

ENERGY FLOW IN A NATURAL POPULATION OF THE HERBIVOROUS GASTROPOD *TEGULA FUNEBRALIS*¹

Robert T. Paine²

Department of Zoology, University of Washington, Seattle 98105

ABSTRACT

The gastropod *Tegula funebris* (A. Adams, 1855) is confined to the intertidal. At Mukkaw Bay, Washington, it typically occurs in patches of characteristic individual size structure. Various energy flow parameters have been determined for a high intertidal (+1.8 to +0.9 m) and a low intertidal (+0.6 to -0.15 m) subpopulation; these values were then combined in a 3:1 ratio to generate a composite population.

Direct and indirect calorimetry and direct observation on the natural population suggest the following: *Tegula* spawns once per year; the dry weight-shell diameter relationships for males and females can be expressed by a single regression; different caloric values characterize immature (5.2 kcal/ash-free g), mature males (5.4), intermediately mature females (5.8), and fully mature females (6.1); rates of aquatic and aerial respiration are different (at 13.5°C an average low intertidal individual, 211 mg dry wt, respire at a rate of 75 μ l O₂/hr in water and 43 μ l/hr in air).

The energy budget, in which ingestion was obtained by summation, suggests an assimilation efficiency of about 70%, a gross efficiency of growth of 16.7%, and an ecological efficiency of predators of 4.9%. Other efficiencies are discussed. In *Tegula*, 60% of energy transferred to other levels is to decomposers. Comparison of the rate of annual consumption by *Tegula*, 1,071 kcal m⁻² yr⁻¹, and net primary production estimated by cropping, 1,167 kcal m⁻² yr⁻¹, indicate a near balance. Importation of primary production may be necessary to the maintenance of the rocky intertidal community at Mukkaw Bay.

INTRODUCTION

The study of energy flow within individuals and between populations is useful to ecologists in many ways. The calorie is certainly the most logical unit with which to quantify allocation of energy by an organism to a variety of tasks or needs and has been the primary unit of measurement for a number of laboratory and field studies (Richman 1958; Engelmann 1961). Calculations based on energy parameters have been used to suggest reasons underlying seasonal patterns of occurrence (Anraku 1964), the degree to which subpopulations are energy-limited (Paine 1965), and the extent to which a generalized resource is drawn on by some set of consumers (Odum et al. 1962).

¹ This research was supported by National Science Foundation Grants GB-341 and GB-2950.

² It gives me pleasure to acknowledge the interest and support offered by Prof. J. E. Morton and other members of the Department of Zoology, University of Auckland, where this paper was written. I am indebted both to R. M. Cassie for assistance with statistical matters and to Peter Frank who has served as a sounding board and general critic.

Reviews of the literature (Slobodkin 1962; Engelmann 1966) have pointed to three problem areas: many of the studies have assumed an ecological steady state; measurements on individuals or populations usually involve only a selected phase of their life history; some metabolic end products such as various secretions, urine, exuviae, are usually not considered because of difficulty of quantification, and thus contribute an error of undiagnosed magnitude. This latter point should not be underestimated. Stephens (1968) has shown that many marine and estuarine organisms, plant and animal, are capable of using dissolved organic nutrients that enter metabolic pathways by unconventional, or at least non-classical, pathways. For instance, he found that the malidanid worm *Clymenella* could meet its minimal energy demands by active uptake alone. Johannes et al. (1969) have indicated that release of energy-rich compounds also occurs, perhaps in sufficient quantity to balance those actually taken in. Khailov and Burlakova (1969) suggest that between 23 and 39% of gross production

in seaweeds may be released as dissolved organic matter. Thus, there are growing indications that for these energy-rich compounds the quantities involved are too great to be ignored. Given usually undiagnosed errors of this potential magnitude, it is legitimate to question the value of studies on population or community energetics that do little beside acknowledge the existence of such additional pathways. I do not believe that the answer is close at hand on either technical or mensural bases.

