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# An Energy Budget for Individual Barnacles *(Balanus glandula)**

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**Abstract**

An annual energy budget was constructed for individual adult barnacles (*Balanus glandula* Darwin) for the first year after settlement. The production of body tissue, egg, shell, aquatic and aerial respiration, molting and faecal production was determined and consumption was derived from the summation of these budget items. To provide an estimation of the accuracy of the budget equation, energy budgets were constructed for three small groups of barnacles ($n$ = 40) kept under laboratory conditions, in which the budget items, including consumption, were determined independently. The results of the laboratory energy budgets indicated that consumption values derived from the summation methods for the three groups of barnacles were 7.4% higher and 16.2 and 15.6% lower than those determined by actual feeding experiments. The average consumption, assimilation and production of individual barnacles were estimated to be 699.5, 647.3 and 159.6 cal year$^{-1}$, respectively. *B. glandula* has an exceptionally high assimilation efficiency (92.5% from the annual budget and 99.3% from the laboratory budgets) but a low gross production efficiency (22.8%) and net production efficiency (24.7%). A very large proportion of energy (67.4%) was lost in respiration. The second most important budget item was egg production (12.3%); followed in decreasing order by: shell production (6.6%)> production of body tissue (3.9%)>molting (2.3%).

## Introduction

Barnacles are one of the universal species on the rocky shore in temperate waters (Stephenson and Stephenson, 1949; Lewis, 1964). Along the Pacific coast from the Aleutian islands to the northern border of Mexico, *Balanus glandula* Darwin is the major barnacle species (Barnes and Barnes, 1956). The mean number and biomass in barnacle beds in Monterey Bay, California, USA, have been estimated as 11820 m$^{-2}$ and 2100 g dry weight m$^{-2}$, respectively (Glynn, 1965). Connell (1970) reported that the population density of *B. glandula* at Point Roberts near the mouth of the Fraser River ranged between 3000 and 32000 m$^{-2}$. Based on the resettlement on several denuded quadrats, Glynn (1965) estimated that the production of this barnacle was 3.2 g dry weight m$^{-2}$ month$^{-1}$, although it is obvious that only the new settlement was accounted for in his study. With such a large number and biomass, the barnacles may channel a large amount of energy from the pelagic environment into the littoral community and play an important role in the food web dynamics of littoral systems. Energetic studies have been carried out on a variety of other littoral animals [e.g. the gastropods *Littorina irronata* (Odum and Smalley, 1959), *Tegula funebralis* (Paine, 1971), 3 species of *Nerita* (Hughes, 1971a); the limpet *Fissurella barbadensis* (Hughes, 1971b), the isopod *Tylos punctatus* (Haynes, 1974); the bivalves *Modiolus demissus* (Kuenzler, 1961), *Scrobicularia plana* (Hughes, 1970) and the oyster *Crassostrea virginica* (Dame, 1976)]. Surprisingly, the energetics of barnacles have not been studied; except by Perkins (1975) who gave a very crude

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estimation on the energy flow of the *B. glandula* population in his intertidal association-energy flow model.

The present study investigated the energy budget of *Balanus glandula* during the first year after settlement. Most data are from an experimental population in the field in coastal British Columbia, but a short-term laboratory experiment was conducted to verify values for the balanced energy equation. Loss of biomass was not considered when extrapolating to field production and energy flow.

## Terminology

Following the IBP terminology (Petruswicz and MacFadyen, 1970), the energy budget for an individual barnacle can be represented by the equation:

$$C = P_{BT} + P_E + P_S + R_{AER} + R_{AQ} + M + F,$$

where: $C$ = consumption, $P_{BT}$ = production of body tissue, $P_E$ = production of egg[1], $P_S$ = production of shell, $R_{AER}$ = aerial respiration, $R_{AQ}$ = aquatic respiration, $M$ = molting, $F$ = faecal production; and

$$A = C - F$$

$$P = P_{BT} + P_E + P_S$$

$$R = R_{AET} + R_{AQ}$$

where: $A$ = assimilation, $P$ = production, $R$ = respiration.

The loss of dissolved organic matter (DOM), which may be important in some animals (e.g. 42% of consumption and 68% of assimilation in sea urchins according to Miller and Mann, 1973) is assumed to be unimportant for *Balanus glandula* in this study.

## Materials and Methods

### *Experimental Populations*

In March 1975, two roughened Plexiglas plates of 0.61 $m^2$ (78 x 78 $cm^2$) were put at the same tidal level (2.6 to 3.3 m above chart datum) on two pilings of the wharf at Pacific Environment Institute, West Vancouver, British Columbia (123° 15'W; 49°20'N). *Balanus glandula* Darwin spat settled at an initial density of ~200000 $m^{-2}$ on the panels in late May. An analysis of variance showed no significant difference ($P = 0.05$) in the growth rates of the barnacles on these two pilings after they had grown for 1 month. The barnacle density on the panels decreased to ~12295 $m^{-2}$ in late October, when the individuals have attained their maximum size.

### *Determination of Dry Weight, Ash-Free Weight and Calorific Value*

In this study, the dry weight of all the barnacle materials (i.e., body tissue, ovarian tissue, egg masses, naupliar embryos, molted exoskeletons, faecal pellets and shell) was obtained by weighing with a Cahn G2 electrobalance after drying in an oven at 100°C for 48 h.

