Escape swimming and fast-starts are common behaviors of aquatic organisms and critical components of predator–prey interactions. The mechanics of unsteady locomotion have been investigated for a variety of vertebrate and invertebrate animals (e.g. Webb, 1979; Daniel, 1983; Gal and Blake, 1988; Domenici and Blake, 1991; Lovvorn et al., 1991; Katz and Gosline, 1993). Although it is known that size affects the mechanics and performance of escape locomotion behaviors (e.g. Webb, 1976; Daniel and Meyhöfer, 1989; Jordan, 1992; Williams et al., 1996; James and Johnston, 1998), the specific characteristics and magnitude of these effects remain unclear.

We tested hypotheses concerning the scaling of escape swimming performance by examining the morphology of an aquatic exoskeletal animal, the California spiny lobster *Panulirus interruptus*, and quantifying the kinematics and performance of its tail-flip escape locomotion. The tail-flip system offers the following advantages for a scaling study: (1) it is a common escape response exhibited by crustaceans including mysids, shrimp, euphausiids, crayfish and lobsters (Brusca and Brusca, 1990); (2) it is a well-defined mechanical and behavioral event; and (3) post-larval *P. interruptus* display tail-flip behavior throughout their extensive size range (four orders of magnitude in body mass \(M_b\)). The size range examined in the present study includes and extends the range of body sizes considered in previous studies of tail-flipping by other crustaceans (Webb, 1979; Newland et al., 1988; Daniel and Meyhöfer, 1989; Cromarty et al., 1991; Spanier et al., 1991; Arnott et al., 1998).

A combination of resistive (drag) and reactive (acceleration and jet) mechanisms have been proposed to generate thrust during the tail-flip. On the basis of the mathematical model of Daniel and Meyhöfer (1989), the tail (the abdomen and uropods) acts as a paddle while adducting to the thorax, and a jet forms as water between the two surfaces is expelled. This
results in the animal rotating off the substratum into the water column and accelerating backwards (Fig. 1). The swimming event may recur cyclically; each cycle is composed of the tail-flip power stroke and a glide period during which the tail is extended while the animal decelerates.

Decreased tail-flip performance with growth has been attributed to changes in the ethology and neurophysiology of crustaceans. For example, Lang et al. (1977) reported that the tail-flip performance (measured as the frequency of tail-flip responses to a standardized stimulus) of the American lobster *Homarus americanus* decreased with growth. However, Lang et al. (1977) noted that when an adult animal’s chelipeds (claws) were removed, the frequency of its response was similar to that of juvenile animals. They interpreted this result as a case of developmental neuroethology: as *H. americanus* increases in size and develops claws, it preferentially displays new defensive behavior patterns. Edwards et al. (1994a) determined that, with growth, the threshold level of stimulation required for tail-flipping by crayfish increases, and stimulus habituation effects are seen. They associated these effects with changes in the integrative properties of the nervous system and increases in the excitatory input required by the lateral giant axons to stimulate the tail-flip (Edwards et al., 1994b).

Alternatively, decreased performance with increased size can be predicted on the basis of the mechanics of the system (Hill, 1950; Daniel and Meyhöfer, 1989; O’Reilly et al., 1993; Richard and Wainwright, 1995). On the basis of the assumptions that growth is isometric, that peak muscle stress is independent of $M_b$, and that the animal always responds at maximal capacity, six predictions can be made for tail-flip kinematics and performance at increased $M_b$. (1) The distance moved by the tail will increase as $M_b^{1/3}$ because of isometric growth. (2) Tail-flip duration will increase as $M_b^{1/3}$ if muscle contraction frequency scales as $M_b^{-1/3}$ (Hill, 1950). (3) The velocity of the tail and body will be independent of size if the distance moved by the tail scales as $M_b^{1/3}$ and tail-flip duration scales as $M_b^{1/3}$. (4) Angular displacements of the body will be independent of size; the angular velocity of the body will scale as $M_b^{-1/3}$ (i.e. $M_b^{0}/M_b^{1/3}$) given that rotational velocity = linear velocity/length (Wainwright and Richard, 1995). (5) The translational acceleration of the tail and the body will scale as $M_b^{-1/3}$. On the basis of the geometric similarity model (McMahon, 1984) muscle area, and thus force, scales as $M_b^{2/3}$. Thus, given Newton’s second law ($F=ma$, where $F$ is force, $m$ is mass and $a$ is acceleration), acceleration will scale as $M_b^{-1/3}$. (6) Rotational acceleration of the body ($\alpha$) will scale as $M_b^{-1/3}$. Added-mass and jet forces dominate this acceleratory motion (Daniel and Meyhöfer, 1989), and these forces are dependent on body volume. If translational forces scale as $M_b^1$, then the torque ($\tau$), which is produced during the tail-flip because the abdominal muscle is posterior to the center of mass, will scale as $M_b^{4/3}$ (translational force $\times$ moment arm; Daniel and Meyhöfer, 1989). The value of $\alpha$ is determined by $\tau$ and the moment of inertia ($I$). For a solid beam rotating about its center of gravity, $I=ml^2/12$ (where $m$ is beam mass and $l$ is beam length). Given geometric similarity, $I\propto m^{3/2}$; thus, $\tau=I\alpha$, $\alpha\propto m^{-1/3}$.

Thus, scaling rationales based on the mechanics of the system predict decreased rotational velocity, rotational
acceleration and translational acceleration with increased body size. Such mechanical limitations because of isometric growth, combined with a physiological limit to maximum muscle stress, led Daniel and Meyhöfer (1989) to suggest the novel prediction that there is a size limit to the tail-flip escape response. However, Panulirus interruptus tail-flips over a range of $M_b$ of more than three orders of magnitude. How is tail-flip performance sustained at large body sizes? Allometric growth (e.g. muscle mass increasing at a rate greater than $M_b$) or behavioral changes (e.g. initiating the flip with the tail partially flexed) could contribute to sustaining tail-flip performance with growth.

