

LOCOMOTION IN THE ABALONE *HALIOTIS KAMTSCHATKANA*: PEDAL MORPHOLOGY AND COST OF TRANSPORT

DEBORAH A. DONOVAN* AND THOMAS H. CAREFOOT

Department of Zoology, University of British Columbia, Vancouver, Canada V6T 1Z4

Accepted 3 February 1997

Summary

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 \log_{10} -transformed data, $b=0.83$; expected slope for isometry, $b_0=0.67$) 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 \log_{10} -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 \dot{V}_{O_2} (in $\mu\text{l O}_2 \text{g}^{-1} \text{h}^{-1}$) increased linearly with increasing absolute speed v (in cm min^{-1}): $\dot{V}_{\text{O}_2}=40.1+0.58v-0.15m$ ($r^2=0.35$, $P=0.04$), where m is body mass (in g). Minimum cost of transport, calculated from the slope of absolute speed on \dot{V}_{O_2} , was $20.3 \text{J kg}^{-1} \text{m}^{-1}$. 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 $86.0 \text{J kg}^{-1} \text{m}^{-1}$ and $29.7 \text{J kg}^{-1} \text{m}^{-1}$, 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: $\log_{10}\text{COT}_T=3.35-0.90\log_{10}v-0.21\log_{10}m$ ($r^2=0.89$; $P<0.006$) and $\log_{10}\text{COT}_N=2.29-0.69\log_{10}v-0.09\log_{10}m$ ($r^2=0.48$; $P<0.006$), respectively.

Key words: cost of transport, pedal waves, locomotion, *Haliotis kamtschatkana*, Gastropoda, abalone.

Introduction

Abalone display a dramatic escape response when confronted with seastar predators. The response begins with a vigorous twisting of the shell to dislodge the predator's tube feet, followed by rapid locomotion away from the threat. Escape locomotion is visibly different from ordinary locomotion and is characterized by an elevated shell, large-amplitude pedal waves and a trough running from anterior to posterior such that the middle of the foot is lifted off the substratum. The energetically expensive nature of adhesive crawling (Denny, 1980) suggests that these characteristics of high-speed locomotion, in addition to providing propulsive force, may also have energy-saving benefits to allow abalone to locomote more rapidly than might otherwise be possible.

Most gastropods locomote by generating rhythmic waves on the ventral surface of their broad pedal muscle. The wave pattern differs among species depending on the direction in which the wave travels and the portion of the foot it occupies.

Waves that travel from the back of the foot to the front (i.e. in the same direction as the animal is traveling) are direct waves, while waves traveling from front to back are indirect, or retrograde. A wave that reaches from one side of the foot to the other as it travels along the foot is monotaxic, while a wave that occupies only half the foot is ditaxic. In this case, another wave out of phase with the first is found on the other half of the foot. Most marine gastropods are ditaxically retrograde, while the abalone is ditaxically direct. In most marine gastropods, the waves are generated rhythmically (Miller, 1974; Trueman, 1983).

Gastropods with rhythmic pedal waves increase speed by increasing step frequency and/or step length. A step is the distance that a point on the pedal sole travels when a wave passes through it (Miller, 1974). Step frequency can be increased by increasing the velocity of the pedal waves or by increasing the number of waves present on the foot at any given time. Step size

*e-mail: donovan@zoology.ubc.ca.

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 funebris* 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 to form a sheet between the foot and the substratum. Mucus production may be a primary reason that adhesive crawling is so energetically expensive compared with other forms of locomotion (Denny, 1980). While these morphological and physiological changes are noticeable at high speeds, it is not clear to what extent they are employed at lower speeds. Subtle changes to the pedal sole may occur such that energy is conserved throughout a range of speeds.