The percentage of ash-free weight of all these barnacle materials, except the shell, was determined by ashing a known weight of dried sample in a furnace at 500°C for 4 h.

The dried body tissue, ovarian tissue, egg masses, naupliar embryos, molted exoskeleton and faecal pellets were homogenized separately with a mortar and pestle, and pelleted. The caloric value of the materials was determined by burning the pellet in a Phillipson microbomb calorimeter. In determining the caloric values of the molted exoskeleton and faecal pellets, the materials were mixed with benzoic acid to burn since the combustibilities were low. No correction was made for acid production, or the burning of the firing wire, since these were considered to introduce negligible error (Paine, 1964).

Barnacle shell is mainly composed of $CaCO_3$, chitin and protein (Barnes *et al.*, 1976). In this study, the percentages of the latter two components in the barnacle shells were determined, using the method described by Barnes *et al.* (1976). The total energy content of the shell was then found by the summation of the energy content of the chitin and protein fractions, assigning a caloric value of 5.65 and 4.10 for protein and chitin, respectively (Crisp, 1971).

### *Production ($P_{BT}$, $P_E$, $P_S$)*

Twenty samples of barnacles were taken at random from one of the panels each month. They were cleaned in running sea water with a brush before dissection. The egg and the body tissue were dissected from the barnacles. The testes were difficult to isolate and were incorporated into "body tissue" in this study. Dry weight, ash-free weight and caloric value of the various components of the barnacle (including the shell) were determined, using the methods already described. The energy standing

[1] Egg is defined as the totality of ovarian tissue, egg masses and naupliar embryos in this study.

crop of the various tissue components for each individual barnacle was then found by multiplying their dry weight and percentage of ash-free weight by the caloric values.

The monthly mean energy production of the body tissue ($P_{BT}$), egg ($P_E$) and shell ($P_S$) was found by the difference in the energy standing crop of each item between consecutive monthly samplings. In estimating egg production, the summation of the difference in the energy standing crop of ovarian tissue, egg masses as well as naupliar embryos was considered. Negative production of egg masses or naupliar embryos was neglected and assigned a zero value since this merely indicated the discharge of larvae between sampling periods. Negative production of ovarian tissue was accounted because this would indicate reabsorption (Barnes and Archituv, 1976).

*Aerial Respiration* ($R_{AER}$)

The ovarian tissue, egg masses and naupliar embryos were dissected from *Balanus glandula* and their $O_2$ consumptions were measured by a Gilson differential respirometer at 5°, 10°, 15° and 20°C, after acclimatizing at the experimental temperature for 1 h. The tissues were then dried and the $O_2$ consumption rates were expressed as µl $O_2$ mg dry tissue$^{-1}$ h$^{-1}$.

The aerial $O_2$ consumption rate of the barnacle body tissue was measured in a factorial designed experiment with 4 weight groups and 4 temperatures. Barnacles on mussel shells were collected near the Pacific Environment Institute during low tides. After cleaning in running sea water with a brush, they were sorted into 4 size groups with mean body tissue weight of 0.95 ± 0.25 and 8.27 ± 0.60 mg (mean ± standard deviation). The barnacles were acclimatized in an incubator at the experimental temperature for at least 12 h before the experiment. Pneumatostomes indicating aerial respiration (Grainger and Newell, 1965) were observed in nearly all the experimental barnacles. The aerial respiration of the whole barnacle was measured by a Gilson differential respirometer at 5°, 10°, 15° and 20°C. Pieces of barnacle and mussel shell were used as controls in the experiments. The body tissue, ovarian tissue, egg masses and naupliar embryos of the barnacle were dissected and dried separately at the end of the experiment. The $O_2$ consumption of the body tissue was then found by subtracting the $O_2$ consumption of the associated ovarian tissue, egg masses or naupliar embryos from that of the whole barnacle at the same temperature. The $O_2$ consumption rate of the body tissue was then calculated and expressed as µl $O_2$ mg dry body tissue$^{-1}$ h$^{-1}$.

*Aquatic Respiration* ($R_{AQ}$)

Preliminary experiments have shown that salinities within the range of 13 to 23‰ have no significant effect upon the aquatic respiration of *Balanus glandula* (Wu, unpublished data). Since the salinities near the present study area usually fall within such a range (Stockner and Cliff, 1976) salinity was considered to be unimportant in the present study. Subsequently, sea water of 23‰ S was used in all the experiments to measure the aquatic respiration of barnacle tissues.

The $O_2$ consumption of the dissected ovarian tissue and egg masses were measured at 5°, 10°, 15° and 20°C in a respiration vial (YSI model 53) with fully saturated sea water. Occasional stirring using a magnetic stirrer was provided every 15 min; measurements were obtained over a 1 h period. The $O_2$ concentration was determined by an $O_2$ electrode with a Radiometer PHM 72 unit. The $O_2$ consumption of the tissue was then found by the difference in $O_2$ concentration before and after the experiment and expressed as µl $O_2$ mg dry tissue$^{-1}$ h$^{-1}$. The aquatic respiration of the naupliar embryos was not measured because stirring caused a release of the swimming nauplii which increased the $O_2$ consumption.

