EFFECT OF ACTIVITY ON ENERGY ALLOCATION IN THE NORTHERN ABALONE, HALIOTIS KAMTSCHATKANA (JONAS)

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ABSTRACT. The effect of activity, in the form of increased respiratory energy expenditure and secretion of mucous, on the summer and winter energy budgets of Haliotis kamtschatkana was assessed. Abalone exhibited seasonal variations in field activity with 20% of all individuals observed crawling during June to October, compared with <5% during December to February. In the laboratory, abalone exhibited diurnal as well as seasonal variation in activity. The laboratory activity budget showed that an average abalone spends 9.6 h day−1 quiescent, 23.0 h day−1 silent, 0.7 h day−1 feeding, and 1.3 h day−1 crawling during the summer, and 15.8 h day−1 quiescent, 5.5 h day−1 silent, 2.3 h day−1 feeding, and 0.4 h day−1 crawling during the winter. Videodogs of abalone made over 24-h periods revealed that abalone usually crawl at a rate of one shell length min−1. Locomotion is not continuous; rather, abalone stop and then start again, on average twice per meter. Components of the energy budget, C = F + U + P + P + R + M were measured during summer and winter months. None of the slopes of regressions of log10 energy (J day−1) on log10 (m) (g) was significantly different between summer and winter for any of the energy budget components, except those of osmotic growth on mass. Summer values intercepts were all significantly higher than winter y-intercepts, indicating that energy consumption and expenditures were higher during the summer. Respiratory energy expenditure was the largest component of both summer and winter budgets. Activity accounted for 23% of total consumed energy during the summer and 13% during the winter.

KEY WORDS: abalones, activity, energy budget, Haliotis kamtschatkana, secretion of mucous

INTRODUCTION

Increasing world demand for abalones has caused severe declines in most populations, including those of British Columbia’s Haliotis kamtschatkana (Eummert and Jamieson 1988). Efforts have been made to manage this resource, including closure of the fishery (1990), farming, and reintroducing abalone into depopulated areas. Studies have shown that transplanting H. kamtschatkana from exposed habitats to more sheltered habitats leads to increased growth and ultimately greater population densities (Breen 1986, Eummert and Jamieson 1988), suggesting that this may be a feasible strategy to enhance depleted British Columbia stocks. Successful reestablishment and stock enhancement will depend on identification of suitable habitat, which will in turn depend on complete knowledge of the biology of the abalone. Eummert and Jamieson (1980) point out that H. kamtschatkana do not grow to marketable size in high wave-exposure areas, but also note that the cause of the decreased growth is not known. Suggestions of inadequate food supplies or high rates of mortality illustrate the need for more information about the energy balance of H. kamtschatkana.

A poorly understood aspect of abalone biology is, indeed, of gastropods in general, is the energetic cost of activity. Abalone must crawl in order to forage, escape predators, find adequate refugia, and reproduce. Several studies have documented the movements of individual abalone and have shown that abalone vary widely in their mobility (Momma and Sato 1969, Poore 1972, Shepherd 1973). Diurnally, abalone crawl mostly at night, and the amount of movement depends on size (Shepherd 1973, Sloan and Breen 1988), availability of food or shelter (Momma and Sato 1969, Poore 1972, Shepherd 1986, Sloan and Breen, 1988), and type and degree of predation (Schel and Wildens 1987).

Activity is energetically costly to gastropods because of both increased metabolic rate and secretion of mucous. Many studies have shown a rise of oxygen consumption (V_{O_2}) during activity in gastropods (Newell and Roy 1973, Calow 1974, Filch 1975, Crisp 1979). Cost of transport, or the amount of energy needed to transport a unit mass over a unit distance, has also been measured (Denay 1980, Huislin and Iones 1982, Imes and Huislin 1985, Donovan and Carefoot 1997). Calow (1974) estimated that 20% of "routine metabolism" of the pulmonate snail Planorbidus coronatus was devoted to activity. Likewise, several authors have pointed out the importance of mucous as a contribution to molluscan energy expenditure (Paine 1971, Calow 1974, Horn 1986, Davies et al. 1990), and Denay (1980) attributes the relatively high energetic cost of gastropod crawling to production of mucous. Calow (1974) estimated production of mucous as 13–32% of absorbed energy in P. coronata, and Carefoot (1967) estimated that mucous accounted for 15% of the energy budget of the pulmonate Archidoris pseudogrisea.

