Morphological analyses of pedal sole area and pedal waves were conducted for a range of speeds and body sizes in the abalone Haliotis kamtschatkana. The pedal sole of resting abalone increased in size disproportionately with animal volume (slope of log10-transformed data, $b_0=0.67$) and length ($b=2.51$; $b_0=2.0$). Pedal wave frequency increased linearly with speed, confirming that abalone increase speed by increasing the velocity of pedal waves. Total area of the pedal sole decreased by 2.1% for each shell length per minute increase in speed. Likewise, the area of the foot incorporated into pedal waves increased by 1.8% for each shell length per minute increase in speed. Together, these changes translated into a 50% decrease in the pedal sole area in contact with the substratum at a maximum escape speed of 15 shell lengths min$^{-1}$, relative to the pedal sole at rest. The amount of mucus secreted by resting animals during adhesion to the substratum increased isometrically with foot area (slope of log10-transformed data, $b=1.08$). The amount of mucus secreted during locomotion did not vary with speed, but was less than the amount needed for adhesion. We suggest that these morphological and physiological changes reduce the energy expenditure during locomotion. Cost of transport was investigated for a range of speeds and abalone sizes. The rate of oxygen consumption $V_{O_2}$ (in $\mu$L O$_2$ g$^{-1}$ h$^{-1}$) increased linearly with increasing absolute speed $v$ (in cm min$^{-1}$): $V_{O_2}=40.1+0.58v-0.15m$ ($r^2=0.35, P=0.04$), where $m$ is body mass (in g). Minimum cost of transport, calculated from the slope of absolute speed on $V_{O_2}$, was 20.3 J kg$^{-1}$ m$^{-1}$. Total cost of transport ($COT_T$) and net cost of transport ($COT_N$) were high at low speeds and decreased as speed increased, to minima of 86.0 J kg$^{-1}$ m$^{-1}$ and 29.7 J kg$^{-1}$ m$^{-1}$, respectively, at speeds measured in the respirometer. Log$_{10}$-transformation of both cost of transport and speed data yielded linear relationships with the following regression equations: log$_{10}$($COT_T$) = 3.35 – 0.90 log$_{10}$ – 0.21$log_{10} m$ ($r^2=0.89; P<0.006$) and log$_{10}$($COT_N$) = 2.29 – 0.69 log$_{10}$ – 0.09$log_{10} m$ ($r^2=0.48; P<0.006$), respectively.

Key words: cost of transport, pedal waves, locomotion, Haliotis kamtschatkana, Gastropoda, abalone.
can be increased by changing the length or amplitude of the pedal waves. Abalone increase their locomotory rate by increasing the velocity and, hence, the frequency, of their pedal waves (Voltzow, 1986), and there is no evidence in the literature that they change pedal wave length. Miller (1974) describes several gastropod species which dramatically increase pedal wave length in order to increase speed. For example, *Tegula funebralis* increases its wave length from approximately one-third of total foot length during normal locomotion to greater than half total foot length during escape. Conversely, *Calliostoma ligatum*, a species with waves similar in type and size to those of *Haliotis* spp., apparently does not change the size of its waves. Miller (1974), however, measured only the length of the waves; there may be other more subtle changes to wave area during rapid locomotion that could be measured.

In fact, characteristics of the escape response described above suggest that the wave morphology of *Haliotis* spp. does change during rapid locomotion. First, abalone differ from most other gastropods in that their pedal waves are lifted off the substratum as opposed to gliding across a mucus layer, and amplitude (the distance that the wave is lifted off the substratum) is known to increase with increasing velocity (Miller, 1974). One might expect that an increase in wave amplitude could increase speed since more propulsive force could be generated as the wave pushes off the substratum, but it may also decrease the energy needed for locomotion since, as the waves are lifted off the substratum, they travel over water instead of mucus. In this case, less force is required since water is less viscous than mucus. Second, at rapid escape velocities, abalone often lift up the middle portion of their foot, and the only part in contact with the substratum is a band along each side. Such a strategy, i.e. removing a portion of the foot from being able to produce waves which make contact with the ground and thus generate propulsive force, does not seem likely to contribute to an increase in speed. Rather, it seems designed purely for energy saving since, again, less force would need to be produced when more of the foot is traveling over water. Decreasing pedal surface area would also be energetically beneficial in that less mucus would need to be produced. Adhesive crawling involves the secretion of a thin layer of mucus from glands in the foot while the foot adhering to the glass surface. Wet mass (including shell) and shell length of the abalone were recorded.

