Energetics of swimming to shore in the puerulus stage of a spiny lobster: Can a lobster post-larva afford the cost of crossing the continental shelf?

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Running head: Larval lobster swimming energetics

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Abstract

A model that analyzes the hydrodynamic forces during swimming in the puerulus stage of the spiny lobster *Jasus edwardsii* is described. The model calculates the steady swimming speed at which forward propulsion balances drag. Calculated speeds agree with observations of pueruli swimming. The computed mechanical work is converted to metabolic energy consumption using an assumed mechanical efficiency. Values agree well with reported estimates of the utilization of the biochemical energy reserves, composed of lipid, in pueruli crossing the continental shelf.

Assuming no more than half the total lipid content of a puerulus is available to fuel migration, the model suggests that distances of order 50 km and durations of 5 days active swimming are the approximate limits to endurance. Sustained swimming exceeding 15 cm s\(^{-1}\) will likely exhaust energy reserves before an animal can reach the coast, while swimming at less than 5 to 7 cm s\(^{-1}\) is inefficient because of the overhead of non-swimming, inactive metabolism. The results indicate that successful onshore migration of this species operates in a narrow window for the effective use of the finite energy reserve. Reduced energy reserves at the outset due to prior poor feeding, or delays encountered en route due to unfavorable currents, could be lead to exceeding the stored reserves of the pueruli, and death. These results have implications for the potential for relatively small shifts in coastal ocean climate conditions to generate marked changes in recruitment to important spiny lobster fisheries, as has recently been observed.
Introduction

[1] The post larval or puerulus stage in the life cycle of the spiny lobster (Palinuridae) is a critical link between the pelagic larval development in offshore waters and benthic juvenile-adult phase in inshore waters (Herrnkind et al. 1994). The manner in which the non-feeding pueruli move inshore is poorly understood, but there is evidence that this movement involves active swimming that utilizes significant lipid reserves built up over the long (9-24 month) larval development period depending on the species (Kittaka 1990; Nishida et al. 1990; Lemmens 1994; Takahashi et al. 1994; Jeffs et al. 1999; 2001).

[2] Demonstrating this method of migration is problematic because pueruli are difficult to study in the field due to their low abundance, wide dispersal, and highly cryptic behavior and appearance (Herrnkind et al. 1994). Laboratory flume tank experiments intended to directly measure the energetic costs of swimming in the nektonic pueruli of New Zealand’s red spiny lobster, Jasus edwardsii, were previously thwarted by clinging behavior of the pueruli when placed in the flume (Jeffs and Holland 2000; Jeffs 2001). However, estimates of the effort associated with the onshore migration of pueruli have been derived from measuring changes in the biochemical energy stores of pueruli caught at different distances offshore. This is possible because the pueruli stage does not feed, and so relies entirely on stored energy in the form of lipid (Nishida et al. 1990; Takahashi et al. 1994; Jeffs et al. 1999). Comparison of the biochemical composition of pueruli arriving at the coast with those caught 20 km immediately offshore on the south-east coast of the North Island, New Zealand, showed marked differences in energy stores associated only with their lipid content (Jeffs et al. 1999; 2001). The rate of consumption of lipid reserves in pueruli of J. edwardsii crossing 20 km of the continental shelf was estimated at 0.154 mg of lipid per kilometer, which is equivalent to energy expenditure of
5.6 J km\(^{-1}\) or a total of 113 J of energy (Jeffs et al. 1999). This therefore represents an estimate, based on metabolism, of the likely effort entailed in the 20 km migration from offshore to the coastal environments suitable for settlement.

[3] The objective of this study is to estimate the effort expended by pueruli during sustained swimming using a simple model of the hydrodynamics of their swimming motion. Assuming a mechanical efficiency typical of that cited for similar crustacea, we then relate sustained swimming speed and implied hydrodynamic swimming effort to probable distances and elapsed times that can be achieved by pueruli of *J. edwardsii*, and reconcile these with the stores of energy they hold as determined by lipid content studies.

