg O$_2$/g/h) (●) is also plotted as a function of the dissolved oxygen tension.
oxygen level. $M_{O_2}$ of active lobsters decreased with decreasing dissolved oxygen levels but the rate did not become significantly different until the dissolved oxygen tension was 86.3 Torr. The $P_c$ for active lobsters was calculated to be 93 Torr. The aerobic scope for activity decreased with the dissolved oxygen tension and was controlled by the active $M_{O_2}$. The scope at 86.3 Torr is 73% of that of the maximum, however, at 55 Torr the scope is only 25% of the maximum aerobic scope.

4. Discussion

The oxygen consumption response of *J. edwardsii* to intrinsic and extrinsic factors is characteristic of decapod crustaceans. Activity had the largest influence on oxygen consumption, causing a tripling of the standard rate at 13°C. In common with other studies, no significant differences in oxygen consumption between sexes were recorded (Laird and Haefner, 1976; Cockcroft and Wooldridge, 1985; Dall, 1986; Villarreal, 1990; Carvalho and Phan, 1997).

The dependence of total oxygen consumption on body weight is well documented for many crustaceans. Bridges and Brand (1980) summarised the relationship for a series of decapod crustaceans and found scaling exponents ($b$) ranging from 0.286 to 0.877 for a temperature range of 8.5–17.8°C. The $b$ values obtained in this study for both the standard and active oxygen consumption rates (0.595 and 0.690, respectively) fall within this range. Bridges and Brand (1980) noted that crustaceans in the large weight ranges tend towards a $b$ value of >0.75, which suggested that oxygen consumption was more dependent on mass in larger crustaceans. However, the upper weight range of crustaceans reported in Bridges and Brand (1980) is limited (max. 770 g). Zoutendyk (1989) obtained $b$ values of 0.68 and 0.65 (at 8 and 10°C, respectively) for *J. lalandii* ranging in weight from 20 to 2500 g (at higher temperatures $b$ values of 0.8–0.9 were obtained). These results suggest that oxygen consumption may be more dependent on surface area ($b$ of around 0.67) in larger crustaceans, as hypothesised by Zeuthen (1953). Other factors such as temperature may influence the $b$ value.

Standard rates of oxygen consumption vary widely with species, even under a similar temperature regime (Table 2). For example, the oxygen consumption rate of *J. edwardsii* in this study at 13°C was higher than obtained by Waldron (1991) for the same species, even though that study was conducted at 15°C. As similar procedures were used for both studies the reason for the differences are unclear, but may highlight intra-species variations found at different locations (i.e., Tasmania vs. New Zealand). However, in common with Waldron (1991) we found that oxygen consumption was lower than that reported for most other species at similar temperatures. In some cases the extremely high rates obtained in other studies appear to be artefacts of experimental procedures, such as insufficient acclimation time (McMahon and Wilkens, 1983; Waldron, 1991).

Scope for activity (SFA) represents the amount of energy available to an organism through aerobic metabolism beyond that needed for maintenance; for most metazoans this a good indication of their capacity for sustained work (Fry, 1947). The oxygen consumption increase and the weight-specific aerobic SFA for lobsters of 700 g ($=0.05$
Table 2
Comparison of standard rates of oxygen consumption of the southern rock lobster, *Jasus edwardsii*, with published values for some other large decapod crustaceans

<table>
<thead>
<tr>
<th>Species</th>
<th>Wet mass (g)</th>
<th>Temperature (°C)</th>
<th>$M_{o_2}$ (mg/kg/h)</th>
<th>Reference</th>
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<td>729</td>
<td>5</td>
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<td>27</td>
<td>Zoutendyk (1989)</td>
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<td>12</td>
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<td>380–520</td>
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<td>220–510</td>
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mg O₂/g/h) are similar to that measured for other large decapod crustaceans (Spoek, 1974; McMahon et al., 1979; Booth et al., 1982; Waldron, 1991) and compare closely to values obtained for sluggish fish species (McMahon and Wilkens, 1983). *J. edwardsii* only has a limited ability to carry out sustained aerobic work, as would be expected for a benthic, relatively inactive animal.

The response to temperature of *J. edwardsii* was typical of that seen in many crustaceans, with standard oxygen consumption increasing with temperature (Vernberg, 1983). Active oxygen consumption also increased with temperature, however a maximal rate was attained at an intermediate, non-lethal temperature (13°C) and it remained constant at higher temperatures (17 and 21°C). Thus, the SFA was maximal at 13°C, decreasing at temperatures above and below that point. The response of active $M_{O_2}$ and SFA was similar to that seen in many poikilotherms (Bennett, 1978) and the freshwater crayfish, *Pacifastacus leniusculus* (Rutledge and Pritchard, 1981). The lowest temperature at which maximal oxygen consumption is attained, and the temperature where SFA is maximal, is often the preferred body temperature or the normal field temperature (Bennett, 1978). In this study, 13°C was the temperature of acclimation and it is a typical mean water temperature where *J. edwardsii* is found in its natural environment.

