

## AN ENERGY BUDGET FOR A POPULATION OF THE LIMPET *PATELLA VULGATA*

J. R. WRIGHT\* AND R. G. HARTNOLL

Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man

(Figs. 1-6)

An energy budget has been assembled for a population of the limpet *Patella vulgata* inhabiting the mid-tide level of a moderately sheltered shore in the Isle of Man. The average biomass during the two year study was  $346 \text{ kJ m}^{-2}$ , and the energy budget in  $\text{kJ m}^{-2} \text{ year}^{-1}$ :

$$1605 = 68 + 96 + 498 + 884 + 59$$
$$(C = P_g + P_r + R + F + U).$$

This budget is compared with those for other intertidal herbivorous gastropods. Notable features include the high proportion of total production appearing as gametes, and the low  $P/B$  ratio. However, the latter is not low in relation to similarly long-lived molluscs.

### INTRODUCTION

Only a few energy budgets are available for rocky-shore herbivorous gastropods (Table 7), and not many for intertidal molluscs in general. This is scarcely surprising. It is difficult enough to derive a short-term energy budget for a single animal in the laboratory, but vastly more complicated to produce an annual budget for a population in the field. Nevertheless we felt that it was a worthwhile exercise, for some understanding of the dynamics of energy flow is basic to an appreciation of the functioning of a rocky-shore ecosystem. *Patella vulgata* L. was selected for study because it is the major grazer in the mid-shore region, and a major influence on community composition due to its restriction of algal growth (Jones, 1948; Lodge, 1948; Southward, 1964; Southward & Southward, 1978). The study was conducted at mid-tide level on a moderately sheltered shore, a situation in which the effects of *Patella* are marked. On practical grounds, the abundance and relatively large size of *Patella*, together with its adoption of a fairly constant home base (Hartnoll & Wright, 1977), greatly facilitated the design and execution of the programme.

The basic equation for the components of an energy budget is, according to IBP terminology (Petrusewicz, 1967; Ricker, 1968), as follows:

$$C = P_g + P_r + R + F + U.$$

$C$  is the energy content of the food consumed,  $P_g$  is the energy content of the tissue added to the population by growth and recruitment,  $P_r$  is the energy content of the gametes liberated during spawning,  $R$  is the energy lost as a result of respiration,  $F$  is the energy content of the faeces,  $U$  is the energy lost as urine and other exudates,  $C - F - U$  is the food assimilated ( $A$ ),  $P$  is the total production, derived by adding  $P_g$  and  $P_r$ .

\* Present address: St Mary's Sixth Form College, Middlesbrough.

The aim of our investigation was to determine each component of the energy budget for a defined population of *Patella vulgata*, so that the final balance of the equation would indicate the accuracy of the work: most of the other studies in Table 7 lack this internal check. The basic strategy involved selecting a fairly large region of apparently homogeneous composition ('the ledge'), and locating within this a fixed area of 5 m<sup>2</sup> ('the quadrats') containing the population under study. The limpets in the quadrats were undisturbed, other than for monthly *in situ* measurements of shell length, and monitoring of recruitment and mortality. Limpets were removed elsewhere from the ledge as required for biometric analysis and laboratory experiment, in order to provide data for the calculation of the energy budget components of the limpets in the quadrats. In this way, energy budgets for the quadrats were compiled for the two twelve-month periods of March 1974 to February 1975, and March 1975 to February 1976; these are preferable to calendar years since the termination of the main breeding season in December to January would complicate the assessment of a budget for a period ending in December. However, the two periods will generally be referred to as '1974' and '1975' respectively.

#### METHODS

Details of the methods used for determining each component of the budget are presented in the appropriate section, but several widely used procedures can conveniently be described here. Data are generally presented in terms of dry weight, ash-free dry weight, or calorific content. Dry weights were determined by drying at 80 °C in an oven to constant weight. Ash weights were determined by heating in a muffle furnace at 500 °C for 4 h. Calorific content was determined with a Phillipson oxygen micro-bomb calorimeter (Gentry Instruments) linked to a Unicam AR 35 potentiometer recorder: the procedure described by Phillipson (1964) was followed. The components of the energy budget were determined for the 5 m<sup>2</sup> quadrat area, but the final budget is presented in kJ m<sup>-2</sup> year<sup>-1</sup>. The joule and kilojoule are used since they are the S.I. units for energy. Previous studies have worked in calories, and so in Table 7 the energy budget for *Patella* is presented in both kJ and kcal, and those for other species in kcal.

Some terminology needs to be defined. Biomass is the weight of the whole animal. Shell weight is the weight of the shell. Flesh weight is the weight of the animal without the shell. Somatic weight is the weight of the flesh with the gonads removed. Gonad weight is the weight of the gonads. Non-gonad biomass is the weight of the limpet without gonad, namely the sum of the shell and somatic weights.

#### RESULTS

##### *The population investigated*

Previous investigations have shown that different populations of the same gastropod species can have very different energy budget characteristics. Paine (1971) demonstrated this for high and low shore populations of *Tegula funebris* (Adams), and Hughes (1971*b*) for neighbouring populations of *Nerita peloronta* L. There is abundant evidence that populations of *Patella vulgata* vary enormously in such features as growth rate, age structure and size-frequency distribution (Jones, 1948; Lewis & Bowman, 1975; Southward, 1953), and consequent energy budget differences must be anticipated. So in order to place this study in its proper context, it is essential to define in some detail the environment and population characteristics of the limpets investigated.

The study was carried out at Derbyhaven, Isle of Man, on a moderately sheltered shore which rated point five on the Ballantine scale (Ballantine, 1961). The limestone rock has almost horizontal strata, so that the shore is composed of level platforms separated by vertical steps. The platform at mean tide level, measuring 110 m long by on average 6.5 m wide, was selected as the study ledge. It had a fairly evenly distributed

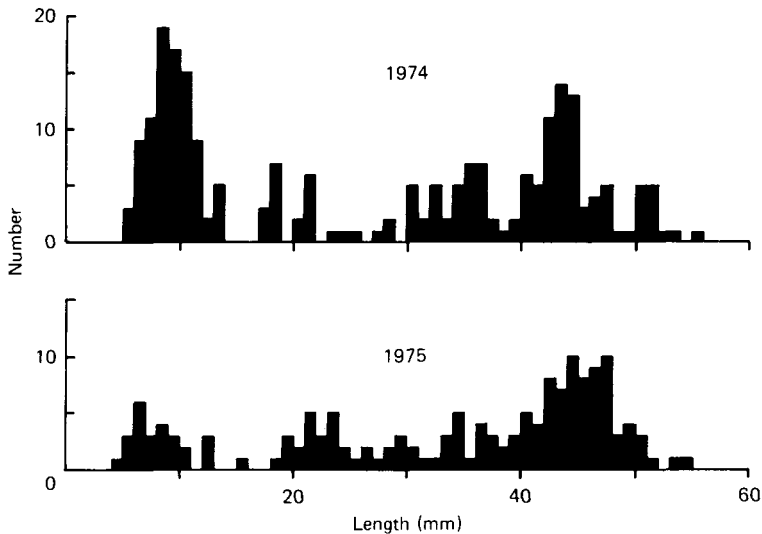


Fig. 1. Length-frequency histograms for the quadrat limpets in October 1974 and October 1975 (1 mm length classes).

community, of which the prominent components were *Fucus serratus* L. and *Fucus vesiculosus* L. in roughly equal amounts, the barnacle *Balanus balanoides* (L.), and the gastropods *Patella vulgata*, *Littorina littoralis* (L.) and *Nucella lapillus* (L.). Total algal cover was of the order of 25%, and barnacle cover also about 25%, with appreciable amounts of bare rock. The quadrats were five contiguous 1 m<sup>2</sup> quadrats running along-shore near the middle of the ledge. During the study the quadrats contained between 130 and 232 limpets, the fluctuation being mainly due to recruitment, followed by the subsequent early death of the young limpets.