Since abalone have body parts with very different densities (i.e. shell, viscera and muscle), the volume of the animal, rather than its wet mass, was used as a measure of abalone size for morphological comparison with foot area. Wet mass was converted to volume by deriving a relationship between mass and volume for *H. kamtschatkana*. Abalone (*N*=10; 67–111 mm shell length) were weighed in air and in sea water. Abalone volume (*V*) was calculated using the equation:

\[ V = \frac{m_a - m_w}{d_w}, \]

where *m*<sub>a</sub> is the mass of abalone in air, *m*<sub>w</sub> is the mass of abalone in sea water, and *d*<sub>w</sub> is the density of sea water (assumed to be 1.025 g cm<sup>-3</sup>).
Frequency of pedal waves

Wave frequency was compared with speed by counting the waves during periods (usually 20 s duration) in which abalone were moving at a constant speed. Pedal waves were video-taped as abalone (N=8; 66–75 mm shell length) traveled at different speeds across the side of a glass aquarium. A pedal wave is defined as a portion of the foot which is contracting, and is visible as a dark region moving across the pedal muscle from posterior to anterior (Fig. 1). A stopwatch within the camera recorded elapsed time onto the film so that a period of constant speed could be selected, and the number of waves traveling up the foot during that period was counted using the OPTIMAS digital analysis system (Bioscan, WA, USA).

Pedal area and pedal wave variables during locomotion

Abalone (N=8; 46–72 mm shell length) were video-taped as described above against a grid of 1 cm×1 cm markings placed along the side of the aquarium for size and distance reference. Speeds during periods of constant locomotion (five for each animal) were calculated, then a frame from each of these time periods was captured onto computer and measurements were made of the abalone’s foot. These measurements included total foot area, pedal wave area, foot length and foot width. Care was taken to analyze the same wave configuration for each animal. Specifically, the foot was analyzed when one wave on the right side of the foot was at the midpoint of the foot and the two waves on the left side were at the front and back of the foot (see Fig. 1).

Maximum speed

Abalone (N=10; 40–99 mm shell length) were placed individually in a large tank which had markers every 10 cm along its side. A live predatory seastar, Pycnopodia helianthoides (Brandt), was held behind the abalone to stimulate rapid escape locomotion. As the abalone traveled between markers, the seastar was continuously held behind the abalone to simulate a chase. The movement of the abalone was timed between the markers, and maximum absolute velocity was recorded along with animal shell length and wet mass.

Mucus secretion

The amount of mucus needed for an abalone to adhere to the substratum was determined by allowing individual abalone (N=16; 50–101 mm shell length) to attach to clean glass plates immersed in a tank continuously supplied with fresh sea water. Each abalone was then removed quickly from the plate using a spatula after it had been stationary for 10 min following adherence. This period was chosen because Davies (1993) found that stationary limpets stop producing mucus 10 min after attachment. It is probable that abalone cease to produce mucus much sooner since our observations suggest that they are able to attach to a surface faster than limpets and are difficult to remove from a surface only 30 s after being placed on it. The plate was then rinsed with distilled water to remove salt residues, and dried at 60 °C for 30 min. The dried mucus was carefully scraped from the plate and its carbon content determined using carbon analysis (NA-1500 Elemental Analyzer, Carlo Erba Strumentazione). Mass of carbon (µg) was converted to dry mass of mucus (µg) by assuming that gastropod pedal mucus is 24.5 % carbon (Peck et al. 1993).