To address these possibilities and to test the scaling predictions proposed above, we measured nine external morphological variables for animals from 1 to 4000 g $M_b$ and abdominal muscle mass for animals of 50–700 g $M_b$. We also quantified five kinematic and six performance variables for animals of 1–1000 g $M_b$. The five kinematic variables examined (the animal’s stance, the distance traveled by the tail, the velocity and acceleration of the tail, and the duration of the tail-flip) are the major kinematic variables contributing to tail-flip performance. Tail-flip performance was evaluated by determining the translational distance, speed and acceleration of the center of mass ($C_m$), and the body rotation, rotational velocity ($\omega$) and rotational acceleration ($\alpha$).

Materials and methods

Panulirus interruptus (Randall) weighing less than 20 g $M_b$ were collected in the puerulus (last larval) stage using the methods of Serfling and Ford (1975); larger animals ($M_b > 100$ g) were collected in near-shore waters off San Diego, USA, using SCUBA. The animals were maintained in tanks with flow-through sea water on a diet of chopped mussels and smelt.

Morphological analyses

Data were collected on a series of intermolt individuals. Growth of a group of individuals over time was not examined because Panulirus interruptus has a slow growth rate (the age of a 1000 g animal is estimated to be 7 years; Serfling and Ford, 1975). Animals were blotted dry, and $M_b$ was determined using a digital balance. Animals weighing less than 50 g $M_b$ were considered juveniles. Sex was determined for animals weighing more than 50 g $M_b$ (the onset of sexual dimorphism) by the presence of enlarged pleopods and a subchelate dactyl (a pincher) on the fifth walking leg of females. Using a Mecanic 6901 Vernier caliper, the following morphological variables were measured to the nearest 0.1 mm: the length ($L_C$), width ($W_C$) and height ($H_C$) of the cephalothorax, the length of the abdomen ($L_A$), the width ($W_A$) and height ($H_A$) of the second abdominal segment, and the length ($L_U$) and width ($W_U$) of the uropods. The linear measurements of animals weighing more than 2000 g $M_b$ were made to the nearest 1 mm using a large caliper made from a meter stick.

Selected individuals were killed by freezing. Abdominal muscles were dissected, and muscle mass was determined to the nearest 0.1 g using a digital balance. The abdominal muscles have a complex helical trajectory within the abdomen (Daniel, 1931), so that measurements of abdominal muscle cross-sectional area based on abdominal cross-sectional area were obviously inaccurate and were not pursued.

The scaling relationships of morphological characteristics were analyzed in relation to animal size (represented by $M_b$) assuming the exponential relationship $y = aM_b^c$, where the slope ($c$) and $y$ intercept ($a$, at $M_b = 1$) of the relationship determine the scaling equation. Using Statgraphics (STSC, MA, USA) statistical software, the data were log-transformed and fitted with a linear regression model ($\log_{10}y = \log_{10}a + c\log_{10}M_b$) as proposed by Huxley (1932).

The use of an ordinary least-squares (OLS) regression model has been criticized because it assumes that $x$ ($M_b$ in this case) is an independent variable (i.e. that the values are determined without error; LaBarbara, 1989). As this assumption is not made for reduced-major-axis regression (RMA) models, we also calculated RMA slopes and the standard error of the slope for comparison with the OLS model characteristics (RMA slope = OLS slope/correlation coefficient; the standard error of the RMA calculation is numerically equal to the standard error of the OLS calculation; LaBarbara, 1989). For ease of viewing, the morphological data presented in graphical form are plotted untransformed on logarithmic scales. Statistically significant relationships are indicated by power regression models (the slope and $y$ intercept of the power regression model is equivalent to that of a linear regression model fitted to log$_{10}$-transformed data).

The center of mass ($C_m$) was assumed to be at the midline of the body because the animal is bilaterally symmetrical. The axial and dorsal–ventral positions of the $C_m$ were determined for four dead animals (12–800 g $M_b$) for full extension, partial flexure and full flexure of the tail. When the animal was suspended, the body rotated so that the $C_m$ was positioned directly beneath a plumb line (based on Webb, 1979). For each tail position, the animal was suspended from three different points on the carapace, and a video image of each position was recorded from a lateral view using a Sony CCD-iris camera and a Panasonic Ag-7355 VCR. When the three images for each body position were overlaid, the intersection of the plumb lines indicated the $C_m$ for that body position.

Kinematic and performance analysis

Swimming animals of 1–1000 g $M_b$ were videotaped for kinematic analysis. All the animals were in the intermolt phase; animals larger than the size of the onset of sexual dimorphism (approximately 50 g $M_b$) were females. The animals were videotaped in artificial light in sea water at 18±2 °C. The swimming area was at least three times the width and five times the length of the animal. Animals larger than 200 g $M_b$ were filmed from a lateral view using a Sony CCD-iris camera positioned perpendicular to the side of the tank, a time code
generator and a Panasonic AG-7355 video recorder recording at 60 fields s\(^{-1}\). Animals less than 200 g \(M_b\) were filmed from a lateral view using a NAC high-speed video system at 250 fields s\(^{-1}\) and a single camera. Simultaneous ventral and lateral views of selected small (less than 5 g \(M_b\)) animals were also obtained with the high-speed NAC system by using a second camera that viewed a mirror placed at 45° to the bottom of the tank. The video recording speeds were selected to ensure that approximately 15–30 images were collected for each tail-flip event. High-speed video equipment was not available when data were collected for 150 g and 240 g animals, so only duration data collected at 60 Hz were analyzed for these animals.

The direction, height and number of tail-flips in a given swimming sequence are dependent on the type of stimulus, on the point on the body of stimulus application and on whether the animal is in an intermolt or intramolt period (Cromarty et al., 1991). Work on crayfish has shown that stimulation to the anterior region of the cephalothorax excites the medial giant nerves and that the trajectory of the resulting tail-flip is essentially straight backwards (Newland et al., 1992). To standardize the stimulus, tail-flips were elicited using a 6 V a.c. electrical stimulus applied to the antennae (based on Webb, 1979). This stimulus repeatedly elicited the tail-flip response, and no side effects from the stimulus were observed. Tail-flip sequences were selected for analysis on the basis of visual confirmation that the stimulus contacted the animal before the tail-flip was initiated, the animal completely left the substratum during the tail-flip and the animal traveled approximately parallel to the long axis of the tank and did not contact the tank walls during the tail-flip. Four tail-flips were digitized for each animal.