The aquatic $O_2$ consumption of the body tissue of *Balanus glandula* was measured in a factorial designed experiment with four different water temperatures and four different weight groups. Barnacles on mussel shells were collected at low tide. They were cleaned in running sea water with a brush and sorted into four groups with mean body tissue weight of 0.44 ± 0.01, 2.43 ± 0.30, 4.06 ± 0.29 and 9.98 ± 0.26 mg. The barnacles were allowed to acclimatize at the experimental temperature for 24 h before the experiments. Continuous aeration was supplied during the period of acclimatization. The $O_2$ consumption of the various size groups at water temperatures of 5°, 10°, 15° and 20°C were measured.

Immediately before the experiment, the barnacles were transferred to the respiration chamber. The sea water in the respiration chamber had the same salinity and temperature as the acclimatizing sea water, except that it had been filtered through a 30 µm plankton mesh to remove large-size plankton. The res-

piration chambers were placed in a constant water temperature bath (± 0.2 C°). A current simulating the natural condition was provided by a magnetic stirrer placed under the mesh-gauze (which separated the barnacles and the stirrer) in the respiration chamber. The result of $O_2$ consumption was accepted only if over half the barnacles were observed to have active cirral beat during the period of measurement. The $O_2$ saturation of the sea water in the respiration chamber was never allowed to fall below 60%, since according to Prasada Rao and Ganapati (1969), $O_2$ saturation above this level would have little effect on respiration. $O_2$ concentration of the sea water before and after 1 h experiment was measured by a polarographic $O_2$ electrode and a Radiometer PHM 72 unit.

The $O_2$ consumption was found by the difference of $O_2$ concentration before and after the experiment. As in the aerial respiration experiment, the $O_2$ consumption of the body tissue was found by subtracting the $O_2$ consumption of the associated ovarian tissue, naupliar embryos or egg masses from the $O_2$ consumption of the whole active barnacle. The $O_2$ consumption was expressed in µl $O_2$ mg dry body tissue$^{-1}$ h$^{-1}$.

The aerial and aquatic $O_2$ consumption of the body tissue, ovarian tissue, naupliar embryos and egg masses was converted into calories by multiplying an oxycaloric value of 4.8 cal/ml $O_2$ (Crisp, 1971) after correcting the $O_2$ consumption at normal temperature and pressure. Such an oxycaloric value assumes a mixed diet of protein, carbohydrate and fat for the animal (Crisp, 1971) which would be appropriate for barnacles, as they normally feed on plant (phytoplankton) and animal (zooplankton) materials.

The total hours of submergence and emergence for the month were calculated for the experimental population from a local tide table. Energy lost to aerial and aquatic respiration for the month was calculated for an individual barnacle, taking into account the mean body weight of the animal, the associated ovarian tissue, naupliar embryos and egg masses, and the mean air and water temperature of the month (Environment Canada/Atmospheric Environment, 1973; Institute of Oceanography, The University of British Columbia, 1973).

*Faecal Production and Molting Rate (F and M)*

Both faecal production and molting rate were determined for every month in the same experiment. Barnacles on mussel shells (approximately the same size as the individuals on the settling plate) were collected from the pilings 1 day before the experiment. They were cleaned with a brush in running sea water and submerged from the wharf in a cage overnight. The faecal production and molting rate of the barnacles were measured in an experimental period of 24 h. The barnacles were taken out of the water at the start of the experiment. Five replicates with about 100 barnacles per tray were exposed to air at the mean temperature of the month for a certain period of time, then into running sea water for the rest of the 24 h experimental period. The relative time for the barnacles exposed to air and submerged in running sea water, within the 24 h experimental period, was determined accordingly by the total submergence:emergence ratio of the month at the 3 m tidal level.

At the end of the experiment, the barnacles were dissected and the mean dry weight of their body tissue determined. The molted exoskeletons and faecal pellets were collected and their dry weights, ash-free weights and caloric values determined, using the methods already described. The molting frequency of a single individual within the month was estimated from the percentage of molting in the experiment and expressed as no. molts individual$^{-1}$ month$^{-1}$. The faecal production rate was expressed in mg dry faeces mg dry body tissue$^{-1}$ month$^{-1}$.

The energy lost in faecal production for each month was then calculated from the caloric value, the ash-free weight content of the faecal pellets, and the faecal production rate. The energy lost in molting for the month for an individual was calculated from the caloric value, the ash-free weight percentage of the molted exoskeleton, the mean weight of the molted exoskeleton and the molting frequency of an individual in the month.

An annual energy budget was then constructed for an individual *Balanus glandula* by summing up the values of the 12 months for each item. Consumption was then found by summing all the budget items on the right-hand side of the equation.

*Laboratory Energy Budget*

To estimate the error involved in estimating the consumption values by the summation method, a short term (36 days) experiment was performed in the laboratory in August, 1976. Energy budgets were constructed for three small groups of *Balanus glandula* in which all the budget items, including consumption, were measured independently.

*Balanus glandula* on mussel shells were collected during low tides near the Pacific Environment Institute. Individuals with mean dry body weight of 6.4 ± 0.4 mg were sorted for the experiments. The standing crop energy of the body tissue and ovarian tissue in 30 individuals were determined before the experiment, using the methods described above. Another 120 sorted individuals were equally divided into three groups. They were put in separated trays in a filtered running sea water system (in which fresh sea water was filtered sequentially through: commercial sponge-glass wool-100 µm mesh-30 µm mesh-10 µm mesh-Whatman No. 1 filter paper). The sea water of the system was checked daily with an inverted microscope to ensure the absence of microscopic algae and dinoflagellates. The water temperature was continuously recorded by a thermograph (Ryan model F). The faecal materials and molted exoskeletons produced by each group were collected daily, and energy loss in faecal production and molting was then estimated by the same method described above.