Metabolic rates of marine organisms depend on a myriad of internal and environmental factors that interact in different ways at different times of the year (Newell 1973). Seasonal temperature differences affect both oxygen consumption (see Bayne and Newell 1983, Carefoot 1987) and activity (Newell 1969, Poore 1972, Newell and Keeford 1977). Newell and Pye (1971) showed interaction between activity level and temperature in Littorina littorea in that the active rate of respiration was more temperature dependent than the standard rate, suggesting that activity would have a different effect on a gastropod’s energy budget at different times of the year. Indeed, Widdows and Bayne (1991) found that both filtration rate and oxygen consumption in the mussel Mytilus edulis were affected by acclimation to high and low temperatures, which in turn, changed the animal’s energy allocations. Evidence
for effects of temperature on secretion of mucus is more scarce, but Kideys and Hartnoll (1991) found that secretion of mucus in the whelk _Buccinum undatum_ decreased at low temperatures. Changes in secretion of mucus at different temperatures and during different seasons would cause further changes in the effect of activity on an energy budget.

From observations of abalone, it is evident that activity and locomotion play important roles in their daily lives, yet there has been no study on the effects of activity on respiratory energy loss, secretion of mucus, and energy balance of abalone, and these are the bases of this study. We determined time-energy budgets for _H. kamtschatkana_ for both summer and winter in order to assess the effect of activity on them.

**MATERIALS AND METHODS**

Energy budgets were calculated for _H. kamtschatkana_ by measuring all components of the energy budget _C_ = _F_ + _U_ + _P_ _e_ + _P_ _r_ + _R_ + _M_. The components not directly affected by activity, consumption (_C_), production of feces (_P_ _e_), nitrogen excretion (_U_), somatic growth (_P_ _s_), and reproductive growth (_P_ _r_), were measured once during summer (June to August 1995) and once during winter (November 1995 to January 1996), except for _P_ _e_, which was measured monthly (March 1995 to July 1996), and _P_ _r_, which was measured once at the end of the experiment (August 1996). The two components directly affected by activity, respiration (_R_) and secretion of mucus (_M_), were estimated by developing summer (June 1995) and winter (December 1995) time budgets and then integrating amounts of time spent in each activity state with energy equivalents for each state.

**Collection of Animals**

Abalone were collected in Barkley Sound near the Bamfield Marine Station, Bamfield, British Columbia, and transported to the Shannon Point Maritime Center, Anacortes, WA. They were held in a large tank with a constant supply of fresh seawater and fed _ad libitum_ on _Nereocystis luetkeana_, a preferred kelp food (Paul et al. 1977).

**Time Budgets**

Activity states of _H. kamtschatkana_ were monitored in both laboratory and field, and time budgets were determined from the amount of time spent in each different activity state. In total, five states that appeared important to the energetics of _H. kamtschatkana_ were identified: (1) quiescent (shell held tightly to the substratum, cephalic and mantle tentacles retracted), (2) alert (shell raised off the substratum, tentacles extended), (3) active (back and forth movements in a small area without moving any appreciable distance), (4) crawling (moving an appreciable distance in one direction), and (5) feeding. In addition to laboratory and field observations, videotapes were made of crawling abalone.

**Laboratory**

Abalone were placed in a large open-air tank exposed to natural light and with a constant supply of fresh seawater. They were observed hourly, and the number of abalone in each of four states (quiescent, alert, crawling, and feeding) was recorded. This experiment was conducted in summer (June 1994; _n_ = 105) and winter (January 1996; _n_ = 70). Daily activity budgets were calculated from these summer and winter data.

**Field**

Activity states (quiescent, alert, and crawling) of field abalone were recorded during daytime SCUBA dives in Barkley Sound, near the Bamfield Marine Station. Dives were made between 9 am and 12 pm, in alternate months from April 1994 to April 1995. Divers followed 100-m transects and recorded the activity state of all abalone seen (_n_ = 52–203 for each outing). These data were used to compare the amount of activity in the laboratory and the field.