**Methods**

*Mechanics and energetics of swimming*

[4] Although it can be problematic to directly measure the metabolic power used in swimming by small crustaceans, estimates of swimming energetics can be made by considering simplified models of the hydrodynamical thrust and drag of the swimming appendages and body. Morris et al. (1985; 1990) used this methodology to estimate the propulsion efficiency, swimming speed and jump distance of small cyclopoid and larger calanoid copepods. We used a similar approach to estimate the hydrodynamical power required to maintain a constant swimming velocity in the puerulus stage of the spiny lobster by calculating the propulsive and drag forces of the swimming appendages integrated over a complete swimming beat, and balancing these with the steady drag force on the animal. The angular displacements and velocities of the pleopods (the swimming appendages beneath the tail of the puerulus) were obtained from video imagery, while the
pleopod dimensions (which differ in effective hydrodynamical cross-section between the power and recovery strokes) were measured from sample animals.

[5] The copepods studied by Morris et al. (1985; 1990) accelerate significantly on each power stroke, and decelerate on the recovery stroke, which is a factor that is incorporated into their swimming model. In contrast, the lobster pueruli considered here are observed to maintain a constant velocity during sustained forward swimming (Jeffs and Holland 2000). This is consistent with their substantially greater mass (typically 0.3 g), and hence inertia, compared to small crustaceans such as copepods. The assumption of a steady swimming velocity is not valid for the rapid backward swimming behavior of pueruli during an escape reaction, but our interests here are not in the swimming energetics during the evasion of predators but rather in the net force balance for sustained forward swimming during migration across the continental shelf to the coast. The assumption of a constant swimming velocity simplifies the swimming model compared to that of Morris et al. (1985; 1990) (for copepods), but the nonlinearity of the quadratic drag force on a puerulus-sized animal nevertheless necessitates an iterative solution for the swimming speed at which propulsive and drag forces are balanced. For typical observed beat rates of the pueruli swimming appendages, it will be shown that computed swimming speeds agree well with those observed, providing a useful check on the validity of the swimming model.

Model of swimming energetics

[6] Our swimming model comprises three basic elements: the propulsive forces generated by the regular beat of the swimming appendages, the drag on the appendages during the recovery stroke, and the drag on the body itself. When these forces are balanced, a steady swimming velocity is achieved. Inputs to the model are the pleopod dimensions, the observed angular
movements of the pleopods, the beat rate of the swimming motion, and the dimensions of a

typical puerulus body (which determines the drag).

Motion of the swimming appendages

[7] The swimming behavior in the pueruli of *J. edwardsii* has been described previously by Jeffs

and Holland (2000). Using video imaging they examined an ensemble of some 30 pelagic pueruli

held in a seawater tank within a few hours of capture and observed relatively uniform swimming

velocities averaging around 16 cm s\(^{-1}\). The four pairs of pleopods that propel the animal in steady

swimming were seen to beat in synchronous metachronal waves at a rate of about 6.5 beats s\(^{-1}\).

[8] In our swimming model we describe the sweep of the pueruli pleopods in terms of the

angle each pleopod makes to the direction of motion as a function of time, \(\beta_i(t)\), for the \(i^{th}\)

pleopod, numbering from the head to the tail. The minimum and maximum angular

displacements of the pleopods (Fig. 1) were estimated by analyzing the movements of six

swimming pueruli using a high speed video recorder with a macro lens through a glass tank in a

manner similar to that described by Jeffs and Holland (2000). Measurements for each of the four

pleopods taken from six pueruli were averaged to give the parameters of the pleopod strokes in

our swimming model.

[9] The pleopods from two of these pueruli were removed and scale drawings made using

a microscope and camera lucida. Measurements taken from the drawings determined the width

of each appendage as a function of the distance along the pleopod, starting from the articulated

joint with the abdomen (Fig. 2). In our video observations the expodites (the biramous terminal

paddles on the pleopods; see Jeffs and Holland 2002, their Fig. 2) were seen to spread apart on
the power stroke, whilst on the recovery stroke they were brought together. This action reduces
the hydrodynamic cross-section and decreases the drag on the recovery stroke. This difference in
effective cross-section on power and recovery strokes is indicated in Fig. 2 by the solid and light
lines, respectively, and was determined from our measurements of the sample exopodites.

[10] The power and recovery strokes of the pleopod motion are separated by resting
intervals at the change of stroke direction. The sum of stroke, recovery, and resting intervals
comprises one beat (Fig. 3), and the duration of the respective components of the beat scale
proportionately as the animal varies the beat frequency.