Video images were digitized using a Panasonic AG-7355 video recorder and imported into a Macintosh Quadra 700 using MediaGrabber 2.2 software (RasterOps Corp.). Using the NIH Image program (developed at the US National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/), four points on the image were followed through time: the anterior and posterior margins of the cephalothorax, the tip of the uropods and a reference point on the background grid (Fig. 2). Tail-flip duration was defined as the time from the initiation to the end of tail closure. The \(x\) and \(z\) coordinates of the \(C_m\) and the angle of the body to the horizon (\(\theta\)) were calculated on the basis of the positions of the anterior and posterior margin of the cephalothorax. The position of the \(C_m\) was used for calculations of body translational velocity and acceleration; \(\theta\) was used to determine maximum rotation of the body and for calculations of body angular velocity and acceleration.

The calculation of velocity and acceleration data from a time series of position data collected by image analysis is a common method (e.g. Daniel and Meyhöfer, 1989; Biewener and Full, 1992), but its utility has been questioned. Acceleration values calculated from position data are susceptible to high levels of noise that is inherent in digitized position data and originates from sources including camera vibrations and digitizing errors (Biewener and Full, 1992). More accurate data would have been collected with implanted accelerometers (e.g. Harper and Blake, 1989), but their use was precluded by the small size of several of the animals used in this study (1–10 g \(M_b\)). To resolve this problem, we processed the position data to remove the high-frequency noise. Data were imported into Acknowledge software (BIOPAC Systems), and a zero-lag Blackman digital filter was applied. The duration of the event was considered to represent the period of its fundamental frequency (\(f_o\)); the filter frequency for each data set equaled 3.33\(f_o\).

Velocity was calculated as:

\[
U_t = (x_{t+i} - x_{t-i})/(2\Delta t),
\]

where \(U_t\) is velocity at time \(t\) and \(x_{t+i}\) or \(x_{t-i}\) is the position at time \(t+i\) or \(t-i\), respectively (Winter, 1989). Acceleration was calculated by substituting \(U\) for \(x\) in equation 1.

Statistical analyses were conducted using Statgraphics software. Unless stated otherwise, statistical significance was established using a probability value of 0.05. As described in detail for the morphology data, the log\(_{10}\)-transformed data were analyzed using OLS linear regression models, but the data are presented untransformed and plotted on logarithmic scales for ease of viewing.

Variation within individuals was accounted for by averaging the data from four tail-flip events and basing the regression analysis on these average values. Individuals of very similar size were only available for animals weighing less than 5 g \(M_b\) because these animals were raised from larvae on site. Therefore, as an index of variation among individuals, the kinematics and performance of three animals of similar size (1.22 g, 1.30 g and 1.39 g \(M_b\)) were compared.
Results

Morphology

External morphological measurements closely approximated isometric growth (Fig. 3; Table 1), although the slopes of approximately half the variables examined were statistically different from the isometric value of 0.333 (Table 1). The use of the OLS regression model was supported by the fact that the RMA slope values were similar to the OLS slope values (RMA slope = OLS slope/OLS correlation coefficients; Table 1). The characteristics of males, females and juveniles in relation to $M_b$ were similar (Fig. 3; Table 1). Subtle sexual dimorphisms were seen because the $W_A$ and $L_U$ of females were relatively greater than those of males.

Abdominal muscle was 22±4 % (mean ± s.d.) of $M_b$, of this, 85% was flexor muscle ($M_F$) and 15% was extensor muscle ($M_E$; Table 1). The scaling variables of the muscle masses were not significantly different (Fig. 4; Table 1). The slope of the regression model fitted to the $M_E$ data was not significantly different from the isometric value of 1. The slope of the regression model fitted to the $M_F$ data was not significantly different from 1 at a $P$ value of 0.02.

The position of $C_m$ was similar in animals from 12 g to 800 g $M_b$, which was supported by the other morphometric data indicating isometric growth. The average position of the $C_m$ was between the third and fourth walking leg and just ventral to the midline of the rostrum, or 33±3 % of rostral length and 55±2 % of rostral height (Fig. 2). The change in the position of the $C_m$ during the swimming event was 5 % or less of the body length and 10 % or less of the rostral height of each animal. On the basis of the consistent placement of the $C_m$ over almost two orders of magnitude of $M_b$ and the small change in the position of the $C_m$ during the tail-flip, an average position for the $C_m$ calculated from these data was used for the analysis of translational distance, velocity and acceleration of the body.

Kinematics and performance

The following sequence of events occurred during the tail-flips: (1) the tail adducted towards the abdomen and moved through an angle of 90° to the body axis; (2) the body began to rotate, and the legs left the substratum; and (3) the tail closed against the body. Animals characteristically initiated the tail-flip with the tail fully extended, and the position of the tail at the initiation of the tail-flip did not differ significantly with body size (Fig. 5).