**Videotaped Crawling Activity**

Abalone (_n_ = 15; 70–120 g live mass) were placed three at a time in a glass aquarium (30 x 50 x 15 cm) with an adequate flow of fresh seawater (2 L min⁻¹) and were videotaped over a 24-h period. Videotapes were analyzed for (1) rate of crawling, (2) total distance moved during crawling, and (3) number of crawling bouts.

**Energy Budgets**

Because we were initially interested in potential gender differences in energy budget parameters, 10 females and 10 males were used for each component of the energy budget (unless otherwise stated). The animals ranged in live mass from 13 to 175 g so the effect of mass on energy budget parameters could also be investigated.

**Consumption (C)**

Abalone were kept in plastic mesh cages and fed pieces of kelp of known mass each day at 3 pm over a 4-day period. Uneaten kelp was removed each following day at 3 pm and weighed. Each day, three pieces of kelp were placed in empty cages as controls and change of mass was recorded. The mass of the uneaten kelp from each abalone’s cage was subtracted from the initial mass of the piece, and the result was corrected for any difference in mass exhibited by the mean of the controls to determine the wet mass of kelp consumed.

To determine the energy content of food eaten, samples of kelp were weighed fresh and then dried at 60°C to constant mass. Samples of dried kelp were combusted in a Phillips microbomb calorimeter to determine their energy content. Average daily energy consumption (J day⁻¹) for each abalone was calculated by multiplying the daily wet mass of consumed kelp by the energy content per gram wet mass of the kelp.

**Feces Production (F)**

Abalone (_n_ = 5; 20–128 g live mass) were held individually in 1-L aerated plastic containers filled with filtered (5 μm pore size) seawater at ambient temperature over a 4-day period. Kelp of known mass was fed to each animal on the first day, and uneaten remnants were removed and weighed on the following day. The abalone were held in the containers for three more days, during which feces were collected daily. The feces were dried at 90°C to constant mass and then combusted in a microbomb calorimeter. The mean energy value for the feces was used to calculate _F_ in the energy budget.

**Nitrogen Excretion (U)**

Individual abalone were placed in sealed containers and maintained at ambient temperature. Duplicate 1-mL aliquots of the
for effects of temperature on secretion of mucins is more scarce, but Kiley and Hattan (1991) found that secretion of mucins in the abdominal cavity increased with core temperature. Changes in secretion of mucins at different temperatures and during different seasons would cause further changes in the effect of activity on an energy budget.

From observations of abalone, it is evident that activity and locomotion play important roles in their daily lives, yet there has been no study on the effects of activity on respiratory energy loss, secretion of mucins, and energy balance of abalone, and these are the basis of this study. We determined time-energy budgets for H. heterostomus and L. topaziana during winter and summer to assess the effect of activity on them.

MATERIALS AND METHODS

Energy budgets were calculated for H. heterostomus by measuring all components of the energy budget C = F + A + P + R + E/ M. The components not directly affected by activity, consumption (C), production (P), and respiration (E), nitrogen excretion (N), and growth (G) were measured once during summer (June to August 1995) and once during winter (November 1995 to January 1996), except for P, which was measured monthly (March 1995 to July 1996), and R, which was measured once at the end of the experiment (August 1996). The two components most affected by activity, respiration (R) and secretion of mucins (M), were estimated by developing summer (June 1995) and winter (December 1995) time budgets and then integrating amounts of time spent in each activity state with energy equivalents for each state.

Collection of Animals

Abalone were collected in Barkley Sound near the Bamfield Marine Station, Bamfield, British Columbia, and transported to the Shawna Point Marine Centre, Anacortes, WA. They were held in a large tank with a constant supply of fresh seawater and fed alfalfa on Nereocystis leutkeana, a preferred kelp food (Paul et al. 1997).

Time Budget

Activity states of H. heterostomus were monitored in both laboratory and field, and time budgets were determined from the amount of time spent in each activity state. To determine the activity states that appeared important to the energetics of H. heterostomus, we identified: (1) quiescent (shell held tightly to the substrate, no visible gill or mantle movements) associated with movements in a small area (0.01 m²), (2) active (shell and feet movements), and (3) feeding. The energy expenditure associated with the activity state was determined from the average daily energy consumption of each state. The total energy consumption was calculated by multiplying the dead energy of all samples of kelp by the energy content per gram wet mass of the kelp.