Mucus secretion during locomotion was determined by inducing similarly sized abalone (N=7; 95–99 mm shell length; mean ± S.E.M. resting pedal area 42±4 cm²) to locomote over glass plates. Three clean 8 cm×31 cm glass plates were placed in series on glass bowls resting in the tank. An abalone was placed on the first plate and allowed to travel over the middle plate onto the third. The time taken to traverse the middle plate was recorded, the plate was removed, and the mucus collected as described above. This procedure was repeated until each abalone had traversed the middle plate at five different speeds with as wide a range of speed as possible. Locomotory rates ranged from 9.6 to 105.1 cm min⁻¹ for the seven animals. Trials for an individual abalone were at least 24 h apart.

Oxygen consumption and cost of transport

Abalone (N=29; 31–96 mm shell length) were placed individually in round, Perspex respirometry chambers (100, 450, 720 and 1850 ml) at 10 °C and were allowed to move freely. A shelf located 1 cm above the bottom of the chamber supported a plastic mesh screen, beneath which rotated a magnetic stir bar. The abalone often circled the respirometer, either on the wall or on the shelf protecting the stir bar. During these revolutions, speeds were measured by recording the time at which distance markers around the side of the respirometer were passed. Oxygen consumption was monitored continuously using a polarographic oxygen electrode connected to a computerized data-acquisition system (DATACAN, Sable Systems, Inc.). Since this system allowed the times between markers to be recorded, oxygen consumption during periods of known speeds could be calculated. Movement usually occurred within the first 15 min of a trial, and at no time did the oxygen partial pressure drop to below 75 % of saturation during the trial. Energy expenditure (J h⁻¹) was calculated from oxygen consumption (µl O₂ h⁻¹) by multiplying by an oxycalorific coefficient (Qox) of 21.10 ml µl O₂⁻¹. This represents an accepted value for the catabolism of carbohydrate (Elliot and Davison, 1975) and was chosen because most gastropods rely on glycogen stores for energy during activity (Carefoot, 1987).
Resting metabolic rates were determined for each abalone by measuring oxygen consumption during quiescent periods. If the abalone were active, resting oxygen consumptions were measured for at least 20 min after the activity bouts in order to ensure that there was no residual elevation of metabolic rate. Resting oxygen consumption was measured 1–3 times for each abalone, and the resting metabolic rate used to calculate net cost of transport for each animal was the average from the individual animal’s trials.

Minimum cost of transport for *H. kamtschatkana* was calculated from the slope of the regression of absolute speed on total oxygen consumption during locomotion (Taylor et al. 1970; Full et al. 1990). Total cost of transport was calculated for individual abalone for each period of known speed and energy consumption by dividing total mass-specific energy expenditure (J kg\(^{-1}\) h\(^{-1}\)) by absolute speed (m h\(^{-1}\)). Net cost of transport, or the transport costs above resting metabolic rate, was calculated by subtracting resting mass-specific oxygen consumption from total mass-specific oxygen consumption during locomotion for each abalone, then dividing by the speed at which that abalone had traveled. Net cost of transport represents the energy devoted solely to locomotion, which here includes any postural costs. This method of calculating net cost (as opposed to also subtracting out postural costs) was chosen since total oxygen consumption during locomotion and resting oxygen consumption were both measured directly for each animal, whereas the postural cost for locomoting abalone was calculated indirectly from the difference between average resting mass-specific oxygen consumption for all the animals and the y-intercept of the regression of speed on total oxygen consumption.

### Results

**Pedal morphology**

Log\(_{10}\)-transformed resting foot area increased linearly with \(\log_{10}(\text{volume})\) (Table 1). The slope of 0.83 is significantly higher than the predicted slope for isometry (\(b_0\)) of 0.67 (\(t=4.12;\ P<0.001\)). Likewise, \(\log_{10}(\text{foot area})\) increased allometrically with \(\log_{10}(\text{shell length})\) (\(t=3.75;\ P<0.002\)). This indicates that the sole of the foot grows disproportionately larger as abalone increase in size.