The size-frequency distribution is one informative characteristic of a limpet population. The length distribution of the limpets in the quadrats varied seasonally due to recruitment, growth and mortality, and from year to year due to different levels of recruitment. Histograms of length-frequency for October in 1974 and 1975 are presented in Fig. 1, so that they can be compared with the distributions for the same time of year given by Lewis & Bowman (1975, fig. 6). The size of the Derbyhaven limpets, of which a large proportion exceeded 40 mm length, was greater than any of their East coast populations. However, the overall pattern of length-frequency is most like their site 9, 'mid-level, bare rock and *Fucus*': this roughly describes the Derbyhaven habitat, so the population structure seems typical for this type of environment. The distribution in Fig. 1 also resembles that from the more sheltered site at Port St Mary in the Isle of Man

described by Southward (1953). Very different length–frequency patterns are described by both Southward (1953) and Lewis & Bowman (1975) from more exposed sites or from different shore levels, implying very different energy budgets.

The second important population characteristic is growth rate, and the repeated measurement of known individuals over a two-year period enabled a growth curve to be constructed (Fig. 2). This is based on observation for the first six years of life – beyond

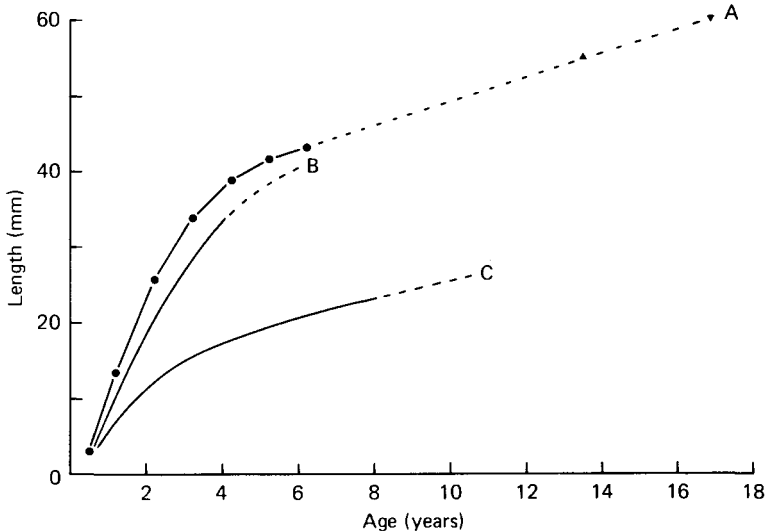


Fig. 2. Growth curves for *Patella vulgata*, the solid portions observed, the broken portions extrapolated. (A) The quadrat limpets of the present study ( $\blacktriangle$ , largest limpet in quadrats;  $\blacktriangledown$ , largest limpet on ledge). (B) Lewis & Bowman (1975) site 9, 'mid shore bare rock and *Fucus*'. (C) Lewis & Bowman (1975) site 2, 'high shore barnacles and mussels'.

that it is extrapolated. Growth is rapid during the first four years, but the rate declines markedly with the onset of sexual maturity: however, some growth does continue throughout life. The growth rate of the quadrat specimens is probably relatively rapid for the species, since Lewis & Bowman (1975, fig. 7) have demonstrated that this is so for 'mid level bare rock and *Fucus*' populations. The curve indicates that the largest limpet found in the quadrats was about thirteen years old, the largest limpet on the ledge about seventeen. Fig. 1 shows that a large proportion of the population is between 40 and 50 mm in length, and Fig. 2 indicates that these limpets will be mature, slow growing, and between five and ten years old.

#### Growth production – $P_g$

Growth production is the production of tissue other than gametes, and is made up of two components.

$$P_g = \Delta B + E,$$

where  $\Delta B$  is the change in non-gonad biomass of the population and  $E$  is the balance between the loss of non-gonad biomass by mortality and its addition by recruitment. In

order to determine  $P_g$ , the length of each limpet in the quadrats was measured monthly, and appropriate conversions (see below) used to calculate the calorific value of shell and somatic tissue. The difference in the totals for two successive months gave  $\Delta B$  for the intervening period. Specimens lost by mortality and added by recruitment were identified and their non-gonadal calorific value determined in the same way to give  $E$ . If recruitment exceeded mortality, then the difference was deducted from  $\Delta B$  to give  $P_g$ . If, as is more usual, mortality exceeded recruitment, then the difference was added to  $\Delta B$ . The values of  $P_g$  for the monthly or longer periods were summed to give a total for the year.

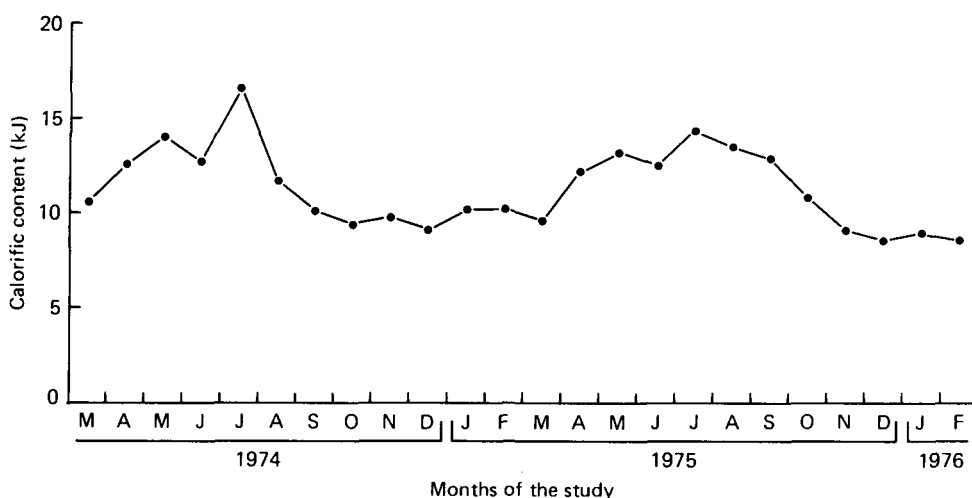


Fig. 3. Calorific content of the somatic tissue of a 40 mm-long limpet calculated for each month of the study.

The maximum shell length of the limpets in the quadrats was measured *in situ* each month with vernier calipers reading to 0.01 mm. Limpets were not marked, in case marking might affect mortality. However, individuals returned to fixed home-sites very consistently, and knowledge of the size and position of each limpet at the previous survey enabled specimens to be identified. Consequently, the loss of specimens (by mortality or emigration) and the gain of specimens (by recruitment or immigration) was detected. Over the course of a year, immigration and emigration can be assumed to balance, and hence ignored as factors in the determination of  $P_g$ .