This study of the bioenergetics of the herbivorous intertidal gastropod *Tegula funebris* (A. Adams, 1855) was intended to complement a more numerical analysis (Paine 1969). I have measured those energy budget components that are usually measured and have supplemented them with estimates of other biologically real, yet unmeasured, parameters. Comparison of the partially artificial figure of consumption of plant material by *Tegula* with crude estimates of the productivity of the study area can suggest the relative degree to which available plant energy might be limiting *Tegula*. Further, energy analysis of the population broken down by sex, age, and distribution indicates patterns of overall individual well-being or reproductive contribution that are essential to a satisfactory understanding of some of the determinants of the species' ecology.

MATERIALS AND METHODS

Data were collected at Mukkaw Bay, just south of Cape Flattery at the exposed western tip of the Olympic Peninsula, Washington. The general locality should be classified as slightly less than exposed outer coast, in the scheme of Rickotts and Calvin (1952), because certain characteristic organisms (i.e., the brown algae *Postelsia palmaeformis* and *Lessoniopsis littoralis*) are absent. The study area itself is a gradually sloping rocky platform about 150 m wide from high to low water marks, bounded laterally by two sizable rock outcrops. The shoreward 20 m or so are a sand beach; the platform ends abruptly near the low water mark where the shore's

TABLE 1. *The size structure of Tegula funebris inhabiting different portions of the environment at Mukkaw Bay*

Female reproductive category and size range (mm)	High area		Low area	
	N/m ²	%	N/m ²	%
Immature				
0.0- 0.9				
1.0- 1.9	0	0.0		
2.0- 2.9	3	0.7		
3.0- 3.9	5	1.2		
4.0- 4.9	4	1.0		
5.0- 5.9	7	1.7		
6.0- 6.9	22	5.2		
7.0- 7.9	29	6.9		
8.0- 8.9	36	8.5		
9.0- 9.9	49	11.6		
10.0-10.9	83	19.7	0	0.0
11.0-11.9	70	16.6	2	0.6
12.0-12.9	54	12.8	18	5.6
13.0-13.9	30	7.1	34	10.5
Intermediate				
14.0-14.9	11	2.6	38	11.7
15.0-15.9	8	1.9	46	14.2
16.0-16.9	1	0.2	56	17.3
17.0-17.9	9	2.1	52	16.0
Fully mature				
18.0-18.9	0	0.0	38	11.7
19.0-19.9	1	0.2	24	7.4
20.0-20.9	0	0.0	7	2.2
21.0-21.9			6	1.9
22.0-22.9			1	0.3
23.0-23.9			1	0.3
24.0-24.9			1	0.3
25.0-25.9			0	0.0

slope steepens. *Tegula* occurs throughout this area on suitable rock or pebble substrates, confined to the intertidal. Small individuals settle high (+0.9 to +1.8 m) in this area and spend at least the initial 5-6 years of their life there (Paine 1969). Some, but not all, then begin to migrate and appear in quantity lower down (+0.6 to -0.2 m). I have chosen to treat the residents of these two areas as separate subpopulations because of the local differences in size (age) structure.

The typical size structure of these subpopulations (Table 1) is based on individuals collected in 22 quadrats (16 × 16 cm or 32 × 32 cm) placed randomly throughout the area in April and June 1965 and then pooled. Three phenomena are indi-

TABLE 2. *Dry weight (Y)-shell diameter (X) regression equations for pre- and postspawned Tegula funebralis samples. The 1965 and 1966 samples have been pooled to provide a relation for the "average" population. Weight is measured in mg dry wt; shell diameter in mm*

