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Citation	, 50(2), 61-70
Issue Date	1999-08
Doc URL	http://hdl.handle.net/2115/24184
Type	bulletin (article)
File Information	50(2)_P61-70.pdf

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Energy Requirement for Metabolism in a Population of the Limpet *Lottia kogamogai* (Formerly *Collisella heroldi*)

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Abstract

The annual metabolic cost of the limpet *Lottia kogamogai* population was determined. Respiration rates (R : $\mu l\ O_2$/ind/h), both in air and water, were related to dry body weight (W : mg) and temperature (t : °C) by the functions : $R_t = (0.0321t + 0.0520) W^{0.7366}$ ($-1.5 \leq t \leq 27.5$, air) and $R_t = 10^{(0.0558t + 0.9663)} W^{0.7160}$ ($3 \leq t \leq 20$, water). The oxygen uptake per unit weight of *L. kogamogai* decreased as body size increased. The measurements for Q_{10} were 2.00 for aerial and 3.61 for aquatic respiration between 5 and 25°C. The annual energy cost due to respiration for the *L. kogamogai* population was 13.19 kcal/m² at Usujiri in southern Hokkaido.

Key words : Energy metabolism, *Lottia kogamogai*, Oxygen consumption, Aerial respiration, Aquatic respiration

Introduction

Limpets are important members of the rocky intertidal community. They feed chiefly by scraping rock surfaces with their long, toothed radula, rasping off the microscopic film of algae on rocks (Hawkins and Hartnoll, 1983), and are fed upon by intertidal carnivorous gastropods (Branch, 1978). Thus, limpets play an important role in the energy flow of the rocky intertidal ecosystem. For this reason, bioenergetic studies of limpets have received much attention (e.g., Branch, 1981). The energy required for metabolism is an important part in the energy budget of an animal. Some papers on energy requirements of metabolism for herbivorous gastropod populations have been published (Hughes, 1971a, b ; Wright and Hartnoll, 1981 ; Horn, 1986). However, most of the studies were carried out within a narrow range of temperatures. Furthermore, none of these works considered tidal rhythm when they applied the metabolic data of an individual to calculate the metabolic energy cost of the corresponding natural population.

A small limpet found in southern Hokkaido that was identified as *Collisella heroldi* (Dunker) in our previous studies (Niu and Fuji, 1989, Niu et al., 1992, 1994a, b), has since been corrected to *Lottia kogamogai* by Sasaki and Okutani (1994). This is a numerically dominant species in the rocky intertidal community at Usujiri, southern Hokkaido, Japan. In the present study, we measured the aerial and aquatic respiration rates of *L. kogamogai* within the range of temperatures they

usually experienced and calculated the metabolic energy requirement of the population with detailed tidal and temperature data collected from the field.

Methods

Study site

The present study was carried out along a rocky intertidal shore at Usujiri, Hokkaido (42°21′N : 140°57′E). Heights of the three tidal levels (MTL, MLWL, and MHWL) in this area were 95 cm, 43 cm and 143 cm, respectively. Salinity was relatively constant throughout the year (31.6–33.9‰, Niu et al., 1992).

Fig. 1 shows the seasonal changes in seawater temperature at the study site. Measurements were made daily at 8 : 00 am over a three-year period. Each dot represents the average value over a ten-day period. The lowest temperature recorded was approximately 3°C in February. The temperature rose to a peak of about 20°C in August and September. To examine the distinctly variable air temperature at the site, a recording thermometer, which continuously recorded the surrounding temperature, was placed at the site over a one-year period. Assuming the period from 6 : 00 am to 6 : 00 pm is daytime and the other period is nighttime, seasonal changes in air temperature at the site during daytime and nighttime are shown in Fig. 2. The lowest average value was about −1.5°C during nighttime in late February. Early September was the hottest period, with an average value of 27°C during daytime.

