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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 mucus, 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 9.8 h day^{-1} quiescent, 12.0 h day^{-1} alert, 0.7 h day^{-1} feeding, and 1.5 h day^{-1} crawling during the summer, and 15.8 h day^{-1} quiescent, 5.5 h day^{-1} alert, 2.3 h day^{-1} feeding, and 0.4 h day^{-1} crawling during the winter. Videotapes 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, $C = F + U + P_g + P_r + R + M$ were measured during summer and winter months. None of the slopes of regressions of $\log_{10}$energy (J day^{-1}) on $\log_{10}$mass (g) was significantly different between summer and winter for any of the energy budget components, except those of somatic growth on mass. Summer *y*-intercepts were all significantly higher than winter *y*-intercepts, indicating that energy consumption and expenditure 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: abalone, activity, energy budget, *Haliotis kamtschatkana,* secretion of mucus

INTRODUCTION

Increasing world demand for abalone has caused severe declines in most populations, including those of British Columbia's *Haliotis kamtschatkana* (Emmett 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 density (Breen 1986, Emmett and Jamieson 1988), suggesting that this may be a feasible strategy to enhance depleted British Columbia stocks. Successful reintroduction and stock enhancement will depend on identification of suitable habitat, which will in turn depend on complete knowledge of the biology of the abalone. Emmett and Jamieson (1988) 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 and, 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 motility (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 (Schiel and Welden 1987).

Activity is energetically costly to gastropods because of both increased metabolic rate and secretion of mucus. Many studies have shown a rise of oxygen consumption ($\dot{V}O_2$) during activity in gastropods (Newell and Roy 1973, Calow 1974, Fitch 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 (Denny 1980, Houlihan and Innes 1982, Innes and Houlihan 1985, Donovan and Carefoot 1997). Calow (1974) estimated that 20% of ''routine metabolism'' of the pulmonate snail *Planorbis contortus* was devoted to activity. Likewise, several authors have pointed out the importance of mucus as a contribution to molluscan energy expenditure (Paine 1971, Calow 1974, Horn 1986, Davies et al. 1990), and Denny (1980) attributes the relatively high energetic cost of gastropod crawling to production of mucus. Calow (1974) estimated production of mucus as 13–32% of absorbed energy in *P. contortus,* and Carefoot (1967) estimated that mucus accounted for 15% of the energy budget of the opisthobranch *Archidoris pseudoargus.*

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 Køfoed 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 energy budget at different times of the year. Indeed, Widdows and Bayne (1971) 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 $C = F + U + P_g + P_r + R + M$. The components not directly affected by activity, consumption (C), production of feces (F), nitrogen excretion (U), somatic growth (P_g), 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_g, 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 Marine 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 × 50 × 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 Phillipson 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

water in the containers were collected after 1 h and analyzed for (Solorzano 1969). Because nitrogen excretion by *H. kamtschatkana* does not fluctuate daily (Taylor and Carefoot unpubl.), nitrogen excretion was measured at 9 am and the values were extrapolated to a 24-h period. Energy costs (J day^{-1}) were calculated from micrograms of ammonia excretion by multiplying by 24.83 J mg of NH_3^{-1} (Elliot and Davison 1975).

Somatic Growth (P_g) and Reproductive Growth (P_r)

Mass and length of each abalone were recorded monthly for the duration of the experiment (16 mo). At the end of the experiment, when the animals were ready to spawn (August 1996), they were weighed a final time and removed from their shells. Each abalone was separated into five components: (1) shell, (2) pedal and adductor muscles with head and tentacles, (3) visceral mass including stomach, digestive gland, and gills, (4) gonad, and (5) hemolymph, mucus, and mantle water that drained off of the abalone during dissection. During dissection, the visceral mass was separated from the large pedal muscle and the gonad was removed from around the digestive gland by aspirating it into a clean glass vial. Wet mass of shell, muscle, viscera, and gonad was recorded for each animal. The soft tissues from each animal were homogenized individually and dried, and energy content was determined by combustion in a microbomb calorimeter. Shell caloric content was estimated from Paine (1971), assuming that abalone shell was 1.1% protein and protein has an energy value of 23.83 J mg^{-1}. Because it proved impossible to collect enough mucus and hemolymph from each animal for analysis, and lacking an estimate for the energy value of hemolymph, this mucus and hemolymph portion was assumed to be similar in energy value to pedal mucus (23.97 J mg^{-1}; Calow 1974).