Each group of barnacles was fed or exposed to air once or twice daily. The barnacles were fed in a Plexiglas chamber (same as the respiration chamber described above) which was incubated in a constant temperature (± 0.2 C°) water bath. 400 ml of a log-phase growing diatom (*Skeletonema costatum*) was fed to the barnacles. Continuous stirring of the culture was provided by the magnetic stirrer throughout the experiment. An equal number of empty barnacle shells were used in the control of the feeding experiment. The numbers of diatoms were counted using a haemacytometer and the total consumption of the barnacle group was found by the difference in the total number of diatoms before and after the experiment. The energy value of *S. costatum* consumed was then calculated based on (1) the number and dry weight conversion factor and the chemical component analysis of *S. costatum* given by Parsons *et al.* (1961), and (2) assigning a calorific value of 5.65, 4.10 and 9.50 cal $mg^{-1}$ for protein, carbohydrate and fat, respectively (Crisp, 1971).

For aerial exposure, the barnacle groups were put in an incubator with a known, constant temperature (ranging from 10° to 20°C). The duration of aerial exposure, the air temperature, the feeding temperature, the feeding time and the feeding concentration varied among the three barnacle groups. The $O_2$ consumption of each barnacle group was then calculated from the series of equations derived from the earlier aerial and aquatic respiration experiments (see "Results"), taking into account the duration of exposure and submergence and the respective air-water temperature that each particular group was subjected to. The total energy loss in aerial and aquatic respiration for each barnacle group was then calculated.

At the end of the experiment, the barnacles were killed and the total energy content stored in the body and ovarian tissues was determined. The production of body tissue and ovarian tissue for each group during the experimental period was then found by the difference in the total energy content of the respective item before and after the 36 day period.

The production of shell was assumed to be zero in constructing the laboratory budgets, since shell growth of *Balanus glandula* would be minimal after 5 months of adult life (see "Results" and "Discussion").

## Results

### *Caloric Value*

The seasonal changes in the caloric value of the ovarian tissue, body tissue, egg masses and naupliar embryos of *Balanus glandula* are shown in Fig. 1. In general, the highest caloric value was found in the ovarian tissue, followed in decreasing order by: egg masses>naupliar embryos>body tissue. The seasonal variations in caloric value of a single category of tissue were small, however.

### *Production ($P_{BT}$, $P_E$, $P_S$)*

The seasonal changes in the dry weight standing crop of body tissue are shown in Fig. 2. A large seasonal fluctuation was observed. The dry weight standing crop of the body tissue increased rapidly from June to September, decreased to a lower level and fluctuated from November to March, reached a peak in April, and then decreased to a lower level and fluctuated from November to March, reached a peak in April, and decreased again in May.

The monthly $P_S$, $P_E$, $P_{BT}$ as well as $P$ are shown in Fig. 3. Positive values of production of all these items were found in the months of June, July, August, September, December, February and April, and negative values of all these items (except $P_S$ in October) were found in the other months of the year. $P_{BT}$ $P_E$ and $P$ showed a positive and negative peak in August and November, respectively. $P_S$ became negligible after the barnacle was 5 months old.

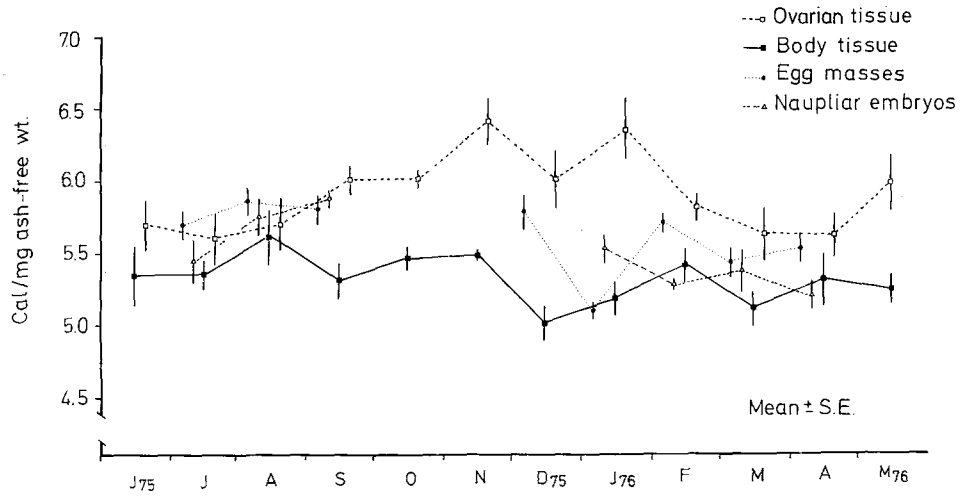


Fig. 1. *Balanus glandula*. Seasonal changes in caloric values of various tissues from June 1975 to May 1976. (Data from 20 individuals per month obtained from settling plates at West Vancouver, British Columbia)