According to the tidal table, a close relationship was found between the average immersion and exposure times in every month and the tidal level. The relationship can be described as the following : $T = a_i + b_i H + c_i H^2 + d_i H^3$, where $T (0 \leqq T \leqq 12$ hours) is exposure time, H is tidal level (cm) and a_i, b_i, c_i, d_i are constants in i-th month, which can be calculated from the tidal table. Using the above equation and
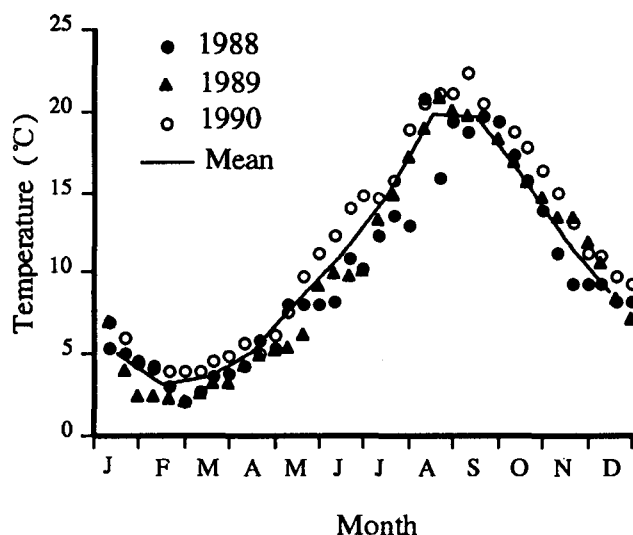

Fig. 1. Seasonal changes in the seawater temperature at Usujiri, southern Hokkaido.
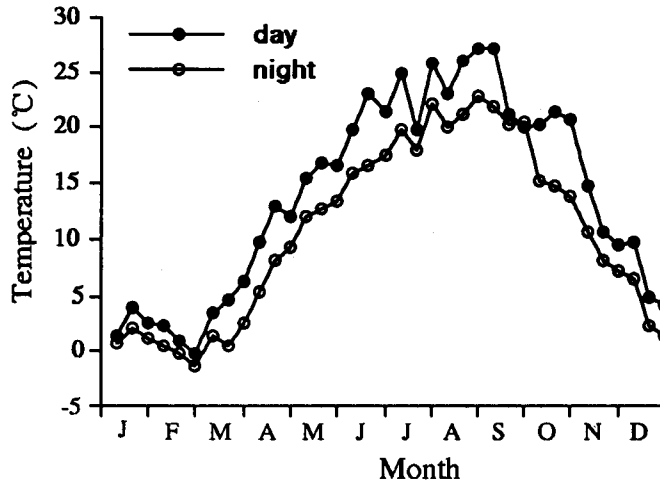
Fig. 2. Seasonal changes in daytime and nighttime air temperatures at Usujiri, southern Hokkaido.

Table 1. Seasonal changes in exposure (day and night) and immersion time (h) at an average height (57.64 cm) of the sampling stations in the intertidal area at Usujiri. ETD: exposure time during day, ETN: exposure time during night, IT: immersion time.

Month	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
ETD	3.58	4.79	7.10	8.04	7.79	7.22	6.04	4.95	4.45	4.65	4.39	3.92
ETN	6.60	6.11	6.45	5.19	3.44	2.82	2.65	3.67	5.06	6.95	7.86	7.77
IT	13.82	13.10	10.46	10.78	12.77	13.96	15.31	15.37	14.49	12.40	11.74	12.31

the mean height 57.64 cm at the sampling stations, the mean exposure times during day and night and the immersion time for one tidal cycle each month were calculated and are shown in Table 1.