In order to calculate calorific values for the quadrat limpets, a sample of limpets was collected each month from the ledge, always avoiding the area adjacent to the quadrats. The length of each limpet was measured, and the shell separated from the flesh. Dry shell weight was determined. The gonads were dissected away from the somatic tissue, and dry somatic weight determined. The calorific value of the somatic tissue was determined each month. The relation between shell length and dry shell weight was similar throughout the year, and is best expressed by the regression of  $\log_{10}$  shell weight (g) on  $\log_{10}$  shell length (mm) with the parameters: correlation coefficient, 0.994; slope, 3.70; intercept, -5.23. Dry shell weight was converted to calories using the value

accepted by Paine (1971) for another herbivorous gastropod,  $0.263 \text{ kJ g}^{-1}$ . The relation between shell length and dry somatic weight varied appreciably from month to month, and so a series of regressions of log dry somatic weight on log shell length were determined (Wright, 1977, table 4). The calorific value of the somatic tissue also varied through the year, due to variation in the composition of the tissues (Wright, 1977, table 6). Polysaccharide (mainly glycogen) is stored in the foot and hepatopancreas, and

Table 1. *The number and biomass of the limpets in the 5 m<sup>2</sup> quadrat area, and the components and total of growth production. Also the gonad calorific content*

Values are given for each month of the study. For each year mean numbers and biomass are given, and total growth production.

Month	Number	Biomass (kJ)	$\Delta B$ (kJ)	$E$ (kJ)	$P_g$ (kJ)	Gonad calorific content (kJ)
1974						
Mar.	168	1465	196.4	1.3	197.6	42.3
Apr.	172	1671	233.2	-18.4	214.8	51.1
May	171	1871	-8.4	54.0	45.6	58.2
June	177	1901	257.1	-18.0	239.1	58.2
July	189	2169	-402.4	43.1	-359.2	69.5
Aug.	232	1972	-338.3	61.1	-277.2	272.1
Sept.	232	1629	-172.1	41.0	-131.0	269.6
Oct.	213	1650	59.9	-11.3	48.6	460.5
Nov.	214	1725	-110.5	98.0	-12.6	476.9
Dec.	178	1319	186.7	8.8	195.5	180.5
1975						
Jan.	177	1419	172.1	23.9	195.9	97.1
Feb.	161	1545	-56.1	-11.7	-67.8	93.8
Year 1974-1975: $\bar{x} = 190$ $\bar{x} = 1696$ $\Sigma x = 17.6$ $\Sigma x = 271.7$ $\Sigma x = 289.3$						
Mar.	160	1482	530.9	-13.0	517.9	42.7
Apr.	160	1758				50.2
May	160	2039	62.4	46.5	108.9	64.1
June	174	2102	-43.1	75.8	33.1	69.9
July	175	2156				75.8
Aug.	176	2160	-219.8	77.5	-142.4	170.4
Sept.	166	2077	-290.6	69.5	-221.1	307.3
Oct.	154	1809	-367.2	56.7	-311.1	328.7
Nov.	156	1507	118.5	61.1	179.7	358.0
Dec.	149	1407				500.3
1976						
Jan.	142	1306	212.7	16.7	229.4	238.6
Feb.	136	1357				123.5
Mar.	130	1486				42.7
Year 1975-1976 $\bar{x} = 159$ $\bar{x} = 1763$ $\Sigma x = 3.8$ $\Sigma x = 390.2$ $\Sigma x = 394.0$						

in June/July its content rises to five times the winter level (Barry & Munday, 1959; Blackmore, 1969). Lipid content rises to a peak in August (Blackmore, 1969). These changes are due to the accumulation of reserves and their subsequent transfer to the maturing gonads, for they are not seen in spat and second-year limpets, which are all immature. The variation in calorific value will be caused predominantly by lipid content, since lipid has a very high calorific value of  $39.6 \text{ kJ g}^{-1}$ . The cumulative effects of changes in somatic weight and calorific value are seen in Fig. 3, which plots the change in

somatic calorific content of a 40 mm-long limpet over the course of the study. The increase during the first half of each year represents the accumulation of reserves, the subsequent decline the transfer of reserves to the developing gonads.

The appropriate conversions were used to calculate the values of  $\Delta B$ ,  $E$  and  $P_g$  for the quadrat limpets in each month of the study (Table 1). This also records the total number

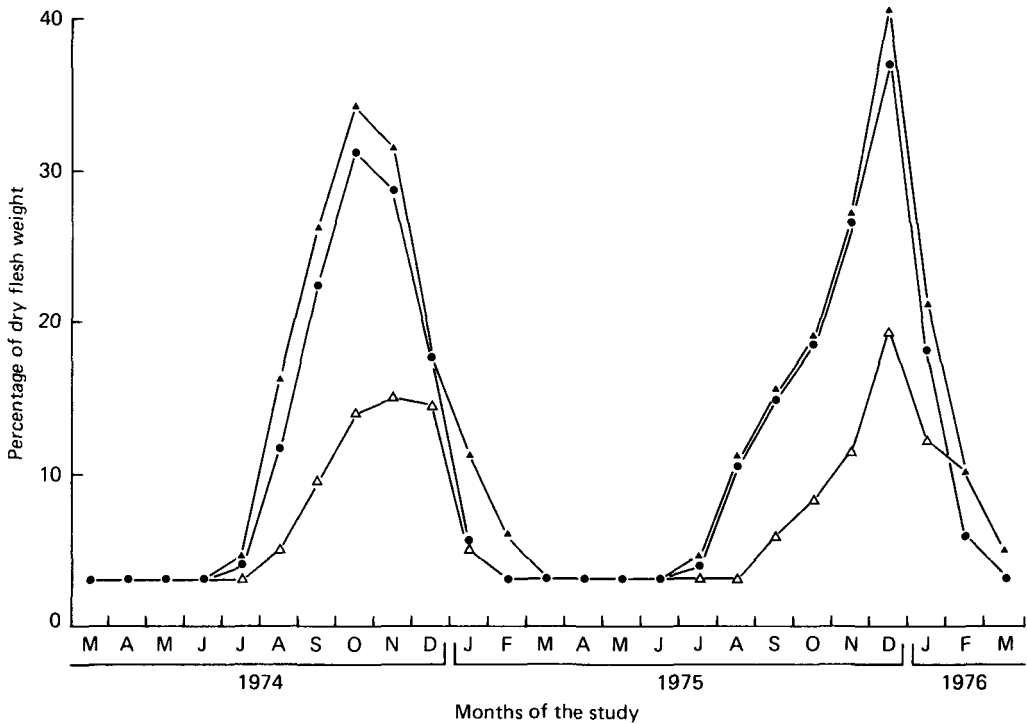


Fig. 4. Gonad dry weight as a percentage of dry flesh weight for each month of the study ( $\Delta$ , third-year males;  $\blacktriangle$ , older males;  $\bullet$ , females).

and biomass of the quadrat limpets each month. The fluctuations in number are mainly due to recruitment of considerable numbers of spat followed by their subsequent rapid mortality. In 1974, recruitment was high and numbers fluctuated between 161 and 232, but in 1975 it was poor and the population ranged only between 136 and 176. Biomass also changed considerably during each year due to the combined effects of recruitment, gonad maturation and spawning, but over the year changes were small. The same constancy is seen in the non-gonad biomass, with a  $\Delta B$  of +17.6 kJ for 1974, and +3.77 kJ for 1975. This is important, for a steady-state system from year to year is a prerequisite for a meaningful energy budget analysis. The total  $P_g$  for the quadrat limpets was 289.3 kJ for 1974 and 394.0 kJ for 1975; in each year, most growth production occurred from December to June, since between July and November resources were used for gonad maturation. Sea temperatures were higher in 1975 than in 1974, which probably accounts for the higher  $P_g$  in the second year of the study.