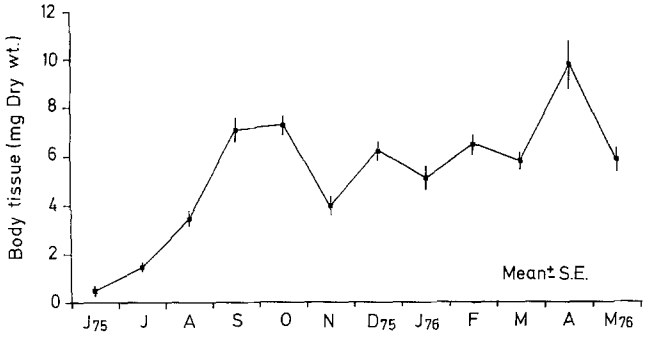


Fig. 2. *Balanus glandula*. Seasonal changes in body tissue weight of individual barnacles for first year after settlement

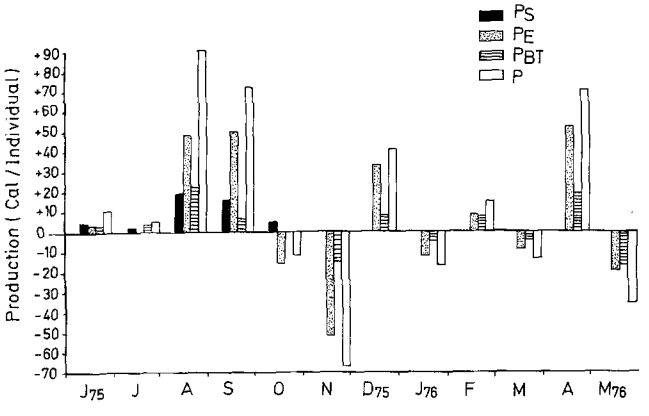


Fig. 3. *Balanus glandula*. Monthly mean production of shell ($P_S$), egg ($P_E$), body tissue ($P_{BT}$) and total production ($P$) of individual barnacles for first year after settlement

*Aerial and Aquatic Respiration ($R_{AER}$ and $R_{AQ}$)*

Covariance analysis showed no significant difference (P = 0.05) between the aerial and aquatic $O_2$ consumption rate of the ovarian tissue. Similarly, no significant difference (P = 0.05) was found between the aerial and aquatic $O_2$ consumption rate of the egg masses. The data of the aquatic and aerial $O_2$ consumption rate were, therefore, pooled for these two items. $O_2$ consumption rate as a function of temperature for egg masses, naupliar embryos and ovarian tissue is shown in Fig. 4. Regression lines were fitted by the least-squares method for each set of data. The relationships between the $O_2$ consumption rate and temperature for the various tissues are given by the following equations:

log $O_2$ consumption rate of ovarian tissue = 0.017 temperature °C - 1.274 ($r$=0.810, $n$=32)

log $O_2$ consumption rate of egg masses = 0.032 temperature °C - 0.663 ($r$=0.985, $n$= 32)

log $O_2$ consumption rate of naupliar embryos = 0.025 temperature °C - 0.663 ($r$=0.941, $n$=24)

Aerial and aquatic $O_2$ consumption rates of the body tissue are plotted against the body weight at 5°, 10°, 15° and 20°C in Figs. 5 and 6. In order to predict the aerial and/or aquatic $O_2$ consumption rate of an individual barnacle with any given body weight and air-water temperature, the following multiple linear regression equations were generated from the same data by an IBM 370 computer:

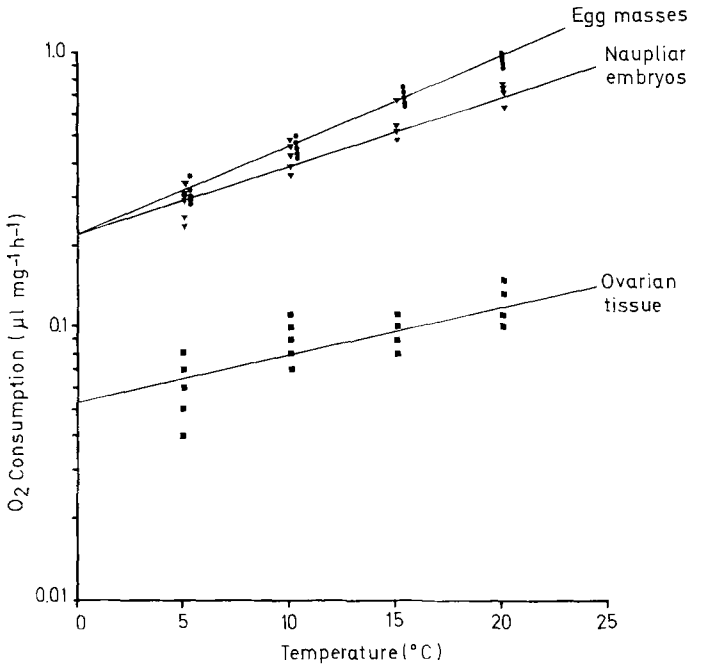


Fig. 4. *Balanus glandula*. $O_2$ consumption rate ($log_{10}$) of egg masses, naupliar embryos and ovarian tissue under different temperatures. Regression lines for various relationships are also shown