Measurement of respiration

Once every two months, limpets with a wide range of body weights were collected randomly from the entire sampling area during exposure time at low tide, transferred to the laboratory, cleaned with seawater, and aged using the methods described in Niu et al. (1992). Aquatic respiration was measured for 2-8 limpets of the same age and similar body weight.. Limpets were placed in 300-ml respiratory chambers (glass jars with airtight screw tops) filled with seawater. For each age group, 3-5 chambers were examined. All chambers were kept inside an incubator at one of five temperatures (5, 10, 15, 20 and 25°C), which was closest to the temperature in the field at the experimental period. Limpets were allowed to adapt to the experimental temperature and starved for at least 5 hours before the experiment. The seawater in each chamber was then replaced with water of the same temperature. The dissolved oxygen content was determined by the Winkler method. The difference between the experimental chamber and the control was the amount of

oxygen consumed by the experimental limpets. Aerial respiration was measured at the same temperature after aquatic respiration. A constant pressure respirometer was used. Incubation time was also more than 5 hours. After all experiments, limpets were killed and their shells were removed. They were then dried, and their dry body weights were measured.

Data analysis

The regressions of log (oxygen consumption (μl O_2/ind/h)) against log (dry body weight (mg)) were calculated for all temperatures. A multiple regression equation describing the relationship among oxygen consumption, body weight and water temperature was calculated. Combining the multiple regression equation, immersion and exposure (day and night) times during one tidal cycle (Table 1), corresponding water temperature and air temperature at day and night (Figs. 1 and 2), and the mean dry body weight of each age group of limpets every month (Fig. 1 in Niu et al., 1994b), the daily oxygen consumption (μl O_2/ind/day) of an individual was calculated for each month. An oxycalorific coefficient of 4.83 cal/ml O_2 at N.T.P. (Hughes, 1971b) was applied to calculate the daily metabolic loss (cal/ind/day) through respiration.

The annual energy requirement for metabolism of the *L. kogamogai* population was estimated from density data (Niu et al., 1992), and the daily metabolic loss data of an individual in each month. The following equation was used:

$$R_a = \sum_{i=0}^{5} \sum_{j=1}^{12} N_{ij} \; R_{ij} \; D_j$$

where R_a is the mean annual metabolic loss of the *L. kogamogai* population, N_{ij} is the number of individuals per m² of i age in j-th month, R_{ij} is the daily metabolic loss i age individual in j-th month, and D_j is the number of days in j-th month.

Results

Relationship of weight-specific oxygen consumption to body weight

Fig. 3 shows the relationship between weight-specific oxygen consumption and the body weight of *L. kogamogai* at 15°C both in water and in air. It is clear that the oxygen uptake per unit weight of the limpet decreases as body weight increases. Weight-specific oxygen consumption is higher in air than in water for an individual. The relationship is similar at other temperatures.

Relationship of respiration rate, body weight, and temperature

The relationship between respiration rate and body weight of *L. kogamogai* at different temperatures is presented in Figs. 4 and 5, with the equations shown in Table 2. Correlation variance analyses of these regression lines are shown in Table 3. There was no statistical difference among their slopes, but distinct differences were found among their intercepts. The slopes were pooled and gave joint slopes of 0.72 and 0.74 for aquatic and aerial respiration, respectively. Consequently, the regression lines were recalculated assuming a uniform slope of 0.72 for aquatic and 0.74 for aerial respiration. We found that the intercepts of these recalculated regressions have a close relationship with temperature ($r^2 = 0.94$, $P < 0.05$ for aquatic
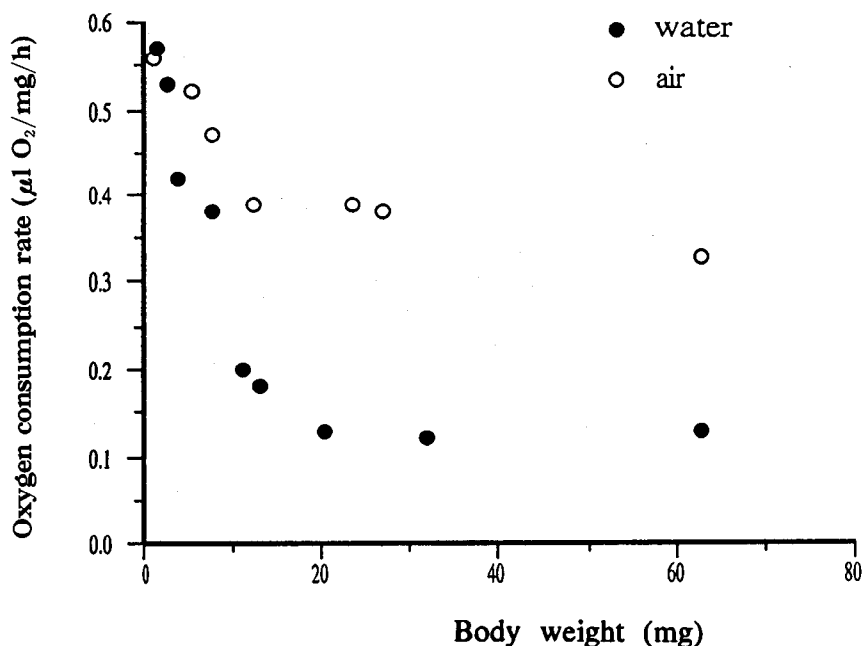
Fig. 3. The relationship between dry body weight and specific oxygen consumption rate both in water and air at 15°C.