Pedal wave frequency increased linearly with speed for all abalone measured (\(N=8\)) (Fig. 2). For individual abalone, all speed (shell lengths min\(^{-1}\)) *versus* frequency (waves min\(^{-1}\)) regression lines were significant (all \(r>4.91;\ all P<0.04\)). The individual regression lines did not differ significantly from each other [\(F_{0.05(2),7.20}=0.44;\ P>0.5\]), so the regression lines were pooled and found to have a common slope (±S.E.M.) of 2.42±0.17. Thus, to increase speed by 1 shell length per minute, abalone generate 2.4 more waves per minute. However, this increase in frequency is not large enough to account for the increase in speed since, speed more than doubles for a twofold increase in frequency (Fig. 2). Therefore, step length (the distance a point on the foot travels during a step) must also increase with increasing speed. Step length was calculated at various speeds using the relationship: \(v=f\times L\), where \(v\) is speed (in shell lengths min\(^{-1}\)), \(f\) is frequency (in waves min\(^{-1}\)) and \(L\) is step length (in shell lengths wave\(^{-1}\)) and the regression equation for the pooled data of speed on wave frequency determined above: \(f=8.71(±0.68)+2.42(±0.17)v\) (Fig. 2). As expected, step length increases with increasing speed (Fig. 3).

Pedal morphology changed with speed such that less of the sole was in contact with the substratum at higher speeds. Total visible sole area decreased with increasing speed (Fig. 4A). Seven out of eight abalone analyzed decreased the area of their foot significantly as they increased speed (all \(r>2.36;\ all P<0.05\)). In these seven abalone, the decrease was linear, and none of the individual regression lines differed significantly from each other [\(F_{0.05(2),7.20}=2.22;\ P=0.07\)]. Their common regression line had a mean slope (±S.E.M.) of −0.021±0.008, indicating that pedal area decreased by 2.1 % for each shell length per minute increase in speed. In addition, the proportion of the total pedal area occupied by waves increased linearly and significantly with speed in all abalone analyzed (Fig. 4B; \(N=8\); all \(r>2.30;\ all P<0.05\)). The individual regression lines did not differ significantly from each other [\(F_{1(7.45)=1.17;\ P>0.25}\). They were

### Table 1. Morphometric relationships between shell length, foot area, abalone volume and mucus secretion for Haliotis kamtschatkana

<table>
<thead>
<tr>
<th>Relationship</th>
<th>(\log_{10}a)</th>
<th>(b)</th>
<th>(r^2)</th>
<th>(N)</th>
<th>Predicted slope for isometry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resting foot area ((\text{cm}^2)) <em>versus</em> abalone volume ((\text{cm}^3))</td>
<td>−0.11±0.07</td>
<td>0.83±0.04*</td>
<td>0.96</td>
<td>20</td>
<td>0.67</td>
</tr>
<tr>
<td>Resting foot area ((\text{cm}^2)) <em>versus</em> shell length ((\text{mm}))</td>
<td>−3.40±0.26</td>
<td>2.51±0.14*</td>
<td>0.95</td>
<td>20</td>
<td>2.0</td>
</tr>
<tr>
<td>Mucus secretion ((\mu\text{g})) <em>versus</em> resting foot area ((\text{cm}^2))</td>
<td>1.11±0.43</td>
<td>1.08±0.30</td>
<td>0.48</td>
<td>16</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Regression statistics are for the equation \(\log_{10}y = \log_{10}a + b\log_{10}x\).

*Indicates that the slope \(b\) differs significantly from the predicted slope for isometry, \(P<0.002\).

Values are means ± S.E.M.
pooled and found to have a common mean slope ($\pm$S.E.M.) of 0.018±0.005. Therefore, for each shell length per minute increase in speed, 1.8% more of the foot was incorporated into waves.

No significant trends were found for either foot width or foot length as a function of speed.

**Maximum speed**

The absolute maximum speed recorded was 113 cm min$^{-1}$ by a 99 mm abalone. This corresponds to a speed of 11.4 shell lengths min$^{-1}$. A smaller abalone (59 mm) achieved a speed of 14.7 shell lengths min$^{-1}$. Mean ($\pm$S.E.M.) maximal speed of the 10 abalone tested was 12.7±0.7 shell lengths min$^{-1}$.

