Ecological energy requirements of the green mussel, _Perna viridis_ Linnaeus from Ennore estuary, Madras

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**ABSTRACT**  
Ecological energies of growth and respiration were computed for individuals of the tropical intertidal green mussel, _Perna viridis_ L. from Ennore estuary Madras for the period 1974-1975. Von Bertalanffy growth curve was fitted to data obtained from rearing marked animals in the field. _Perna viridis_ has a higher rate of growth than all other mussels studied so far. Growth efficiency was computed for mussels of various sizes and the values were 56, 41, 32 and 19% for 2, 40, 80 and 120 mm sized mussels respectively.  


**RÉSUMÉ**  
Besoin en énergies écologiques de la moule verte, _Perna viridis_ Linnaeus de l’estuaire de Ennore, Madras (Inde)  

L’énergie écologique de croissance et de respiration est calculée pour la moule verte du milieu intertidal tropical, _Perna viridis_ L. pendant la période 1974-1975. La courbe de von Bertalanffy a été ajustée à partir des résultats obtenus à l’aide d’une expérience de marquage. Nous avons trouvé que les taux de croissance des moules tropicales étaient beaucoup plus élevés que ceux décrits pour les autres espèces de moules. Le calcul de l’efficacité de croissance nous a donné les résultats suivants : 56, 41, 32 et 19 % respectivement pour les moules ayant une longueur de 2, 40, 80 et 120 mm.  


**INTRODUCTION**  
The distribution of the green mussels, _Perna viridis_ L. extends roughly all around the intertidal coasts of the India Peninsula (Jones, Alagarewamy, 1973). However, mussel culture has only recently gained momentum in India due to its economic importance (Qasim et al., 1977). Even so, ecological studies on green mussels have received little attention to date. Growth and secondary productivity estimates of _Perna viridis_ should be considered very important as this organism represents a true tropical bivalve species usually occurring in dense populations, playing a major role in the functioning of tropical marine ecosystems. Following Lindman’s theoretical considerations of ecological energetics (1942), the productivity and functioning of animals, populations or communities have been largely studied through ecological energy measurements. The present study deals...
with the ecological energy requirements of the green mussel from a population of Ennore estuary ecosystem, near Madras, India.

The following energy budget terminology has been devised by the International Biological Program (Petrusewicz, 1967; Ricker, 1968; Crisp, 1971):

\[ C = P + R + F + U, \]

C is the energy content of the food consumed; P is the energy produced due to growth; R is the energy lost as metabolic heat (represented by respiration or Oxygen consumption); F is the energy lost as feces and U is the energy lost from excreted urine and mucus.

“Energy flow” has been described by Smalley (1960) as the portion of the energy consumed which is assimilated by a population (A) and can be calculated as follows:

\[ A = C - (F + U) = P + R. \]

In individual animals, production can be explained as:

\[ P = P_g + P_r. \]

\[ P_g \] is the energy increase due to growth and \( P_r \) is the energy lost as reproductive materials. So, in individual organisms growth \( P_g \), reproduction \( P_r \) and respiration \( R \) combined in terms of energy form the energy of assimilation \( A \).

The present work deals with the energy requirements of intertidal green mussels for their somatic growth and respiration. Somatic growth and respiration account for a major portion of the energy utilised by most mature organisms (with the exception of olds, non-actively growing individuals), and for all of the energy utilised by immature organisms (Dame, 1972).

While the temperate mussels have been studied in detail (Bayne, 1976), literature regarding the growth of the green mussels \( P. viridis \) is more limited (Paul, 1942; Ranade et al., 1973; Qasim et al., 1977).

This study reports a quantitative aspect of growth and respiration of a tropical mussel in terms of energetics. Some aspects of the respiration and ecology of these green mussels have already been worked out by Shafee (1976, 1977 and 1978) and references are made to these as they pertain to a great part of the present study. Although the study reported here is very organismic in scope, the results may be easily adaptable to other marine tropical bivalves or even to tropical marine invertebrates in general.

MATERIALS AND METHODS

Location

\( Perna viridis \) L. were collected from Ennore estuary 20 km north of Madras (13°N, 80°E). The mussel population found in this estuary was completely exposed at low tide and completely immersed at high tide during an average tidal cycle and the approximate tidal range was one meter at the collection site. Due to the construction of a thermal power station at Ennore, the mouth of the estuary was kept permanently open throughout the period of this study. Temperature and salinity measurements were made at more or less regular monthly intervals. Temperature was measured by a centigrade thermometer and salinity by silver nitrate titrations.