Somatic growth was determined by regressing monthly mass of each abalone on time, with the slope of the regression being then a measure of growth (g mo^{-1}). This method was used, as opposed to subtracting final mass from initial mass and dividing by time, because there was considerable monthly fluctuation in wet mass. Mass change during winter (November to March) was compared with mass change during summer (April to October). Daily gain in live mass was converted to energy gain (J day^{-1}) by partitioning total gain in live mass into gain in mass of individual body parts (shell, muscle, and viscera) estimated from the proportion of whole mass that each of these tissues constituted. Each component was then multiplied by the energy content of the respective tissue.

An attempt was made to spawn the animals during summer (August 1995) with hydrogen peroxide (Morse et al. 1977). However, because only one animal spawned, energy devoted to reproduction (P_r) was estimated from gonad mass (including gametes) at the end of the experiment. Reproductive growth (J day^{-1}) was determined for each abalone by multiplying gonad mass by its energy content.

Respiration (R)

On the basis of the time budget, four states of activity were identified as those most often exhibited by *H. kamtschatkana* (quiescent, alert, feeding, and crawling). Because we were unable to induce abalone to feed in the respirometer, we assumed that energy expended during the feeding state was equivalent to that expended during the active state, which could be measured.

To assess the extent of increase in oxygen consumption from quiescent to alert and alert to active states, abalone (n = 21; 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 a computerized data acquisition system (Datacan; Sable Systems, Inc.). The state of the animal (quiescent, 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 measured 2–4 times, permitting an average for each state to be calculated. Energy costs (J h^{-1}) were calculated from oxygen consumption (μL of O_2 h^{-1}) by multiplying by an oxygen equivalent (Q_{ox}) of 20.88 J mL of O_2^{-1} (Elliot and Davison 1975). This represents a weighted value for the catabolism of carbohydrate, protein, and fat based on the proportion of each found in *N. luetkeana*.

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 extents of increase in oxygen consumption from quiescent to alert and alert to active, determined above, were then applied to these summer and winter quiescent rates to estimate energy expenditure during different activity states at different times of the year. Energy expenditure during crawling was determined from Donovan and Carefoot (1997).

Production of Mucus (M)

Secretion of mucus was measured for two aspects of activity: adherence to the substratum and locomotion. The amount of mucus needed for substratum adherence during summer and winter was determined by allowing individual abalone (n = 20; 13–175 g live mass) to attach to a clean glass plate immersed in a tank supplied with fresh seawater. After an abalone had been stationary for 10 min after adherence, it was removed quickly from the plate. A 10-min period was chosen because Davies (1993) found that stationary limpets stop producing mucus within 10 min after attachment. 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 was determined (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). Dry mass of mucus was converted to energy (J), assuming a conversion of 23.97 kJ g^{-1} of mucus (Calow 1974). Secretion of mucus during crawling was determined from Donovan and Carefoot (1997).

RESULTS

Time Budgets

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% crawling; 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 generally from 7 pm to 12 am, but the percent crawling was no greater than 2–6%. Throughout the day, 60% or more of the abalone were quiescent, with an increase in alertness occurring during the period from 5 pm to 11 pm. Time