**Mucus secretion**

Log$_{10}$-transformed mucus secretion (µg dry mucus) of stationary animals increased in direct proportion to log$_{10}$ (foot area) (cm$^2$) (Table 1). The slope of the regression line was not significantly different from 1.0 ($t$=0.28; $P>$0.5), the predicted slope for isometry. Since abalone foot area does not scale isometrically with volume ($b$=0.83), this means that larger abalone secrete relatively more mucus per unit body volume to adhere to the substratum than do smaller abalone.

None of the regressions of absolute speed (in cm min$^{-1}$) on the amount of mucus was significant ($N=7$; all $P>0.1$), so a mean mass of mucus secreted per centimeter traveled was calculated for each animal. Means ($\pm$S.E.M.) ranged from 2.0±0.4 to 10.0±1.3 µg dry mucus cm$^{-1}$, with a grand aggregate mean of 5.3±0.7 µg dry mucus cm$^{-1}$ ($N=35$).

**Oxygen consumption and cost of transport**

Total mass-specific rate of oxygen consumption ($V_{\text{O}_2}$) increased linearly with increasing absolute speed ($N=29$; $t$=2.19; $P=0.04$), rising by 0.58 µl $O_2$ g$^{-1}$ h$^{-1}$ for every 1 cm min$^{-1}$ increase in speed (Fig. 5). Total $V_{\text{O}_2}$ was also dependent upon mass ($b$=−0.15; $t$=2.59; $P=0.02$), decreasing with increasing abalone mass. The mean ($\pm$S.E.M.) $V_{\text{O}_2}$ of resting abalone (20.7±1.7 µl $O_2$ g$^{-1}$ h$^{-1}$) was nearly half the value of the y-intercept of the line relating $V_{\text{O}_2}$ to speed (40.1±4.5 µl $O_2$ g$^{-1}$ h$^{-1}$) (Fig. 5). The difference of 19.4 µl $O_2$ g$^{-1}$ h$^{-1}$ is likely to represent a ‘postural effect’ of locomotion for crawling abalone.

The minimum cost of transport, calculated from the slope of absolute speed (in m h$^{-1}$) versus $V_{\text{O}_2}$, for $H$. kamtschatkana in this study is 20.3 kg$^{-1}$ m$^{-1}$ (slope of $V_{\text{O}_2}$ versus speed regression line is 0.96 µl $O_2$ g$^{-1}$ m$^{-1}$ when speed is in m h$^{-1}$). Total cost of transport (total amount of energy needed to transport a unit body mass over a unit distance) and net cost of transport (energy above resting metabolism required for transport, here including postural costs) calculated for individual animals locomoting at a variety of speeds (Fig. 6) decreased to minima of 86.0 J kg$^{-1}$ m$^{-1}$ and 29.7 J kg$^{-1}$ m$^{-1}$, respectively, at the highest speed measured in the respirometer (maximum speed, 26.8 cm min$^{-1}$). Because the postural component at high speeds is very small relative to the cost of movement, the total cost of transport should asymptotically approach the net cost of transport, which should in turn approach the minimum cost of transport (Fig. 6). Owing to the closed respirometry system, a whole seastar could not be used to stimulate locomotion in the abalone, so a tube foot of *Pycnopodia helianthoides* was used. Also, the abalone could not be stimulated continuously with the tube foot, so the maximum speed recorded in the respirometer was lower than the maximum speed recorded in the aquarium.
Both relationships between total and net cost of transport and speed became linear when the variables were log10-transformed. Total and net cost of transport (\(COT_T\) and \(COT_N\), respectively, in \(J \cdot kg^{-1} \cdot m^{-1}\)) decreased both with absolute speed (\(v\) in \(cm \cdot min^{-1}\)) and with mass (\(m\), in g), with regression equations (mean ± s.e.m.) \(\log_{10} COT_T = 3.35(± 0.13) - 0.90(± 0.06) \log_{10} v - 0.21(± 0.07) \log_{10} m\) \((r^2 = 0.89, N = 29)\) and \(\log_{10} COT_N = 2.29(± 0.29) - 0.69(± 0.14) \log_{10} v - 0.09(± 0.16) \log_{10} m\) \((r^2 = 0.48, N = 29)\), respectively. All regressions were significant (all \(t > 2.97; \ all P < 0.006)\) except the regression of \(\log_{10}\) (net \(COT_N\)) versus \(\log_{10}\) (mass) \((t = 0.58; \ P = 0.56)\).