There were no statistically significant differences between the kinematic and performance variables of the three individuals of similar $M_b$ because the variation in repeated events of a single individual was similar to the variation among individuals. This indicated that the mean value from single animals was representative of data for animals of that $M_b$. Thus, the data presented here for scaling relationships
Table 1. *Parameters of the linear regression models fitted to the scaling data of Panulirus interruptus*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Group</th>
<th>Body mass range (g)</th>
<th>OLS slope ± s.e.m.</th>
<th>OLS intercept (log_{10} y) ± s.e.m.</th>
<th>OLS r²</th>
<th>OLS S.E.M. of predicted intercept</th>
<th>Significantly different from slope</th>
<th>RMA slope (OLS slope/r)</th>
<th>Significance</th>
<th>Slope</th>
<th>y-intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_B$</td>
<td>All</td>
<td>21.4–516.0 (mm)</td>
<td>0.157–3650</td>
<td>0.33±0.001</td>
<td>1.53±0.003</td>
<td>0.996</td>
<td>0.019</td>
<td>NS</td>
<td>0.334</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_C$</td>
<td>All</td>
<td>8.8–208.0 (mm)</td>
<td>0.157–3650</td>
<td>0.33±0.003</td>
<td>1.52±0.003</td>
<td>0.996</td>
<td>0.022</td>
<td>NS</td>
<td>0.334</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$W_C$</td>
<td>m</td>
<td>28.9–135.0 (mm)</td>
<td>52–3650</td>
<td>0.350±0.010</td>
<td>0.854±0.010</td>
<td>0.988</td>
<td>0.016</td>
<td>S</td>
<td>0.352</td>
<td>m&gt;j</td>
<td></td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>28.6–129.0 (mm)</td>
<td>53–3198</td>
<td>0.348±0.015</td>
<td>0.857±0.015</td>
<td>0.972</td>
<td>0.023</td>
<td>NS</td>
<td>0.353</td>
<td>f&gt;j</td>
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</tr>
<tr>
<td></td>
<td>j</td>
<td>5.0–21.2 (mm)</td>
<td>157–42</td>
<td>0.294±0.009</td>
<td>0.907±0.009</td>
<td>0.955</td>
<td>0.042</td>
<td>S</td>
<td>0.301</td>
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<td></td>
<td>All</td>
<td>5.0–135.0 (mm)</td>
<td>0.157–3650</td>
<td>0.33±0.002</td>
<td>0.894±0.002</td>
<td>0.992</td>
<td>0.026</td>
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<tr>
<td>$H_C$</td>
<td>All</td>
<td>7.7–123.0 (mm)</td>
<td>1.22–3650</td>
<td>0.33±0.002</td>
<td>0.843±0.005</td>
<td>0.996</td>
<td>0.041</td>
<td>S</td>
<td>0.344</td>
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<td></td>
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<tr>
<td>$L_A$</td>
<td>m</td>
<td>51.3–207.0 (mm)</td>
<td>52–3650</td>
<td>0.324±0.002</td>
<td>1.16±0.006</td>
<td>0.996</td>
<td>0.009</td>
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<td>0.325</td>
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<td></td>
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<tr>
<td></td>
<td>f</td>
<td>51.8–204.0 (mm)</td>
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<td>0.336±0.004</td>
<td>1.14±0.011</td>
<td>0.986</td>
<td>0.016</td>
<td>NS</td>
<td>0.339</td>
<td>f&gt;j</td>
<td></td>
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<tr>
<td></td>
<td>j</td>
<td>8.6–45.0 (mm)</td>
<td>157–42</td>
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<td>1.11±0.008</td>
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<td>NS</td>
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<tr>
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<td>All</td>
<td>8.6–207.0 (mm)</td>
<td>0.157–3650</td>
<td>0.34±0.002</td>
<td>1.12±0.002</td>
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<td>0.025</td>
<td>S</td>
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<td>$W_A$</td>
<td>m</td>
<td>26.5–114.0 (mm)</td>
<td>52–3650</td>
<td>0.325±0.004</td>
<td>0.875±0.010</td>
<td>0.986</td>
<td>0.016</td>
<td>S</td>
<td>0.327</td>
<td>f&gt;m</td>
<td>m&gt;f</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>26.6–122.0 (mm)</td>
<td>53–3198</td>
<td>0.351±0.005</td>
<td>0.827±0.012</td>
<td>0.984</td>
<td>0.017</td>
<td>S</td>
<td>0.354</td>
<td>f&gt;j</td>
<td>f&gt;j</td>
</tr>
<tr>
<td></td>
<td>j</td>
<td>4.3–23.3 (mm)</td>
<td>157–42</td>
<td>0.330±0.009</td>
<td>0.835±0.006</td>
<td>0.984</td>
<td>0.027</td>
<td>NS</td>
<td>0.333</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>All</td>
<td>4.3–122.0 (mm)</td>
<td>0.157–3650</td>
<td>0.345±0.002</td>
<td>0.836±0.004</td>
<td>0.994</td>
<td>0.021</td>
<td>S</td>
<td>0.346</td>
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<tr>
<td>$H_A$</td>
<td>All</td>
<td>4.4–65.0 (mm)</td>
<td>1.3–3650</td>
<td>0.338±0.006</td>
<td>0.628±0.013</td>
<td>0.974</td>
<td>0.038</td>
<td>NS</td>
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<tr>
<td>$L_U$</td>
<td>m</td>
<td>23.1–101.0 (mm)</td>
<td>52–3650</td>
<td>0.286±0.006</td>
<td>0.934±0.014</td>
<td>0.970</td>
<td>0.021</td>
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<td>0.290</td>
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<td>f&gt;m</td>
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<td></td>
<td>f</td>
<td>76.9–119.0 (mm)</td>
<td>53–3198</td>
<td>0.337±0.007</td>
<td>0.838±0.017</td>
<td>0.964</td>
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<td></td>
<td>j</td>
<td>4.0–23.6 (mm)</td>
<td>157–42</td>
<td>0.329±0.012</td>
<td>0.855±0.009</td>
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<td>0.045</td>
<td>NS</td>
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<tr>
<td></td>
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<td>4.0–101.0 (mm)</td>
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<tr>
<td>$W_U$</td>
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<td>19.1–296.0 (g)</td>
<td>1.22–3198</td>
<td>0.306±0.008</td>
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<td>10.4–154.0 (g)</td>
<td>52–700</td>
<td>0.915±0.039</td>
<td>−0.450±0.094</td>
<td>0.958</td>
<td>0.054</td>
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<td>$M_E$</td>
<td>All</td>
<td>1.8–23.0 (g)</td>
<td>52–700</td>
<td>0.904±0.061</td>
<td>−1.240±0.146</td>
<td>0.908</td>
<td>0.089</td>
<td>NS</td>
<td>0.949</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_F$</td>
<td>All</td>
<td>8.6–131.0 (g)</td>
<td>52–700</td>
<td>0.913±0.039</td>
<td>−0.519±0.092</td>
<td>0.962</td>
<td>0.056</td>
<td>S</td>
<td>0.931</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

If there was no significant difference between the values for males (m), females (f) and juveniles (j), one regression model was fitted to all the data and the variables of that model are presented here.

The breakdown of the morphological variables showing significant differences in slope or y intercept between sexes or ages is presented ($P<0.05$).

$L_B$ is body length ($L_B=L_C+L_A+L_U$), $L_C$ is cephalothorax length, $W_C$ is cephalothorax width, $H_C$ is cephalothorax height, $L_A$ is abdomen length, $W_A$ is abdomen width, $H_A$ is abdomen height, $L_U$ is uropod length, $W_U$ is uropod width, $M_T$ is total muscle mass, $M_E$ is extensor muscle mass, $M_F$ is flexor muscle mass, OLS is ordinary least-squares regression, NS is not significantly different, S is significantly different, and RMA is reduced-major-axis regression model.