and $r^2 = 0.84$, $P < 0.05$ for aerial respiration).   The relationship among aquatic and aerial oxygen consumption rates, dry body weight and temperature can be described by the following multiple-regression equations :

Aquatic oxygen consumption :

$$R_t = 10^{(0.0558t-0.9663)} W^{0.7160} \tag{1}$$

Aerial oxygen consumption :

$$R_t = (0.0371t + 0.0520) W^{0.7366} \tag{2}$$

where R_t = oxygen consumption (μl O_2/ind/h) at t °C ; W = dry body weight (mg) ; t = temperature (°C), $3°C \leq t \leq 20°C$ (water) and $-1.5°C \leq t \leq 27.5°C$ (air).

Q_{10} in the temperature range 5-25°C

Based on equation (1), in the temperature range 5-25°C, the Q_{10} for aquatic respiration was calculated as :

$$Q_{10} = (R_{25}/R_5)^{10/(25-5)} = 3.6141.$$

Likewise, the Q_{10} for aerial respiration between 5 and 25°C was calculated from equation (2) to equal 2.0051.

Energy requirement for metabolism of the L. kogamogai population

Fig. 6 shows the seasonal changes of daily energy loss due to metabolism for *L. kogamogai* individuals of different age groups.   From August to February, the
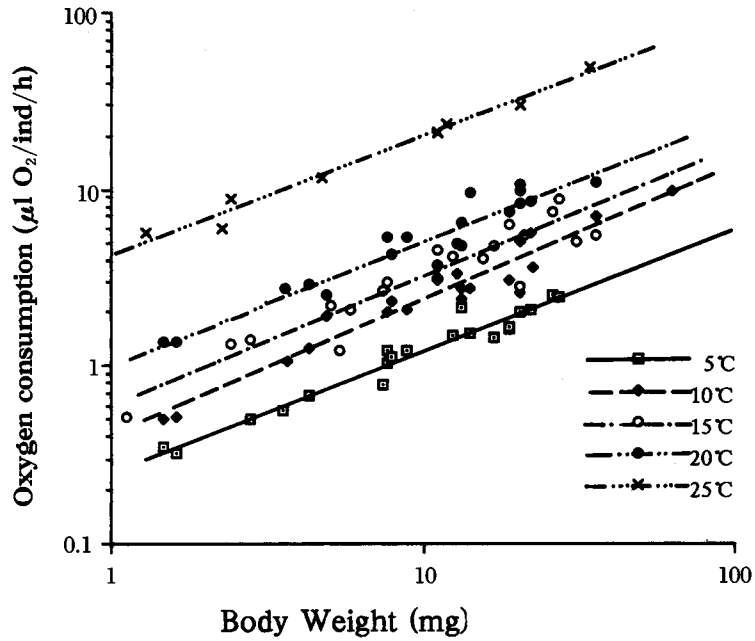
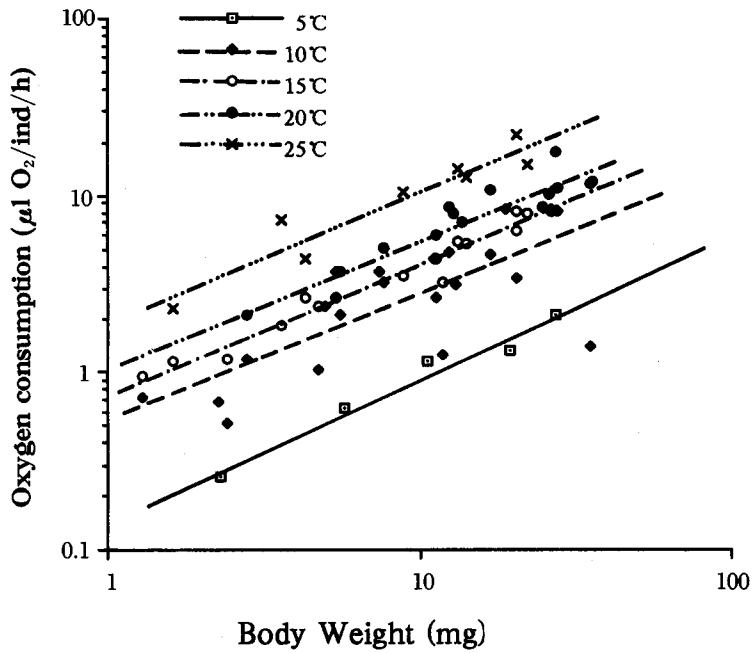Fig. 4. The relationship between dry body weight and aquatic respiration rate (μl O_2/ind/h) at different temperatures.

Fig. 5. The relationship between dry body weight and aerial respiration rate (μl O_2/ind/h) at different temperatures.