Active and standard $M_{O_2}$ usually come together at the upper and lower lethal temperature of the species. Lower and upper lethal temperatures have not been determined for *J. edwardsii* but the results of this study show it is below 5°C and above 21°C for lobsters acclimated to 13°C.

In general $Q_{10}$ values for standard $M_{O_2}$ of crustaceans have been found to vary between two and three; the values usually decrease with increasing temperature (Wolvekamp and Waterman, 1960). Studies of other large decapods have found $Q_{10}$ values similar to *J. edwardsii* (3.0), e.g., for *J. lalandii*, $Q_{10(8-19)} = 2.5$ (Zoutendyk, 1989) and for *Panulirus interruptus*, $Q_{10(13-20)} = 2.5$ (Winget, 1969). In *J. edwardsii* the value of $Q_{10(5-9)}$ of 4.3 is high, but not unusual for crustacean species at the lower end of their temperature range, e.g., for *Penaeus monodon* it is 3.6 (Liao and Murai, 1986), for *P. esculentus* it is 4.7 (Dall, 1986) and for *P. californiensis* it is 4.8 (Villarreal and Rivera, 1993). In the crab, *C. sapidus*, there was also a large drop in $M_{O_2}$ at low temperatures ($Q_{10} = 4.9$)(Mauro and Mangum, 1982). The decreased $M_{O_2}$ in *C. sapidus* was associated with a sharp decrease in the heart rate, ventilation and the intrinsic oxygen demand of the muscle. The authors suggested the crabs could go into metabolic ‘hibernation’ because the high oxygen affinity of haemocyanin limits the ability of the tissues to use oxygen and they become hypoxic. Thus at 5°C *J. edwardsii* may have undergone a cold coma and were reaching the extremes of their range of thermal tolerance; a point where the scope for activity is zero (Newell, 1979).

The $Q_{10}$ value for active oxygen consumption between 5 and 9°C was extremely high. An equivalent literature value could not be found although $Q_{10}$ values of 8.9 and 7.7 were measured for non-temperature acclimated *H. gammarus* and *P. japonicus*, respectively (Whiteley et al., 1990; Paterson, 1993). Lobsters did not display a physical response (e.g., tail flicking) to being handled at 5°C. As activity is one of the major factors causing increases in oxygen consumption (Halcrow and Boyd, 1967; Newell, 1979), active $M_{O_2}$ would not be expected to increase greatly at that temperature. The aerobic expansibility at 5°C was very small but at 9°C when lobsters were much more...
active in response to handling, their aerobic expansibility increased substantially. Therefore, the high active $Q_{10.5-9}$ value appears to be due to the inability of lobsters to increase activity at the lower temperature. $Q_{10}$ values are as much reflections of changed activity as of the temperature dependence on the metabolic reactions underlying the activity (Halcrow and Boyd, 1967). Active $Q_{10}$ values of close to 1.0 were measured at temperatures above 13°C. Similar values have been recorded as temperature increases above the ‘preferred’ body temperature in many species of lower vertebrates (Bennett, 1978).

The extended time period taken to return to standard $M_{O_2}$ after handling and emersion suggests that a large oxygen debt was incurred. Large decapod crustaceans typically take around 8 h to return to pre-exercise levels of oxygen consumption after a period of exercise and/or emersion (McMahon et al., 1979; Waldron, 1991). The slightly shorter timeperiod in this study may be a reflection of the low water temperature. Whiteley and Taylor (1990) found that $H.\ gammarus$ took longer to recover from the effects of aerial exposure at 20°C compared to 10°C, and the timeperiod of recovery of $P.\ cygnus$ increased as temperature increased (Crear, 1998).

The increase in oxygen consumption and activity at night matches that observed in other subtidal decapods, which typically show a diurnal rhythm in their behaviour patterns (Ansell, 1973; Naylor, 1988; Hammond and Naylor, 1977; Lipcius and Herrnkind, 1982; Du Preez, 1983; Dall, 1986). The routine $M_{O_2}$ of 24% above standard $M_{O_2}$ is comparable with the routine rate calculated by Dall (1986) for the prawn $P.\ esculentus$ of 8–12% above the standard rate. Such a small increase above standard rates is probably appropriate for benthic animals with limited activity (Dall, 1986). Where diurnal rhythms are present, light is the prime entraining factor (Naylor, 1988; Williams and Dean, 1989). In the wild, $J.\ edwardsii$ commences foraging just before dusk and continues through the night, ceasing at dawn (Fielder, 1965). The oxygen consumption data in this study indicates that a similar activity pattern is maintained in captivity.