*N* varies because all variables could not be measured for each individual.

*S.E.M.* of the estimate is the s.d. of the residuals, which can be used to construct prediction limits for new observations.

**Predicted slope is 0.33 for length variables and 1.00 for mass variables.**
Scaling of lobster escape response

represent the average values of multiple tail-flips by single individuals.

The kinematic and performance results are summarized in Table 2. In general, the predicted scaling relationships for tail-flip duration, tail distance and velocity, and the translational distance and velocity variables were supported by the data, while tail and translational acceleration variables were not. In contrast, predictions for rotation and rotational velocity were not supported, while the rotational acceleration data matched the predicted value.

Mean values of tail-flip duration for a given individual varied from 0.034 to 0.196 s; and tail-flip duration scaled as $M^{0.22}$, which was significantly different from the predicted relationship of $M^{0.33}$ (Fig. 6; Table 2).

Table 2. Characteristics of the regression models of $y = aM^c$ which were fitted to kinematic and performance data

<table>
<thead>
<tr>
<th>Figure number</th>
<th>Variable</th>
<th>Predicted OLS slope, $c$</th>
<th>Calculated OLS slope ± S.E.M.</th>
<th>log$_{10}$ of c ± S.E.M.</th>
<th>OLS $r^2$</th>
<th>OLS S.E.M. of estimate</th>
<th>RMA slope (OLS slope/r)</th>
<th>Variable range</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>Flip duration (s)</td>
<td>0.33</td>
<td>0.22±0.038</td>
<td>−1.51±0.07</td>
<td>0.74</td>
<td>0.114</td>
<td>0.25</td>
<td>0.034–0.196</td>
</tr>
<tr>
<td>7a</td>
<td>Tail $d$ (m)</td>
<td>0.33</td>
<td>0.25±0.014</td>
<td>−1.55±0.025</td>
<td>0.97</td>
<td>0.041</td>
<td>0.26</td>
<td>0.030–0.145</td>
</tr>
<tr>
<td>7b</td>
<td>Tail $U$ (m s$^{-1}$)</td>
<td>0</td>
<td>0**</td>
<td>0</td>
<td>0.01</td>
<td>0.006</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>7c</td>
<td>Tail $a$ (m s$^{-2}$)</td>
<td>−0.33</td>
<td>0</td>
<td>−1.66±0.026</td>
<td>0.98</td>
<td>0.042</td>
<td>0.28</td>
<td>0.022–0.160</td>
</tr>
<tr>
<td>8a</td>
<td>Translational $d$ (m)</td>
<td>0.33</td>
<td>0.28±0.015</td>
<td>−1.66±0.026</td>
<td>0.98</td>
<td>0.042</td>
<td>0.28</td>
<td>0.022–0.160</td>
</tr>
<tr>
<td>8b</td>
<td>Translational $U$ (m s$^{-1}$)</td>
<td>0</td>
<td>0**</td>
<td>0</td>
<td>0.01</td>
<td>0.006</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>8c</td>
<td>Translational $a$ (m s$^{-2}$)</td>
<td>−0.33</td>
<td>0</td>
<td>−1.66±0.026</td>
<td>0.98</td>
<td>0.042</td>
<td>0.28</td>
<td>0.022–0.160</td>
</tr>
<tr>
<td>9a</td>
<td>Rotation (degrees)</td>
<td>0</td>
<td>0.08±0.031</td>
<td>1.54±0.053</td>
<td>0.44</td>
<td>0.085</td>
<td>0.12</td>
<td>32–67</td>
</tr>
<tr>
<td>9b</td>
<td>$\omega$ (degrees s$^{-1}$)</td>
<td>−0.33</td>
<td>0</td>
<td>0</td>
<td>0.01</td>
<td>0.006</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>9c</td>
<td>$\alpha$ (degrees s$^{-2}$)</td>
<td>−0.33</td>
<td>−0.28±0.084**</td>
<td>5.34±0.144</td>
<td>0.58</td>
<td>0.146</td>
<td>−0.37</td>
<td>217,755–270,601</td>
</tr>
</tbody>
</table>

d is distance, $U$ is velocity, $a$ is acceleration, $\omega$ is rotational velocity, $\alpha$ is rotational acceleration, OLS is ordinary least-squares regression, S.E.M. is standard error of the mean and RMA is reduced-major-axis regression.

* S.E.M. of the estimate is the S.D. of the residuals, which can be used to construct prediction limits for new observations.

** Slope is not significantly different from the predicted value.
Maximal values for the distance moved by the tail, a function of abdomen length and the preflip stance, ranged from 0.030 to 0.145 m and increased as $M_b^{0.25}$, which was significantly different from the predicted relationship of $M_b^{0.33}$ (Fig. 7A). Maximal tail velocities varied from 0.75 to 2.5 m s$^{-1}$ (Fig. 7B) and were independent of size, as predicted. Maximal tail accelerations varied from 25 to 165 m s$^{-2}$ (Fig. 7C) and were independent of size, which did not support the predicted relationship of $M_b^{-0.33}$.

The distance moved by the body ranged from 0.02 to 0.16 m and increased as $M_b^{0.28}$, which was significantly different from the predicted relationship of $M_b^{0.33}$ (Fig. 8A). Distance values ranged from 0.41 to 0.65 body lengths ($BL$) and decreased slightly with increased size (Fig. 8A). Maximal translational velocities ranged from 0.6 to 1.6 m s$^{-1}$ (Fig. 8B) and were independent of body size, as predicted. Relative to body length, maximum velocity values ranged from 4.3 to 24.6 $BL$ s$^{-1}$ and decreased with increased size (Fig. 8B). Maximum translational acceleration values ranged from 22 to 79 m s$^{-2}$ (Fig. 8C) and were independent of body size, which did not support the predicted relationship of $M_b^{-0.33}$. Relative to body length, maximal acceleration values ranged from 49 to 1356 $BL$ s$^{-2}$ and decreased with increased size.

