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The ontogeny of physiological response to light intensity in early stage spiny lobster (*Jasus edwardsii*) larvae

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ABSTRACT

Early stage phyllosoma larvae of the spiny rock lobster *Jasus edwardsii* were examined for swimming speed, feeding, oxygen consumption and nitrogen excretion as instantaneous performance indicators when exposed to different irradiance levels. Swimming speed was measured in recently hatched Stage I larvae while all other parameters were measured in larvae from hatch to mid-Stage V. The swimming speed of recently hatched Stage I phyllosoma increased logarithmically between light intensities of 2.9×10^{14} and 1.8×10^{16} quanta s^{-1} cm^{-2} indicating that, within this range, swimming activity was only suppressed at the lowest irradiance level. Larvae examined under dark (no light) conditions showed lower feed intake, oxygen consumption and nitrogen excretion than larvae under low (7.7×10^{12} q s^{-1} cm^{-2}) and high (3.9×10^{14} q s^{-1} cm^{-2}) light intensities, and this was a consistent pattern observed throughout development from hatch to Stage V. There was no difference in feeding, oxygen consumption and nitrogen excretion between larvae exposed to low and high light intensities. However, from mid-Stage I to mid-Stage V, the metabolic feeding efficiency (feed intake:oxygen consumption ratio) was consistently higher in larvae exposed to low light intensity than in phyllosoma assessed in the dark and under high irradiance. A light intensity of about 7.7×10^{12} quanta s^{-1} cm^{-2} and no higher than 3.9×10^{14} quanta s^{-1} cm^{-2} is recommended to stimulate feeding and optimise metabolic feeding efficiency in early larval stages of *J. edwardsii*.

1. Introduction

The aquaculture of spiny lobsters represents a unique opportunity to increase the production of lobster fisheries, which are already extensively exploited around the globe. Currently, the commercialisation of spiny lobster culture is hampered by low survival in the hatchery through the protracted larval phase (Kittaka and Booth, 1994). In Australia, research into the development of rearing techniques for aquaculture has focused on the southern and tropical rock lobsters (*Jasus edwardsii* and *Panulirus ornatus*, respectively) (Ritar et al., 2006).

Defining optimal environmental conditions is an essential first step in the successful propagation of animals since they may influence behaviour (e.g., locomotor activity, feeding) and metabolic processes (e.g., basal metabolic rate, food assimilation) as previously demonstrated in *J. edwardsii* larvae for culture temperature (Bermudes and Ritar, 2004) and salinity (Bermudes and Ritar, 2005). The primary environmental factors include temperature, salinity and light. Light and gravity are the principal orienting stimuli governing the directional response of animals in the vertical plane (Fraenkel and Gunn, 1961). However, the responses and their amplitudes can be altered by other environmental parameters such as light intensity, temperature and salinity (Sulkin, 1984). While gravity is essentially a constant parameter with depth, light is highly variable in the marine environment. Factors such as season, time of the day, depth, water quality and weather conditions can all affect light intensity and spectral composition (Clarke, 1970). In decapod larvae, light can act as a stimulus to locomotor activity (see review by Sulkin, 1984). Bermudes and Ritar (2004) showed that, depending on ambient temperature, locomotor activity can represent a large part (between 52% and 82%) of the metabolic demand of active recently hatched *J. edwardsii* larvae. In a previous study in the same species, Moss et al. (1999) found greater larval growth increment at low light intensity than at high intensities. They concluded that given the lack of effect of light intensity on feed intake, the higher growth rates observed under low irradiance would primarily be explained by greater energy expenditure with increasing light intensity. However, to date, there has not been any direct investigation of the effect of light intensity on the level of metabolic expenditure in spiny lobster larvae.