The energetic costs of locomotion have been studied intensively for running, swimming and flying, but the costs of adhesive crawling are not as well understood. Several studies have shown that crawling snails increase their energy expenditure above resting costs (Newell and Roy, 1973; Calow, 1974), but only two have correlated oxygen consumption with speed to determine cost of transport, the energy needed to transport a unit mass over a unit distance (calculated by dividing

mass-specific energy expenditure by speed). Denny (1980) calculated the cost of transport for the terrestrial slug *Ariolimax columbianus*, and Houlihan and Innes (1982) investigated transport costs for four marine gastropod species. Both studies showed adhesive crawling to be energetically more expensive than other types of locomotion. Houlihan and Innes (1982) briefly investigated the effects of animal size on cost of transport for the marine gastropod *Monodonta turbinata*, and found that total mass-specific cost of transport decreased as size increased.

The first purpose of the present study was to investigate morphological differences in pedal sole area and pedal waves of the Northern abalone *Haliotis kamtschatkana* over a range of speeds and body sizes, to determine whether there may be energy-saving strategies employed during increases in locomotory speed. The second purpose was to investigate the cost of transport of *H. kamtschatkana* over a range of speeds and body sizes to further our understanding of the effects of size on the costs of adhesive crawling in marine gastropods.

Materials and methods

Animal collections

Northern abalone, *Haliotis kamtschatkana* (L.), were collected at Bamfield Marine Station, Vancouver Island, British Columbia, Canada, and transported to Shannon Point Marine Station, Anacortes, Washington, USA. They were held in large tanks with a continuous supply of fresh sea water at a mean temperature of 10°C during the experiments. The abalone were fed *ad libitum* on kelp, *Nereocystis luetkeana*.

Pedal area at rest

Abalone ($N=21$; 31–102 mm shell length) were placed individually in a glass aquarium with a constant supply of fresh sea water and were allowed to adhere to the side of the tank. An animal was left undisturbed until its foot was fully expanded. A 1 cm×1 cm piece of plastic was placed next to the abalone as a reference and a photograph was taken. The photographs were analyzed using the SIGMA-SCAN area-measurement software system (Jandel Scientific, CA, USA) to determine the area of 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_a is the mass of abalone in air, m_w is the mass of abalone in sea water, and d_w is the density of sea water (assumed to be 1.025 g cm⁻³).

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

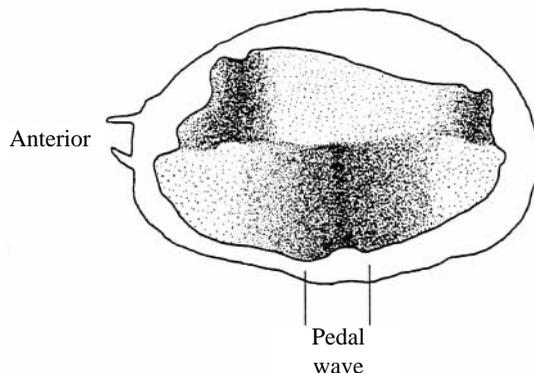


Fig. 1. Ventral view of a locomoting abalone as seen through a glass plate. The dark areas represent pedal waves.

($N=16$; 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 \pm S.E.M. resting pedal area $42 \pm 4 \text{ cm}^2$) 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 ($\mu\text{l O}_2 \text{ h}^{-1}$) by multiplying by an oxycaloric coefficient (Q_{ox}) of $21.10 \text{ mJ } \mu\text{l O}_2^{-1}$. 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 ($\text{J kg}^{-1} \text{h}^{-1}$) 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} (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} (foot area) increased

allometrically with \log_{10} (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 $t>4.91$; 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 (\pm 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: $f=8.71(\pm 0.68)+2.42(\pm 0.17)v$ (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 the sole of their foot significantly as they increased speed (all $t>2.36$; all $P<0.05$). In these seven abalone, the decrease was linear, and none of the individual regression lines differed significantly from each other [$F_{(2),6,42}=2.22$; $P=0.07$]. Their common regression line had a mean slope (\pm 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 $t>2.30$; 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*

Relationship (y versus x)	$\log_{10}a$	b	r^2	N	Predicted slope for isometry
Resting foot area (cm^2) versus abalone volume (cm^3)	-0.11 ± 0.07	$0.83\pm 0.04^*$	0.96	20	0.67
Resting foot area (cm^2) versus shell length (mm)	-3.40 ± 0.26	$2.51\pm 0.14^*$	0.95	20	2.0
Mucus secretion (μg) versus resting foot area (cm^2)	1.11 ± 0.43	1.08 ± 0.30	0.48	16	1.0

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 \pm S.E.M.