Date	Reproductive condition	Sample size	Regression equation	Standard error of regression coefficient
17 Apr 1965	pre	36	$\ln Y = -4.326 + 3.439 \ln X$	0.005
20 Jul 1965	post	40	$\ln Y = -5.194 + 3.727 \ln X$	0.025
Total 1965		76	$\ln Y = -4.605 + 3.524 \ln X$	0.010
7 Apr 1966	pre	43	$\ln Y = -4.612 + 3.574 \ln X$	0.009
19 Aug 1966	post	63	$\ln Y = -5.412 + 3.780 \ln X$	0.011
Total 1966		106	$\ln Y = -5.357 + 3.790 \ln X$	0.010
Total 1965 + 1966		182	$\ln Y = -5.016 + 3.670 \ln X$	0.008

cated. No small (<11 mm) *Tegula* were encountered in the lower intertidal, suggesting that this subpopulation must be maintained by immigration. Very small individuals (<6 mm) are probably under-represented in the high areas because of their small size and the presence of numerous hiding places. Most of the fully mature individuals (>18 mm) occur lower down.

Based on quantitative samples taken throughout the years 1963-1968 (Paine 1969), I have estimated an average density of 800/m² in the upper intertidal and 412/m² lower down. Although these concentrations seem high for a sizable snail, they are consistent with the data of others: Glynn (1965) records 365/m² in the lower portion of his study site, and Wara and Wright (1964) indicate densities up to 1,400/m² in the areas they examined.

Between October 1964 and August 1966 a number of samples were taken in which the size (the maximum shell diameter measured from the lip across the umbilicus), dry weight (specimens dried at 80C), sex, and intertidal position of each individual were noted. Dry weight-shell diameter regressions were fitted for all of these, and then analyses of covariance (Snedecor 1959) were used to compare particular samples. No difference in the regression lines was detected for the comparison of male with female specimens collected either high or low in the intertidal on any specific date, which permitted all samples to be pooled by sex. Further, no difference in slope or

intercept was found for any samples collected at the same time, regardless of their intertidal position. Thus one weight-length regression is satisfactory for all specimens collected at any date. Finally, the samples could be sorted by date into pre- and post-spawning categories. These regressions differed significantly from each other for both 1965 and 1966 samples, indicating that the change in weight associated with spawning is reflected in the weight-diameter relationship. However, analysis of covariance indicated no difference between years when 1965 and 1966 samples were pooled. The double-log regression equations for these samples are given in Table 2. Because of the seasonal change in regression, all weight-length relationships, with one exception, were determined from the total regression for 1965 and 1966, as I felt this represented a satisfactory compromise between the ripe and spawned condition. The exception is those prespawning individuals whose weight was used to judge what the caloric loss associated with gamete release might be.

The percent ash value is based on 208 incinerations of whole *Tegula*, removed from the shell, dried, pulverized, and then placed in a muffle furnace for 3-4 hr at 500C. These gave an average ash value of 9.02%.

We can now generate some constants to be used in establishing the energy budget. The mean dry weight, based on the population structure shown in Table 1, is 46 mg (11.1-mm shell diam) in the high area and

211 mg (16.9-mm shell diam) lower down, or 36.8 and 86.9 g/m² respectively. On an ash-free basis these values would be: high area, 42 mg per individual and 33.6 g/m²; low area, 192 mg per individual and 79.1 g/m².

COMPONENTS OF THE ENERGY BUDGET

The energy entering an organism is allocated to a variety of pathways in varying proportions and rates. It is the summation of these categories that provides an estimate of energy flow through a population and, in conjunction with information on the rate of production of suitable food for the animal in question, provides one estimate of the effect that a particular species exercises in a particular situation. Those categories that could be estimated are discussed sequentially below, the units of energy flux being kcal m⁻² yr⁻¹.

Egestion

The energy equivalent of egested material was calculated as follows. From October 1964 to September 1966 from 5–20 *Tegula* were collected in the field, placed immediately in jars of clean seawater, and maintained in these jars for periods up to 36 hr. Occasionally the fecal matter was collected before the end of the run, to determine if the rate of fecal pellet production diminished during the experimental interval. At the end of each run the animals were measured, their dry weight established (Table 2), and the fecal matter collected, dried at 80C, and weighed.