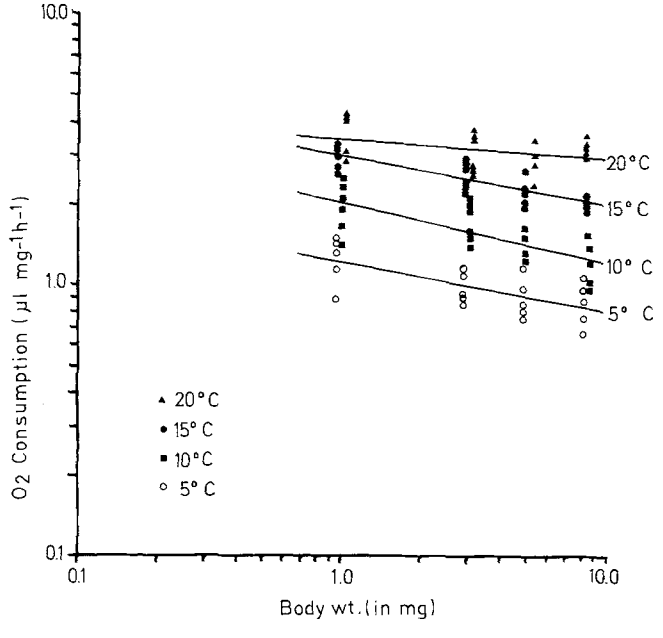


Fig. 5. *Balanus glandula*. Aerial $O_2$ consumption rate ($log_{10}$) of body tissue in relation to body weight ($log_{10}$) and temperature

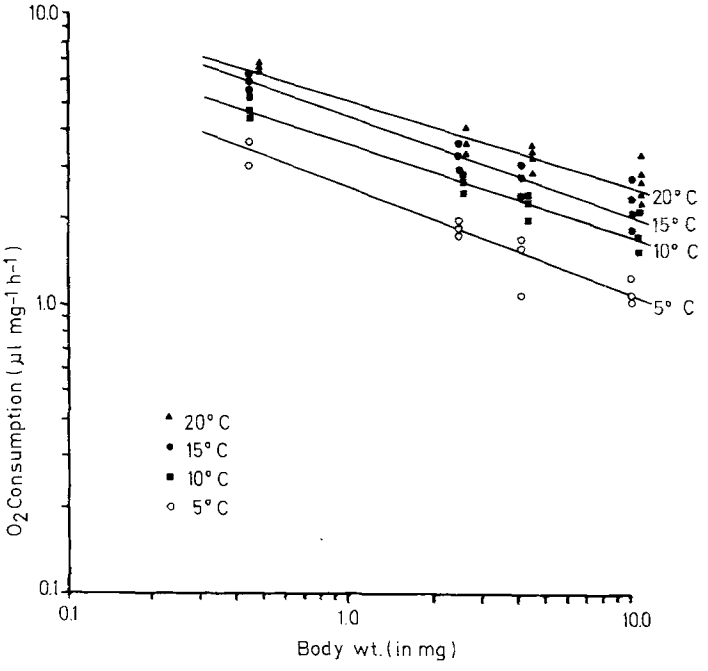


Fig. 6. *Balanus glandula*. Aquatic $O_2$ consumption ($log_{10}$) of body tissue in relation to body weight ($log_{10}$) and temperature

log aerial $O_2$ consumption rate of body tissue = (−0.075 ± 0.027) + (0.034 ± 0.001 temperature °C) − (0.168 ± 0.023 log mg body weight) ($r$ = 0.892, $n$ = 79),

log aquatic $O_2$ consumption rate of body tissue = (0.309 ± 0.022) + (0.021 ± 0.001 temperature °C) − (0.334 ± 0.016 log mg body weight) ($r$ = 0.914, $n$ = 60).

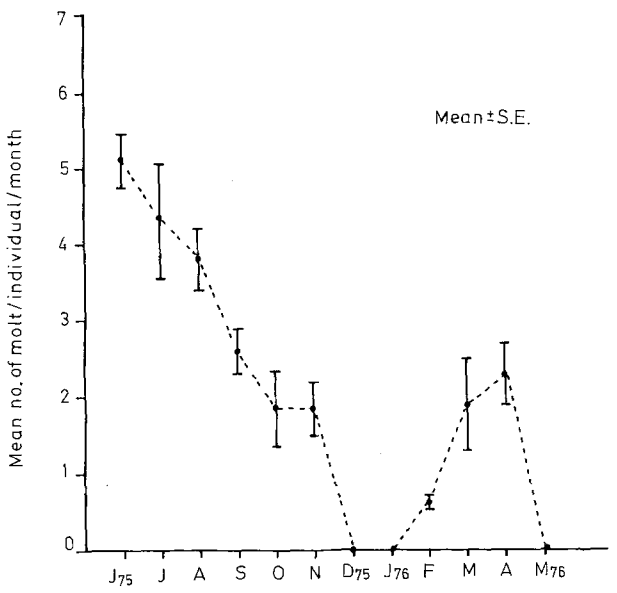


Fig. 7. *Balanus glandula*. Molting frequency over period June 1975 to May 1976. 500 individuals were observed for each date