**Growth**

Green mussels of different sizes were collected during the years 1974 and 1975, brought to the laboratory, separated from the clumps and cleaned in sea-water. The byssus threads were removed and the shells were numbered with white paint. The total length of the mussels was measured to the nearest 0.1 mm. These mussels were placed in a nylon net and suspended approximately midway in the intertidal zone of the Ennore estuary. Some mussels were placed in a plastic bucket, perforated to allow water circulation, and subsequently placed in the water, beside the suspended nylon nets. During the course of the study, many spa threads were found attached to the bamboo stakes for mussel culture work located near the experimental site. In such cases, the stakes were also numbered in order to study the spat growth. The site was visited on many occasions during the course of this study (1974-1975), and the increases in length were noted on each occasion.

The percent of protein matrix per unit of the shell weight was determined by ashing the weighed shells in a muffle furnace for approximately 24 hours at 550°C. The difference between the initial and final weights was assumed to represent the mass of organic material present in the shell. This value was divided by the original weight of the shell to yield the fraction of organic matter by weight in the shell.

The byssus production per animal was studied by collecting mussels of different sizes, along with their byssus threads, from the field population. The byssus were removed from the respective shells, cleaned well and dried in an air oven at 60°C. The dry weight of the byssus per length of the shell was determined. The amount of organic matter present in the byssus was determined by ashing them in the muffle furnace for 12 hours at 550°C.

Table 1

<table>
<thead>
<tr>
<th>Months</th>
<th>Temperature (°C)</th>
<th>Salinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>26.04</td>
<td>32.91</td>
</tr>
<tr>
<td>February</td>
<td>28.35</td>
<td>33.30</td>
</tr>
<tr>
<td>March</td>
<td>28.03</td>
<td>33.63</td>
</tr>
<tr>
<td>April</td>
<td>28.70</td>
<td>33.10</td>
</tr>
<tr>
<td>May</td>
<td>27.85</td>
<td>32.54</td>
</tr>
<tr>
<td>June</td>
<td>26.93</td>
<td>34.01</td>
</tr>
<tr>
<td>July</td>
<td>26.50</td>
<td>34.14</td>
</tr>
<tr>
<td>August</td>
<td>27.00</td>
<td>33.10</td>
</tr>
<tr>
<td>September</td>
<td>27.85</td>
<td>32.95</td>
</tr>
<tr>
<td>October</td>
<td>28.60</td>
<td>31.81</td>
</tr>
<tr>
<td>November</td>
<td>26.50</td>
<td>19.39</td>
</tr>
<tr>
<td>December</td>
<td>25.00</td>
<td>28.44</td>
</tr>
</tbody>
</table>
During the course of this study, mature and immature mussels were brought to the laboratory from the same site, and the biometric relationships between the length and whole live weight of the mussels were studied. Measurements were made as described by Shafee (1977).

Statistical treatment

All statistical analyses such as means, variances, standard errors, 95% Confidence Intervals, linear and non linear regressions were computed with the aid of the Hewlett Packard 9825 A Electronic Desk Computer at the "Centre Océanologique de Bretagne (COB)", using the programs given to the author by Dr. Gérard Conan.

RESULTS

Table 1 gives the values of salinity and water temperature of the Ennore estuary during the months of 1974. Salinity and temperature showed little variation except for a low value of salinity (19.39%) during the month of November, which occurred immediately following a rainfall. Such small changes in salinity and temperature were not considered important in the present study.

Growth

The length data obtained while rearing the marked mussels in the field during various time intervals were fitted to von Bertalanffy growth curves, as explained by Fabens (1965) and Tomlinson (in Abramson, 1971). Both are iterated least square techniques involving no transformation of variates \( L_t \) (initial size) and \( L_{t+1} \) (final size). Parameter \( K \) and \( L_m \) can be accurately estimated. Parameter \( t_0 \) cannot be estimated from such data since no information is available on size at age and \( t_0 \) was set equal to 0. Figure 1 shows the growth curve fitted to the equation \( L_t = L_m (1 - e^{-Kt}) \). The observed values are also plotted in the same figure.

The average percent protein matrix per mussel shell from ten determinations was 11.68 with a standard error of 1.42. The regression between length and whole weight of the mature and immature animals is described in Table 2. The mussels measuring less than 40 mm in length were considered to be immature, while those measuring more than 40 mm in length were assumed to be mature (Shafee, 1977). The relation between dry byssus weight and mussel length is also described in Table 2. The mean percent protein matrix in the byssus threads was found to be 72.33%, with a standard error of 5.38.