Feces Production (F)

Abalone (n = 5; 20–128 g live mass) were held individually in 1.4-L aerated plastic containers filled with filtered (5 µm pore size) seawater at ambient temperature over a 4-day period. Samples of kelp were fed to the abalone on the first day, and seaweed remnants were removed and weighed on the following day. The abalone were kept in the containers for three more days, during which feces were collected daily. The feces were dried at 90°C to constant mass and then combusted in a microbomb calorimeter.

Nitrogen Excretion (E)

Abalone were placed in sealed containers maintained at ambient temperature. Duplicate 1-mL aliquots of the water in the containers were collected after 1 h and analyzed for urea (Solorzano 1969). Because nitrogen excretion by H. heterostomus is low and difficult to quantify, excretion measurements were made at 4°C and 20°C, and the nitrogen excretion at 20°C was extrapolated to 4°C using an Arrhenius relationship. Nitrogen excretion was measured at 9 and the values were extrapolated to a 24-h period. Energy costs (J day⁻¹) were calculated from nitrate (mg N) from Nike (1977) and energy budget.

Somatic Growth (P) and Reproductive Growth (P)

Mass and length of each abalone were recorded monthly for the duration of the experiment (16 mo). At the end of the experiment, when each abalone was ready to spawn, April 1996, they were weighed, a final time, and removed from the tanks.

Consumption (C)

Abalone were kept in plastic mesh cages and fed pieces of kelp of known wet mass each day at 3 pm on a 4-day period. Un eaten kelp was removed each following day. Each day, three pieces of kelp were placed in empty cages as controls and change of mass was recorded. The mass of the unaltered kelp from each abalone’s cage was subtracted from the initial mass of the piece, and the result was corrected for any differences in mass exhibited by the mean of the controls to determine the wet mass of kelp consumed.

To determine the energy content of food eaten, samples of kelp were weighed fresh and then dried at 60°C to constant mass. The total energy consumed by each abalone was determined by multiplying the dead energy of consumed kelp by the energy content per gram wet mass of the kelp.

RESULTS

Energy Allocation in Abalone

Respiration (R)

On the basis of the time budget, four states of activity were identified as those most often exhibited by H. heterostomus (quiet, alert, feeding, and combing). Because we were unable to induce abalone tofeeding in the respirometer, we assumed that energy expenditure during the various states of activity was constant and comparable to that expended during the active state, which could be measured.

To assess the extent of increase in oxygen consumption from quietness to alertness and active states, abalone (n = 31; 13–144 g live mass) were placed in round, Perspex respirometry chambers. Temperature was maintained at 10°C, and oxygen consumption was monitored continuously with a polarographic oxygen electrode connected to an oxygen analyzer (Yellow Springs Instrument Company). The state of the animal (quiet, alert, active) was recorded every 2 min during the duration of the trial. Often, each animal did not exhibit all states during one trial, so animals were placed in the respirometer multiple times over a period of several days (separated by at least 48 h). Thus, oxygen consumption for each state was determined over 4–8 times, permitting an average for each state to be calculated. Energy costs (J·h⁻¹) were calculated from oxygen consumption (µL of O₂·h⁻¹) by multiplying by an oxygen equivalent mass of 20.89 mg·µL⁻¹·h⁻¹ (Clark and Devlin 1975). This represents a weighted value for the carbohydrate, protein, and fat based on the proportion of each foodstuff in L. topaziana.

Summer and winter quiescent metabolic rates of abalone (n = 20; 13–175 g live mass) were measured individually over 1-h periods in respirometers as described above. The extent of increase in oxygen consumption from quiescent to alert and active state, determined above, was then applied to these summer and winter quiescent measurements to compare energy consumption of different activity states at different times of the year. Energy expenditure during cawing was determined from Donovan and Carefoot (1997).