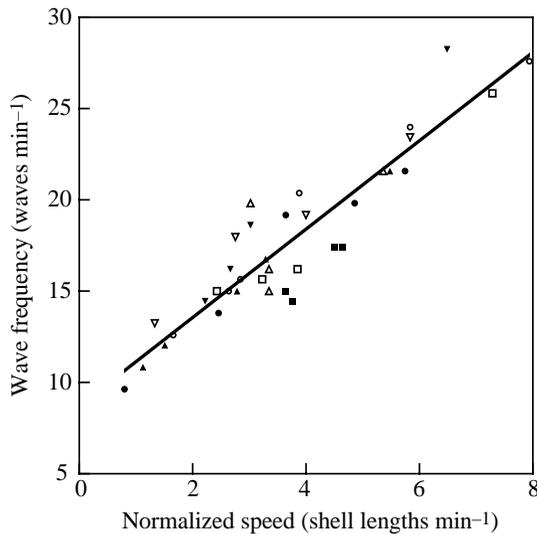


Fig. 2. Frequency of pedal waves of locomoting abalone as a function of speed. Statistically significant regression lines were generated for all eight abalone tested. These were not found to be statistically different and they had a common slope (\pm S.E.M.) b of 2.42 ± 0.17 . Each symbol represents an individual abalone.

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 $10.0 \pm 1.3 \mu\text{g}$ dry mucus cm^{-1} , with a grand aggregate mean of $5.3 \pm 0.7 \mu\text{g}$ dry mucus cm^{-1} ($N=35$).

Oxygen consumption and cost of transport

Total mass-specific rate of oxygen consumption (\dot{V}_{O_2}) increased linearly with increasing absolute speed ($N=29$;

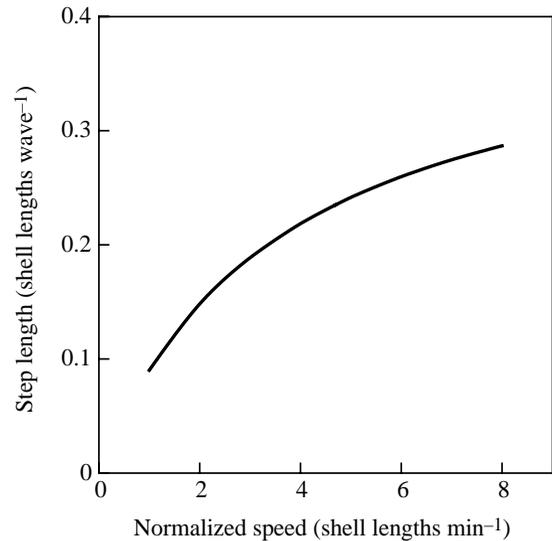


Fig. 3. Step length as a function of speed in locomoting abalone. The data were calculated using the equation $v=L \times f$, where v is speed (in shell lengths min^{-1}), f is frequency (in waves min^{-1}) and L is step length (in shell lengths wave^{-1}) and the linear regression equation from Fig. 2 of speed on wave frequency for all abalone: $f=8.71(\pm 0.68)+2.4(\pm 0.17)v$ (\pm S.E.M.).