Table 2

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Group</th>
<th>Regression</th>
<th>Equation</th>
<th>( 95% ) CI</th>
<th>( a )</th>
<th>( b )</th>
<th>( r )</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length (L) (mm) and whole live weight (W) (mg)</td>
<td>Immature</td>
<td>( x ) on ( y )</td>
<td>( nL = 3.0141 + 0.3797 \ln W )</td>
<td>3696</td>
<td>.0857</td>
<td>0.98</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Functional</td>
<td>( y ) on ( x )</td>
<td>( \ln W = -7.5573 + 2.5183 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Functional</td>
<td>( x ) on ( y )</td>
<td>( \ln W = -7.7458 + 2.5734 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Functional</td>
<td>( y ) on ( x )</td>
<td>( \ln W = -8.6587 + 2.8009 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td></td>
<td>( \ln W = -8.7234 + 2.8163 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>( x ) on ( y )</td>
<td>( \ln L = 2.1236 + 0.4222 \ln WB )</td>
<td>2.2367</td>
<td>0.5001</td>
<td>0.97</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Functional</td>
<td>( y ) on ( x )</td>
<td>( \ln WB = -4.5197 + 2.2504 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Functional</td>
<td>( \ln WB = -4.7710 + 2.3086 \ln L )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Energy requirements

From the growth data reported above and the respiration observations of Shafee (1976), the annual energy expenditure for mussels of various sizes (2, 40, 80 and 120 mm) was calculated. The growth in mussel length per year (T) was calculated from the formula described by Gulland (1969):

\[ l_{t+T} = L_s (1 - e^{-kt}) + L_s e^{-kt} \]  

(1)

where \( l_s \) is the length at the beginning of the experiment, \( L_s \) is the maximum length derived from the von Bertalanffy growth curve (Fig. 1), \( K \) is a constant which describes the rate at which the growth rate of the animal decreases with age and \( e \) is the base of natural logarithms.

The lengths were converted to dry body weights by using the relationships:

\[ \log W_d = -0.9670 + 1.9863 \log L_s \]  

(2a)

for immature mussels and

\[ \log W_d = -2.5582 + 3.0283 \log L_s \]  

(2b)

for mature mussels, where \( W_d \) is the dry body weight in grams and \( L_s \) is the length in millimetres (Shafee, 1977). The increase in dry body weight \( W_d \) per given time may be calculated from the equation:

\[ W_{dA} = W_{dA} - W_{dA} \]  

(3)

where \( W_{dA} \) is the dry body weight of the animal prior to the experiment and \( W_{dA} \) is the dry body weight of the mussel after a given time period.

To calculate the growth energy due to increase in body tissues \((G_b)\), the increase in dry body weight was converted to caloric equivalents using the formula:

- 1 mg ash free dry body of immature mussel = 5.332 kcal.

- 1 mg ash free dry body of mature mussel = 5.440 kcal (Shafee, 1978).

The growth energy used to form shell protein matrix \((G_s)\) was calculated using the formula:

\[ G_s = (W_s) (0.51) (0.1168) (5.5) \]  

(4)

and

\[ W_s = (W_{sA}) - W_s \]  

(5)

where \( W_s \) is the whole weight of the animal prior to the experiment and \( W_{sA} \) is the whole weight of the animal after a given time. \( W_{sA} \) and \( W_s \) were determined using the relationships described in Table 3, 0.51 is the proportion of the whole which is shell (Shafee, 1977), 0.116 is the proportion of protein by weight/unit of the shell, and 5.5 Kcal/g is the assumed caloric value of shell protein matrix (Morrowitz, 1968; Dame, 1972).

The energy cost of byssus production \((G_{by})\) was calculated from the equation:

\[ W_{by} = W_{byA} - W_{by} \]  

(6)

and

\[ P_s = W_{by} \times 0.723 \times 5.5 \]  

(7)

\( W_{byA} \) is the weight of the dry byssus in grams after a given time and \( W_{by} \) is the weight of the byssus in grams at the beginning of the experiment. 0.723 is the proportion of the organic matter found in byssus and 5.5 is assumed to be the equivalent caloric content of organic matrix (Morrowitz, 1968). \( W_{by} \) and \( W_{byA} \) may be calculated from \( l_s \) and \( l_{s+T} \) by utilising the relationships described in Table 2.