*Reproductive production - P<sub>r</sub>*

*Patella vulgata* spawns once each year in winter. If the calorific value after spawning is deducted from that before spawning, this gives the annual  $P_r$  for a limpet. This was done for the quadrat limpets, and an allowance added for specimens which died during the period of gonad maturation, to give the total annual  $P_r$ . The gonad calorific content of the quadrat limpets was calculated from their shell length, using conversions derived from the monthly samples from the ledge described in the preceding section.

Table 2. *Calorific values of male and female gonads (kJ g<sup>-1</sup> dry wt)*

Standard error in brackets.			
Males			
Spent/resting	Dec.	19.2	(0.42)
	Jan-July	19.0	(0.21)
Maturing	Aug.	19.6	(0.17)
	Sept.	19.7	(0.71)
	Oct.-Dec.	19.8	(0.46)
Females			
Spent/resting	Jan.	22.7	(0.50)
	Feb./July	18.7	(0.29)
Maturing	Aug.	19.8	(0.13)
	Sept.	25.0	(0.29)
	Oct.	25.3	(0.29)
	Nov.	25.3	(0.38)
	Dec.	25.2	(0.80)

A complication is that *Patella vulgata* is a protandrous hermaphrodite, with no external sexual characters. Examination of over 1000 specimens during the study showed that all first- and second-year limpets were neuter. All third-year specimens, 92.5% of fourth-year specimens, and 58% of those older than four years were male. After the fifth year there was no further change in the sex ratio, so it is clear that some males change sex whereas others remain male throughout life: this suggests that *Patella vulgata* could be diandric, with two genetically different forms of male. Other studies have similarly recorded appreciable proportions of males in the largest size groups (Ballantine, 1961; Blackmore, 1969; Das & Seshappa, 1948; Lewis & Bowman, 1975).

The above sex ratios were used to estimate the proportions of males and females in each year class of the quadrat limpets. The calorific content of the gonads was then calculated using the appropriate conversions. The flesh weight was determined from the monthly regression of log dry flesh weight on log shell length (Wright, 1977, table 4), and the gonad weight determined as the specified percentage of the flesh weight (Fig. 4). The calorific content was calculated using the calorific value of the gonad (Table 2). Separate conversions were required for third-year males, older males, and for females. Third-year males commence gonad maturation in August/September, and the testes develop to a maximum of 19% of the flesh weight. Older males begin to mature earlier in July, and the testes can reach 40% of the flesh weight. All female year classes commence maturing in July, and mature ovaries average up to 37% of flesh weight. The calorific value of the testes only increased slightly with maturation, from 19.05 to 19.8 kJ g<sup>-1</sup>,



whilst that of the ovaries did so markedly, from 18.9 to 25.3 kJ g<sup>-1</sup>, no doubt due to increased lipid content. The sexes spawn simultaneously, and this commenced early in December in 1974, but in late December in 1975.

The total gonad calorific content for the quadrat limpets in each month is given in the final column of Table 1. After spawning begins, the content falls rapidly over about two months, which represents mainly loss of gametes. This is followed by a slow return to the resting value due to resorption of the few remaining. The total  $P_r$  for each year is calculated as follows:

1974	Gamete production at spawning	476.9 - 97.1 = 379.8 kJ
	Gametes lost by mortality	95.8 kJ
	Total $P_r$	475.6 kJ
1975	Gamete production at spawning	500.3 - 123.5 = 376.8 kJ
	Gametes lost by mortality	102.6 kJ
	Total $P_r$	479.4 kJ

The totals for the two years are interestingly very close, in contrast to the marked difference in  $P_g$ . This suggests that if there is a scarcity of resources, then gamete production has a higher priority than somatic growth.

#### *Respiration - R*

It is not practicable to measure energy output by direct calorimetry in poikilotherms, and so it was determined indirectly by measuring the oxygen consumption during respiration, and applying an oxycalorific coefficient. This was the general coefficient of 14.2 J mg<sup>-1</sup> oxygen, or 20.2 J ml<sup>-1</sup> oxygen at N.T.P. (Ivlev, 1935). In order to determine  $R$ , limpets were collected from the ledge each month, and their rate of respiration in air and water at ambient temperature determined in the laboratory. This information was used to calculate the overall respiration of the quadrat limpets each month, since they occur at M.T.L. and spend about half this time in air and half in water.

To measure aquatic respiration, limpets were collected from the ledge half an hour before immersion by the tide, taken to the laboratory and placed in 500 ml respiratory chambers: these were glass jars with airtight screw tops. The chambers were kept at the ambient seawater temperature at Derbyhaven. At the time of immersion of the ledge, the chambers were filled with sea water at ambient temperature and sealed for 6 h (the duration of immersion of the ledge). The oxygen content of the water was determined by the micro-Winkler technique, both before the experiment, and after the experiment in the chamber and in a control. The difference between the chamber and the control was the oxygen used by the experimental limpet.

To determine aerial respiration, limpets were collected from the ledge whilst immersed and kept immersed during transport to the laboratory. At the time of emersion of the ledge, they were transferred to constant-pressure respiratory chambers (Davies, 1966; modification of Scholander, 1942, for medium-sized animals) at ambient field air temperature. Oxygen uptake was recorded at half-hour intervals for 6 h. For both aquatic and aerial respiration, about twelve animals were assessed on each occasion.

The methods described above measured respiration at the time of immersion or

emersion in the field as appropriate, and for the full period of those conditions. This is very important, for both our own observations and those of Gompel (1937), show that the oxygen consumption rate of *Patella vulgata* varied with the tides. During emersion, respiration falls to a minimum at the time of low water: the methods used could not reveal variations in rate while immersed, but a similar rhythmicity must be anticipated.

Table 3. *Monthly totals for the quadrat limpets in respect of respiration and ammonia production*

All figures in kJ month<sup>-1</sup>.

Month	Aerial oxygen consumption	Aquatic oxygen consumption		Ammonia production
		Uncorrected	Corrected	
1974				
Mar.	30.8	72.6	108.8	0.44
Apr.	41.1	88.7	140.4	0.66
May	58.2	99.5	165.9	0.75
June	65.7	108.6	185.5	0.88
July	80.3	140.1	233.3	1.06
Aug.	76.8	140.6	228.6	1.15
Sept.	59.9	121.4	187.2	0.78
Oct.	50.4	108.4	158.1	0.75
Nov.	40.0	104.3	143.4	0.79
Dec.	44.8	77.0	102.7	0.51
1975				
Jan.	33.6	69.4	95.4	0.58
Feb.	28.7	57.1	80.8	0.46
Mar.	32.0	63.0	94.5	0.42
Apr.	44.8	93.4	148.0	0.67
May	60.9	104.8	174.7	0.81
June	75.5	125.8	214.8	0.99
July	82.4	138.1	230.2	1.24
Aug.	91.2	152.2	247.4	1.25
Sept.	70.5	139.8	227.1	1.14
Oct.	52.5	111.4	162.4	0.88
Nov.	38.0	91.4	125.7	0.68
Dec.	34.2	79.9	106.8	0.58
1976				
Jan.	31.9	65.3	89.7	0.47
Feb.	27.4	54.2	76.8	0.39

Any methods which ignore these tidal rhythms must be suspect. It was also considered important to carry out experiments during the first cycle of immersion or emersion after collection, and at the appropriate ambient temperature. This minimized risks associated with the development of arrhythmicity and the effects of acclimation.