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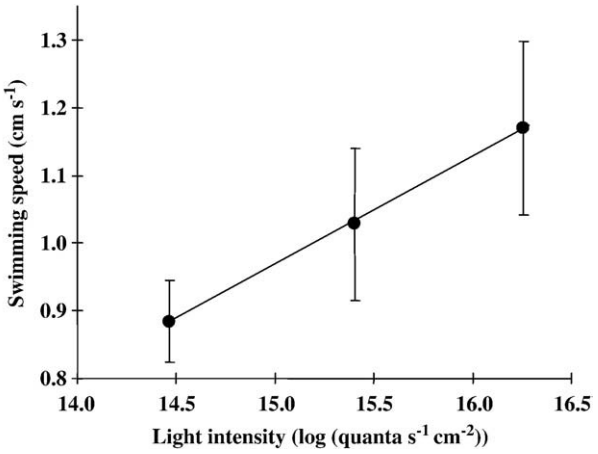

Fig. 1. Mean (±SE) swimming speed of recently hatched Stage I *Jasus edwardsii* larvae in relation to log-transformed light intensity (quanta s^{-1} cm^{-2}). The relationship was fitted with a linear regression on the raw data.

In the present study, we explored the effects of light intensity on the balance between feed intake and energy expenditure. The swimming speed was also quantified in recently hatched Stage I larvae to ascertain the effect of light on the level of activity. Feed intake, oxygen consumption and nitrogen excretion were measured to provide an instantaneous assessment of metabolism of phyllosoma under different light intensities.

2. Materials and methods

2.1. Larvae

Larvae were obtained from ovigerous females caught in coastal waters around Tasmania and kept in captivity at the TAFI Marine Research Laboratories. Recently hatched larvae from 15 females were collected from hatching tanks during spring at ambient temperatures ranging from 12.0 to 17.1 °C. Larvae from separate broods were reared at 18 °C in 10 l flow-through tanks (Ritar, 2001), initially stocked with 1000 recently hatched phyllosoma. Phyllosoma were fed juvenile *Artemia* (~2 mm) at a ration of 180 mg dry mass per 10 l water (approximately 2 *Artemia* per ml). Uneaten food and dead larvae were removed daily, and tanks were exchanged and cleaned weekly. The influence of light intensity on the physiology of phyllosoma was examined at Day 0 (recently hatched), 4–6 (mid-Stage I), 15–18 (mid-Stage II), 25–30 (mid-Stage III) and 52–55 (mid-Stage V). Mean±SE individual dry weights of recently hatched Stage I, mid-Stage I, II, III and V were 68.9±4.6 μg, 128.6±4.8 μg, 274.7±7.7 μg, 501.6±24.1 μg and 1234.8±120.2 μg, respectively. To avoid interference from possible circadian behavioural patterns, all experiments were conducted between 0900 and 1700 h. The effects of light intensity on oxygen consumption and nitrogen excretion were determined in two separate broods. Feed intake was examined in 15–20 larvae from a minimum of three broods at each age class and under each environmental condition tested. Different broods were used at each stage due to the numbers required for each experiment and to occasional mass mortality events during culture.

2.2. Swimming activity

Recently hatched Stage I *J. edwardsii* larvae are strong swimmers with a predictable positive phototaxis to directional light. To assess the effect of light intensity on the swimming activity of phyllosoma, recently hatched larvae were allowed to swim toward a directional light source (20 W quartz halogen) adjusted at three increasing intensities: 2.9×10^{14}, 2.5×10^{15}, and 1.8×10^{16} q s^{-1} cm^{-2} as measured at the middle of the experimental chamber with a light meter (QSL 100, Biospherical Instrument Inc., San Diego, CA). The different light intensities were obtained by placing layers of aluminium fly screen and drawing paper in front of the light source. These filters did not affect the peak wavelength of the light source (652 nm) as measured with a portable spectroradiometer (LI-1800, Li-Cor Biosciences Ltd., Lincoln, Nebraska). After the light was turned on, larvae were released from a small cage placed at the middle of the chamber. Their swimming towards the light was recorded with an overhead camera connected to a video recorder. Swimming speed (cm s^{-1}) was later measured on a monitor as the time taken for larvae to cover a 10-cm horizontal section of the chamber. A total of 20 larvae from each of four broods were examined at each light intensity.