Energy requirements for respiration were calculated using the equation:

\[ \log [O_2] = 0.817 + 0.7001 \log W_{dA} \]  

(8)

where \([O_2]\) is the oxygen consumed in microlitres per hour and \( W_{dA} \) is the average dry weight in milligrams (Shafee, 1976). The mean monthly dry weight \((W_{dA})\) may be calculated as follows:

\[ W_{dA} = \frac{W_{dA} + W_{dA} + W_{dA}}{2} \]  

(9)

where \( W_{dA+1} \) is the dry body weight of the animal after 30 days and \( W_{dA} \) is the dry body weight of the mussel prior to the experiment (assuming that every month has 30 days). The energy required for respiration in water \((R_s)\) for mussels was calculated using the relationship:

\[ R_s = 0.00483 \times 360 \times [O_2] \]  

(10)

where 0.00483 is the kilocalories per millilitre of oxygen consumed (Dame, 1972), 360 is the number of hours on the average that an intertidal mussel is submerged in an average month (30 days) and \([O_2]\) is the oxygen consumed in millilitres per hour as calculated using equation (8), while the mean dry body weight was calculated using the equation (9). The monthly energies are summed to yield

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**Table 3**

Comparison of the annual energy requirements in kilocalories by the green mussels of different sizes (refer text for explanation of symbols).

<table>
<thead>
<tr>
<th>Size of the mussel at ( l_s ) (mm)</th>
<th>( G_b )</th>
<th>( G_s )</th>
<th>( G_{by} )</th>
<th>( P ) (( G_b + G_s + G_{by} ))</th>
<th>( R_s ) (( R_s \times 2 ))</th>
<th>( R_s ) (0.79 ( R_s ))</th>
<th>( R_s ) (( R_s + \alpha ))</th>
<th>A (( P + R_s ))</th>
<th>%G</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.7513</td>
<td>1.0994</td>
<td>0.1855</td>
<td>2.9462</td>
<td>1.6404</td>
<td>0.6480</td>
<td>2.2884</td>
<td>5.2346</td>
<td>56.</td>
</tr>
<tr>
<td>40</td>
<td>22.6208</td>
<td>28.9912</td>
<td>1.6077</td>
<td>53.2197</td>
<td>55.9428</td>
<td>22.0974</td>
<td>78.0402</td>
<td>131.2599</td>
<td>40.55</td>
</tr>
<tr>
<td>80</td>
<td>27.4743</td>
<td>32.2831</td>
<td>1.5527</td>
<td>61.31</td>
<td>91.7722</td>
<td>36.2500</td>
<td>126.0222</td>
<td>189.3322</td>
<td>32.78</td>
</tr>
<tr>
<td>120</td>
<td>21.7628</td>
<td>24.1603</td>
<td>1.0374</td>
<td>46.9605</td>
<td>143.5319</td>
<td>56.6951</td>
<td>200.2270</td>
<td>247.3875</td>
<td>19.00</td>
</tr>
</tbody>
</table>
an abundance of food throughout the year, very large social effects, and changes in salinity and temperature. (Paul, 1942). Seed (1975) has summarized the growth rates of various bivalve species and found that the growth rates differ even in the same species, due to many ecological and geographical factors. Many mathematical models have been developed to evaluate growth in bivalves and each of them has been found to give different estimates of growth, even when fitted to the same general data. The growth curves fitted to the von Bertalanffy equation in the present study give a higher growth rate for *Perna viridis* L., than all the temperate mussels that have been studied but is comparable with the findings of Paul (1942), Ranee et al. (1973) and Qasim et al. (1977).

Shafee (1976) has described the standard rate of respiration in *Perna (Mytilus) viridis*. However the routine rate of respiration is usually greater than the standard rate and it is dependent upon various ecological and physiological factors. Findings of McLusky and Stirling (1974) reveal that tropical bivalves may consume ten times more oxygen when they are active and approximately five times more during periods of spontaneous activity (routine rate), than when they are inactive (standard rate). Newell and Bayne (1973) have shown that the oxygen consumption of active *Mytilus* is approximately 3 times that of inactive mussels. The "scope for activity" as described by Fry (1957) was found to be approximately twice the standard rate of oxygen consumption in *M. edulis* (Bayne, 1974). In this study, routine rate of oxygen consumption is assumed to be twice that of the standard rate. This assumption is strengthened by the works of Trevallion (1971) who arrived at a similar conclusion while working on *Tellina tenius*.

**DISCUSSION**

Due to a relatively constant temperature (27.3°C) throughout the year, very slight changes in salinity and an abundance of food throughout all seasons, tropical animals are reported to grow faster than temperate animals (Paul, 1942). Seed (1976) has summarized the growth rates of many temperate mussels and found that the growth rates differ even in the same species, due to many ecological and geographical factors. Many mathematical models have been developed to evaluate growth in mussels and each of them have been found to give different estimates of growth, even when fitted to the same basic data. The growth curve fitted to the von Bertalanffy equation in the present study gives a higher growth rate for *Perna viridis* L., than all the temperate mussels hither reported but is comparable with the findings of Paul (1942), Ranee et al. (1973) and Qasim et al. (1977).