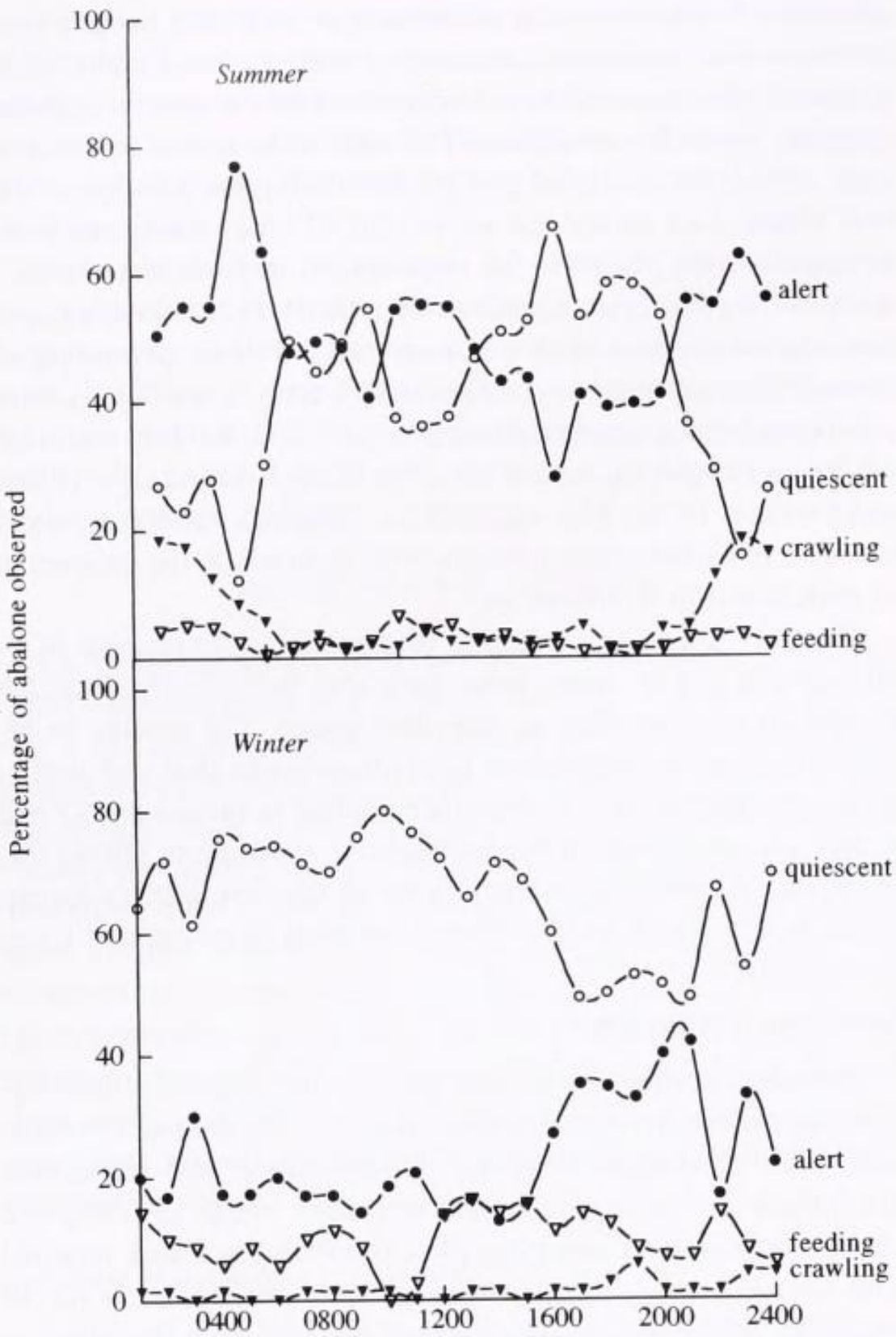

Figure 1. Seasonal differences in activity of *H. kamtschatkana* in the laboratory.