Production of Mucus (M)

Secretion of mucus was measured for two aspects of activity: adhesion to the substratum and locomotion. The amount of mucus needed for substratum adhesion during summer and winter was determined by allowing individual abalone (n = 20; 13.75–175 g live mass) to attach to a clean glass plate immersed in a tank supplied with fresh seawater. After an abalone had been stationed for 10 min after attachment, the amount of mucus was determined by adding salt to the plate until the salt resisted and dried at 60°C for 30 min. The dried mucus was carefully scraped from the plate, and its carbon content was determined (NAEA: 1981 Analytical Analyst: Carlos Erba Strumentazione, Cuneo). Mass of carbon (µg) was converted to dry mass of mucus (µg) by assuming that gastropod pedal mucus was 24.5% carbon (Peck et al. 1993). The mass of carbon converted to energy (J·day⁻¹) was assumed a conversion of 23.97 J·g⁻¹ of mucus (Calow 1974). Secretion of mucus during cawing was determined from Donovan and Carefoot (1997).

Laboratory Activity

During the summer, definite diurnal trends were seen, with greater locomotion during the night (18%) and increased quiescence during the day (only 1–2% cawing; Fig. 1, top). Peak quiescence occurred during daytime, with usually 50% or more abalone being in this state. The abalone fed steadily throughout the day because kelp was plentiful in the tank.

During the winter, abalone were more quiescent and less active than in the summer, and there was less of a diurnal trend (Fig. 1, bottom). Peak locomotion was from 7 pm to 10 pm, and the percent cawing was no greater than 2–6%. Throughout the day, 50% or more of the abalone were quiescent, with an increase in alertness occurring during the period from 5 pm to 11 pm. Time
spent by an average laboratory-held abalone at each activity during summer and winter is shown in Table 1.

Field Activity

Abalone exhibited more activity in the warm summer months (Fig. 2). For example, about 20% of all abalone were observed to be crawling during June, August, and October. Few animals were crawling during the winter months; instead, they were most often quiescent or alert. No animals were observed feeding.

Videotaped Crawling Activity

Locomotion was not continuous, and the average abalone stopped and started again twice for every meter moved. Average rate of crawling was 1 body length min⁻¹.

**TABLE 1.**

Average amount of time spent each day by *H. kantshakana* in different activity states during summer and winter.

<table>
<thead>
<tr>
<th></th>
<th>Quiescent</th>
<th>Alert</th>
<th>Feeding</th>
<th>Crawling</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>9.8</td>
<td>12.0</td>
<td>0.7</td>
<td>1.5</td>
<td>24</td>
</tr>
<tr>
<td>Winter</td>
<td>15.8</td>
<td>5.5</td>
<td>2.3</td>
<td>0.4</td>
<td>24</td>
</tr>
</tbody>
</table>

Figure 2. Field activity of *H. kantshakana* during daytime in Barkley Sound, British Columbia from April 1994 to April 1995.

**Energy Budgets**

There were no differences in values for any of the energy budget components between male and female abalone (all t < 2.0, all p > 0.06), save for some aspects of reproduction. Gonad energy content was higher in females than in males (females, 23.4 ± 0.4 mg of dry gonad mass⁻¹ ± 0.9 SE; males, 20.0 ± 0.5; t = 3.21, p = 0.01). However, there was no gender difference in total gonad mass (females, 10.3 mg of dry gonad mass g live abalone mass⁻¹ ± 1.7 SE; males, 9.4 ± 1.6; t = 0.38, p = 0.71) and ultimately no difference in yearly reproductive energy expenditure (females, 4.2 kJ y⁻¹ ± 0.7 SE; males, 2.8 ± 0.3; t = 1.89, p = 0.09). Thus, values for both males and females were combined for the regressions of energy budget components on mass.

Regression equations for the five energy budget components not directly affected by activity (C, F, U, Pᵣ, and Pₑ) are presented in Table 2. None of the slopes of the summer regression equations were significantly different from the winter regressions (all t < 0.66, all p < 0.10), except for the slopes of somatic growth on mass (t = 2.02, p < 0.05). However, all y-intercepts of the summer regressions were significantly higher than those of the winter regressions (all t > 3.44, all p < 0.005). Thus, except for somatic growth, the scaled relationship between energy and size remained constant between summer and winter, but summer values were greater than winter values.