The rate of production of egested material expressed in g dry wt g⁻¹ hr⁻¹ was relatively constant for the initial 12 hr, but it diminished rapidly during the remainder of the run. Thus on an average 24-hr basis, 70% of the egested material is defecated in the initial 12 hr. The data in Table 3 have been corrected, wherever appropriate, to a 24-hr basis, using a factor of 1.4 to adjust for this discrepancy, on the assumption that under natural conditions ingestion might be fairly continuous and that there would be no lessening of the defecation rate. There is no seasonal trend to these

TABLE 3. The number of individuals used (N) to determine the rate of fecal pellet production [g dry wt feces (g dry wt *Tegula*)⁻¹ day⁻¹] of *Tegula funebralis*

Date	N	Rate	Date	N	Rate
Oct 1964	16	0.037	Feb 1966	8	0.041
Dec 1964	5	0.000	Mar 1966	10	0.036
Jan 1965	18	0.014	Apr 1966	9	0.035
Feb 1965	16	0.041	May 1966	10	0.029
Mar 1965	20	0.043	May 1966	10	0.028
Apr 1965	6	0.030	Jun 1966	13	0.039
May 1965	18	0.015	Jun 1966	12	0.022
Jun 1965	12	0.025	Jul 1966	10	0.083
Oct 1965	9	0.018	Aug 1966	10	0.032
Nov 1965	12	0.025	Sep 1966	10	0.050
Jan 1966	11	0.026			
					$\bar{x} = 0.032$
					(SD = 0.016)

data, so I have accepted their average value, 0.032 g g⁻¹ day⁻¹. The fecal matter contained much ash. Incinerated samples gave values of 86, 91, 96, 89, 75, and 83%—an average value of 86.7% ash. The organic residue, 13.3% or 0.0042 g g⁻¹ day⁻¹ has been assumed to have the caloric value of starch, 4.2 kcal/g. On these bases, then, the rate of fecal pellet production is (0.0042)(365)(4.2)(dry wt/m² in the low or high intertidal). This amounts to values of 560 and 237 kcal m⁻² yr⁻¹ in the low and high intertidal respectively.

Respiration

Maintenance energy requirements were measured in both air and water over a range of temperatures comparable with those *Tegula* meets under natural conditions.

Aerial respirations were obtained using a Beckman polarographic electrode. The rate of oxygen consumption for mean-sized individuals at 13.5C is 206 μ l O₂ g⁻¹ hr⁻¹ based on the mean of 13 individuals (95% confidence limits, $\pm 42 \mu$ l O₂). Comparable data at 23.0C, based on 21 determinations, yielded a rate of 413 μ l O₂ (± 66).

Aquatic respiration was measured by the Winkler technique at three different ambient temperatures, 6.5, 10.0, and 17.0C. Individuals were collected and first allowed to acclimatize for 24–72 hr. Most of the experimental animals were active during

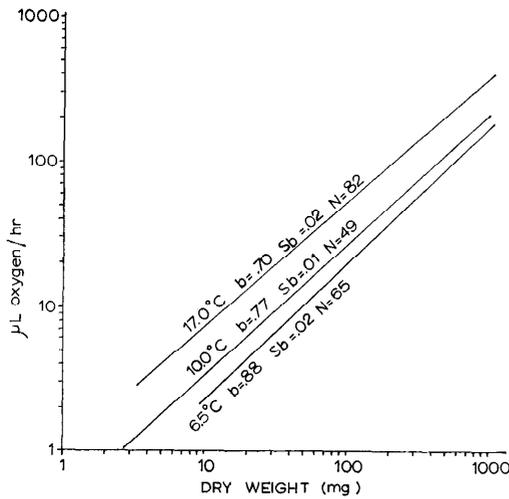


FIG. 1. Double-log plots of rates of aquatic respiration of *Tegula funebralis* determined at three temperatures. The lines, fit by least squares, have been drawn over the range of dry weights used in the determinations.

the measurement period. The results are shown in Fig. 1.