[11] The video imagery of puerulus swimming action shows that on the power strokes the
pleopods move separately and, we assume, develop their thrust independent of the motion of the
adjacent pleopods. If there were partial interference in the flow around the pleopods due to wake
turbulence we would be presented with a virtually intractable hydrodynamic problem. We simply
postulate here that any interference in the hydrodynamics of the appendages would result in a
decrease in overall swimming efficiency, and that this is unlikely in an animal for which efficient
sustained swimming is critical to this particular life stage. The angular displacement versus time
of each of the four pleopods assumed in the swimming model is shown in Fig. 3. For
convenience, a cosine function is adopted for the transition from starting to ending displacement,
and back. Differentiating the angular displacement with respect to time gives the angular
velocity, $\omega$, which enters in the swimming model. From Fig. 3 it is apparent that each pleopod
has essentially completed the stroke before the adjacent pleopod commences, supporting the
conjecture that there is minimal hydrodynamic interference of neighboring pleopods during the
power stroke. The thrust developed by the four pairs of pleopods is therefore computed
independently and summed to give the total propulsive force of the swimming action.
In contrast to the power strokes, the recovery stroke is characterized by a synchronized motion of the four pleopods, presumably to minimize drag, on the return. Accordingly, we compute the combined drag of all appendages on the recovery stroke as simply that for the pleopod experiencing the greatest drag during the course of the return movement.

Forward propulsion force from pleopod motion

[13] The propulsive force calculation is achieved by discretizing each pleopod along its length into a finite number of segments (we use \( N_R = 50 \)), computing the force on each segment in accordance with its local velocity and cross-section dimension, and then summing over all segments. This computation is repeated at a finite number of time intervals (we use \( N_T = 200 \)) during the cycle of power and recovery stroke, and the total propulsive force integrated over the time of a complete beat.

[14] The forces on a single pleopod segment during the power stroke are defined as at time \( t \), the angular velocity of the \( i \)th pleopod is \( \omega_i(t) = d\beta_i/dt \) and the speed perpendicular to the leg associated with the sweep action is \( r_{ij}\omega_i \), where \( r_{ij} \) is the radial distance along the leg from the joint to segment \( j \) for pleopod \( i \) (Fig. 4). To this we add the component of the steady swimming velocity (\( V_S \)) that is perpendicular to the leg to obtain the actual speed of segment \( j \) through the water:

\[
U_{ij} = r_{ij}\omega_i - V_S \sin \beta_i \quad .
\]

The hydrodynamic drag force on this segment is denoted \( \Delta D_{ij} \) and its component in the direction of motion:
\[ \Delta F_i = \Delta D_i \sin \beta_i \]  

(2)

is the thrust the segment contributes to the animal’s propulsion.

[15] Thus far we have followed rather closely the conceptual model of swimming dynamics proposed for copepods by Morris et al. (1985). However, unlike in their model, we need not consider unsteady movement of the body and the role that the cycle of acceleration and deceleration on each stroke plays in the hydrodynamic added mass of the animal. This is because our video observations show that puerulus swimming speeds are quite steady over the course of a beat, and the acceleration is negligible (Jeffs and Holland 2000).

[16] We compute the propulsive force on each swimming appendage as the sum of a quadratic drag term and an inertia force associated with the effect of hydrodynamic added mass due to displacement of the water (Morison et al. 1950) during acceleration of the pleopods:

\[ \Delta D_i = \frac{1}{2} \rho C_D A_i U_i^2 + \rho K_A \hat{V}_i \frac{dU_i}{dt} . \]  

(3)

Here \( \rho \) is the density of seawater, \( C_D \) is a drag coefficient, \( A_i \) is the projected cross-sectional area of the segment normal to the flow, \( K_A \) is the added mass coefficient, and \( \hat{V}_i \) is the volume of the segment. We again follow Morris et al. (1985) and use an empirical formula for the drag coefficient of a cylinder normal to the flow:

\[ C_D = 1 + 10 \text{Re}^{-2/3} , \]  