Table 2. Regression lines showing the relationship between oxygen consumption (R: μl/h/ind) and body weight (W: mg) for unfed *L. kogamogai* individuals at different temperatures (t: °C). N: Number of animals.

t	N	Aquatic R-W	N	Aerial R-W
5	20	$\text{Log}R = 0.6869\log W - 0.5986$	5	$\text{Log}R = 0.8170\log W - 0.8510$
10	21	$\text{Log}R = 0.7642\log W - 0.3848$	22	$\text{Log}R = 0.6519\log W - 0.3568$
15	19	$\text{Log}R = 0.6789\log W - 0.2562$	15	$\text{Log}R = 0.7741\log W - 0.3267$
20	20	$\text{Log}R = 0.7471\log W - 0.0019$	15	$\text{Log}R = 0.6574\log W + 0.0276$
25	8	$\text{Log}R = 0.6737\log W + 0.6304$	8	$\text{Log}R = 0.7642\log W - 0.1236$

Table 3. Analysis of variance for the regression lines of aquatic (top) and aerial (bottom) relationships shown in Table 2.

Reduced form	SS	f	V	F_s	F
Separate line	0.8777	78	0.0112		
Slope diff.	0.0209	4	0.0052	0.4647 < 2.45	
Parallel lines	0.8986	82	0.0110		
Positional diff.	10.0052	4	2.5013	228.34 > 2.45	
Single line	5.2855	86			

Reduced form	SS	f	V	F_s	F
Separate line	1.9077	55	0.0347		
Slope diff.	0.0366	4	0.0092	0.2641 < 2.53	
Parallel lines	1.9443	59	0.0330		
Positional diff.	2.7636	4	0.6909	20.965 > 2.53	
Single line	4.7079	63			

energy loss to metabolism decreased to its lowest value. Energy loss through aquatic respiration was higher than aerial respiration in most months—only during March to May were aerial respiration losses a little higher, a result of the prolonged exposure time.