2.3. Measurement of physiological responses

Light-proof chambers were used to compare the physiological response of larvae placed in the dark (no light), or exposed to low (7.7×10^{12} q s^{-1} cm^{-2}) or high (3.9×10^{14} q s^{-1} cm^{-2}) light intensities. In the light treatments, a quartz halogen light source (20 W; waveband: 350–800 nm; peak: 652 nm) was reflected on a white ceiling 0.5 m above the animals to provide even distribution of light throughout the chambers. Each light-proof chamber was fitted with a water bath maintained at 18 °C. The methods used to measure oxygen consumption (VO_2), nitrogen excretion and feed intake in *J. edwardsii* larvae can be found in Bermudes and Ritar (2004). Briefly, VO_2 was measured by oxygen depletion in closed 12 ml glass respirometers for Stage I (including recently hatched), II and III larvae, and in 17 ml respirometers for Stage V animals, in groups of 8–10, 4–5, 3 and 2 animals per respirometer, respectively. Throughout these trials, oxygen saturation in the respirometers was kept above 80%, as recommended by Ikeda et al. (2000). Percent oxygen saturation of water samples drawn from

Table 1
Akaike's Information Criterion and coefficient of determination adjusted for degrees of freedom ($R^2_{adj.}$, in brackets) obtained for the modelling of *y* (oxygen consumption, nitrogen excretion or feed intake) against *x* (age in days) in *Jasus edwardsii* larvae exposed to dark, low or high light intensity

Model[a]	Oxygen consumption			Nitrogen excretion			Feed intake		
	Dark	Low	High	Dark	Low	High	Dark	Low	High
(1) $y=a+bx+cx^2$	−195.2 (0.58)	−181.5 (0.78)	−172.3 (0.73)	−346.1 (0.42)	−324.4 (0.47)	−324.9 (0.53)	282.3 (0.63)	305.2 (0.65)	329.8 (0.57)
(2) $y=\frac{a}{1+bx}$	−195.7[b] (0.58)	−176.9 (0.75)	−167.6 (0.69)	−348.4[b] (0.43)[b]	−329.8[b] (0.49	−325.6 (0.53)	275.2[b] (0.65)	299.6[b] (0.66)	319.6[b] (0.61)[b]
(3) $y=a\times e^{-bx}$	−193.4 (0.56)	−166.2 (0.69)	−161.2 (0.65)	−348.3 (0.43)	−325.9 (0.46)	−327.0[b] (0.54)[b]	283.1 (0.62)	309.4 (0.63)	329.9 (0.57)
(4) $y=y_0+a\times e^{-bx}$	−191.1 (0.59)[b]	−199.1[b] (0.85)[b]	−173.5[b] (0.73)[b]	−346.7 (0.42)	−328.9 (0.54)[b]	−325.1 (0.53)	301.1 (0.66)[b]	334.5 (0.67)[b]	341.6 (0.61)

[a](1) quadratic regression; (2) rational expression with two parameters; (3) exponential function with two parameters; (4) exponential function with three parameters.
[b]Indicates the most parsimonious model (i.e. AIC) and/or the model with the least unexplained error (i.e. $R^2_{adj.}$) at each light intensity. Boxed values indicate the model selected for further analysis.