Oxygen consumption increased with activity level over a wide range of abalone mass (Fig. 3). The slopes of the log₁₀-log₁₀ transformed regressions of oxygen consumptions on mass for quiescent, alert, and active abalone were not significantly different ($F_{10,0.05,2.892} = 0.43$, p > 0.05; analysis of covariance [ANCOVA]), but the y-intercepts were ($F_{10,0.05,2.892} = 32.7$, p < 0.001; ANCOVA). For a 50-g abalone, then, oxygen consumption increased 33% from quiescent to alert, and by a further 29% from alert to active.

Regressions of log₁₀ respiratory energy on log₁₀ mass during summer and winter for quiescent abalone are described by the equations log₁₀R = 0.34 + 0.74 log₁₀m ($r^2 = 0.77$, t = 7.70, p <
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Figure 1. Seasonal differences in activity of H. kantschinka in the laboratory.

There were no differences in values for any of the energy budget components between male and female abalone (all \( p > 0.06 \)), save for some aspects of reproduction. Gonad energy content was higher in females than in males (females, 23.4 \( \mathrm{mg} \) of dry gonad mass \( \pm 0.9 \) SE; males, 20.0 \( \pm 0.5 \); \( t = 3.21, p = 0.01 \)). However, there was no gender difference in total gonad mass (females, 10.3 mg of dry gonad mass g\(^{-1}\) live abalone mass; \( t = 2.7 \) SE; males, 9.4 \( \pm 1.6 \); \( t = 0.38, p = 0.71 \)) and ultimately no difference in yearly reproductive energy expenditure (females, 4.2 kJ d\(^{-1} \) g\(^{-0.7} \) SE; males, 2.8 \( \pm 0.3 \); \( t = 1.89, p = 0.09 \)). Thus, values for both males and females were combined for the regressions of energy budget components on mass.

Table 1 presents the time budgets for the five energy budget components not directly affected by activity (C, F, U, P\(_{0}\), and P\(_{1}\)) are presented in Table 2. None of the slopes of the summer regression equations were significantly different from the winter regressions (all \( p > 0.06 \), all \( p > 0.10 \)), except for the slopes of somatic growth on mass growth (\( t = 2.02, p < 0.05 \)). However, all \( y \)-intercepts of the summer regressions were significantly higher than those of the winter regressions (all \( t > 3.44, p < 0.005 \)). Thus, except for somatic growth, the scaled relationship between energy and size remained consistent between summer and winter, but summer values were greater than winter values.


### TABLE 1

<table>
<thead>
<tr>
<th>Time (h)</th>
<th>Season</th>
<th>Quiescent</th>
<th>Alert</th>
<th>Feeding</th>
<th>Crawling</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Summer</td>
<td>9.8</td>
<td>12.0</td>
<td>0.7</td>
<td>1.5</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>15.8</td>
<td>3.5</td>
<td>2.3</td>
<td>0.4</td>
<td>24</td>
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</tbody>
</table>

### TABLE 2

<table>
<thead>
<tr>
<th>Energy Budget Component</th>
<th>Log (E)</th>
<th>Log (M)</th>
<th>Log (A)</th>
<th>Log (P)</th>
<th>Log (C)</th>
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<tr>
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<td>Winter</td>
<td>0.70</td>
<td>0.76</td>
<td>0.78</td>
<td>0.77</td>
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### DISCUSSION

In order to assess the effect of activity on the seasonal energy budgets of H. kantschinka, daily respiratory energy expenditure and secretion of mucus in the absence of activity must be estimated. For respiratory energy, this can be accomplished by extrapolating summer and winter quiescent energy equivalents (40 and 24 h\(^{-1} \)) over a 24-h period. Thus, a 50-g abalone would consume 241.5 h\(^{-1} \) in the quiescent state, 32.2 h\(^{-1} \) in the alert state, and 41.7 h\(^{-1} \) in the active state. Additionally, respiratory energy expenditure during diurnal locomotion can be estimated from the consumption of energy at 8.1 m\(^{-3} \) noted above to get an overall energy cost of 13.3 h\(^{-1} \).