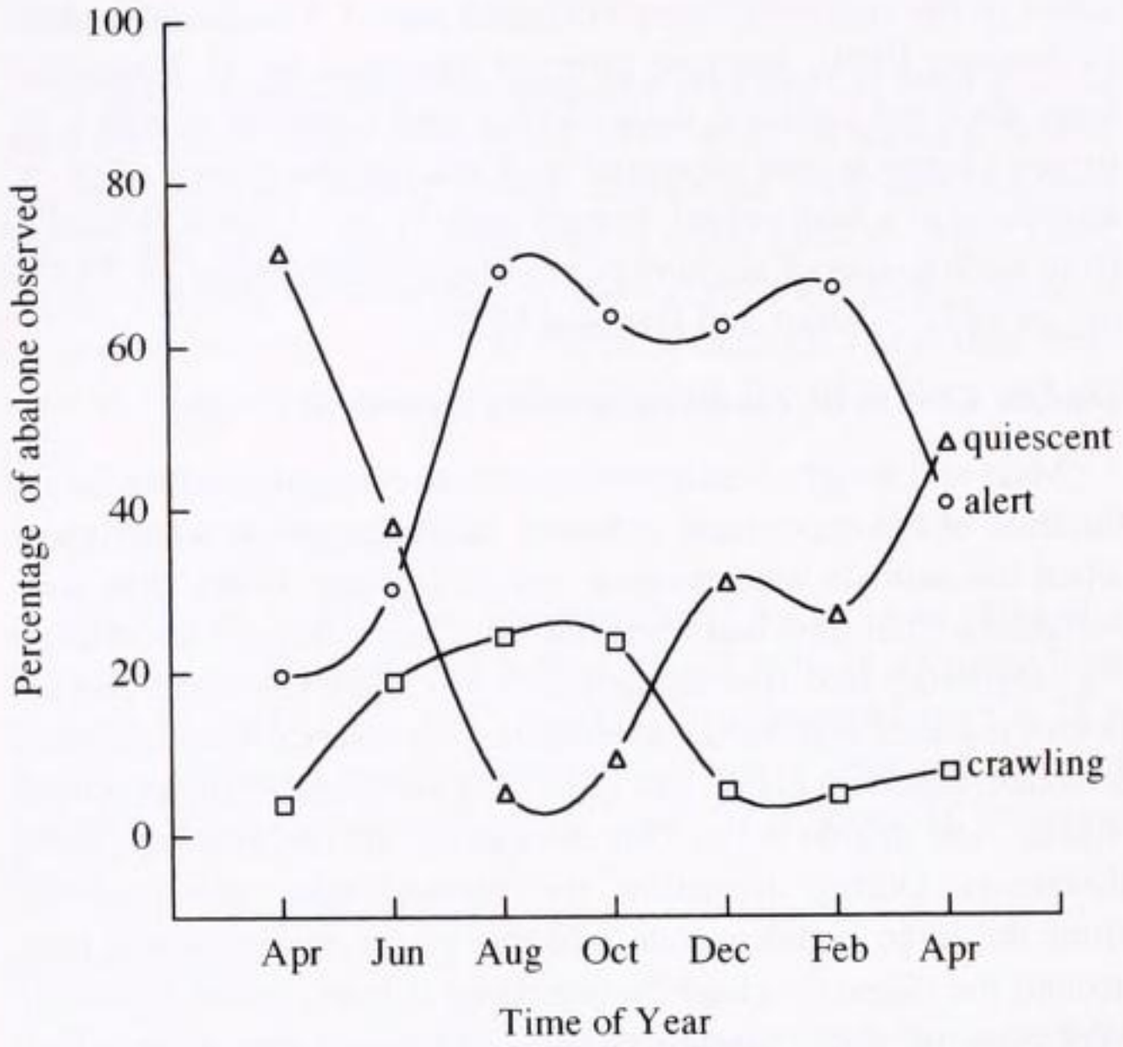

Figure 2. Field activity of *H. kamtschatkana* during daytime in Barkley Sound, British Columbia from April 1994 to April 1995.

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. kamtschatkana* in different activity states during summer and winter.

	Time (h)				
Season	**Quiescent**	**Alert**	**Feeding**	**Crawling**	**Totals**
Summer	9.8	12.0	0.7	1.5	24
Winter	15.8	5.5	2.3	0.4	24

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 J 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, P_g, and P_r) 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 $\log_{10}$-$\log_{10}$ transformed regressions of oxygen consumptions on mass for quiescent, alert, and active abalone were not significantly different ($F[_{0.05(2),2,56}] = 0.43$, $p > 0.05$; analysis of covariance [ANCOVA]), but the y-intercepts were ($F[_{0.05(2),2,56}] = 32.7$, $p < 0.001$; 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 $\log_{10}$ respiratory energy on $\log_{10}$ mass during summer and winter for quiescent abalone are described by the equations $\log_{10}R = 0.34 + 0.74 \log_{10}m$ ($r^2 = 0.77$, $t = 7.70$, $p <$

TABLE 2.

Regression statistics for the components of summer and winter energy budget components that are not directly affected by activity for the abalone *H. kamtschatkana* (n = 20).