Table 2
Parameters of the exponential expression applied to the oxygen consumption in early stage *Jasus edwardsii* larvae exposed to different light intensities (Fig. 2)

$y = y_0 + a \times e^{(-bx)}$*						
	Light intensity					
	Dark		Low		High	
Parameter	Estimate	*P*	Estimate	*P*	Estimate	*P*
y_0	29.818[a]	<0.0001	40.214[b]	<0.0001	40.514[b]	<0.0001
a	21.594	<0.0001	34.363	<0.0001	34.678	<0.0001
b	0.048[a]	<0.05	0.114[b]	<0.0001	0.068[ab]	<0.001

*Where *y* is oxygen consumption (nmol O_2 mg DW^{-1} h^{-1}) and *x* is age (days). This model was selected according to the procedure outlined in Table 1.
Coefficients within same row with different superscripts were significantly different (KLR, $P<0.05$).

the respirometers was measured with a polarographic electrode connected to a digital controller (Rank Brothers, UK). In each treatment, VO_2 was assessed in five replicate respirometers and two controls without phyllosoma. Nitrogen excretion was measured in 9.5 ml vials in the younger stages and in 25 ml vials for the larger Stage V phyllosoma. Following a 8- to 9-h incubation period, a 3-ml water sample was drawn from each of five replicate vials and two controls without larvae for each treatment. Larval excretion was determined by substitution of control levels following analysis of ammonia concentrations according to the method described by Solórzano (1969). Feed intake by individual larvae was examined in plastic jars in 30 ml seawater and with 15 preys per individual, using 1.2–2.0 mm *Artemia* for Stages I–III larvae and larger 2.2–3.0 mm *Artemia* for Stage V larvae. The dry mass of test animals was determined from three samples of larvae rinsed in 0.9% ammonium formate and dried for 24 h at 60 °C (Lovegrove, 1962). The mass of each sample was measured to the nearest 10 µg on a precision balance (Mettler AT261 DeltaRange, Mettler-Toledo, Switzerland). Oxygen consumption, nitrogen excretion and feed intake were expressed in nmol O_2 mg DM^{-1} h^{-1}, nmol NH_3–N mg DM^{-1} h^{-1} and µg *Artemia* mg DM^{-1} h^{-1}. The convection requirement index (CRI), an indicator of metabolic feeding efficiency (Newell and Branch, 1980), was calculated as the quotient of feed intake and oxygen consumption. Note that oxygen consumption and feed intake were each measured in separate groups of larvae. Consequently, given the computation of the CRI (i.e., using group means at each light intensity and stage), statistical analysis was not applicable. Therefore, interpretation of the data was made according to the statistically tested effect of light intensity on oxygen consumption and feed intake.

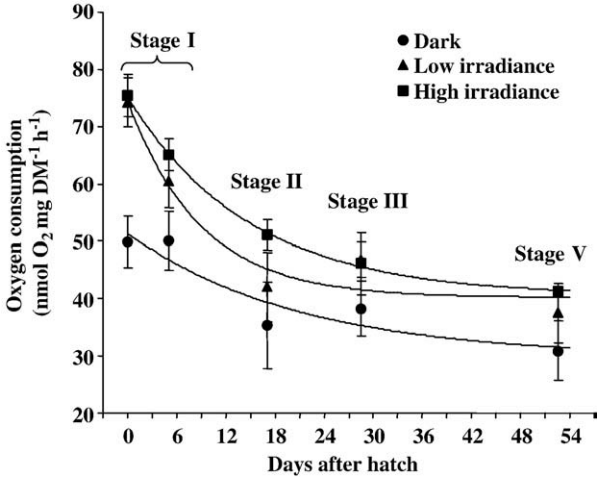

Fig. 2. Mean (±SD) oxygen consumption (nmol O_2 mg DM^{-1} h^{-1}) in early stage *Jasus edwardsii* larvae placed in the dark, or under low (7.7×10^{12} q s^{-1} cm^{-2}) or high (3.9×10^{14} q s^{-1} cm^{-2}) light intensity. An exponential expression was fitted to the raw data at each light intensity (Table 2).