Maximum rotation during a tail-flip ranged from 32 to 67° (Fig. 9A) and increased slightly as $M_b^{0.08}$, which did not support the predicted mass-independent relationship (Table 2). Maximal $\omega$ values ranged from approximately 950 to 2700° s$^{-1}$ (Fig. 9B) and were independent of $M_b$, which did not support the predicted relationship of $M_b^{-0.33}$. Maximal $\alpha$ values ranged from approximately 2.1×$10^4$ to 2.7×$10^5$°s$^{-2}$ and decreased as $M_b^{-0.28}$, which was not significantly different from the predicted value of $M_b^{-0.33}$ (Fig. 9C).

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**Fig. 8.** Translational body distance (A), maximum velocity (B) and maximum acceleration (C) in relation to body mass. $BL$ is body length. Symbols represent means ± s.d. ($N=4$). The solid lines represent the statistically significant least-squares power regression equations of the measurements. Hypothesized scaling relationships (dotted lines) were supported for distance (A, predicted slope 0.33, slope of the data 0.28, $r^2=0.98$) and velocity (B, predicted to be independent of $M_b$, but not for acceleration (C, predicted slope $-0.33$). Relative to body length, distance, maximum velocity and maximum acceleration decreased ($r^2=0.58$, 0.84 and 0.71, respectively).

**Fig. 9.** Maximum rotation (A), maximum rotational velocity ($\omega$, B) and maximum rotational acceleration ($\alpha$, C) in relation to body mass ($M_b$). Symbols represent means ± s.d. ($N=4$) of the measured values; the solid lines represent the calculated least-squares power regressions of body rotation and $\alpha$ on body mass ($r^2=0.44$ and 0.58, respectively). The predicted scaling relationships (dotted lines) for rotation (independent of body size) and $\omega$ ($M_b^{-0.33}$) were not supported, but the scaling of $\alpha$ ($M_b^{-0.28}$) was not significantly different from the predicted slope of $M_b^{-0.33}$.
Discussion
Scaling of morphology

The isometric growth pattern of *Panulirus interruptus* validates the use of scaling predictions based on isometric growth for this locomotory system, but did not support the hypothesis that allometric growth patterns contributed to tail-flip performance at large body size. The isometric growth of *Panulirus interruptus* contrasts with crustacean species which show either allometric growth during the post-larval stages, e.g. *Homarus americanus* (Lang et al., 1977), or a significant change in body proportions at sexual maturity (e.g. the abrupt increase in the abdomen width of the brachyuran *Corystes cassivelaunus* after the ‘puberty molt’; Hartnoll, 1985). The subtle sexual dimorphisms of *Panulirus interruptus* (the relatively larger WA and LU of females compared with males) is a common pattern for crustaceans. Allometry of the female abdomen is generally considered to be related to increased surface area for the external brooding of eggs (Kanciruk, 1980). Although the relatively larger abdomen and uropods of females could contribute to increased tail-flip performance compared with males, the effects on performance would be limited because the dimorphism of these characteristics is small.

Compared with other crustaceans, *Panulirus interruptus* has an intermediate amount of its body mass devoted to abdominal muscle (22% versus approximately 40% for the shrimp *Pandalus danae*, Table 3). The 22% of body mass devoted to escape muscle in *Panulirus interruptus* is lower than the values for cephalopods (30–45%), which use a jet escape response, but similar to that of teleost fish (teleosts are 30–55% muscle but only half of that is in use at a given time; Webb, 1978).

Scaling of tail-flip kinematics and performance

The general scaling relationships for the kinematic variables of tail-flip duration, tail distance, maximum velocity and maximum acceleration were predicted by the mechanics of the system three out of four times. For example, tail-flip duration increased as $M_b^{0.22}$. Since the pre-flip stance was independent of $M_b$, the increase in duration was the result of the tail traveling longer distances with similar maximal velocities. Brown shrimps *Crangon crangon* also increase tail-flip duration with growth (Arnott et al., 1998); increases in the time course of a kinematic event with growth are common in the scaling of locomotion (e.g. Marsh, 1988; Katz and Gosline, 1993) and feeding (Richard and Wainwright, 1995).

Increased tail-flip duration was predicted here on the basis of a decrease in muscle contraction frequency of $M_b^{-0.33}$ (Hill, 1950; O’Reilly et al., 1993). Although our kinematic data showed that trend, it is problematic to conclude anything more specific about the abdominal muscle than that its shortening frequency is likely to decrease with growth because the connection between the scaling of kinematics and muscle performance is not necessarily direct. For example, James and Johnston (1998) determined that, for fast-starts by the shorthorn sculpin *Myoxocephalus scorpius*, the rostral muscle shortening duration scaled as $BL^{1.42}$, but tail-beat duration scaled as $BL^{0.54}$; these slopes were significantly different. Thus, the scaling of kinematics indicated the sign but not the magnitude of the scaling of muscle properties.

In general, the slowing of the rate of skeletal muscle contraction with increased size has been demonstrated for vertebrates by several investigators (e.g. Altringham and Johnston, 1990; Rome et al., 1990; Anderson and Johnston, 1992; Altringham et al., 1996); however, the change in shortening velocity for fast muscle may not be large. Data from Rome et al. (1990) on small and large mammals indicated that the scaling of maximum shortening velocity for fast muscle ($M_b^{0.08}$) was significantly different from that for slow muscle ($M_b^{0.18}$). Rome et al. (1990) suggested that the difference in slopes reflects the maintenance of a high mechanical power output in fast muscle and of a high efficiency in slow muscle. Supporting this hypothesis is the scaling of optimal cycle frequency ($f_{\text{opt}}$) for maximum power output in the fast and slow muscles of the frog *Xenopus laevis* ($M_b^{0.07}$ and $M_b^{0.23}$, respectively; Altringham et al., 1996). The scaling of flagellar beat frequency of the green crab *Carcinus maenas* as $M_b^{0.07}$ implies that the $f_{\text{opt}}$ of flagellar muscle scales similarly (Josephson and Stokes, 1994) and also supports the hypothesis of Rome et al. (1990). These data suggest that fast muscle largely maintains its contraction frequency and that there may be a large discrepancy between the scaling of tail-flip duration of *Panulirus interruptus* and the scaling of the abdominal muscle $f_{\text{opt}}$. However, Johnson et al. (1993) found that fast muscle frequency and limb cycle frequency in the lizard *Dipsosaurus dorsalis* scaled as $M_b^{-0.24}$, indicating a close match between the scaling of kinematics and muscle characteristics. This variability in results limits our ability to infer muscle frequency characteristics from the present kinematic data.