The rates of oxygen consumption and the respective Q_{10} values under both environmental conditions are quite comparable, as might be expected in a species confined to the intertidal. The mean-size individual from the low intertidal, weighing 211 mg dry wt, respire under water at a rate of 75 $\mu\text{L/hr}$ at 13.5C (value read from Fig. 1). The Q_{10} value measured between 6.5–17.0C is 2.64. Similarly, the respiratory rate in air at 13.5C for an average individual is 43 $\mu\text{L O}_2/\text{hr}$. The Q_{10} value determined between 13.5–23.0C is 2.08. I have calculated the aquatic respiration rate on the basis of $\text{ml O}_2 \text{ kg wet wt}^{-1} \text{ hr}^{-1}$ as 39 ml O_2 at 6.5C, 50 ml at 10.0C, and 104 ml O_2 at 17.0C. Even though *Tegula* is a smaller animal, these values seem high in comparison with rates for some other herbivorous marine gastropods: *Haliotis*, 24–87 $\text{ml O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$ at 24C (Ghiretti 1966); *Aplysia*, 21–38 ml O_2 at 14–15C (Nicol 1967); *Aplysia*, 24 ml O_2 at 15C (Carefoot 1967a). However McLean (1962) working with *T. funebralis* measured aquatic rates equivalent to 108 $\text{ml O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$ at 11C and 190 ml O_2 at

19C. He also found rates of aerial respiration of 98 ml O_2 at 19C. Although these rates are even higher than mine, they substantiate that *Tegula* can respire when exposed to air and that the overall rates are high when compared with other gastropods.

To apply these metabolic data to Mukkaw Bay *Tegula*, I have assumed these mean monthly water temperatures: December, January, and February, 7.2C; March, 8.0; April and November, 9.5; May and October, 11.0; June–September, 13.0. These values are based on occasional personal measurements and on the minimum (5.9C) and maximum (13.5C) surface water temperature given by Rigg and Miller (1949). They also are in close agreement with the mean monthly temperatures given by the USCGS (1952). They are inaccurate to the degree that coastal air temperatures depart from seawater temperatures, that the temperature of tide pools or shallow intertidal depressions depart from surface water temperatures, and according to the amount of time that the average *Tegula* is exposed or immersed at low water. I have no way to evaluate these and other variables, so the above temperature schedule is an approximation.

I calculated annual respiration for each subpopulation by assuming 75% of the gas exchange takes place in water, a Q_{10} of 2.64 for all ambient temperatures, and an RQ of 0.85 (Kuenzler 1961), yielding an oxy-caloric equivalent of 4.86 cal/ml O_2 . I then calculated the caloric equivalent of the oxygen consumed by a population of known size structure (Table 1) and weight–shell diameter relationship (Table 2) for each month and summed over the year. The rates for the high intertidal are 459 $\text{kcal m}^{-2} \text{ yr}^{-1}$ and 921 kcal for the lower area.

Reproduction

Tegula is dioecious and its gametes are liberated freely into the surrounding water mass. Data on the season and intensity of spawning come from an intensive program of oxygen bomb calorimetry (with a Parr semimicro oxygen bomb calorimeter) car-