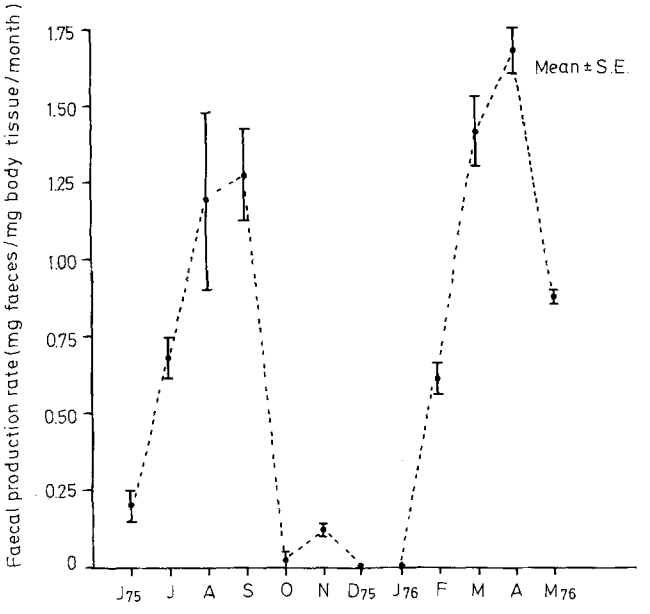


Fig. 8. *Balanus glandula*. Faecal production rate over period June 1975 to May 1976. 500 individuals were observed for each date

Table 1. *Balanus glandula*. Annual energy budget for an individual barnacle of first year settlement, based on measurements at West Vancouver, B.C. over period June 1975 to May 1976. (For explanation of abbreviations, see "Terminology")

| | $C$ | = | $P_{BT}$ | + $P_E$ | + $P_S$ | + $R_{AER}$ | + $R_{AQ}$ | + $M$ | + $F$ | $A$ | $P$ | $R$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Calories | 699.5 | | 27.5 | 86.0 | 46.2 | 101.6 | 370.3 | 15.8 | 52.2 | 647.3 | 159.6 | 471.9 |
| % | (100) | | (3.9) | (12.3) | (6.6) | (14.5) | (52.9) | (2.3) | (7.5) | | | |

Table 2. *Balanus glandula*. Laboratory energy budgets for three groups of barnacle ($n$ = 40), with independent measurement for each budget item (in calories). $*C_S$ = consumption derived from summation method; $*C_F$ = consumption derived from feeding experiments. (For explanation of other abbreviations, see "Terminology")

| | $P_{BT}$ | $P_E$ | $R_{AER}$ | $R_{AQ}$ | $M$ | $F$ | $*C_S$ | $*C_F$ | $A:C_S$ | $A:C_F$ | $\frac{C_S - C_F}{C_F} \times 100\%$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 26.7 | -356.7 | 527.2 | 2392.0 | 44.4 | 22.3 | 2655.9 | 2473.0 | 0.992 | 0.991 | + 7.4% |
| 2 | -33.4 | -571.6 | 421.7 | 2183.9 | 50.3 | 18.7 | 1069.6 | 2470.0 | 0.991 | 0.992 | - 16.2% |
| 3 | 119.2 | -222.3 | 831.8 | 2011.8 | 53.2 | 21.2 | 2814.9 | 3336.0 | 0.992 | 0.994 | - 15.6% |

*Assimilation efficiency ($A:C$) = 92.5%; gross production efficiency ($P:C$) = 22.8%; net production efficiency ($P:A$) = 24.7%.

*Faecal Production and Molting Rate (F and M)*

The monthly molting frequency and faecal production rate for an individual barnacle are shown in Figs. 7 and 8, respectively. Both the molting frequency and faecal production were low and negligible in December and January.

*Annual Energy Budget*

An annual energy budget for an individual *Balanus glandula* during its first year after settlement is shown in Table 1. The percentage of energy channelled to each budget item is shown in parentheses by assuming that consumption = 100%. A

high assimilation efficiency (*A*:*C*) and low gross production efficiency (*P*:*C*) and net production efficiency (*P*:*A*) were found from the annual energy budget (92.5, 22.8 and 24.7%, respectively). When comparing the proportion of energy used in the various budget items, it is apparent that *B. glandula* uses a very large proportion (67.4%) of energy intake in respiration. Egg production ($P_E$) was the second most important (12.3%), followed in order of decreasing importance by: $P_S$ (6.6%)>$P_{BT}$ (3.9%)>molting (2.3%).

*Laboratory Energy Budgets*

The laboratory energy budgets constructed for the three barnacle groups are presented in Table 2. The consumption values derived from both the summation method and actual feeding experiments are also shown. The consumption values determined by summation were 7.4% higher and 16.2 and 15.6% lower than those determined by actual feeding experiments for the three barnacle groups.

Gross and net production efficiencies were not calculated from the laboratory energy budgets since negative production was found in all three barnacle groups. The assimilation efficiencies derived from the three independent barnacle groups were similarly high (99.3 ± 0.1%) and agreed with that derived from the annual energy budget (Table 1).

## Discussion

*Balanus glandula* settled in May, grew rapidly and attained their maximum size and sexual maturity in September (4 months after their settlement). High production values for both shell, body tissue and egg, associated with a high molting frequency and faecal production, were found in August and September. At this time the abundance of phytoplankton was high (Stockner and Cliff, 1976) and the adults were at their juvenile stage. Shell production became negligible after October (5 months after barnacle settlement). Negative productions of both body tissue and egg were observed in October to January (except for December), and the molting frequency and faecal production were also negligible during this period. Negative production of body tissue and egg was marked in November, when plankton abundance was the lowest for the year (Stockner and Cliff, 1976). High production was observed in April, during the spring bloom. Negative production was, however, found in May when the plankton abundance was presumably still high. Except for negative production in December, the production of the barnacle then showed a positive correlation with the abundance of the plankton in the waters.