An alternative explanation for the increased event duration with growth seen here is that it reflects a physiological limit to peak muscle stress. As discussed above, if growth is isometric, muscle cross-sectional area (and therefore force) scales as $M_b^{2/3}$, but the force demands on the muscle for this acceleration-based motion scale as $M_b^1$. The dichotomy between the scaling of muscle force production and the magnitude of force required for sustained performance has led to suggestions that size limits escape performance in shrimps (Daniel and Meyhofüer, 1989) and scallops (Cheng and DeMont, 1996). Increased event duration is one way round this limitation because it decreases the force demands on the muscle. Daniel and Meyhofüer (1989) calculated that increases in tail-flip duration cause exponential decreases in the maximum muscle stress required to sustain performance. The decreased load with increased duration is probably complemented by increased force production by the muscle because of the inverse force–velocity relationship of muscle (Hill, 1938).

The scaling of the tail acceleration of *Panulirus interruptus* was predicted to decrease as $M_b^{-0.33}$, but it was independent of body size. This variable is key for determining the scaling of
### Table 3. Comparison of the available data on crustacean tail-flip locomotion

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>$L_B$ (m)</th>
<th>$L_C$ (m)</th>
<th>$M_b$ (g)</th>
<th>Image</th>
<th>Tail-flip duration (s)</th>
<th>Maximum Distance (m, BL)</th>
<th>Maximum Velocity (m s$^{-1}$, BL s$^{-1}$)</th>
<th>Maximum Acceleration (m s$^{-2}$, BL s$^{-2}$)</th>
<th>Maximum Rotation (degrees)</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Crangon</em> crangon</td>
<td>Brown shrimp</td>
<td>0.11–0.69</td>
<td>–</td>
<td>0.013–4.550</td>
<td>–</td>
<td>Visual 200</td>
<td>0.01–0.12 2.8</td>
<td>0.59–0.31 25–60</td>
<td>–</td>
<td>–</td>
<td>Arnott et al. (1998)</td>
</tr>
<tr>
<td><em>Homarus</em> americanus</td>
<td>American lobster</td>
<td>–</td>
<td>0.026–0.035</td>
<td>13.4</td>
<td>Visual 60</td>
<td>0.17 (includes tail extension)</td>
<td>0.065 0.5** 3.5*</td>
<td>–</td>
<td>–</td>
<td></td>
<td>Cromarty et al. (1991)</td>
</tr>
<tr>
<td><em>Nephrops</em> norvegicus</td>
<td>Norway lobster</td>
<td>–</td>
<td>0.025–0.064</td>
<td>–</td>
<td>Tactile 60</td>
<td>–</td>
<td>0.019 0.5** –</td>
<td>–</td>
<td>–</td>
<td>Newland et al. (1988)</td>
<td></td>
</tr>
<tr>
<td><em>Orconectes</em> virilis</td>
<td>Crayfish</td>
<td>0.08</td>
<td>–</td>
<td>18</td>
<td>Electrical 250</td>
<td>0.044 0.031 0.87 50.9 636</td>
<td>0.019 0.5** –</td>
<td>–</td>
<td>–</td>
<td>Webb (1979)</td>
<td></td>
</tr>
<tr>
<td><em>Pandalus</em> danae</td>
<td>Dock shrimp</td>
<td>0.07</td>
<td>–</td>
<td>–</td>
<td>Tactile 200 or 500</td>
<td>0.030 0.05 0.7 0.015 3 43 150 2140 75</td>
<td>–</td>
<td>–</td>
<td>Daniel and Meyhöfer (1989) Meyhöfer and Daniel (1990)***</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Panulirus</em> interruptus</td>
<td>Spiny lobster</td>
<td>0.035–0.338</td>
<td>0.013–0.131</td>
<td>0.3–1000</td>
<td>Electrical 60, 250 0.034–0.196</td>
<td>0.022–0.160 0.6–1.6 16–80 30–1470 40</td>
<td>–</td>
<td>–</td>
<td>Present study</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Scyllarides</em> latus</td>
<td>Slipper lobster</td>
<td>0.22–0.31</td>
<td>–</td>
<td>–</td>
<td>Tactile 25</td>
<td>–</td>
<td>1 3.74** –</td>
<td>–</td>
<td>–</td>
<td>Spanier et al. (1991)</td>
<td></td>
</tr>
</tbody>
</table>

The morphological data shown for *Panulirus interruptus* are for the size range of the individuals for which kinematic data were collected; the kinematic data for *P. interruptus* are the range of the mean values for each variable.

$L_B$ is body length, $L_C$ is cephalothorax length, $M_b$ is body mass and $BL$ is body lengths.

*Data were calculated to reflect relative values, which limits the utility of the comparison.

**Average values calculated over the duration of a tail-flip.
tail-flip performance because added-mass forces dominate thrust production, giving a direct relationship between tail acceleration and force production (Daniel and Meyhöfer, 1989). Thus, the size-independence of tail acceleration suggested that tail-flip performance would be preserved in larger animals.

Our data indicated that tail-flip performance was preserved in larger animals. Relative to body size, distance increased, velocity was independent and, surprisingly, acceleration was independent. Eight out of ten of the animals outperformed the prediction. Arnott et al. (1998) also found that maximum velocity and acceleration of the body were independent of size for tail-flips by the brown shrimp. Sustained maximum velocity and acceleration performance have also been documented for fast-starts in fish by Webb (1976) and Domenici and Blake (1993). The sustained acceleration performance of fishes during growth was attributed by Webb and Johnsrude (1988) to the summation of muscle switches.