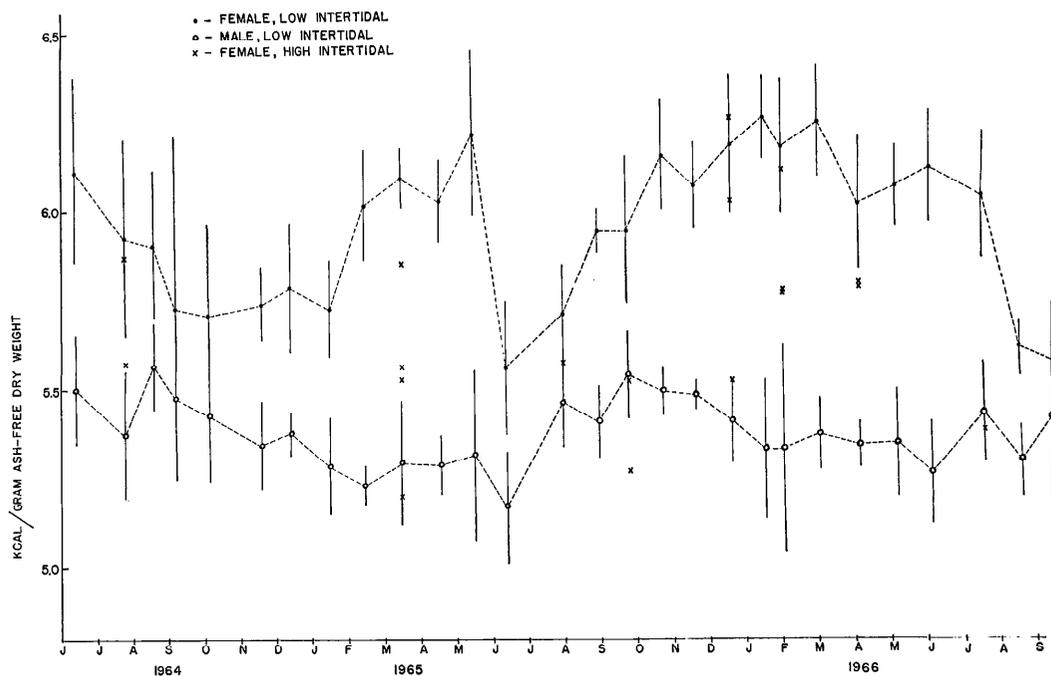


FIG. 2. Seasonal trends in caloric value shown by large (>20 mm) male and female *Tegula funebilis*. The lines are the 95% confidence limits of the mean; the notation X indicates values for individual female *Tegula* collected high in the intertidal.

ried out from June 1964 to September 1966. The basic procedures are discussed in Paine (1966). Two types of analysis of these data are given below, because individual size (state of maturity), sex, season of measurement, and intertidal position all influence the individual caloric value.

Figure 2 shows the results of calorimetry on sexually mature individuals larger than 20-mm diam. Most of these adult individuals were collected in the low intertidal; those obtained elsewhere are appropriately designated. Usually 5-6 individuals of each sex were combusted at each date. Males have a fairly constant caloric value of about 5.4 kcal/ash-free g—some 12% below the approximate peak of 6.1 attained by low-zone females before spawning. The value for females is much less constant and the three periods of decrease, June-September 1964, May-June 1965, and July-September 1966, are presumably due to the liberation of energy-rich

gametes. When female *Tegula* spawned, the caloric value decreased from 6.1 kcal/ash-free g to about 5.7 in 1964, and 5.55 in both 1965 and 1966, an average drop of 0.5 kcal or 8.2% of the prespawning value. I have accepted 5.6 kcal as the female caloric baseline for reproductively capable individuals.

In Fig. 2 the results of 18 combustions of females collected high in the intertidal also are given, 15 of which were collected before spawning. The 13 of these large (>20 mm) females that were ripe, as judged by the criteria of gonad condition and color, averaged 5.8 kcal/ash-free g, suggesting both that energy for reproductive purposes is less available in the high intertidal and that only 0.2 kcal worth of gametes (5.8-5.6), representing 3.4% of the prereproductive condition, are released at spawning.