2.4. Statistical procedures

The effect of the log-transformed light intensity on swimming speed was described with linear regression analysis. The ontogenic changes in the VO_2, nitrogen excretion and feed intake response of phyllosoma were described at each light intensity with mathematical expressions (e.g., rational expressions, exponential functions). Two criteria were used to fit the best type of model possible to the raw data, and to facilitate interpretation and the comparison of models between treatments: the Akaike's Information Criterion (AIC; Haddon, 2001); and the coefficient of determination adjusted for degrees of freedom (R^2_{adj}). Note also that, to be statistically comparable, models have to be the same at all light intensities. Therefore, compromise was sometimes required between the two criteria in order to obtain models that would be representative of the data and would also be relevant to the analysis. AIC and R^2_{adj} were computed in SigmaPlot 6.0, JMP 3.1 and Microsoft Excel. The Kimura Likelihood Ratio (KLR) test was used to assess for the effect of light intensity on oxygen consumption, nitrogen excretion and feed intake by testing for changes in the value of model parameters between the three light intensities examined (Haddon, 2001). Comparison of model intercepts was used to test for the effect of light intensity on the level of response, while the other coefficients of a model were compared to seek changes in the shape of the curve caused by light intensity. The KLR analyses were carried out following the Microsoft Excel spreadsheet procedure described by Haddon (2001).

3. Results

3.1. Swimming speed

The swimming speed of recently hatched Stage I larvae increased in a logarithmic fashion with increasing light intensity (linear regression, $r^2=0.356$, $F_{1,10}=5.534$, $P<0.05$; Fig. 1) described by the following expression:

$$SS = -1.421 + 0.159(\log_{10}(LI))$$

where *SS* is the swimming speed (cm s^{-1}) of recently hatched Stage I larvae and *LI* is the light intensity (quanta s^{-1} cm^{-2}).

3.2. Oxygen consumption

The developmental decline in weight specific oxygen consumption was described with an exponential function (Tables 1 and 2, Fig. 2) for larvae in the dark ($R^2_{adj}=0.59$, $F_{2,47}=35.82$, $P<0.0001$), larvae exposed to low light intensity ($R^2_{adj}=0.85$, $F_{2,46}=133.28$, $P<0.0001$) and larvae exposed to high light intensity ($R^2_{adj}=0.73$, $F_{2,47}=68.02$, $P<0.0001$). Light

Table 3
Parameters of the rational expression applied to the nitrogen excretion in early stage *Jasus edwardsii* larvae exposed to different light intensities (Fig. 3)

$y = \frac{a}{1+bx}$*						
	Light intensity					
	Dark		Low		High	
Parameter	Estimate	*P*	Estimate	*P*	Estimate	*P*
a	3.413[a]	<0.0001	4.874[b]	<0.0001	5.526[b]	<0.0001
b	0.064	<0.01	0.093	<0.01	0.068	<0.01

*Where *y* is nitrogen excretion (nmol NH_3–N mg DW^{-1} h^{-1}) and *x* is age (days). This model was selected according to the procedure outlined in Table 1.
Coefficients within same row with different superscripts were significantly different (KLR, $P<0.05$).

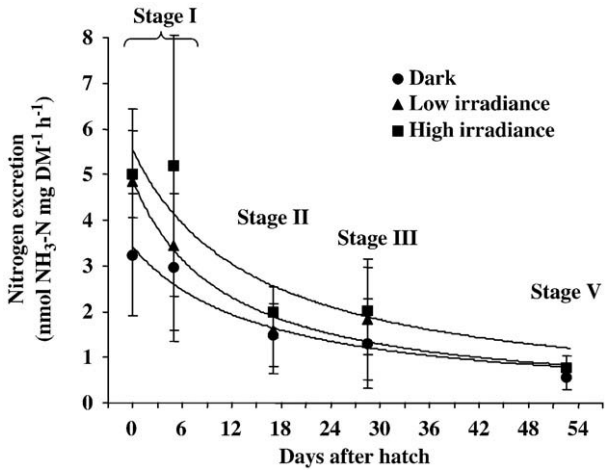

Fig. 3. Mean (±SD) nitrogen excretion (nmol NH_3–N mg DM^{-1} h^{-1}) in early stage *Jasus edwardsii* larvae placed in the dark, under low (7.7×10^{12} q s^{-1} cm^{-2}) or high (3.9×10^{14} q s^{-1} cm^{-2}) light intensity. A rational expression was fitted to the raw data at each light intensity (Table 3).