Values for daily respiratory energy expenditure and secretion of mucus for a 50-g abalone during summer and winter are presented in Table 3. These calculations combine the time budgets from Table 1 with the energetic costs of the different activity states. In turn, these secretion and respiration of mucus values are presented with values for the other energy budget components (calculated from the regressions in Table 2 for a 50-g abalone) in Table 4.

### Figure 2

Figure 2. Field activity of H. kantschinka during daylight in Barkby Sound, British Columbia from April 1994 to April 1995.

### Figure 3

Figure 3. Regressions of log\(_{10}\) energy expenditures (J h\(^{-1} \)) on log\(_{10}\) mass for abalone at three activity states. Regression equations are quiescent energy consumption: \( y = -2.82 + 0.67 \log_{10} \text{mass} \), alert energy consumption: \( y = -2.78 + 0.76 \log_{10} \text{mass} \), active energy consumption: \( y = 2.53 + 0.63 \log_{10} \text{mass} \). All regressions were significant (all \( r > 11.26, p < 0.001 \)).
TABLE 3.
Total daily respiratory and energy expenditures of mucus for a 50-g abalone.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Time (h)</th>
<th>Energy Equivalents (J h⁻¹)</th>
<th>Distance Moved (m day⁻¹)</th>
<th>Cost of Transport (J m⁻¹)</th>
<th>Total Energy (J day⁻¹)</th>
<th>No. of Adherences Per Day</th>
<th>Energy Equivalents (J adherence⁻¹)</th>
<th>Distance Moved (m day⁻¹)</th>
<th>Energy Equivalent (J m⁻¹)</th>
<th>Total Energy (J day⁻¹)</th>
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<td>Summer</td>
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<tr>
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<td>48</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quiescent</td>
<td>15.8</td>
<td>24</td>
<td></td>
<td></td>
<td>379</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alert</td>
<td>5.5</td>
<td>32</td>
<td></td>
<td></td>
<td>176</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feeding</td>
<td>2.3</td>
<td>41</td>
<td></td>
<td></td>
<td>94</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crawling</td>
<td>2</td>
<td>8</td>
<td></td>
<td></td>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The daily time budget (Table 1) was integrated with energetic costs of each activity. Summer and winter quiescent respiratory energy rates (J h⁻¹) were calculated from regressions of respiratory energy on mass (see Text for regression equations). Alert and feeding rates (the latter assumed to be equivalent to active rates) were calculated from increases over quiescent rates determined by measuring oxygen consumption during different activity states. Distance moved (m day⁻¹) was calculated from average time spent crawling (1.5 h in summer, 0.4 h in winter; Table 1) and average crawling rate (7.1 cm min⁻¹; videotape data). Energetic cost of this movement (cost of transport) was estimated from Donovan and Carefoot (1997). Number of adherences per day was estimated from number of crawling bouts per minute over total distance (videotape data), and energy equivalent of mucus was estimated from Donovan and Carefoot (1997).

Predators of H. kantschakana include octopus, crabs, fish, and sea stars (Sloan and Breen 1988), and H. kantschakana exhibits a dramatic crawling escape response in the presence of the seastar Pycnopodia helianthoides. Our comparison of activity levels in laboratory and field also supports the idea that field abalone are more active than laboratory-held abalone. During observations of field abalone by SCUBA divers in June, 19% of all abalone observed were crawling during daytime. This was not the case during the daytime summer observations in the laboratory, where only 2–5% of abalone were crawling. Winter daytime values were closer to each other, with 5% of abalone crawling in the field in both December and February and 0–2% crawling in the laboratory.

As expected, values of summer and winter energy budget components differed for H. kantschakana, much of it due to differences in activity level. For a representative 50-g abalone, winter consumption was only 45% of summer consumption, with nearly all consumed energy going toward maintenance (R, M, and U: Table 4). The largest component of the winter energy budget was respiration, accounting for 77% of all consumed energy. Respiration was also the largest component of the summer budget, but the proportion of consumed energy going toward this component was only 59%, owing to increases in somatic and reproductive growth. Costs of mucus were nine times greater in summer than winter, and mucus accounted for 16% of consumed energy during summer. The proportions of energy lost as feces and nitrogenous waste remained relatively constant between summer and winter. For the summer budget, all energy consumed was accounted for (actually, overestimated by 3%), and for the winter budget, 94% was accounted for.