The sustained acceleration performance of Panulirus interruptus over a three-orders-of-magnitude increase in $M_b$ is probably at least partially attributable to the increased tail-flip duration. As discussed above, increased tail-flip duration is likely to increase muscle force production, because of decreased contraction velocity, and to result in exponential decreases in force demands on the muscle because of decreased added mass. The sustained performance may also be attributable to increased muscle force production relative to body size because of relatively increased muscle cross-sectional area (e.g. the ungulate plantaris muscle; Pollock and Shadwick, 1994). This is unlikely with P. interruptus, however, because the abdomen was packed with muscle at all body sizes, and the abdominal cross-sectional area and muscle mass scaled isometrically, so a relative increase in muscle cross-sectional area would depend on a relative decrease in muscle fiber length. Alternatively, maximum muscle performance relative to body size could increase because of changes in muscle fiber characteristics. For example, Somero and Childress (1990) determined that the strongly positive scaling of glycolytic enzyme activities in the white muscle of pelagic fish allows larger fishes to exhibit greater burst performance. Changes in myosin light or heavy chain composition or troponin-T isoforms with size could contribute to changes in muscle performance (James et al., 1998). The scaling of lobster abdominal muscle composition and performance remains to be investigated, but it is known that the developmental dynamics of some crustacean muscle includes continuous fiber growth and fiber-type transformation (Mellon, 1992).

On the basis of the translational data, it appears that the scaling predictions for acceleratory behavior are simply insufficient for describing this system. However, in terms of body rotational acceleration, the prediction that $\alpha$ would scale as $M_b^{0.33}$ was supported, with $\alpha \propto M_b^{0.28}$. A decrease in $\alpha$ with increased size has also been documented for brown shrimp (Arnott et al., 1998). In the case of Panulirus interruptus, the scaling of $\alpha$ was not due to a change in pre-flip stance (and thus to a change in the moment arm of the force). Thus, these data suggest that the torque produced by the animal scaled with a mass exponent greater than 1.

Torque is an unavoidable component of the tail-flip because force is produced at some distance from the animal’s $C_m$. Daniel and Meyhöfer (1989) predicted that there is a trade-off between the translational and rotational moments generated by the animal, which is based on the ratio of the length of the tail ($L_T$) to the length of the cephalothorax ($L_C$), and that the optimum $L_T/L_C$ ratio for maximum translation during the tail-flip was 1. Panulirus interruptus has an $L_T/L_C$ ratio of $1.5\pm0.07$ (mean ± s.d., $N=222$), which suggests that rotation should be difficult for a spiny lobster of any size. Despite this potential problem in morphological design, the maximum rotation of Panulirus interruptus was almost half that reported for Pandalus danae, in which $L_T/L_C$ is 1.3 ($M_b$ 1–10 g, $N=22$; Daniel and Meyhöfer, 1989). This difference may reflect counterbalancing by Panulirus interruptus using other morphological structures. For example, the legs and the first antennae of Panulirus interruptus extend anterior to the $C_m$ during the tail-flip, are robust, and are under muscular control. They may be used to counterbalance body rotation during the tail-flip, as in scyllarid lobsters that use antennal plates to control rotation during the tail-flip (Jacklyn and Ritz, 1986).

Comparison with other crustaceans

The values for tail-flip duration, distance and velocity for the larger specimens of Panulirus interruptus are comparable with those reported previously for a variety of crustaceans of similar size (Table 3) including the American lobster Homarus americanus (Cromarty et al., 1991), the Norway lobster Nephrops norvegicus (Newland et al., 1992) and the slipper lobster Scyllarides latus (Spanier et al., 1991). Values for the smaller individuals of Panulirus interruptus are similar to those presented for the crayfish Orconectes virilis (Webb, 1979), the dock shrimp Pandalus danae (Daniel and Meyhöfer, 1989) and the brown shrimp Crangon cragon (Arnott et al., 1998).

One might expect that the presence of chelipeds would reduce tail-flip performance. Although Homarus americanus (Cromarty et al., 1991) achieves lower maximum velocities and accelerations than Panulirus interruptus, this comparison is limited by the fact the acceleration values for H. americanus were calculated to reflect relative differences between the animals and not absolute performance. Webb (1979) used similar methods to those described here to study crayfish (an electrical stimulus was used to elicit the tail-flips, and the images of position data were collected at 250 Hz). Compared with spiny lobsters of similar size, crayfish have a similar amount of body mass devoted to flexor muscle (16%), and the tail-flip duration, body distance, velocity and acceleration during a tail-flip are comparable. These data suggest that the size of the chelipeds relative to the body, rather than their presence or absence, is the important factor for tail-flip performance.

The complication of large claws affecting performance is avoided by comparing Panulirus interruptus with the shrimp
Pandalus danae (Daniel and Meyhöfer, 1989). Both Pandalus danae and Panulirus interruptus grow isometrically, but there are morphological differences between the species besides the $L_T:\text{LC}$ ratio that may affect tail-flip performance. The maximum uropod width of Panulirus interruptus during the tail-flip is approximately 15% larger than that of Pandalus danae; however, abdominal muscle mass is a greater proportion of $M_b$ in Pandalus danae (approximately 40%; Meyhöfer and Daniel, 1990) than in Panulirus interruptus (22%). Thus, although the lobster has a longer and wider tail for flipping, its tail carries a heavier load, and this load is probably only partially compensated for by the fact that these animals are moving through water.

The kinematic data clearly show that the dock shrimp outperform the lobster in tail-flipping (Table 3). Tail-flip durations for lobsters of any size are longer than those of the dock shrimp and, although both animals move a similar distance relative to their body length (approximately 0.7BL), the maximal velocities and accelerations for the shrimp were up to double those of the lobster. Thus, in terms of maximal velocity and acceleration, the escape response of Panulirus interruptus is inferior to that of Pandalus danae.

The relatively heavily armored body of Panulirus interruptus probably contributes to this difference in performance between the two animals. Other potential factors are body posture or stance, association with a substratum, the distribution pattern of muscle along the abdomen for mechanical advantage, and the contractile characteristics of the abdominal muscle. An interesting extension to this study and to that of Meyhöfer and Daniel (1990) would be the characterization of flexor and extensor muscle properties for a size range of individuals of Panulirus interruptus and of a superior tail-flip performer such as Pandalus danae. This would provide the first information on the scaling of muscle properties in marine invertebrates, which is the next step to understanding the ‘black box’ of muscle power for the tail-flip escape response in crustaceans.

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References


Scaling of lobster escape response