$t=2.19$; $P=0.04$), rising by $0.58 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for every 1 cm min^{-1} increase in speed (Fig. 5). Total \dot{V}_{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.) \dot{V}_{O_2} of resting abalone ($20.7 \pm 1.7 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was nearly half the value of the y -intercept of the line relating \dot{V}_{O_2} to speed ($40.1 \pm 4.5 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) (Fig. 5). The difference of $19.4 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ 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 \dot{V}_{O_2} , for *H. kamtschatica* in this study is $20.3 \text{ J kg}^{-1} \text{ m}^{-1}$ (slope of \dot{V}_{O_2} versus speed regression line is $0.96 \mu\text{l O}_2 \text{ g}^{-1} \text{ m}^{-1}$ 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 $86.0 \text{ J kg}^{-1} \text{ m}^{-1}$ and $29.7 \text{ J kg}^{-1} \text{ m}^{-1}$, 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 \log_{10} -transformed. Total and net cost of transport (COT_T and COT_N , respectively, in $\text{Jkg}^{-1}\text{m}^{-1}$) decreased both with absolute speed (v in cmmin^{-1}) and with mass (m , in g), with regression equations (mean \pm S.E.M.) $\log_{10}COT_T = 3.35(\pm 0.13) - 0.90(\pm 0.06)\log_{10}v - 0.21(\pm 0.07)\log_{10}m$ ($r^2 = 0.89$, $N = 29$) and $\log_{10}COT_N = 2.29(\pm 0.29) - 0.69(\pm 0.14)\log_{10}v - 0.09(\pm 0.16)\log_{10}m$ ($r^2 = 0.48$, $N = 29$), respectively. All regressions were significant (all $t > 2.97$; all $P < 0.006$) except the regression of $\log_{10}(\text{net } COT_N)$ versus $\log_{10}(\text{mass})$ ($t = 0.58$; $P = 0.56$).

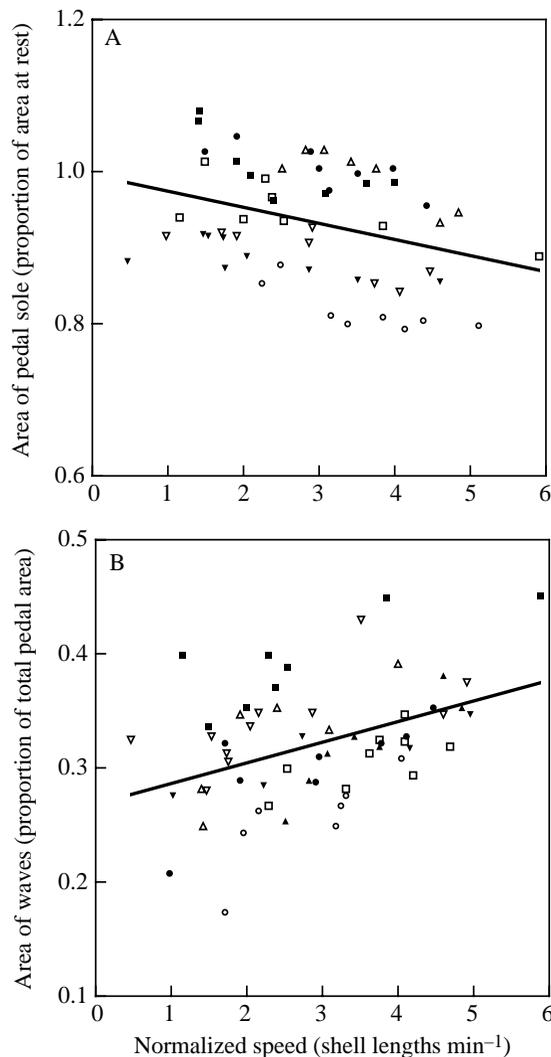


Fig. 4. (A) Total area of the pedal sole of locomoting abalone visible through a glass aquarium as a function of speed. Statistically significant regression lines were generated for seven out of eight abalone tested. These were not found to be statistically different and they had a common slope (\pm S.E.M.) b of -0.021 ± 0.008 . (B) Area of the pedal waves of locomoting abalone as a function of speed. Statistically significant regression lines were generated for all eight abalone tested. These were not found to be statistically different and they had a common slope (\pm S.E.M.) b of 0.018 ± 0.005 . Each symbol represents an individual abalone.