(4)

where \( \text{Re} = Ud/\nu \) is the flow Reynolds number based on cylinder diameter, \( d \), and \( \nu = 10^{-6} \text{ m}^2 \text{ s}^{-1} \) is the kinematic viscosity of water. Here, the cylinder diameter is \( d_i \), the width of the relevant pleopod segment (Fig. 2b), recalling that this width changes between recovery and power strokes.
when the pair of overlapping expodites on each pleopod separates. The area $A_{ij}$ in equation (3) is the product of $d_{ij}$ and the small radial length of each segment, $\delta r_{ij} = L_i/N_R$, where $L_i$ is the full length of the $i^{th}$ pleopod. We continue with the assumption the pleopod segment is approximately cylindrical to compute the volume of fluid displaced, $\widehat{V}_{ij}$, and use $K_A = 1$ appropriate to a cylinder in an accelerating flow. It can be shown that the ratio of the inertia to drag forces scales with the aspect ratio (diameter/length) of the pleopod, so it is significantly less on the recovery stroke than power stroke. In our computations the added mass inertia is typically $\sim 30\%$ of the drag force on the power stroke.

[17] The thrust generated by a single pleopod at time $t$ is the summation over all segments along the length of the pleopod,

$$F_i(t) = \sum_{j=1}^{N_s} F_{ij} = \sum_{j=1}^{N_s} \Delta D_{ij} \sin \beta_i(t),$$

and is positive on the power stroke but negative, representing drag, on the recovery stroke. We calculate the total forward thrust achieved by the coordinated action of all pleopods by summing the efforts of the eight pleopods (four left and four right) and averaging over the duration of the power stroke, $T_P$, i.e., in the interval $0 < t < T_P$. As noted previously, video imaging shows that on the recovery stroke the pleopods tuck together and move synchronously, thereby shadowing each other and decreasing the extent of drag that would hamper forward motion. Therefore, on the recovery stroke the calculation must find the pleopod that is experiencing the greatest drag at any given time. On recovery the thrust $F_i < 0$, so the greatest magnitude of the drag is actually given by $\min_t F_i(t)$ during $T_p < t < T_B$. The average thrust over a complete beat cycle is then:
\[ F_{\text{T}h\text{rust}} = \frac{2}{T_B} \left( \sum_{i=1}^{4} \int_0^{T_p} F_i(t) \, dt + \int_{T_p}^{T_S} \min F_i(t) \, dt \right), \quad (6) \]

where the factor of 2 accounts for the combined effort of paired left and right pleopods.

[18] In sustained steady swimming this net propulsive force is opposed by drag on the body which we parameterize by adopting a drag coefficient for the puerulus body using an empirical relation based on frontal area for a streamlined body of revolution (Blevins 1984):

\[ C_{Di\text{Body}} = 3 \times 1.328 \, \text{Re}^{-1/2} \left[ \frac{L}{d} + \left( \frac{d}{L} \right)^{1/2} \right] + 0.33 \frac{d}{L}, \quad \text{Re} < 10^5, \quad (7) \]

where \( d \) is the maximum body width, \( L \) is the body length, and the Reynolds number is based on the body length, \( \text{Re} = UL/\nu \). From measurements of more than 100 pueruli collected from the south-east coast of the North Island of New Zealand we obtained average widths \( d = 6 \) mm and lengths \( L = 35 \) mm. Blevins (1984) notes that equation (7) indicates the optimum aspect ratio for minimum drag is about \( L/d = 5 \), and the sample pueruli are close to this criterion. This adds credence to our choice of drag coefficient because we expect the puerulus stage to be adapted to minimize drag for efficient swimming in the migration to shore.

[19] The drag force at swimming speed \( V_S \) is then

\[ F_{\text{Dr}a\text{g}} = \frac{1}{2} \rho C_{Di\text{Body}} \frac{\pi}{4} d^2 V_S^2. \quad (8) \]

[20] An assumption embodied in equation (1) is that the segments of the leg developing the thrust lie outside the frictional boundary layer that forms around the puerulus body, otherwise we would need to use a value smaller than \( V_S \) when \( r_{ij} \) is less than the boundary layer thickness. We justify this by considering the Blasius solution for the thickness of the boundary layer that
grows on a flat plate; \( \delta = 2 \sqrt{\nu x / V} \), where \( x \) is the distance from the leading edge (here, from the head of the puerulus). For \( V = 8 \) cm s\(^{-1} \) \( \delta \) is of order 1 mm at the tail of the puerulus \( x = L \) (35 mm) which indicates the swimming surfaces of the pleopods (Fig. 2) indeed lie outside the frictional boundary layer surrounding the body.