The annual energy requirement for metabolism of the *L. kogamogai* population was determined to be 13.19 kcal/m².

Discussion

The weight-specific oxygen consumption has a negative relationship with body weight in the present study. Similar results have been reported in many other studies (Sutherland, 1972; Branch, 1979, 1981; Paul, 1986). There is, however, little information on the comparison of aerial and aquatic weight-specific oxygen consumption rates. Paine (1971) calculated an aerial oxygen consumption rate of 206 μl O_2/g/h and an aquatic respiration rate of 355 μl O_2/g/h at 13.5°C for a herbivorous gastropod *Tegula funebral* (mean size : 211 mg dry weight). This is different with the finding of the present study. Our result showed that weight-
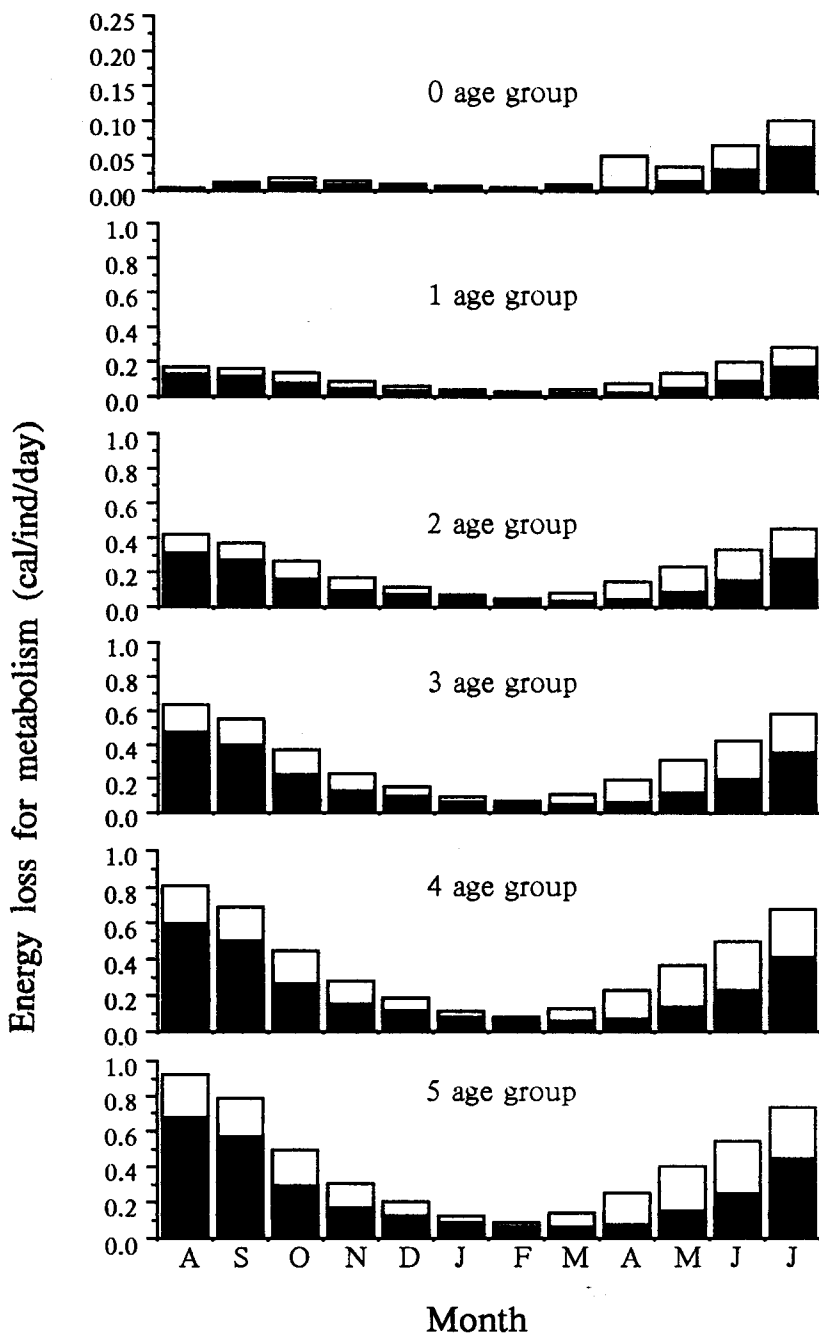
Fig. 6. Seasonal changes in daily energy losses for metabolism of *L. kogamogai* individuals in different age groups. □ : in air, ■ : in water.