The organic matter present in the shell of *Perna viridis* (11.68%) appears to be higher than the organic matter present in the shell of *Mytilus edulis* (Dare, 1975), but compares well with that of *Modiolus demissa* (Kuenzler, 1961).

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Aerial respiration in mussels has been studied by Kuenzler (1961) for *Modiolus demissa*, by Coleman (1973) for *Mytilus edulis* and by Bayne et al. (1976 a) for *Mytilus californianus*. Summarizing all these findings, Bayne et al. (1976 b) expressed the view that oxygen consumption in air by mussels is slightly less than standard oxygen consumption in water. In this study, no experimental work was performed to verify this statement. However, it is assumed that oxygen consumption in air is 79% of the oxygen consumption during standard metabolic rate in water. This value (79%) is the mean of the values reported for other mussels by various authors.

The ratio of growth energy (G) to assimilated energy (A) may be called the growth efficiency (G/A). The immature mussels show higher values (56%) for this parameter. The lower values for mature mussels reflect the energy lost in reproductive products. This is not considered in the present study. The values of growth efficiency obtained in this study may be compared with those of other bivalves. Table 4 shows respiration and growth as a percent of assimilation for different species of bivalves, as computed for either populations or individual organisms. The large amount of variation in efficiencies observed is due to several factors. Seasonal changes in temperature, total food supply or quality of food, and reproduction each affect growth and respiration differently, thus affecting the ratios between growth and respiration in temperate organisms. In addition, the percent growth in relation to

<table>
<thead>
<tr>
<th>Species</th>
<th>%R</th>
<th>%G</th>
<th>Habitat</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crassostrea virginica (a)</td>
<td>57-74</td>
<td>26-43</td>
<td>Intertidal salt marsh</td>
<td>Dame (1971)</td>
</tr>
<tr>
<td>Modiolus demissa</td>
<td>70</td>
<td>25</td>
<td>Intertidal salt marsh</td>
<td>Kuenzler (1961)</td>
</tr>
<tr>
<td>Mytilus californianus (b)</td>
<td>8-15</td>
<td>11-84</td>
<td>Marine intertidal</td>
<td>Fox and Coe (1943)</td>
</tr>
<tr>
<td>Mytilus edulis (a)</td>
<td>44-81</td>
<td>19-56</td>
<td>Intertidal estuary</td>
<td>Jorgensen (1952)</td>
</tr>
<tr>
<td>Perna viridis (a)</td>
<td>50-70</td>
<td>29-50</td>
<td>Subtidal coast</td>
<td>This study</td>
</tr>
<tr>
<td>Patinopecten yessoen</td>
<td>76-79</td>
<td>21-24</td>
<td>Intertidal mudflat</td>
<td>Fuji and Hashizume (1974)</td>
</tr>
<tr>
<td>Scrobicularia plana (c)</td>
<td>71-87</td>
<td>13-29</td>
<td>Intertidal sand</td>
<td>Hughes (1970)</td>
</tr>
<tr>
<td>Tellina tenius (c)</td>
<td>71-87</td>
<td>13-29</td>
<td>Intertidal sand</td>
<td>Trevallion (1971)</td>
</tr>
</tbody>
</table>

(a) Reproduction energy is not included.
(b) Data taken from Trevallion, 1971.
(c) Production energy is used in place of growth energy.
assimilation may be influenced by the size and age of the animal (Jorgensen, 1952; Dame, 1972).

It may be noticed that all workers listed in Table 4 except for Trevallion (1971) have considered only the standard rate of respiration as respiration energy losses. The present study bears experimental results only for the standard rate of respiration in water. If aerial respiration which has not been studied in this work, could be neglected and only the standard rate of respiration could be considered, the percentage of growth by assimilation would give an over estimation of growth efficiency. But, on the other hand, if Bayne's (1976a) approximation is used to evaluate routine and aerial respiration, then this gives a reasonable estimate of Growth Efficiency.

Phillipson (1966) has noted that poikilotherms usually utilise more assimilated energy in growth than homotherms and that this characteristic renders poikilotherms more economical as a source of animal protein. The energies utilised by tropical mussels for their growth and respiration show that these animals may play a major role in the functioning of tropical marine ecosystems, where they live in dense populations. Although some growth energy is essentially lost in the functioning of tropical marine mussels: their physiological ecology and metabolism, edited by B. L. Bayne, Cambridge University Press, 1976. Cambridge University Press. 506 p.


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