Discussion

This study demonstrates that the pedal morphology of \textit{Haliotis kamtschatkana} changes with speed such that the area of the pedal sole in contact with the substratum decreases with increasing speed. This may decrease the amount of energy required for locomotion, potentially allowing abalone to move faster than might otherwise be possible. Indeed, abalone are capable of locomoting more rapidly than are most other gastropod species. The fastest absolute speed recorded in the present study (113 cm min\(^{-1}\) by a 9.9 cm abalone) is 1.5 times faster than the maximum absolute speeds reported for other crawling gastropods by Miller (1974) in a comprehensive survey of locomotion in a large variety of gastropods. The only species having faster rates of locomotion belonged to the specialized leaping Strombidae (223.2 cm min\(^{-1}\) for \textit{Strombus maculatus} and 153.6 cm min\(^{-1}\) for \textit{S. gigas}).

The linear relationship between wave frequency and speed confirms that abalone increase step frequency by increasing the velocity of their pedal waves rather than by increasing the number of waves present on the foot at any moment. This is supported by the observation that no more than three waves were present on the foot at any speed. Likewise, step length increased with increasing speed as a result of a change in pedal morphology. In fact, the pedal morphology of \textit{H. kamtschatkana} changed in two ways as velocity increased: the total visible area of the sole decreased (Fig. 4A) and, of the pedal area visible, relatively more was incorporated into pedal waves (Fig. 4B). Although a maximum speed of only 8 shell lengths \(min^{-1}\) was recorded in the video-taped experiments, abalone were able to locomote at nearly
transport for each animal. Individual abalone were then plotted against the adjusted cost of adding it to the measured cost of transport. The speeds of the individual abalone were then plotted against the adjusted cost of transport for each animal.

15 shell lengths min\(^{-1}\) when continuously stimulated using a predatory seastar in a large tank, but they could only sustain this speed for a few minutes. If the linear decrease in pedal sole area found in the present study (a 2.1% reduction for each shell length per minute increase in speed) can be extrapolated to this maximum speed, pedal sole area could decrease by as much as 32% during the fastest escape responses relative to that at rest. Furthermore, an additional 27% of the remaining pedal area would be incorporated into pedal waves (i.e. an increment of 1.8% for each shell length per minute increase in speed). To put this into perspective, if an abalone had a resting visible sole area of 10 cm\(^2\), only 6.9 cm\(^2\) would be visible at 15 shell lengths min\(^{-1}\). Of those 6.9 cm\(^2\), 1.9 cm\(^2\) would be incorporated into waves, leaving only 5.0 cm\(^2\) in contact with the substratum. Thus, the pedal area subjected to friction from the substratum may decrease by as much as 50% at maximal escape velocity relative to the pedal area at rest. It is important to note that such changes will occur throughout a range of speeds. Even at an intermediate speed of 5 shell lengths min\(^{-1}\), pedal adjustment yields an 18% decrease in resting foot area.

The amount of mucus needed to travel a unit distance was highly variable between animals, and no clear trends were evident with increasing speed. However, the mean amount of mucus secreted during locomotion was low compared with the amount of mucus required to adhere to the substratum. For example, a 95 mm \(H. \text{kamtschatkana}\) secreted 640 \(\mu g\) of dry mucus during adhesion (calculated using the regressions of shell length on resting foot area, and resting foot area on mucus secretion while stationary; Table 1). If this abalone were to crawl 10 shell lengths (95 cm) while secreting the same amount of mucus per shell length as used for stationary adherence, then 6400 \(\mu g\) of mucus would be produced. However, since the average amount of mucus secreted per centimeter during locomotion was 5.3 \(\mu g\) dry mucus cm\(^{-1}\), only 504 \(\mu g\) of mucus would actually be produced by this abalone to travel 95 cm. Although these values are only estimates, they corroborate the conclusions of Peck et al. (1993) that rates of mucus secretion differ between stationary and locomoting limpets. Davies and Williams (1995) measured a value of 21–152 \(\mu g\) dry mucus cm\(^{-1}\) for locomoting limpets, \(C. \text{grata}\), which is considerably larger than the value of 5.3 \(\mu g\) dry mucus cm\(^{-1}\) determined in the present study for \(H. \text{kamtschatkana}\), despite the 10-fold larger foot area of the abalone.