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**Steady swimming velocity**

While swimming velocity obviously affects the drag on the body, it also affects the total thrust generated by the beating pleopods via equation (1). The steady swimming speed achieved by a puerulus is therefore not an independent parameter of the swimming model, but rather the velocity the animal attains when drag matches the net forward thrust, \( F_{\text{Thrust}} = F_{\text{Drag}} \).

[22] It is not possible to combine equations (6) and (8) to derive an explicit algebraic expression for \( V_s \), but the condition \( F_{\text{Thrust}} = F_{\text{Drag}} \) is readily solved iteratively using a bisection algorithm to compute \( V_s \) as a function of beat frequency (Fig. 5). The model gives steady swimming speeds of 13 to 16 cm s\(^{-1} \) at beat frequencies of 6 to 7 s\(^{-1} \). This result is in very good agreement with the measurement of steady swimming speeds in freely swimming pueruli by Jeffs and Holland (2000) and provides further reassurance of the validity of the swimming model.

Sensitivity to parameters

[23] Numerous assumptions have been made in formulating the puerulus swimming model, not the least of which is that the pleopods have a simple rotational movement and that they may be treated, for hydrodynamic purposes, as piecewise cylinders with dimensions held fixed on the
power and recovery strokes. Accepting for the moment that the model is conceptually sound, it is nonetheless prudent to examine how uncertainties in model parameters will carry through to the calculated net force balance, steady swimming velocity, and energetics.

[24] The observed variance in the dimensions of bodies and appendages is remarkably low – at most a few percent (Jeffs et al 1999). We also have confidence from the video imagery that the timing and angular displacements of pleopod motion are well measured. Uncertainty in the balance between propulsive and drag forces therefore arises principally from the poorly known drag coefficients in equations (6) and (8), and the simple treatment of added mass inertia in the pleopod thrust calculation.

[25] Whatever the actual source of uncertainty in the thrust calculation, we can explore its impact by allowing sizeable variation in $C_D$ in equation (3). The shaded region in Fig. 5 shows the range in steady swimming speed is about ±8% when $C_D$ is varied by ±30%. This relative insensitivity arises because the total thrust is only partially dependent on $C_D$ (due to the independent added mass inertia term) and because the drag force that balances net thrust is proportional to the square of swimming speed. For example, a 17% increase in total thrust would be required to produce an 8% increase in swimming speed. Fig. 5 also shows the sensitivity to ±30% changes in $C_{D|Body}$ (dashed lines) and we see the effect on swimming speed is comparable to, but opposite, the pleopod drag. The swimming speed at fixed beat frequency is insensitive to $K_d$ because the inertia effect is a linear function of flow acceleration and is essentially symmetrical on power and recovery strokes. However, the animal must do work against this force in both stroke directions so sensitivity to $K_d$ does become evident in net energy consumption – a point we return to below.
Energetics

To compute the effort expended in sustained swimming, we use the principle that the work done by the swimming appendages in the course of one complete pleopod beat is the product of force times distance swept by each pleopod segment, integrated over the duration of the beat. Recalling that the velocity of each pleopod segment is $r_j \omega_i(t)$, the work done in a small time interval $dt$ is $|\Delta D_j r_j \omega_i(t)| dt$ where we take the absolute value because the animal expends this effort regardless of which direction the pleopod is moving. The average mechanical work (or energy) per time associated with swimming is then

$$P_{MECH} = \frac{2}{T} \sum_{i=1}^{4} \int_0^{T_B} \sum_{j=1}^{N_a} |\Delta D_j r_j \omega_i(t)| dt,$$

(9)

where the summation over the eight pleopods (four left and four right) has been applied, and the division by beat period yields a result in units of power, i.e., $J s^{-1}$ or Watts. To convert this rate of mechanical work to an estimate of metabolic effort, $P_{MET}$, we assume the same muscle efficiency $\mu = 0.25$ proposed by Morris et al. (1985) for other crustacea, and compute $P_{MET} = \mu^{-1}P_{MECH}$.