Energy Budget Component (*Y*)	log*a*	*b*	r^2	*t*	p*
Summer					
Consumption (C)	2.19	0.64	0.59	5.15	<0.001
Feces (F)	1.45	0.64	0.59	5.15	<0.001
Nitrogen (U)	−1.19	0.61	0.21	2.11	0.050
Somatic growth (P_g)	1.08	0.56	0.33	2.72	0.016
Reproductive growth (P_r)	0.45	0.79	0.60	4.20	0.001
Winter					
Consumption (C)	2.00	0.55	0.46	3.68	0.002
Feces (F)	1.11	0.55	0.46	3.68	0.002
Nitrogen (U)	−2.03	0.91	0.27	2.56	0.020
Somatic growth (P_g)	−2.39	1.33	0.57	3.99	0.002

Regression statistics are for the equation $\log Y = \log a + b \log m$, where Y is an energy budget component in J day^{-1} and m is mass in g.
* Values are derived from student's *t*-tests.

0.001) and $\log_{10}R = 0.05 + 0.78 \log_{10}m$ ($r^2 = 0.73$, $t = 6.97$, p < 0.001), respectively, where R represents respiratory energy (J h^{-1}) and m represents mass (g). When respiratory energy expended by a 50-g abalone, calculated from these equations, is combined with increases measured in respiratory energy for the different activity states, it can be seen that during the summer, a 50-g abalone will expend 40 J h^{-1} in the quiescent state, 53 J h^{-1} in the alert state, and 68 J h^{-1} in the active state. Additionally, respiratory energy expenditure during crawling can be estimated from the cost of transport of *H. kamtschatkana*. The total cost of transport of a 50-g *H. kamtschatkana* crawling at one shell length·min^{-1} (7.1 cm min^{-1}) is 169 J $kg^{-1}m^{-1}$ (calculated from the multiple regression of $\log_{10}$ total cost of transport on $\log_{10}$ mass and $\log_{10}$ speed; Donovan and Carefoot 1997). Thus, a 50-g abalone uses 8 J m^{-1} while crawling.