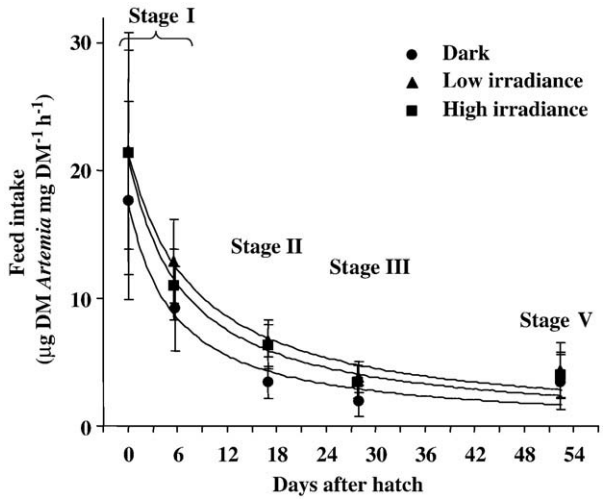

Fig. 4. Mean (±SD) feed intake (µg DM *Artemia* mg DM^{-1} h^{-1}) in early stage *Jasus edwardsii* larvae placed in the dark, under low (7.7×10^{12} q s^{-1} cm^{-2}) or high (3.9×10^{14} q s^{-1} cm^{-2}) light intensity. A rational expression was fitted to the raw data at each light intensity (Table 4).

intensity had a significant effect on VO_2 throughout the development from hatching to Stage V (KLR: *d.f.* = 3, χ^2 = 118.99, P<0.0001). According to the difference in the coefficient *b* of the model (i.e., inflection of the exponential response), the shape of the oxygen consumption response through time was affected by light intensity (KLR: *d.f.* = 1, χ^2 = 4.55, P<0.05). The initial ontogenic exponential decline in oxygen consumption was significantly larger in larvae exposed to low light intensity than in larvae in the dark (KLR on *b*: *d.f.* = 1, χ^2 = 4.49, P<0.05). However, there was no effect of light intensity on the overall VO_2 decline from hatching to Stage V (KLR on *a*: *d.f.* = 1, χ^2 = 2.72, P = 0.099). The intercept of the model was also influenced by light intensity (KLR: *d.f.* = 1, χ^2 = 12.39, P<0.001), and the comparison of intercepts between curves of significantly similar shape indicated that larvae exposed to high light intensity showed significantly higher VO_2 than larvae in the dark throughout early development.

3.3. Nitrogen excretion

Nitrogen excretion declined in a curvilinear fashion during development. Data were fitted with a rational expression (Tables 1 and 3, Fig. 3) for the response observed in the dark (R^2_{adj} = 0.43, $F_{1,42}$ = 33.93, P<0.0001), under low light intensity (R^2_{adj} = 0.49, $F_{1,41}$ = 41.38, P<0.0001), and under high light intensity (R^2_{adj} = 0.53, $F_{1,43}$ = 50.28, P<0.0001). There was an overall effect of light intensity on the nitrogen excretion of phyllosoma throughout the developmental period examined (KLR: *d.f.* = 2, χ^2 = 20.80, P<0.0001). The amplitude of the decline in nitrogen excretion through time (i.e. coefficient *b* in the rational expression) was not significantly different between the three light intensities tested (KLR: *d.f.* = 1, χ^2 = 0.91, P = 0.340). However, there was an overall effect of light intensity on the excretory rate of phyllosoma (KLR on *a*: *d.f.* = 1, χ^2 = 15.37, P<0.0001), and nitrogen excretion was lower in the dark than in low (KLR: *d.f.* = 1, χ^2 = 8.19, P<0.01) and high (KLR: *d.f.* = 1, χ^2 = 14.73, P<0.001) light intensities as indicated by ad-hoc testing between the intercept (*a*) at each intensity.