The relation between oxygen consumption and flesh weight can be expressed as

$$O_2 = aW^b \quad (1)$$

or as

$$\log O_2 = \log a + b \log W \quad (2)$$

Equation 2 gives a linear relation between log oxygen consumption and log weight, and the parameters of this regression for each set of measurements of aquatic and aerial respiration are given by Wright (1977, tables 26 and 27). There is considerable variation

between months, basically as a function of temperature. Each month the quadrat limpets were measured, and their dry flesh weights determined from the appropriate regressions (Wright, 1977, table 4). From these weights, the total monthly aerial (Table 3) and aquatic (Table 3) respiration for the quadrat limpets was calculated using the results of the monthly respiration experiments. The major imponderable is the degree to which the transfer from field to laboratory conditions affected activity, and in consequence respiration rates. In the field, the population studied was active only when foraging whilst immersed in daylight (Hartnoll & Wright, 1977). In the laboratory, there was little movement at all whilst respiration was being determined. Thus the laboratory estimates are probably realistic in respect of aerial respiration, and of nocturnal aquatic respiration. The figure for daytime aquatic respiration was probably low, and to this an arbitrary correction of  $\times 2$  was applied, as various others have done previously (Brody, Proctor & Ashworth, 1934; Winberg, 1956; Odum, Connell & Davenport, 1962; Mann, 1964, 1965; Carefoot, 1967*a*; Trevallion, 1971). The uncorrected and corrected totals for aquatic respiration each month are given in Table 3.

The total annual oxygen consumption of the quadrat limpets was (1974):  $609.1 \text{ kJ}$  (aerial) +  $1830.1 \text{ kJ}$  (corr.aquatic) =  $2439.2 \text{ kJ}$ ; (1975):  $641.3 \text{ kJ}$  (aerial) +  $1898.1 \text{ kJ}$  (corr.aquatic) =  $2539.4 \text{ kJ}$ .

#### *Consumption and faeces – C and F*

These two components of the energy budget are best considered together, since faeces energy content was not measured directly. Instead, the absorption efficiency was determined, and faeces energy then derived from the energy content of the consumed food. This was not ideal, but appeared unavoidable: it does of course reduce the rigour of the internal check on the balance of the energy budget.

The population of limpets under study fed only during daytime immersion by the tide (Hartnoll & Wright, 1977), with about 75% of them feeding on any one day. The pattern of foraging behaviour is different in other habitats in the Isle of Man (Hawkins, 1979), and in *Patella vulgata* elsewhere (see Hartnoll & Wright, 1977). The limpets browsed on detritus and small algal growth on the rock surface, rasping the rock with the radula and apparently unselectively ingesting any material there: *Patella* does not normally browse upon large algae. It was not possible to measure the area of rock grazed naturally by an *in situ* limpet during a tidal immersion, so artificial substrates were provided. These were slates (50 by 25 cm), enclosed in wire cages to exclude or enclose limpets as appropriate, and bolted to the ledge. They were left with limpets excluded until covered by an obvious algal mat, and a limpet then placed on the slate. The area grazed during a tidal cycle was quite obvious as a cleared track. The algal film remaining on the slate was removed and its calorific content determined, which enabled the calorific value of the area of food ingested to be calculated. Attempts to conduct these feeding trials in the laboratory failed, because the limpets would not feed despite efforts to reproduce natural conditions. Therefore they were all carried out in the field, and this was only possible during the summer months: at other seasons, the slates were damaged by storms before an adequate algal mat developed.

The results for the field observations are given in Table 4. Clearly ingestion increases

with size, although ingestion per unit of size appears to decrease slightly. Ingestion is related to dry flesh weight by the equation:

$$I = aW^b$$

or

$$\log I = \log a + b \log W.$$

Table 4. *The ingestion in one daylight tidal immersion by limpets on slates on the shore during June, August and September*

Month	Length (mm)	Dry flesh weight (g)	Ingestion (J)	Ingestion ( $J g^{-1}$ dry flesh weight)
June	51.33	1.6784	800	477
	50.44	1.7892	687	381
	45.68	1.0053	519	515
	44.50	1.1121	557	502
	35.96	0.4389	176	402
	23.70	0.0922	59	620
Aug.	53.61	2.2981	1147	498
	51.41	1.9031	1017	536
	46.04	1.4532	469	332
	43.79	1.2147	431	356
	40.62	0.6499	373	574
	38.67	0.6254	364	586
	31.26	0.2431	155	628
	21.52	0.0618	25	414
Sept.	53.01	2.2268	955	427
	50.09	1.7241	691	402
	45.92	1.0762	414	385
	40.60	0.7342	264	360
	40.62	0.8357	394	473
	22.00	0.0624	29	498

Table 5. *Parameters for the regression of  $\log_{10}$  ingestion ( $Jd^{-1}$ ) on  $\log_{10}$  dry flesh weight (g) for observations in the month indicated and total ingestion (kJ) for the quadrat limpets in that month based upon these regressions*

Month	Correlation coefficient	Intercept	Slope	Monthly ingestion	
				1974	1975
June	0.991	2.665	0.905	1244	1440
Aug.	0.979	2.674	0.974	1328	1464
Sept.	0.996	2.617	0.945	1050	1210

The data for June, August and September were used to calculate separate linear regressions for log ingestion on log dry flesh weight (Table 5). The length of the quadrat limpets was measured each month, and dry flesh weights calculated from the regressions in Wright (1977, table 4). Then the total ingestion of the quadrat limpets was calculated for each of the months during which ingestion measurements were made (Table 5). It had to be assumed that ingestion on the natural rock was equivalent to that on the rather more profusely covered protected slates, and that transfer to the slates did not inhibit the limpets' feeding: hopefully these factors have introduced compensating bias.

Since the observations of consumption were restricted to the summer, estimation of the total annual consumption involved major assumptions. It was presumed that the monthly consumption as a proportion of the annual consumption is in the same ratio as that month's respiration is to the annual respiration. This is problematical, for many factors in addition to general metabolic level might affect consumption: thus the demands of gonad maturation might stimulate it, whilst the occupation of body space by the ripe gonads could inhibit feeding. Nevertheless, in the absence of any better alternative, this procedure was followed for the combined data for June, August and September of each year.

1974

Respiration for these months	803.7 kJ
Respiration for the whole year	2439.2 kJ
Consumption for these months	3622 kJ
Total annual consumption	$3622 \times 2439.2/803.7 = 10993$ kJ

1975

Respiration for these months	926.5 kJ
Respiration for whole year	2539.4 kJ
Consumption for these months	4114 kJ
Total annual consumption	$4114 \times 2539.4/926.5 = 11276$ kJ

The ingestion index was also calculated, being the daily consumption (kJ) divided by the flesh tissue (kJ) times 100. For 1974 the value was 1.75, and for 1975 1.77.