Such changes in pedal morphology and mucus secretion during rapid locomotion presumably lead to a decrease in tenacity. Miller (1974) found that gastropods with larger pedal areas had greater tenacity, that gastropods had maximum tenacity while stationary, and that tenacity decreased as speed increased. Although tenacity was not measured in our study, three observations suggest that our measurements of decreased pedal area associated with increased speed are consistent with a decreased tenacity: (1) abalone moving at high speeds are often unable to cling to the vertical side of an aquarium and fall to the bottom, (2) abalone moving at any speed are easier to remove from the substratum than are stationary animals, and (3) abalone escaping from predators in the field appear to skim the surface of the substratum.

The energetics of locomotion observed in our study were similar to those found for five other gastropod species for

![Graph of total cost of transport and net cost of transport as a function of absolute speed.](image)

**Fig. 6.** Total cost of transport and net cost of transport as a function of absolute speed. Regression equations for log\(_{10}\)-transformed data are given in the text. The data presented on the graph have been adjusted for the mass components of the log–log regression equations given in the text by calculating the mass component for each abalone and adding it to the measured cost of transport. The speeds of the individual abalone were then plotted against the adjusted cost of transport for each animal.

![Graph of minimum cost of transport of abalone.](image)

**Fig. 7.** Minimum cost of transport of abalone (\(H. \text{kamtschatkana}\)) compared with that of other marine snails (\(M. \text{articulata, Monodonta turbinata, G. richardi and G. rarilineata}\); Houlihan and Innes, 1982) and a terrestrial slug (\(A. \text{columbianus}\); Denny, 1980). Regression lines for running, flying and swimming animals were taken from Schmidt-Nielsen (1972).
which this type of data is available (Denny, 1980; Houlihan and Innes, 1982). Total \( V_O_2 \) increased linearly with absolute speed (Fig. 5), while cost of transport was high at low speeds and quickly decreased to a minimum as speed increased (Fig. 6). Minimum cost of transport is equal to the slope of the regression line of total \( V_O_2 \) versus absolute speed (Taylor et al. 1970; Full et al. 1990) and, at high speeds, total cost of transport should reach this value asymptotically as the rate of oxygen consumption increases and resting metabolic costs and postural effects become a smaller proportion of the total metabolic rate. Indeed, total cost of transport was nearly equal to net cost of transport at a speed approximately equal to the maximum velocity of \( H. kantschatkana \) recorded in this study (113 cm min\(^{-1}\)). Thus, 20.3 J kg\(^{-1}\) m\(^{-1}\) appears to be the minimum cost of transport for \( H. kantschatkana \). This value is much lower than values for other gastropod species for which similar measurements are available (Fig. 7). This may be due to the comparatively large size of abalone, and it would be of interest to measure the cost of transport in larger marine gastropod species to determine whether this trend is consistent. For the terrestrial slug \( Ariolimax columbianus \) (Denny, 1980), the high cost of transport of 912 J kg\(^{-1}\) m\(^{-1}\) compared with 64 J kg\(^{-1}\) m\(^{-1}\) for a similarly sized abalone may be due to differences in the cost of crawling in air versus water. Abalone would benefit from the buoyancy provided by water, and mucus requirements may be less in a wet environment. Also, Denny (1980) measured total \( V_O_2 \) over a 24 h period and so recorded the oxygen consumption after activity ceased, thus taking into account any \( O_2 \) debt incurred by anaerobic metabolism. Interestingly, the cost of transport for an abalone (20.3 J kg\(^{-1}\) m\(^{-1}\)) is slightly less than the cost of transport of a similarly sized running vertebrate (26 J kg\(^{-1}\) m\(^{-1}\); Fedak and Seeherman, 1979; see Fig. 7), but is twice that of a similarly sized flying bird (10 J kg\(^{-1}\) m\(^{-1}\); Tucker, 1973) and seven times that of a swimming fish (3 J kg\(^{-1}\) m\(^{-1}\); Beamish, 1978). Houlihan and Innes (1982) also found that transport costs for their largest individuals of the marine gastropod \( Monodonta turbinata \) were below those of similarly sized running vertebrates (the value represented in Fig. 7 is for an average-sized \( M. turbinata \)).