3.4. Feed intake

The weight specific consumption of *Artemia* declined in a curvilinear fashion throughout early development as described by the rational expression (Tables 1 and 4, Fig. 4) for larvae in the dark (R^2_{adj} = 0.69, $F_{1,92}$ = 208.48, P<0.0001), larvae under low light intensity (R^2_{adj} = 0.69, $F_{1,92}$ = 204.87, P<0.0001), and larvae under high light intensity (R^2_{adj} = 0.64, $F_{1,92}$ = 166.13, P<0.0001). There was a significant effect of light intensity on feed intake throughout development (KLR: *d.f.* = 2, χ^2 = 16.90, P<0.001). Although the shape of the response was consistent across treatments (KLR on *b*: *d.f.* = 1, χ^2 = 1.12, P = 0.290), light intensity significantly influenced the feed intake of phyllosoma during early ontogeny (KLR on *a*: *d.f.* = 1, χ^2 = 9.43, P<0.01). Feed intake by larvae in the dark was significantly lower than under low (*d.f.* = 1, χ^2 = 8.69, P<0.01) and high light intensities (*d.f.* = 1, χ^2 = 6.30, P<0.05), but there was no difference in *Artemia* consumption between larvae under low and high light intensity (*d.f.* = 1, χ^2 = 0.05, P = 0.816).

3.5. Convection requirement index (CRI)

The CRI appeared to decline during early larval development, and from mid-Stage I to mid-Stage V, the CRI was consistently higher in larvae exposed to low light intensity than in larvae in the dark or under high light intensity (Table 5).

Table 4
Parameters of the rational expression applied to the feed intake in early stage *Jasus edwardsii* larvae exposed to different light intensities (Fig. 4)

$y = \frac{a}{1+bx}$*						
	Light intensity					
	Dark		Low		High	
Parameter	Estimate	*P*	Estimate	*P*	Estimate	*P*
a	17.666[a]	<0.0001	21.579 [b]	<0.0001	21.261 [b]	<0.0001
b	0.183	<0.0001	0.126	<0.0001	0.152	<0.0001

*Where *y* is feed intake (µg *Artemia* mg DW^{-1} h^{-1}) and *x* is age (days). This model was selected according to the procedure outlined in Table 1.
Coefficients within same row with different superscripts were significantly different (KLR, P<0.05).

Table 5
Convection requirement index (CRI), computed as the quotient of the data on feed intake and oxygen consumption, for recently hatched and mid Stages I, II, III and V *Jasus edwardsii* larvae subjected to different light intensities

Larval stage	Light intensity		
	Dark	Low	High
Recently hatched	15.85	13.02	12.65
I	8.21	9.51	7.61
II	4.32	7.11	5.59
III	2.33	3.64	3.37
V	5.03	5.24	4.33

4. Discussion

The combination of behavioural assessment (swimming and feeding) and metabolic studies (oxygen consumption and nitrogen excretion) provided further understanding of the mechanisms through which light intensity can influence growth in *J. edwardsii* larvae. Recently hatched *J. edwardsii* larvae are known to display strong, positively phototactic swimming towards the water surface as they hatch at dawn (MacDiarmid, 1985). In this study, light stimulated locomotor activity in recently hatched phyllosoma swimming towards a directional light source. The swimming speed of phyllosoma increased logarithmically with increasing light intensity, thereby tending toward a maximum at the highest intensity tested (1.8×10^{16} q s^{-1} cm^{-2}). Mikami (1995) reported a similar logarithmic pattern in the swimming speed of recently hatched *Thenus orientalis* larvae exposed to illuminance of different intensities. The effect of light intensity on swimming speed has been reported in other larval decapod species (reviewed by Sulkin, 1984). The presence of photokinesis in *J. edwardsii* larvae indicates that they vary locomotor activity according to ambient lighting, which may have energetic implications such as reduced growth and survival.