Faeces production could not be measured directly because it was impossible to collect the entire faecal production of an individual in the field, and because the laboratory feeding trials were unsuccessful. However, it was possible to obtain samples of faecal pellets produced by limpets feeding on the slates, since the pellets are discrete cylindrical bodies. The possession of faeces from an animal feeding upon a known diet enables the percentage absorption to be calculated by the ash ratio method of Conover (1966). Conover termed it 'percentage assimilation', but since assimilation ( $C - F - U$ ) has a different meaning in IBP terminology, absorption ( $C - F$ ) will be used. This assumes that digestion has significant effects only upon the organic components of the food, and to calculate the absorption, one must know the fraction of organic matter (ash-free dry weight/dry weight) in the food ( $F$ ) and the faeces ( $E$ ).

$$\text{Absorption efficiency} = \frac{(F - E)}{(1 - E)F} \times 100.$$

The organic fraction of the algal mat was 0.350, and that of the faeces 0.282, which gave an absorption efficiency of 27.1% by the above formula. This is in terms of weight of organic material, but *Patella* clearly digests this food selectively, for the calorific value of the algal mat was 18.5 kJ g<sup>-1</sup> ash-free dry weight, compared with 14.0 kJ g<sup>-1</sup> for the faeces. Allowing for this, the percentage absorption in terms of energy content is 44.9%. Therefore the energy content of the faeces is calculated as 55.1% of that of the consumption: 1974, 6057 kJ; 1975, 6213 kJ.

*Urine - U*

The main nitrogenous excretion of *Patella* is in the form of ammonia (Fretter & Graham, 1962), and excretory loss as other forms of nitrogen was ignored. The production of mucus was also ignored, and in retrospect this was perhaps a mistake. Paine (1971) draws attention to several studies on molluscs where the mucus component is regarded as significant, though it does not seem to have been accurately measured. In the opisthobranch *Navanax* it was assumed to be 7% of the consumption (Paine, 1965), and in three other opisthobranchs 15% of the assimilation (Carefoot, 1967*b*).

Ammonia production was determined by keeping the animals in the same respiratory chambers as were used for measuring aquatic oxygen consumption. Ammonia concentration was measured by the Berthelot procedure (Solórzano, 1969; Harwood & Huysen, 1970). Energy content was derived using the Brafield & Solóman (1972) coefficient of 288 kJ mol<sup>-1</sup>.

The relationship between ammonia production (*U*) and flesh weight (*W*) can be represented by

$$U = a W^b$$

or

$$\log U = \log a + b \log W.$$

Several series of ammonia production experiments were conducted at different seasons. For each series, the parameters of the linear regression of  $\log U$  on  $\log W$  were calculated (Wright, 1977, table 40). The regressions vary with temperature, and each month the ammonia production was calculated using the regression for the temperature nearest to the ambient sea temperature. The flesh weight of the quadrat limpets was derived from their length using the regressions in Wright (1977, table 4), so that each month the total ammonia production of the quadrat limpets was calculated (Table 3). This varied from about 0.4 kJ month<sup>-1</sup> in winter to nearly 1.3 kJ month<sup>-1</sup> in midsummer. The annual ammonia excretion was 8.81 kJ for 1974 and 9.52 kJ for 1975. These values are insignificant in relation to the other components of the energy budget, and ammonia excretion could safely have been ignored as a significant element in the budget.

## DISCUSSION

The components of the energy budget, as described in the introduction, are summarized in Table 6. They are presented per square metre, to facilitate comparison with other studies, and are given for 1974, 1975, and for the two years combined. Two values are given for consumption:  $C_m$  is the value calculated from the ingestion experiments,  $C_s$  is the value obtained by summing the components on the other side of the equation. The degree of correspondence between them provides some check on the accuracy of the work, although it has already been pointed out that the rigour of this check is reduced by the dependence of *F* on *C*. Considering the two years overall,  $C_s$  is smaller than  $C_m$  by 15%. There are few other molluscan energy budgets which provide any internal check at all. One is that of Hughes (1970) on the deposit-feeding bivalve *Scrobicularia plana* (da Costa), in which he found  $C_m$  smaller than  $C_s$  by 14%. Paine (1965) in a short-term

laboratory study of the carnivorous opisthobranch *Navanax inermis* (Cooper) found  $C_s$  smaller than  $C_m$  by 8%. This laboratory study naturally introduced fewer sources of error than an annual field budget. Considering the many extrapolations and approximations necessarily involved in compiling an annual budget, discrepancies of the order of 15% do not seem unreasonable.

Table 6. *Components of the energy budget for the quadrat limpets*

	Biomass in $\text{kJ m}^{-2}$ , energy components in $\text{kJ m}^{-2} \text{ year}^{-1}$ .									
	$B$	$C_m$	$C_s$	$P_g$	$P_r$	$R$	$F$	$U$	$P$	$A$
1974	339	2199	1854	57.9	95.1	487.8	1211	1.76	153.0	640.8
1975	352.5	2255	1927	78.8	95.9	507.8	1243	1.90	174.7	682.5
1974/5	346	2227	1890	68.3	95.5	497.8	1227	1.83	163.8	661.6

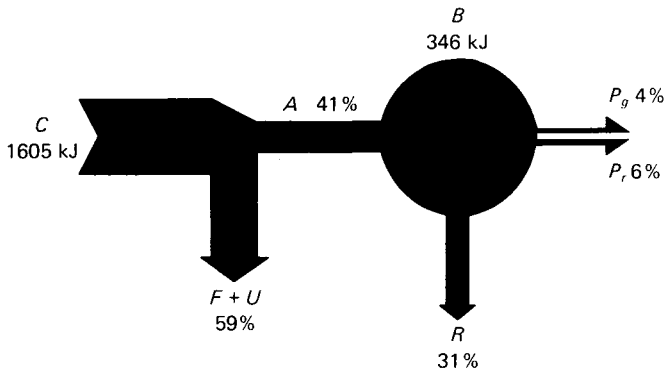


Fig. 5. Annual energy flow per square metre for the quadrat limpets. Budget components expressed as percentage of consumption.

In the present study, the estimates of some components of the energy budget are more reliable than others.  $P_g$  and  $P_r$  are based on reliable data with no major assumptions.  $R$  is based on comprehensive data, but includes the untested correction for activity.  $U$  is negligible, but makes no allowance for mucus production: perhaps between 5 and 10% of assimilated energy is lost in this way.  $C$  is based upon limited data and major assumptions, and is the least reliable.  $F$  depends upon  $C$ , though the value for the absorption efficiency itself should be reasonably accurate. A balanced budget is necessary for comparative purposes, and one was formulated making two assumptions. One is that mucus production comprises 8% of the energy absorbed from the food. The other is that the absorption efficiency of 45% is reliable. This budget for 1974 plus 1975, in terms of  $\text{kJ m}^{-2} \text{ year}^{-1}$  is:

$$1605.3 = 68.3 + 95.5 + 497.8 + 884.3 + 59.4$$

$$(C = P_g + P_r + R + F + U).$$

The flow of energy is depicted in Fig. 5. The implication is that  $C_m$  was in practice a considerable overestimate, probably because the tiles provided a markedly richer source

of food than the natural rock surface. The fact that the rock surface in the quadrats is kept clear of small algal growth indicates that the limpets are normally consuming all of the available food, and that even this relatively quickly growing population is subsisting appreciably below its potential level of food intake. Presumably at below its potential growth rate too, for Southward & Southward (1978) noted that the few limpets which survived the effects of the 'Torrey Canyon' oil spill grew in the unusually abundant food supply at up to ten times their normal rate.