The large seasonal fluctuation of body and ovarian tissues found in the present study suggests that barnacles consumed a large amount of energy in summer when food was abundant, and stored this in the form of body and ovarian tissues. They could then maintain themselves by remobilizing their energy when food became scarce in the winter months. Barnes and Archituv (1976) found that the ovarian tissue and body tissue of *Balanus balanoides* were not separate compartments and can be mobilized during starvation. Such adaptations may enable barnacles to cope with the large seasonal fluctuation of food in their environment.

An unusually high assimilation efficiency (92.5% from the annual energy budget and 99.3% from the laboratory energy budgets) was obtained in the present study for *Balanus glandula*, but results agree with the only other data on barnacles (*B. improvisus*; Kuznetsova, 1973). Based on the results of her feeding experiments, Kuznetsova found that the assimilation efficiency of *B. improvisus* was very high (94%) when fed with barnacle nauplii, and was lower when fed on the algae *Asterionella* sp. and *Cladopora* sp. (86 and 66%, respectively). Such high values of assimilation efficiency have seldom been reported for other animals, except in the crustacean *Macrocyclops albidus* feeding on *Paramecium* sp. which has been reported to have a maximum assimilation efficiency of 97% (Klekowski and Shushkina, 1966; *in* Lawton, 1970), and in the carnivorous fish *Megalops cyprinoides* (92% according to Pandian, 1967). Other animals feeding on zooplankton and phytoplankton have much lower assimilation efficiencies compared with *B. glandula*. For example, the oyster *Crassostrea virginica*, which is similar to *B. glandula* in some aspects (e.g. both are sessile, filter-feeding macroinvertebrates living in the intertidal zone), has a much lower (42%) assimilation efficiency (Dame, 1976). The marine copepod *Calanus hyperboreus* and the fresh water copepod *Diaptomus gracilis*, both feeding on phytoplankton, had an assimilation efficiency of 60 and 78%, respectively (Conover, 1966; Kibby, 1971). The marine crustacean *Euphausia pacifica* feeding on *Artemia* sp. larvae had an assimilation efficiency of 84% (Lasker, 1966).

Welch (1968) suggested that net production efficiency is inversely proportional to assimilation efficiency. Although a high net production efficiency would be expected for the barnacles since

they are sessile, and a relatively small amount of energy would be required in their normal activities, low net production efficiency (24.7%) as well as low gross production efficiency (22.8%) were found for *Balanus glandula* in this study. The result thus gives some support to the suggestion of Welch (1968).

In an overall analysis of the data, it is obvious that respiration was the most important item in the energy budget of *Balanus glandula*. A very large proportion of energy intake (67.4%) of this barnacle was lost in respiration and became unavailable to the next trophic level. The next important budget item was egg production (12.3%); followed in the order of decreasing importance by: shell production (6.6%)>body tissue production (3.9%)>molting (2.3%). The energy channelled to egg production was 53.9% of production and was about three times more than that of body tissue production, and about two times that of shell production. Indeed, for animals such as barnacles, which must suffer a very high mortality during their planktonic stages and their early settlement, it may be advantageous for them to channel a large proportion of their energy intake into egg production in order to ensure the propagation of the species. Moreover, the adult barnacles may suffer from a high mortality from catastrophes or intensive predation (Dayton, 1971) in the first year after they have settled. The large energy committment to reproduction shortly after settlement in *B. glandula* may well be a good response to such an opportunistic type of life history.

The P:R ratio of *Balanus glandula* derived from the present study (0.34) resembles that for those "short lived poikilotherms" summarised by McNeill and Lawton (1970). McNeill and Lawton also derived equations to predict $P$ from $R$, and *vice versa*. In applying the present values of $P$ and $R$ for *B. glandula* to their equations, the calculated values of $P$ and $R$ were only 4.0% lower and 1.8% higher than the actual values, respectively. The present findings, therefore, support the generalizations made by McNeill and Lawton for the "short lived poikilotherms".

In the present study, the consumption, assimilation and production of an individual *Balanus glandula* was estimated to be 699.5, 647.4 and 159.6 cal $year^{-1}$, respectively. Neglecting mortality loss and applying the population density of 12295 $m^{-2}$ on our settling plates, the barnacle population should consume 8600.4 Kcal $m^{-2}$ $year^{-1}$, thus resulting in an assimilation (energy flow) of 7958.6 Kcal $m^{-2}$ $year^{-1}$ and a total productivity of 1962.3 Kcal $m^{-2}$ $year^{-1}$.

The energy flow values derived from the present estimation, compared with other aquatic populations, would be among the highest that had been reported. Although a very large proportion of intake energy of the barnacle population would be lost in respiration, a significant proportion would be elaborated as barnacle tissue and become available to the next trophic level in the littoral system. The production of 1962.3 Kcal $m^{-2}$ $year^{-1}$ in *Balanus glandula* in British Columbia, compared with production of individuals in other animal populations, would be similar to that of the oyster *Crassostrea gigas* (1545 Kcal $m^{-2}$ $year^{-1}$) (Bernard, 1973) and only lower than that of the newly-settled *Mytilus edulis* (3000 to 6000 Kcal $m^{-2}$ 6 $months^{-1}$) (Dare, unpublished data; cf. Miller and Mann, 1973).

However, the present calculation of energy flow and production for this barnacle population should be viewed with caution since (1) the present annual energy budget data was derived from a fast-growing, first-year settlement, in which the energy flow and the production would be higher than the older age groups, and (2) mortality of the barnacle population has not been taken into account.

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