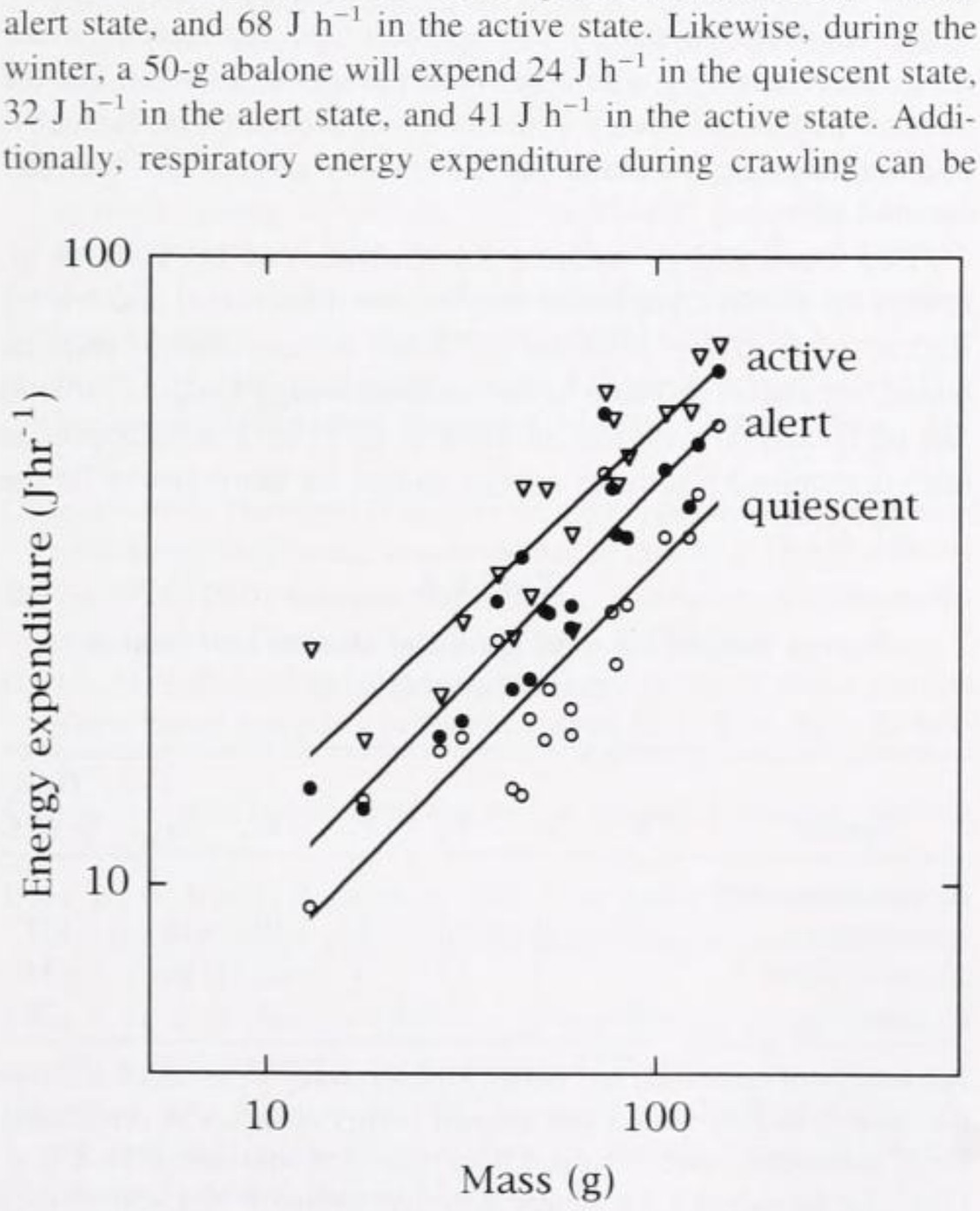

Figure 3. Regressions of $\log_{10}$ energy expenditure (Jh^{-1}) on $\log_{10}$ mass for abalone in three activity states. Regression equations are: quiescent $\log_{10}$energy = −2.82 + 0.67 $\log_{10}$mass; alert $\log_{10}$energy = −2.76 + 0.70 $\log_{10}$mass; active $\log_{10}$energy = −2.53 + 0.63 $\log_{10}$mass. All regressions were significant (all $t > 11.26$, all $p < 0.001$).

Amounts of energy lost as secretion of mucus on adherence to the substratum are described by the regression equations $\log_{10}M = -0.17 + 0.86 \log_{10}m$ ($r^2 = 0.46$, $t = 3.67$, p = 0.002) and $\log_{10}M = -0.65 + 0.85 \log_{10}m$ ($r^2 = 0.27$, $t = 2.60$, p = 0.018), for summer and winter animals, respectively, where M represents energy from secretion of mucus (J $adherence^{-1}$) and m represents mass (g). Thus, a 50-g abalone will expend 20 J of energy adhering to the substratum in summer and 6 J in winter. Abalone secrete 0.12 μg of dry mucus cm^{-2} foot area for every centimeter they crawl (Donovan and Carefoot 1997). A 50-g (71-mm) abalone has a foot area of 18 cm^2 (Donovan and Carefoot, 1997), which yields a secretion rate of mucus of 2.2 μg of dry mucus cm^{-1} crawled. This converts to 5 J m^{-1} lost as mucus during crawling, which can be added to the respiratory energy expenditure during crawling of 8 J m^{-1} noted above to get an overall energy cost of 13 J m^{-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 respiration and secretion 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.

DISCUSSION

In order to asses the effect of activity on the seasonal energy budgets of *H. kamtschatkana*, 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 J h^{-1}, respectively) over a 24-h period. Thus, a 50-g abalone would expend 960 J day^{-1}, during summer and 576 J day^{-1} during winter if it were completely quiescent. Daily secretion of mucus in the absence of activity can be estimated by assuming that the abalone adheres to the substratum once per day and then remains still. In that case, a 50-g abalone would expend 20 J day^{-1} during summer and 6 J day^{-1} during winter. This estimate of respiratory energy expenditure for inactive abalone would then represent 51% of total daily energy consumption in summer, compared with 59% when activity is accounted for (Table 4), a difference of 8%. Likewise, the estimate of secretion of mucus for an inactive abalone in summer would represent only 1% of daily consumption, rather than 16%, a difference of 15%. Thus, activity accounts for 23% of summer energy consumption. In the same manner, activity accounts for 13% of winter energy consumption.