Discussion

This study demonstrates that the pedal morphology of *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 ($223.2 \text{ cm min}^{-1}$ for *Strombus maculatus* and $153.6 \text{ cm min}^{-1}$ for *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 *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 $8 \text{ shell lengths min}^{-1}$ was recorded in the video-taped experiments, abalone were able to locomote at nearly

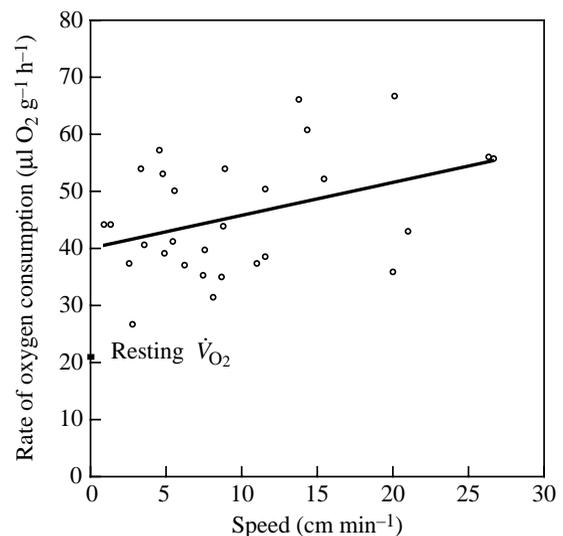


Fig. 5. Total rate of oxygen consumption \dot{V}_{O_2} ($\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) as a function of absolute speed v (cm min^{-1}). The regression line is: $\dot{V}_{O_2} = 40.1(\pm 4.5) + 0.58(\pm 0.26)v - 0.15(\pm 0.06)m$ (\pm S.E.M.; $r^2 = 0.35$; $N = 29$), where m is body mass (in g). The data presented on the graph have been adjusted for the mass component of the regression equation by calculating the mass component for each abalone and adding it to the measured \dot{V}_{O_2} . The speeds of the individual abalone were then plotted against the adjusted \dot{V}_{O_2} values.

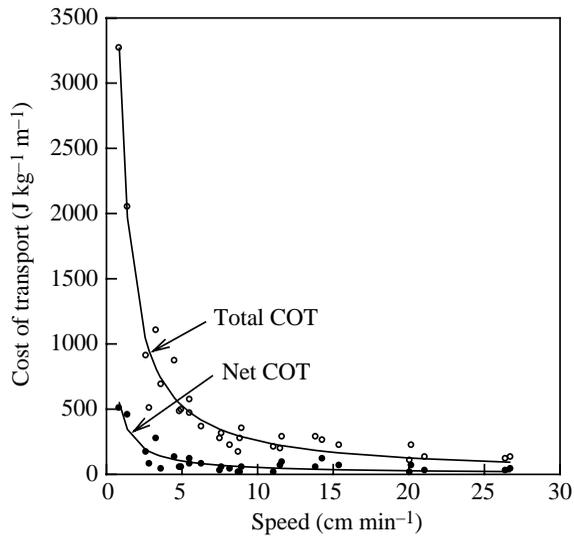


Fig. 6. Total cost of transport and net cost of transport as a function of absolute speed. Regression equations for \log_{10} -transformed data are given in the text. The data presented on the graph have been adjusted for the mass components of the log-log regression equations given in the text by calculating 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.

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. kamtschatkana* secreted $640 \mu\text{g}$ 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