specific oxygen consumption is higher in air than in water for individuals of the same body weight at the same temperature. Although *L. kogamogai* is much smaller (the biggest body size is about 60 mg dry weight) than *T. funebral*, its weight-specific oxygen consumption rate (350 μl O_2/g/h in air and 120 μl O_2/g/h in water for a 60 mg individual at 15°C) is lower than the latter's, indicating that *L. kogamogai* may have a relatively lower metabolic rate than other herbivorous gastropods.

It has been suggested that the respiration rate of ectotherms is proportional to the power 0.75 of body weight (Branch, 1981). In this work, we calculated a joint-weight exponent *b* of 0.72 and 0.74 for aquatic and aerial respiration, respectively. These results are very close to the suggested value. The *b* value in aquatic respiration is a little lower than in aerial respiration. In both cases, *b* is independent of temperature.

In the present study, we obtained Q_{10} values of 3.61 for aquatic and 2.00 for aerial respiration. Davies (1966), in his study of *Patella vulgata* and *P. aspera*, found that the Q_{10} values changed at different temperature intervals. He calculated mean Q_{10} values of 2.03, 1.94 and 2.03 at 5-25°C for aerial respiration of *P. vulgata* at high and low shore, and *P. aspera*, respectively. These values are very similar with the Q_{10} value of *L. kogamogai* for aerial respiration. The low Q_{10} in aerial respiration may be an adaptation of the intertidal limpets to the big variance in temperature during exposure. In contrast with aerial respiration, the Q_{10} value of aquatic respiration for *L. kogamogai* is higher than other herbivorous gastropods (Sutherland, 1972; Branch, 1979, 1981). Branch (1981) suggested that the limpets can be divided into "conservers", which live in conditions of low food supply and must have low Q_{10} values in order to minimize metabolic costs, and "exploiters" which live in conditions of abundant food and have high Q_{10} values. As the present study site in Hokkaido is the northern limit of the distribution for the *L. kogamogai* population, the high Q_{10} value of aquatic respiration in this study may be an energy strategy to maintain high metabolic rates and obtain more food during immersion and grow fast when temperatures are warm and food is abundant, and to reduce metabolic costs during cold seasons, when food supply are low. The growth data (Niu et al., 1992), Fig. 4 and the monthly energy requirement data in Fig. 6 also support this inference.

In addition to temperature and body weight, tidal rhythm is an important factor influencing the metabolic costs of intertidal grazers (Hawkins and Hartnoll, 1983). The present study applied detailed tidal data to estimate the population's metabolic costs. The influences of locomotion and starvation were not considered. We observed that the limpets continually moved inside the experimental container during the initial several hours, but became sessile after the acclimation time. Some studies have shown that the rate of oxygen consumption rises when the animals are given food and allowed to move freely (Branch, 1981). Therefore, the results in the present study may be underestimation. The annual production (P_g + P_r) is 5.88 kcal/m² (Niu et al., 1994b), so the value of R/P is 2.24. This value is lower than other limpets (Hawkins and Hartnoll, 1983; Hughes, 1971b; Wright and Hartnoll, 1981). A more detailed study on the influence of locomotion and food on respiration should be conducted to estimate the metabolic costs of a *L. kogamogai* population.

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