In fact, because abalone crawl less in the laboratory than they do in the wild, we have probably underestimated the activity component of the energy budget of field *H. kamtschatkana*. Abalone are known to increase foraging activity when food is scarce (Poore 1972, Shepherd 1973, Sloan and Breen 1988), which did not occur in the laboratory. Likewise, field abalone must crawl to find refugia and escape predation. Shepherd (1986) has shown that motility of *Haliotis laevigata* is related to crevice space, with abalone increasing the amount they crawl until they find a suitable crevice.

TABLE 3.

Total daily respiratory and energy expenditures of mucus for a 50-g abalone.

Parameter	Time (h)	Energy Equivalents (J h^{-1})	Distance Moved (m day^{-1})	Cost of Transport (J m^{-1})	Total Energy (J day^{-1})		No. of Adherences per Day	Energy Equivalents (J $adherence^{-1}$)	Distance Moved (m day^{-1})	Energy Equivalent (J m^{-1})	Total Energy (J day^{-1})
Respiration (R)						Mucus (m)					
Summer						Summer					
Quiescent	9.8	40			392	Adherence	14	20			280
Alert	12.0	53			636	Crawling			6	5	30
Feeding	0.7	68			48						310
Crawling			6	8	48						
					1,124						
Winter						Winter					
Quiescent	15.8	24			379	Adherence	4	6			24
Alert	5.5	32			176	Crawling			2	5	10
Feeding	2.3	41			94						34
Crawling			2	8	16						
					665						

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 estimated 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 meter over total distance (videotape data), and energy equivalent of mucus was estimated from Donovan and Carefoot (1997).

Predators of *H. kamtschatkana* include octopus, crabs, fish, and seastars (Sloan and Breen 1988), and *H. kamtschatkana* 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. kamtschatkana*, 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. kamtschatkana*.

	Energy (J day-1)								
Season	C	F	U	P_g	P_r	R	M	Total	% Total of C
Summer	1,894	345	<1	108	62	1,124	310	1,949	
% of C		18	<1	6	3	59	16		103
Winter	860	111	<1	1	0	665	34	811	
% of C		13	<1	<1	0	77	4		94

Values for components not directly affected by activity (C, F, U, P_g, and P_r) 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.

Species	F	U	P_g	P_r	R	M	Total % of C
*H. kamtschatkana** (summer)	18	<1	6	3	59	16	103
H. tuberculata†	18	1	13	4	27	26	89
H. midae‡	63	<1	5		8		76

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 P_g and P_r were estimated as a single value.

* This study.

† Peck et al. (1987).

‡ Barkai and Griffiths (1988).

basis of their data for reproduction. *H. kamtschatkana* has a much higher respiration component than does *H. tuberculata* (59% of consumed energy compared with 27%, respectively), whereas *H. tuberculata* diverts more energy to growth and production of mucus. Interestingly, mucus was as large a component for *H. tuberculata* as was respiration, accounting for 26% of consumed energy, whereas it was less for *H. kamtschatkana* (16%). Barkai and Griffiths (1988) found that *H. midae* loses 63% of consumed energy to feces, a much larger proportion than measured for either *H. kamtschatkana* or *H. tuberculata* (both 18%). This is most likely because of the different kelp species used as food in the different studies. Kelp vary widely in morphological and physiological defenses to herbivory (Hay and Steinberg 1992, Lobban and Harrison 1997), resulting in digestibility differences for the herbivores. The respiration component for *H. midae* was only 8% of consumed energy, but the authors note that it would be higher if they had incorporated activity into their measurements. All three energy budgets indicate little energy lost to nitrogen excretion.

This study has shown that activity has potentially large effects on both summer and winter energy budgets of the abalone *H. kamtschatkana*. In the field, it is likely that more energy would be expended on activity, especially in areas where food is scarce or predation intense, and this has potential ramifications to the dynamics of abalone populations. In the case of predators, such as seastars, eliciting a crawling escape response, intense predation would not only affect population dynamics by increasing mortality, but could also cause decreased somatic growth and reproductive effort as energy is diverted from these energy budget parameters to respiratory and mucous components.

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