The linear relationship between energy consumption and speed during adhesive crawling is similar to that found for running homeotherms traveling at their preferred gaits (Hoyt and Taylor, 1981; Taylor et al. 1982). In comparison, this relationship is curvilinear for swimming and flying (Brett, 1965; Tucker, 1968). Likewise, total cost of transport decreases with increasing speed in terrestrial locomotion (Peters, 1983; Full et al. 1990). In all forms of locomotion, mass-specific rate of oxygen consumption and transport costs decrease with animal size (Taylor et al. 1970; Beamish, 1978; Schmidt-Nielsen, 1984).

The decrease in transport costs with increasing body size in abalone indicates that the proportionately larger pedal soles of larger abalone (Table 1) do not increase their cost of locomotion. The function of a larger foot area may be to increase tenacity when the animal is at rest. Juvenile abalone tend to be more cryptic, occupying crevices that would protect them from heavy surge, while adult abalone are found more often in the open (Sloan and Breen, 1988). Thus, larger abalone may need a disproportionately larger pedal area to allow them to remain affixed to more exposed substrata.

The \( y \)-intercept of the regression of total \( V_O_2 \) versus absolute speed (40.1 \( \mu l O_2 g^{-1} h^{-1} \)) was 1.9 times larger than the mean resting \( V_O_2 \) of the abalone (20.7 \( \mu l O_2 g^{-1} h^{-1} \)) (Fig. 5). Since the \( y \)-intercept represents the rate of oxygen consumption when the animal is not moving, the difference between it and the resting metabolic rate represents the postural effect for locomoting abalone. Schmidt-Nielsen (1972) defines a postural effect as the increase in energy expenditure needed to hold the body in the position of locomotion. Postural costs are probably incurred by abalone due to the lifting of their shells and the subsequent shifting of the visceral mass prior to locomotion, as is the case for other snails (Houlihan and Innes, 1982). Postural effects of similar magnitude have been determined for other gastropods (0.9–1.3 times resting metabolic rate; Houlihan and Innes, 1982), mammals (1.7 times resting metabolic rate; Taylor et al. 1970), a lizard \( Trachydosaurus rugosus \) (1.5 times resting metabolic rate; John-Alder et al. 1986) and arthropods (1.5–4.0 times resting metabolic rate; Full, 1987; Herreid et al. 1981).

In the present study, cost of transport was calculated solely from aerobic energy expenditure. As such, it may not represent the total amount of energy needed for locomotion. Given the reliance of marine invertebrates on anaerobic metabolism during times of stress (Hochachka, 1980; Gade, 1988) and the open nature of the abalone circulatory system (Bourne and Redmond, 1977a,b; Jones, 1983), it is likely that abalone make use of anaerobic reserves even at low speeds. In fact, two aspects of the data point to a large anaerobic component during locomotion. First, the steep, negative log\( \log_{10} \)–log\( \log_{10} \) slopes of both total cost of transport and net cost of transport versus speed (0.90 and 0.69, respectively) suggest that energy requirements decrease dramatically at high speeds, when, in fact, it is possible that a substantial portion of the energy expended at these speeds (the anaerobic component) was not measured. While transport costs may indeed decrease with speed, as they do in other locomotory forms, addition of an anaerobic component would cause this decrease to be less substantial. Second, the minimum cost of transport measured in this study was an order of magnitude lower than the minimum cost of transport calculated by Denny (1980). His measurements of \( V_O_2 \) included oxygen consumption after activity had ceased, which would have included any \( O_2 \) debt incurred by anaerobic metabolism. We are presently investigating the extent of the contribution of anaerobiosis to the cost of transport in abalone.

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References