In Table 7, outlines are given of the energy budgets available for other intertidal herbivorous gastropods, in order to compare them with that derived for *Patella vulgata*. These species are not comparable in all respects: the *Littorina* species are relatively short lived compared with *Patella*, whilst the studies on *Nerita* and *Fissurella* are tropical rather than temperate. *Tegula funebris* is the only other long-lived temperate species for which an energy budget is available, and its budget does have much in common with that of *Patella*. It is not the absolute values of the budgets which are important for comparison, but the relationships between their components.

One respect in which *Patella* differs from all the other examples is that  $P_r$  exceeds  $P_g$ , so that 59% of the total production is in the form of gametes. One consequence of this is that *Patella* channels most of its production out of the intertidal benthic ecosystem into the pelagic ecosystem. This emphasis upon reproduction is a consequence of the age structure of the population studied, with limpets exceeding four years of age dominating the biomass: in such limpets,  $P_r$  comprises 90% of  $P$ . Other populations of *Patella* have a much higher proportion of younger individuals (Lewis & Bowman, 1975), and in those  $P_r$  will be less significant.

*Patella* respire 75% of the energy which it assimilates, a fairly high figure, as might be expected in a population dominated by older slow-growing individuals. The shorter-lived *Littorina littoralis* respire only 68% of its assimilation. In contrast, the species of *Nerita* had values in the high eighties, possibly because the high temperatures of their upper-shore tropical environment elevated the metabolic rate. Values recorded for molluscs range from 58 to 88% (Wright, 1977), so in this context, the value for *Patella* appears fairly average.

The assimilation efficiency is the percentage of the food consumed which is assimilated, and the value for *Patella vulgata* is 41%. It feeds unselectively on a variety of diatoms, sporelings and detritus, and it is only to be expected that a considerable proportion of this food will be indigestible due to the lack of suitable enzymes. The keyhole limpet *Fissurella barbadensis* feeds in a similar fashion and has an even lower efficiency of 34%: it appears that all the ingested material except the blue-green algae passes through the gut relatively unchanged (Ward, 1966). *Littorina littoralis* feeds on a selected diet of furoid fronds, and has a high assimilation efficiency of 73%. The assimilation efficiency will doubtless vary with diet – in *Aplysia punctata* Cuvier, it ranged from 45 to 75% depending on the food species (Carefoot, 1967a). Values recorded for marine molluscs range from 34 to 87% (Wright, 1977), and *Patella vulgata* is near the lower end of this range as are most of the other intertidal herbivores featured in Table 7.

The net growth efficiency, gross growth efficiency and ecological efficiency are various indices of the extent to which the energy intake of a species is converted into



Table 7. Components of energy budgets for herbivorous intertidal gastropods

All values in kcal m<sup>-2</sup> year<sup>-1</sup>, except *L. littoralis* in kcal kg<sup>-1</sup> dry wt *Fucus* year<sup>-1</sup>. For *Patella vulgata*, values in kJ m<sup>-2</sup> year<sup>-1</sup> in brackets.

Species	Location	C	A	Pg	Pr	R	$\frac{A \times 100}{C}$	$\frac{A \times 100 * P \times 100 \ddagger}{C}$	$\frac{P \times 100 \ddagger E \times 100 \S}{C}$	$\frac{P}{B}$	Ingestion index	Source		
<i>Patella vulgata</i>	Isle of Man	383 (1605)	158 (661)	16.3 (68)	23 (95)	119 (498)	75	41	25	10.2	4.1	0.47	1.26	This paper
<i>Fissurella barbadensis</i> Gmelin	Barbados	566	190	46	5.3	139	73	34	27	9.0	8.0	4.1	12.21	Hughes, 1971a
<i>Littorina irrorata</i> Say	Georgia	—	290	—	—	—	86	45	14	6.3	—	0.81	3.5	Odum & Smalley, 1959
<i>Littorina littoralis</i> <i>Nerita peloronta</i>	Isle of Man Barbados	236	172	35	20	117	68	73	40	23	15	2.3	2.31	Wright, 1977
<i>Nerita tessellata</i> Gmelin	1 2 Barbados	95 265 614	39 115 247	6.8 11.3 21	0.7 3.0 9	31 101 217	81 88 88	41 43 40	19 12 12	7.9 5.4 4.8	7.2 4.3 3.4	1.25	5.64	Hughes, 1971b Hughes, 1971b Hughes, 1971b
<i>Nerita versicolor</i> Gmelin	Barbados	151	59	6.7	0.9	51	87	39	13	5.0	4.4	0.63	4.00	Hughes, 1971b
<i>Tegula funebralis</i>	Washington	1071	689	95	8	578	84	64	15	9.6	8.9	0.42	1.18	Paine, 1971

\* Assimilation efficiency. †, Net growth efficiency. ‡, Gross growth efficiency. §, Ecological efficiency.

material available for higher trophic levels. *Patella* has net and gross growth efficiencies broadly comparable to the other species in Table 7, but its ecological efficiency is low since most of its production is as gametes rather than as somatic growth. Presumably part of this  $P_r$  is incorporated into the pelagic food chain.

All except one of the intertidal herbivores in Table 7 have ecological efficiencies below, often well below, 10%. Since herbivores will consume only part of the algal production in rocky intertidal ecosystems, the transfer of energy from production at the producer level to production at the primary consumer level within these ecosystems must be of the order of only a few per cent.

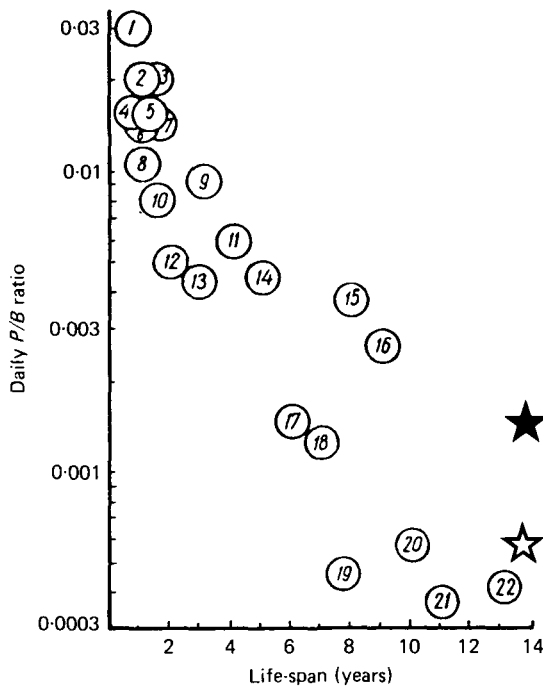


Fig. 6. Daily  $P/B$  ratio plotted against life-span for 22 species of mollusc (after Zaika, 1972). The value for the *Patella vulgata* population investigated is inserted, based upon total  $P$  (★) and upon  $P_g$  alone (☆).

The  $P/B$  ratio and the ingestion index are both measures of the level of metabolic activity, and whilst not closely correlated, they do tend to be similarly high or low in a population. In *Patella vulgata*, both are low compared to the other species in Table 7, and also compared to marine molluscs in general – 0.28 – 5.5 for the  $P/B$  ratio, 1.26 – 12.2 for the ingestion index (Wright, 1977). This is because most of the individuals were old and slow growing in the population of *Patella* investigated. Zaika (1972) has compared the specific production (i.e. the daily  $P/B$  ratio) for 22 species of mollusc by plotting log specific production against life-span (Fig. 6). *Patella vulgata* has a specific production of 0.0013 and a life span of about 14 years: when it is plotted, it is clear that whilst the  $P/B$  ratio for *Patella* appears low, it is in fact relatively high compared with

other molluscs of a similar life span. This is still true even if the  $P/B$  ratio is based only on  $P_{\phi}$ , as is probably the case in most of Zaika's determinations.