Results

Estimates of energy consumption from the swimming model were used to address the question of whether a typical puerulus of *J. edwardsii* has sufficient energy reserves in stored lipid to afford the cost of swimming several tens of kilometers across the shelf to settle at the coast. In our model the swimming effort can only be moderated by varying the frequency at which the pleopods beat and, naturally, the faster they beat the greater the speed the animal can
attain. However, hydrodynamic drag and decreased velocity of the pleopods relative to the surrounding water on the power stroke (equation 1) mean that swimming ever faster incurs an increasing penalty in terms of energy efficiency. Consequently, metabolic effort due to swimming (i.e., $P_{MET}$ measured in J hr$^{-1}$) increases much more rapidly than swimming speed (Fig. 6). Therefore, if metabolic cost were solely due to swimming and there were no other factors limiting the duration of cross-shelf migration, the most efficient migration strategy would be to conserve energy by swimming very slowly. However, pueruli expend metabolic effort whether swimming or not and this would exhaust their energy reserves before settlement if they made insufficient progress in their cross-shelf migration. Lemmens (1994) measured the metabolic rate of recently settled pueruli (i.e., resting and not swimming) of the Western Australian spiny lobster, *Panulirus cygnus*, which enabled him to calculate their individual energy requirement at 0.54 J h$^{-1}$. The pueruli of *J. edwardsii* are of a similar size as *P. cygnus* so we will assume they have a similar basal metabolic energy requirement when inactive. Denoting this rate $P_{INACTIVE}$, the total rate of energy consumption by a swimming puerulus is then

$$P_{SWIM} = P_{INACTIVE} + \mu^{-1}P_{MECH}.$$  \hspace{1cm} (10)

[28] The puerulus stage of spiny lobster species, including *J. edwardsii*, exhibit diurnal vertical migrating behavior, with active swimming only at night in coastal waters to avoid visual predators (Booth and Phillips 1994; Acosta and Butler, 1999). Assuming a 12:12 diurnal periodicity of swimming:inactivity with corresponding energy demands, the average rate of energy consumption in any 24 hours is

$$P_{12:12} = \left(12P_{INACTIVE} + 12P_{SWIM}\right)/24.$$
[29] Including diurnal behavior in our calculations has modest affect on average energy use at high swimming speeds because active swimming dominates the effort, but at slower speeds diurnal inactivity impacts the overall energy requirement because of the effective doubling of the basal metabolism burden for each kilometer of progress (Fig. 7). When speeds fall below 5 cm s\(^{-1}\) for sustained swimming, and below 7 cm s\(^{-1}\) for nighttime-only swimming, the energy use per distance travelled increases as the overhead associated with the base metabolism becomes the major contributor to total metabolic rate. It could be argued that 5 to 7 cm s\(^{-1}\) therefore represents an optimal swimming speed that offers the greatest endurance, if all other factors influencing the duration of the migration can be discounted. Certainly, the swimming model suggests that swimming speeds less than 7 cm s\(^{-1}\) would be an inefficient use of energy.

[30] The total energy consumed \((P_{12:12} \times \text{duration})\) and distances travelled were calculated for a set of nighttime swimming velocities of \(V_s = 7.5, 15\) and 20 cm s\(^{-1}\) (Fig. 8). Distance travelled is based on the 24-hour average speed \(\frac{1}{2}V_s\) because of the daytime inactivity. Swimming speeds of less than 7 cm s\(^{-1}\) are not considered because we have demonstrated these would make poor use of the puerulus’ stored energy. These results indicate that 3 to 8 days are required to traverse the necessary distance (i.e., 20 km) at the range of nighttime swimming speeds considered (Fig. 8). The least energy required for a successful migration is some 135 J for nighttime swimming at 7.5 cm s\(^{-1}\), and for which the journey takes 5.5 days. A more rapid transit at around 15 cm s\(^{-1}\) typical of the speed measured in free-swimming pueruli (Jeffs and Holland 2000) may be advantageous due to the elevated predation risk for pueruli travelling in coastal waters where visual hunting pelagic predators are more abundant and to which they are known to be particularly prone (Gracia and Lozano, 1980; Howard, 1988; Phillips and Sastry, 1980; Smith
and Herrnkind, 1992; Acosta and Butler 1999). If warranted to avoid predation, this accelerated speed would incur a higher energetic cost of some 190 J.