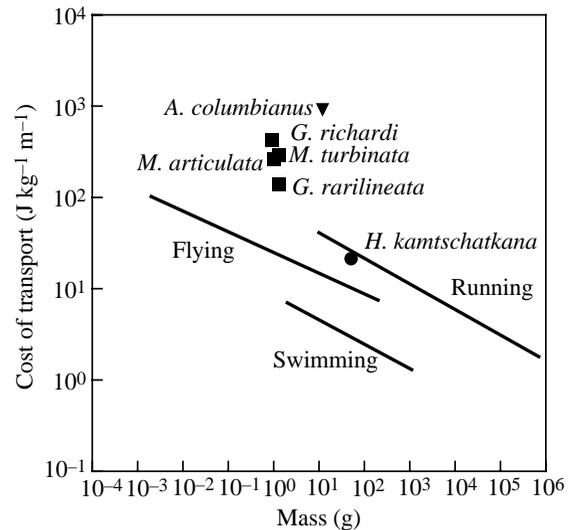


Fig. 7. Minimum cost of transport of abalone (*Haliotis kamtschatkana*) compared with that of other marine snails (*Monodonta turbinata*, *M. articulata*, *Gibbula richardi* and *G. rarilineata*; Houlihan and Innes, 1982) and a terrestrial slug (*Ariolimax columbianus*; Denny, 1980). Regression lines for running, flying and swimming animals were taken from Schmidt-Nielsen (1972).

of mucus per shell length as used for stationary adherence, then $6400 \mu\text{g}$ of mucus would be produced. However, since the average amount of mucus secreted per centimeter during locomotion was $5.3 \mu\text{g dry mucus cm}^{-1}$, only $504 \mu\text{g}$ 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 $21\text{--}152 \mu\text{g dry mucus cm}^{-1}$ for locomoting limpets, *Cellana grata*, which is considerably larger than the value of $5.3 \mu\text{g dry mucus cm}^{-1}$ determined in the present study for *H. 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

which this type of data is available (Denny, 1980; Houlihan and Innes, 1982). Total \dot{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 \dot{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. kamtschaticana* recorded in this study (113 cm min^{-1}). Thus, $20.3 \text{ J kg}^{-1} \text{ m}^{-1}$ appears to be the minimum cost of transport for *H. kamtschaticana*. 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 $912 \text{ J kg}^{-1} \text{ m}^{-1}$ compared with $64 \text{ J kg}^{-1} \text{ m}^{-1}$ 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 \dot{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 ($20.3 \text{ J kg}^{-1} \text{ m}^{-1}$) is slightly less than the cost of transport of a similarly sized running vertebrate ($26 \text{ J kg}^{-1} \text{ m}^{-1}$; Fedak and Seeherman, 1979; see Fig. 7), but is twice that of a similarly sized flying bird ($10 \text{ J kg}^{-1} \text{ m}^{-1}$; Tucker, 1973) and seven times that of a swimming fish ($3 \text{ J kg}^{-1} \text{ m}^{-1}$; 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 \dot{V}_{O_2} versus absolute speed ($40.1 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was 1.9 times larger than the mean resting \dot{V}_{O_2} of the abalone ($20.7 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) (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_{10} – \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 \dot{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.

We are extremely grateful to the faculty and staff of Shannon Point Marine Center for laboratory space and technical support, and to the staff of Bamfield Marine Station for logistical support during collection of the animals. John Gosline and members of his laboratory provided many helpful

comments on various drafts of this manuscript. The work was supported by a University Graduate Fellowship to D.D. and a Natural Science and Engineering Research Council (NSERC) grant to T.C.