## REFERENCES

- BALLANTINE, W. J., 1961. A biologically defined exposure scale for the comparative description of rocky shores. *Field Studies*, **1** (3), 19 pp.
- BARRY, R. J. C. & MUNDAY, K. A., 1959. Carbohydrate levels in *Patella*. *Journal of the Marine Biological Association of the United Kingdom*, **38**, 81–95.
- BLACKMORE, D. T., 1969. Studies of *Patella vulgata* L. II. Seasonal variation in biochemical composition. *Journal of Experimental Marine Biology and Ecology*, **3**, 231–245.
- BRAFIELD, A. E. & SOLOMAN, D. J., 1972. Oxycaloric coefficients for animals respiring nitrogenous substrates. *Comparative Biochemistry and Physiology*, **43A**, 837–841.
- BRODY, S., PROCTER, R. C. & ASHWORTH, U. S., 1934. Growth and development. 34. Basal metabolism, endogenous nitrogen, creatinine and neutral sulphur excretions as functions of body weight. *Bulletin. Missouri Agricultural Experiment Station*, **220**, 1–40.
- CAREFOOT, T. H., 1967a. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *Journal of the Marine Biological Association of the United Kingdom*, **47**, 565–589.
- CAREFOOT, T. H., 1967b. Growth and nutrition of three species of opisthobranch mollusc. *Comparative Biochemistry and Physiology*, **21**, 627–652.
- CONOVER, R. J., 1966. Assimilation of organic matter by zooplankton. *Limnology and Oceanography*, **11**, 338–345.
- DAS, S. M. & SESHAPPA, G., 1948. A contribution to the biology of *Patella* on population distribution and sex proportions in *Patella vulgata* L. at Cullercoats, England. *Proceedings of the Zoological Society of London*, **117**, 411–423.
- DAVIES, P. S., 1966. A constant pressure respirometer for medium sized animals. *Oikos*, **17**, 108–112.
- FRETTER, V. & GRAHAM, A., 1962. *British Prosobranch Molluscs*. 755 pp. London: Ray Society.
- GOMPEL, M. M., 1937. Recherches sur la consommation d'oxygène de quelques animaux aquatiques littoraux. *Compte rendu hebdomadaire des séances de l'Académie des sciences*, **205**, 816–818.
- HARTNOLL, R. G. & WRIGHT, J. R., 1977. Foraging movements and homing in the limpet *Patella vulgata*. *Animal Behaviour*, **25**, 806–810.
- HARWOOD, J. E. & HUYSER, D. J., 1970. Some aspects of the phenolhypochlorite reaction as applied to ammonia analysis. *Water Research*, **4**, 501–515.
- HAWKINS, S. J., 1979. *Field Studies on Manx Rocky Shore Communities*. Ph.D. Thesis, Liverpool University.
- HUGHES, R. N., 1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (Da Costa). *Journal of Animal Ecology*, **39**, 357–381.
- HUGHES, R. N., 1971a. Ecological energetics of the keyhole limpet, *Fissurella barbadensis* Gmelin. *Journal of Experimental Marine Biology and Ecology*, **6**, 167–178.
- HUGHES, R. N., 1971b. Ecological energetics of *Nerita* (Archaeogastropoda, Nerititacea) populations on Barbados, West Indies. *Marine Biology*, **11**, 12–22.
- IVLEV, V. S., 1935. Eine mikromethode zur bestimmung des Kalorienschalte von näkratoffen. *Biochemische Zeitschrift*, **275**, 49–55.
- JONES, N. S., 1948. Observations and experiments on the biology of *Patella vulgata* at Port St Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **56**, 60–77.
- LEWIS, J. R. & BOWMAN, R. S., 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **17**, 165–203.
- LODGE, S. M., 1948. Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **56**, 78–85.
- MANN, K. H., 1964. The pattern of energy flow in the fish and invertebrate fauna of the River Thames. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **15**, 485–495.

- MANN, K. H., 1965. Energy transformations by a population of fish in the River Thames. *Journal of Animal Ecology*, **34**, 253–275.
- ODUM, E. P. & SMALLEY, A. E., 1959. Comparison of population energy flow of a herbivorous and deposit-feeding invertebrate in a salt marsh ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, **45**, 617–622.
- ODUM, E. P., CONNELL, C. E. & DAVENPORT, L. B., 1962. Population energy flow of three primary consumer components of old-field ecosystems. *Ecology*, **43**, 88–96.
- PAINE, R. T., 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology*, **46**, 603–619.
- PAINE, R. T., 1971. Energy flow in a natural population of the herbivorous gastropod *Tegula funebralis*. *Limnology and Oceanography*, **16**, 86–98.
- PETRUSEWICZ, K., 1967. Suggested list of more important concepts in productivity studies (definitions and symbols). In *Secondary Productivity of Terrestrial Ecosystems*, vol. 1 (ed. K. Petruszewicz), pp. 51–82. Warsaw and Cracow.
- PHILLIPSON, J., 1964. A miniature bomb calorimeter for small biological samples. *Oikos*, **15**, 130–139.
- RICKER, W. E. (ed.), 1968., *Methods for Assessment of Fish Production in Fresh Waters*. Oxford and Edinburgh. [I.B.P. Handbook No. 3.]
- SCHOLANDER, P. F., 1942. Volumetric microrespirometers. *Review of Scientific Instruments*, **13**, 32–33.
- SOLÓRZANO, L., 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. *Limnology and Oceanography*, **14**, 799–801.
- SOUTHWARD, A. J., 1953. The ecology of some rocky shores of the south of the Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society*, **59**, 1–50.
- SOUTHWARD, A. J., 1964. Limpet grazing and the control of vegetation on rocky shores. In *Grazing in Terrestrial and Marine Environments* (ed. D. J. Crisp), pp. 265–273. Oxford: Blackwell.
- SOUTHWARD, A. J. & SOUTHWARD, E. C., 1978. Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon oil spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682–706.
- TREVALLION, A., 1971. Studies on *Tellina tenuis* (Da Costa). III. Aspects of general biology and energy flow. *Journal of Experimental Marine Biology and Ecology*, **7**, 95–122.
- WARD, J., 1966. The breeding cycle of the keyhole limpet *Fissurella barbadensis* (Gmelin). *Bulletin of Marine Science of the Gulf and Caribbean*, **16**, 685–695.
- WINBERG, G. G., 1956. Rate of metabolism and food requirements of fish. *Translation Series, Fisheries Research Board of Canada*, no. 194, 202 pp.
- WRIGHT, J. R., 1977. *The Construction of Energy Budgets for Three Intertidal Rocky Shore Gastropods*, *Patella vulgata*, *Littorina littoralis* and *Nucella lapillus*. Ph.D. Thesis, Liverpool University.
- ZAIKA, V. E., 1972. *Specific Production of Aquatic Invertebrates*. Kiev: Naukova Dumka. [In Russian.] [Translated 1973 by Israel Program for Scientific Translations Ltd. Distributed by Halsted Press.]