[31] Our estimates of energy requirements using the swimming model are higher, but are in the vicinity of evidence from a field study that found pueruli of *J. edwardsii* were consuming 3.1 mg of lipid, with a metabolic equivalent of 113 J of energy to execute a migration of 20 km (Jeffs et al. 1999). A subsequent study of a large sample of pueruli (360) caught at various distances offshore estimated that 16.5% of pueruli had insufficient energy reserves to reach inshore settlement grounds. Using the rates of energy consumption calculated from our swimming model would suggest that a significant proportion of pueruli would have insufficient energy reserves to reach inshore settlement grounds at nighttime swimming speeds of 15 and 20 cm s$^{-1}$ respectively which are in the range of swimming speeds for this species (Jeffs and Holland, 2000).

[32] If there were no period of daytime inactivity, then the swimming model suggests a puerulus could execute a 20 km migration by continuous swimming at 5 cm s$^{-1}$ for a total energy demand of 90 J (at 4.5 J km$^{-1}$) (Fig. 7). We do not know whether this behavior is an option a puerulus could elect if its energy reserves were critically low, but it does show that a total effort less that the 113 J estimated by Jeffs et al. (1999) is achievable.

Uncertainty analysis

[33] It was shown above that relatively large variations (±30%) in the force parameters have a modest influence on swimming velocity at fixed beat frequency. But drag also impacts the work done and energy consumed. The two shaded areas in Fig. 6, which are almost coincident,
indicate the sensitivity of energy consumption due to varying the body drag (the slightly larger
shaded region) and added mass coefficient. But in terms of energy used versus swimming speed,
the sensitivity to pleopod drag (dotted line) is small because this coefficient controls the
propulsive thrust and increased effort is harnessed into increased speed. Since energy use appears
most sensitive to $C_{D|\text{Body}}$, we illustrate sensitivity of $P_{12:12}$ to only this parameter in Fig. 7. There
is considerable sensitivity at the higher swimming speeds that we have argued are unlikely to be
sustainable for a full migration, but at lower speeds the results are robust to this parameter
variation. Fig. 7 also shows that varying the drag alters the speed at which energy consumption is
a minimum; this sensitivity is summarized in Table 1 for all parameters.

[34] The sensitivity of total energy consumed during migration at optimum swimming
speed to ±30% change in $C_{D|\text{Body}}$ is indicated in Fig. 8 (dotted lines bracketing the 7.5 cm s$^{-1}$
swimming line). The effect is modest.

[35] In conclusion we have presented a model of the hydrodynamic forces on the
swimming appendages (pleopods) and body of the puerulus stage of spiny lobster larvae and
deduced the mechanical work entailed in maintaining steady swimming speeds. The swimming
speeds predicted for typical beat frequencies of the pleopods concur with laboratory tank
observations of free-swimming pueruli, providing some validation of the formulation of the
swimming model. Furthermore, when energy consumption rates are inferred using an accepted
mechanical efficiency ratio for crustacea, the model gives estimates of the energetic cost to a
puerulus of crossing a 20 km wide continental shelf that accord reasonably well with energy cost
calculations based on the metabolism of lipid reserves in animals caught at either end of this
migratory range.
The puerulus stage of a spiny lobster does not feed, and therefore upon metamorphosis from the preceding larval stage there is an imperative to complete migration to settlement. An inactive, non-swimming puerulus still consumes energy, and so there arises a swimming speed below which the energy used per distance traveled increases, and inefficient swimming progress risks exhausting the energy store of a puerulus. Slower transit times would also increase the exposure of pueruli to the risk of predation which is thought to be extremely high from visual pelagic predators which are abundant in coastal waters. Because of the additional energy costs for periods of diurnal inactivity, there is a difference of only 40% (195 J vs. 135 J) in energy required for diurnal swimming at twice the speed (15 cm s\(^{-1}\)) of the predicted energetic optimum for diurnal swimming of around 7 to 8 cm s\(^{-1}\). This increased speed naturally halves the time of exposure to predation during migration, and would be consistent with the behavior of free-swimming pueruli of this lobster species that have been measured swimming on average at 15 cm s\(^{-1}\).

*Significance to Aquatic Environments*

When compared with data on the actual biochemical energy stores of pueruli, our estimates of overall energy requirements suggest a significant proportion of pueruli would have insufficient energy stores to complete the 20 km migration, especially if the transit is not a straight line across the continental shelf, or if adverse ocean currents impede onshore progress, or if more substantial quantities of energy reserves are required to fuel the post-settlement phase. Poor feeding conditions caused by low productivity during the preceding lengthy larval period
(16-18 months) during which the stored energy reserves are accumulated could further limit the potential swimming range.