Postprandial increases in oxygen consumption have been well studied in fish (see Jobling, 1981 for a review) but relatively few studies have been conducted on crustaceans. The general term for the response is specific dynamic action (SDA). The increase in oxygen consumption is associated with the extra energy produced for transportation of food in the alimentary tract, its digestion, absorption and post absorptive metabolic processes related to the ingested food (Hepher, 1988). Food elicited a strong locomotor response in $J.\ edwardsii$; the increased activity would probably account for the initial rapid increase in oxygen consumption after feeding. Similarly, a large increase in oxygen consumption immediately after feeding was also observed in $P.\ monodon$ (Du Preez et al., 1992); the authors concluded it was due to increased activity and feeding processes, whilst a later peak was due to the absorptive and digestive processes.

Many factors affect the size of the SDA (see Jobling, 1981), but in fish the general response is a peak level of between two and three times standard $M_{O_2}$, with the peak occurring within 12 h after feeding, with a duration of 24–36 h. Therefore, $J.\ edwardsii$ displayed a classic postprandial increase in oxygen consumption. Similarly, oxygen consumption by the crab $C.\ maenas$ was 2.3-fold higher 3 h after a meal (2.6%
wet weight to wet weight), and had returned to its previous value within 24 h (Houlihan et al., 1990). Oxygen consumption by *Cancer pagurus* took 6–9 h to reach maximum postprandial levels (3.8-fold increase) and 24 h to return close to preprandial levels (Ansell, 1973). In *J. edwardsii* the maximum increases in $M_{O_2}$ after feeding was over a third of the lobsters aerobic expansibility at 13°C. Thus, their aerobic scope for activity was severely reduced for an extended period after feeding.

*J. edwardsii* was able to maintain its standard level of oxygen consumption down to a relatively low $P_{O_2}$ (58 Torr), below which $M_{O_2}$ varied in proportion to water $P_{O_2}$. The $P_c$ of *J. edwardsii* is similar to that evaluated for other crustaceans living in well oxygenated environments: *Homarus gammarus* 28 Torr (Spoek, 1974), *H. americanus* 30–40 Torr (McMahon and Wilkens, 1975), *Austropotamobius* sp. 40–50 Torr (Wheatly and Taylor, 1981), *Penaeus esculentus* 40 Torr (Dall, 1986) and *Carcinus maenas* 60–80 Torr (Taylor, 1976). Waldron (1991) obtained a $P_c$ for *J. edwardsii* of 80 Torr, a figure that is considerably higher than found in this study. The reason for the difference is unclear, but the results of this study do not support the view that a low degree of oxygen independence may limit the distribution of *J. edwardsii* (Waldron, 1991).

The critical oxygen tension for a given species is not constant (Reiber, 1995), and in *J. edwardsii* activity caused the $P_c$ to increase by almost 40 Torr. Only a few studies have looked at the $P_c$ of active crustaceans and it has generally been found that $P_c$ is close to saturation (*H. gammarus*, Spoek, 1974; *C. maenas*, Taylor, 1976; *Ebalia tuberosa*, Schembri, 1979; *Corystes cassivelaunus* and *Galathea strigosa*, Bridges and Brand, 1980; *P. esculentus*, Dall, 1986). Animals that are normally oxygen independent down to quite low $P_{O_2}$ levels become oxygen dependent when active. The relatively low $P_c$ evaluated for active *J. edwardsii* was similar to that obtained for *Heterosquilla tricarinata* (80–90 Torr; Innes, 1985). Similar methods were used in evaluating active $P_c$ in the two studies, with the ability of animals to uptake oxygen at specific $P_{O_2}$ values being examined, rather than using the normal method of placing active animals into water and monitoring the depletion of oxygen. The purported lack of ability of crustaceans to remain oxygen independent when active may therefore be an artefact of experimental procedures, and requires further investigation. The low $P_c$ of active *J. edwardsii* means that it can maintain a reasonably high aerobic SFA over a wide range of dissolved oxygen tensions. However, the 27% reduction in the capacity for aerobic SFA at 86 Torr may limit its ability to maintain physiological processes, such as oxygen consumption increases related to feeding. When the closely related species *J. lalandii* was grown at various levels of dissolved oxygen, there was a general decrease in growth and ingestion and an increase in intermoult period, with decreasing levels of oxygen saturation (Beyers et al., 1994). Such results would seem likely if the SFA response of *J. lalandii* to decreasing oxygen levels, which was similar to *J. edwardsii*.

Such a thorough understanding of how extrinsic and extrinsic factors affect oxygen consumption has not been evaluated for any other species of large decapod crustacean. Activity has the largest influence on oxygen consumption rate; holding systems that are designed to supply sufficient oxygen to satisfy the active rate of oxygen consumption will guarantee that environmental oxygen availability does not compromise the ability of lobsters to survive and maintain health in the post-capture environment.
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