In *J. edwardsii* larvae, all three physiological functions examined (i.e. oxygen consumption, nitrogen excretion and feed intake) were influenced by light intensity. Overall, the response by larvae exposed to low or high light intensities did not differ in terms of oxygen consumption, nitrogen excretion and feed intake. These results suggest that the main effect of light intensity in phyllosoma is found between total darkness and light, and that phyllosoma would perform equally at low or high intensities, at least for the range of intensities tested in the present study. Furthermore, the same physiological pattern of response to light intensity prevailed throughout early development as greater rates of respiration, nitrogen excretion and feeding were observed under light than in the dark, from hatch to Stage V.

Overall, the oxygen consumption rates of *J. edwardsii* larvae placed under low and high light intensities were 28% and 36% higher than those observed in larvae in the dark. This agrees with Kils (1979) who reported a 30% increase in oxygen consumption in *Euphausia superba* under light than in darkness. Since light at the levels experienced by phyllosoma in the present study is unlikely to have a direct influence on metabolism, the increase in VO_2 in larvae exposed to light may be attributed primarily to increased locomotor activity as was earlier demonstrated in recently hatched Stage I animals. Nonetheless, the effect of irradiance on metabolism does not occur in all zooplankton; for example, Pearcy et al. (1969) did not find any difference in oxygen consumption between *Euphausia pacifica* placed in the dark or subjected to light. Weight specific nitrogen excretion levels were elevated under light, and as for VO_2, coincided with increasing locomotor activity. This suggests that *J. edwardsii* larvae use protein as a metabolic substrate to fuel the muscular activity involved in swimming. This observation has significant implications in the design of a rearing system since excessive locomotor activity could potentially impair growth. Although metabolic energy losses increase under light, they may be compensated by the greater feed intake seen in larvae subjected to low or high light intensities as opposed to larvae in the dark. These results are consistent with findings by Moss et al. (1999) working on the same species, and with reports of higher feeding rates under light than in the dark in *Ranina ranina* larvae (Minagawa, 1994). However, feeding rates alone do not provide reliable indicators of an animal's potential to grow under various conditions until they are examined as a function of the energy expended under the same conditions.

The CRI was used in the present study to assess metabolic feeding efficiency under different light intensities with a higher CRI indicating that more prey were consumed per unit of energy expended. From mid-Stage I onward, *J. edwardsii* larvae placed under low light intensity showed consistently higher CRI than larvae in the dark, which is partly explained by the significant difference in feeding rates between the two treatments. Although these results were not directly statistically validated, they tend to indicate that under low light intensity there is a positive return for the extra energy expended through swimming possibly via the enhanced frequency of prey encounter. The benefits of light on metabolic feeding efficiency were not increased beyond the low intensity tested as the CRI of larvae under high light intensity was consistently lower than in phyllosoma exposed to low light levels. However, given the lack of statistically significant differences in the oxygen uptake and feeding rate between the two light intensities, any interpretation remains speculative. Nonetheless, these findings are in agreement with those of Moss et al. (1999) who found higher growth increment in *J. edwardsii* larvae fed under low light intensity compared with phyllosoma raised under high light intensity.

In the present study, early stage *J. edwardsii* larvae responded to light exposure with increased swimming activity, feeding, oxygen consumption and nitrogen excretion. These findings have significant implications for the design of larval culture systems that can promote feeding while minimising energy expenditure to improve feed efficiency. While these findings can be directly applied to the fine tuning of light irradiance during larval rearing, another application of the results may be in the control of photoperiod to provide a light phase to enhance feed intake and a dark phase to maximise assimilation. However, further work is required to determine optimal light:dark photoperiod duration, the frequency of photoperiod (i.e., one, two or more light phases in a 24 h cycle) and to determine metabolic and feeding light thresholds under a broader range of intensities than used in this work.

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