Two other energy budgets for abalone, one by Peck et al. (1987) for the European abalone Haliotis tuberculata and one by Barkai and Griffiths (1988) for the South African abalone Haliotis midae, are shown in Table 5. Our summer energy budget (Table 4) can be compared with that of Peck et al. (1987), who appear to have determined a summer energy budget for their species on the

TABLE 4.
Values for each component of summer and winter energy budgets for a representative 50-g H. kantschakana.

<table>
<thead>
<tr>
<th>Energy (J day⁻¹)</th>
<th>% Total of C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>F</td>
</tr>
<tr>
<td>Summer</td>
<td>1,894</td>
</tr>
<tr>
<td>% of C</td>
<td>18</td>
</tr>
<tr>
<td>Winter</td>
<td>850</td>
</tr>
<tr>
<td>% of C</td>
<td>13</td>
</tr>
</tbody>
</table>

Values for components not directly affected by activity (C, F, U, P₈, and P₉) were calculated from regressions from Table 2. Values for respiration (R) and mucus (M) are from Table 3.

TABLE 5.
Energy budgets for three species of abalone expressed as percentages of C.

<table>
<thead>
<tr>
<th>Species</th>
<th>F</th>
<th>U</th>
<th>P₈</th>
<th>P₉</th>
<th>R</th>
<th>M</th>
<th>% of C</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. kantschakana*</td>
<td>18</td>
<td>&lt;1</td>
<td>6</td>
<td>3</td>
<td>59</td>
<td>16</td>
<td>103</td>
</tr>
<tr>
<td>H. tuberculata†</td>
<td>18</td>
<td>1</td>
<td>13</td>
<td>4</td>
<td>27</td>
<td>26</td>
<td>89</td>
</tr>
<tr>
<td>H. midae‡</td>
<td>63</td>
<td>&lt;1</td>
<td>5</td>
<td>8</td>
<td>16</td>
<td>10</td>
<td>76</td>
</tr>
</tbody>
</table>

Percentages of respiration and mucus from this study were calculated from the summer activity budget and summer energy budget. The percentages for H. tuberculata were calculated from regression equations in Peck et al. (1987) for animals of a size similar to the representative 50-g abalone used for this study. The proportions for H. midae have no entry of mucus and P₈ and P₉ were estimated as a single value.

* This study.
† Peck et al. (1987).
‡ Barkai and Griffiths (1988).


**TABLE 3.** Total daily respiratory and energy expenditures of a 54-g albatross.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Energy (J/day)</th>
<th>Distance Moved (m/day)</th>
<th>Cost of Transport (L O2/J)</th>
<th>Total (J/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Respiration (R)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Simulated</td>
<td>70</td>
<td>82</td>
<td>3.7</td>
<td>115</td>
</tr>
<tr>
<td>Actual</td>
<td>34</td>
<td>108</td>
<td>2.9</td>
<td>223</td>
</tr>
<tr>
<td><strong>Feeding (F)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water</td>
<td>15</td>
<td>25</td>
<td>0.6</td>
<td>105</td>
</tr>
<tr>
<td>Land</td>
<td>23</td>
<td>41</td>
<td>0.4</td>
<td>94</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td>406</td>
</tr>
</tbody>
</table>

**Table 3.** Total daily respiratory and energy expenditures of a 54-g albatross. The daily energy budget (Table 3) was integrated with energetic costs of each activity, e.g., expression of respiratory energy as oxygen cost. Total for each albatross reported. During observations a field albatross by SCUBA divers in June, 19% of all albatross observed were swimming during daytime. This was not the case during the daytime summer observations in the laboratory, where only 2-5% of albatross were swimming. Water daytime velocities were closer to each other, with 5% of albatross swimming in the field in both December and February and 0-2% in these observations. As expected, values of summer and winter energy budget components differed for H. kermadecensis, much of it due to differences in distance physical activity. A representative 50-g albatross, winter consumption was only 45% of all consumed energy, whereas summer consumption, accounting for 77% of all consumed energy. Respiration was also the largest component of the summer budget, but the proportion of consumed energy going toward this component was only 55%, owing to increases in somatic and reproductive growth.

**LITERATURE CITED**