[38] If spiny lobster pueruli have little margin in stored energy to overcome adverse migration conditions, then relatively small shifts in coastal circulation associated with climatic variability or longer term ocean climate change have the potential to generate marked changes in the survival of pueruli and subsequent recruitment into spiny lobster fisheries, as has recently been observed in some spiny lobster populations (Caputi et al., 2010).

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References


Table 1  Sensitivity of optimum swimming speed, $V_{S\text{opt}}$, and corresponding rate of energy consumption, $P_{\text{opt}}$, to changes in parameters of swimming model that control the thrust and drag force balance, and mechanical work.

<table>
<thead>
<tr>
<th>Sensitivity analysis</th>
<th>Control case</th>
<th>Parameter varied</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_D$</td>
<td>$C_D$</td>
</tr>
<tr>
<td>variation from control case</td>
<td>$0$</td>
<td>-30%</td>
</tr>
<tr>
<td>$V_{S\text{opt}}$ (cm s$^{-1}$)</td>
<td>7.49</td>
<td>8.11</td>
</tr>
<tr>
<td>$P_{\text{opt}}$ (J km$^{-1}$)</td>
<td>6.68</td>
<td>6.10</td>
</tr>
</tbody>
</table>
Fig. 1. The pleopods of the puerulus of *J. edwardsii* that are actively used for swimming are numbered 1 through 4 from head to tail. The angular displacement at time $t$ for each pleopod, $\beta(t)$, is measured from the direction of travel, and the ranges of motion, $\beta_{\text{min}}$ to $\beta_{\text{max}}$, for each pleopod are given. The puerulus swims forward at a steady speed $V_S$.

Fig. 2. Idealized pleopod widths of the puerulus of *Jasus edwardsii* used in the swimming model. Heavy line is model profile on the power stroke, light line is model profile on the recovery stroke.

Fig. 3. Angular displacement $\beta$ (see Fig. 1) of pleopods P1 through P4 versus time normalized by beat period $T_B$ for a puerulus of *J. edwardsii*. For pleopod 2 (heavy solid line) the portions of the complete stroke that are the power, recovery and rest periods, are indicated.

Fig. 4. Schematic diagram of the forces on a single pleopod segment during the power stroke.

Fig. 5. Steady swimming velocity for a puerulus of *J. edwardsii* as a function of beat frequency computed by solving for speed $V_S$ at which $F_{\text{Thrust}}$ (eq. 6) = $F_{\text{Drag}}$ (eq. 8). Shading shows the sensitivity to ±30% change in pleopod drag coefficient. Dashed line is sensitivity to ±30% change in puerulus body drag coefficient.
Fig. 6. Rate of metabolic energy consumption $P_{MET}$ in J hr$^{-1}$ as a function of steady swimming velocity in a puerulus of *J. edwardsii*. Shading indicates sensitivity to ±30% change in body drag coefficient, and added mass coefficient. Dotted line is effect of ±30% in pleopod drag.

Fig. 7. Rates of energy consumption with ($P_{12:12}$ - solid line) and without ($P_{SWIM}$ - dashed line) diurnal swimming behavior, as a function of active swimming velocity for a puerulus of *J. edwardsii*. Shading shows the sensitivity of $P_{12:12}$ to ±30% change in puerulus body drag coefficient.

Fig. 8. The total energy consumed versus distance traveled when the ratio 12:12 is assumed for a diurnal cycle of active:inactive swimming for a puerulus of *J. edwardsii*. Solid lines with symbols indicate different nighttime swimming speeds of 7.5, 15 and 20 cm s$^{-1}$. Dashed contours indicate elapsed time (including daytime inactivity). Dash-dotted line shows the Jeffs et al. (1999) estimate of puerulus energy usage during migration over 20 km (113 J). Shaded region indicates the regime of “successful migration,” i.e., travel distances > 20 km. Dotted lines bracketing 7.5 cm s$^{-1}$ curve indicate sensitivity to ±30% variation in drag coefficient of puerulus body.
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$\beta_{\text{min}}$ -9° -17° -17° -16°
$\beta_{\text{max}}$ -158° -139° -132° -122°
Fig. 2.

Idealized pleopod widths of the puerulus of *Jasus edwardsii* used in the swimming model. Heavy line is model profile on the power stroke, light line is model profile on the recovery stroke.
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