References

- BEAMISH, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 101–187. New York: Academic Press.
- BOURNE, G. B. AND REDMOND, J. R. (1977a). Hemodynamics in the pink abalone, *Haliotis corrugata* (Mollusca, Gastropoda). I. Pressure relations and pressure gradients in intact animals. *J. exp. Zool.* **200**, 9–16.
- BOURNE, G. B. AND REDMOND, J. R. (1977b). Hemodynamics in the pink abalone, *Haliotis corrugata* (Mollusca, Gastropoda). II. Acute blood-flow measurements and their relationship to blood pressure. *J. exp. Zool.* **200**, 17–22.
- BRETT, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd Can.* **22**, 1491–1501.
- CALOW, P. (1974). Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods, *Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn. *Oecologia* **16**, 149–161.
- CAREFOOT, T. H. (1987). Gastropoda. *Animal Energetics* **2**, 89–172.
- DAVIES, M. S. (1993). Energetic implications of variation in pedal mucus production by *Patella vulgata* L. *Veliger* **36**, 203–208.
- DAVIES, M. S. AND WILLIAMS, G. A. (1995). Pedal mucus of a tropical limpet, *Cellana grata* (Gould): energetics, production, and fate. *J. exp. mar. Biol. Ecol.* **186**, 77–87.
- DENNY, M. W. (1980). Locomotion: the cost of gastropod crawling. *Science* **208**, 1288–1290.
- ELLIOT, J. M. AND DAVISON, U. (1975). Energy equivalent of oxygen consumption in animal energetics. *Oecologia* **19**, 195–201.
- FEDAK, M. A. AND SEEHERMAN, H. J. (1979). Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* **282**, 713–716.
- FULL, R. J. (1987). Locomotion energetics of the ghost crab. I. Metabolic cost and endurance. *J. exp. Biol.* **130**, 137–153.
- FULL, R. J., ZUCCARELLO, D. A. AND TULLIS, A. (1990). Effect of variation in form on the cost of terrestrial locomotion. *J. exp. Biol.* **150**, 233–246.
- GADE, G. (1988). Energy metabolism during anoxia and recovery in shell adductor and foot muscle of the gastropod mollusc *Haliotis lamellosa*: Formation of the novel anaerobic end product tauropine. *Biol. Bull. mar. Biol. Lab., Woods Hole* **175**, 122–131.
- HERREID, C. F., PRAWEL, D. A. AND FULL, R. J. (1981). Energetics of running cockroaches. *Science* **212**, 331–333.
- HOCHACHKA, P. W. (1980). *Living Without Oxygen*. Cambridge, MA: Harvard University Press.
- HOULIHAN, D. F. AND INNES, A. J. (1982). Oxygen consumption, crawling speeds and cost of transport in four Mediterranean intertidal gastropods. *J. comp. Physiol.* **147**, 113–121.
- HOYT, D. F. AND TAYLOR, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.
- JOHN-ALDER, H. B., GARLAND, T. AND BENNETT, A. F. (1986). Locomotory capacities, oxygen consumption and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). *Physiol. Zool.* **59**, 523–531.
- JONES, H. D. (1983). The circulatory systems of gastropods and bivalves. *Mollusca* **5**, 189–238.
- MILLER, S. L. (1974). Adaptive design of locomotion and foot form in prosobranch gastropods. *J. exp. mar. Biol. Ecol.* **14**, 99–156.
- NEWELL, R. C. AND ROY, A. (1973). A statistical model relating the oxygen consumption of a mollusc (*Littorina littorea*) to activity, body size, and environmental conditions. *Physiol. Zool.* **46**, 253–275.
- PECK, L. S., PROTHERO-THOMAS, E. AND HOUGH, N. (1993). Pedal mucus production by the Antarctic limpet *Nacella concinna* (Strebel, 1908). *J. exp. mar. Biol. Ecol.* **174**, 177–192.
- PETERS, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- SCHMIDT-NIELSEN, K. (1972). Locomotion: Energy cost of swimming, flying and running. *Science* **177**, 222–228.
- SCHMIDT-NIELSEN, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.
- SLOAN, N. A. AND BREEN, P. A. (1988). Northern abalone, *Haliotis kamtschatkana*, in British Columbia: fisheries and synopsis of life history information. *Can. Spec. Publ. Fish. aquat. Sci.* **103**, 1–46.
- TAYLOR, C. R., HEGLUND, N. C. AND MALOY, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 1–21.
- TAYLOR, C. R., SCHMIDT-NIELSEN, K. AND RAAB, J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107.
- TRUEMAN, E. R. (1983). Locomotion in gastropods. *Mollusca* **4**, 155–198.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67–87.
- TUCKER, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* **58**, 689–709.
- VOLTZOW, J. (1986). Changes in pedal intramuscular pressure corresponding to behavior and locomotion in the marine gastropods *Busycon contrarium* and *Haliotis kamtschatkana*. *Can. J. Zool.* **64**, 2288–2293.