Adult males, on the other hand, are characterized by no drop in caloric value at

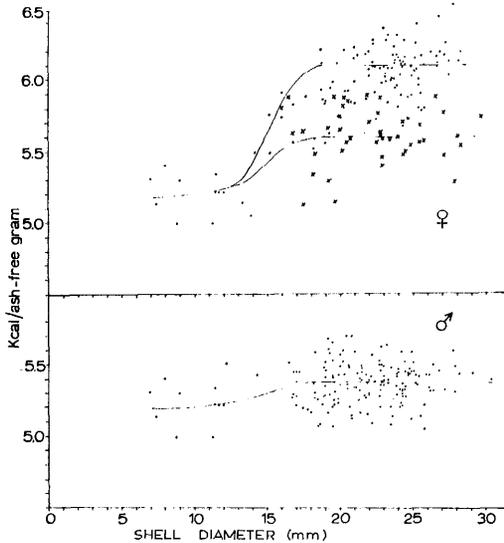


FIG. 3. Ontogeny of caloric value in male and female *Tegula funebralis*. For females, a dot (above a size of 14 mm) indicates an individual believed to be ripe (unspawned) and X indicates an individual believed to be spent (spawned). The lines, though visually approximated, pass through the mean values for all immatures (5.2 kcal), mature males (5.4 kcal), prespawning adult females (6.1 kcal), and postspawning adult females (5.6 kcal).

spawning, and showed no gross morphological change in the gonad's condition (except possibly a change in color from creamy white to faintly brownish). Four combustions of ripe male gonad yielded a mean value of 5.5 kcal/ash-free g. Clearly, within the limits of the precision of the technique, no caloric decrease at spawning could have been recognized.

The relationships between kcal/ash-free g and individual sex and size are given in Fig. 3. The same group of small individuals (<12 mm) is shown for both sexes, but beyond this size males and females are treated separately. An average value of 5.2 kcal/ash-free g is taken as characterizing all prereproductive individuals (0–14 mm shell diam) ($N = 13$; $\bar{x} = 5.17$; $sd = 0.15$). All reproductively capable males (>14 mm) are assumed to have the average value of 5.4. However, because the magnitude of caloric change in female *Tegula* >14 mm

is greater, I have established two further categories: intermediately mature (14–18 mm) individuals with an average prespawning value of 5.8 kcal/ash-free g and fully mature individuals (>18 mm) with a value of 6.1. Figure 3 further illustrates that male and female *Tegula* have significantly different caloric values, and that among females, there is a recognizable difference between pre- and postspawning adults.

I have used the following relationships to assess the caloric loss on spawning. A gonad is clearly recognizable at 14 mm, and all individuals are assumed to initiate some spawning at this size. One burst of spawning occurs per year (Fig. 2) and in mature low-area females an individual >18 mm loses 8.2% of her caloric value in the process. No comparable decrease is observed in males because somatic and reproductive tissue have similar caloric values. However, since males obviously must spawn, I have assumed that they also expend 8.2% of their body calories in the process. Low-zone female *Tegula*, 14–18-mm diam, release 0.2 kcal of gametes (the difference between 5.8 kcal and the baseline postspawning value of 5.6). The 3.4% decrease is assumed to characterize males in the 14–18-mm range as well.

For *Tegula* of the high intertidal, mature females decrease 3.4% in value (5.8 to 5.6) at spawning. A similar percent decrease is assumed to characterize fully mature males. For intermediately developed individuals of both sexes (14–18 mm), the decrease is 1.7% as suggested by the decrease in female values from 5.7 kcal to 5.6.

From the above relationships we can estimate the reproductive contribution by developmental state, sex, and intertidal position, by translating the size structure (Table 1) into an estimate of g dry wt/m² for each reproductive category using the 1966 prespawning weight-length relationship (Table 2). Conversion of this weight to an ash-free basis, multiplication by the appropriate prespawning caloric values and percent loss on spawning gives a value for reproductive output in kcal m⁻² yr⁻¹ (Table 4).

Mortality

At Mukkaw Bay in the low intertidal, 27.6% of the *Tegula* population dies annually (Paine 1969) as judged from the population's age structure. Independently derived mortality estimates, based on the percent of the standing crop consumed per year by the asteroid *Pisaster ochraceus*, lead to a figure of 25% per year. Acceptance of the higher value as a closer estimate of total mortality means that 114 *Tegula*/m² are dying annually or that (114)(0.192 g ash-free)(5.6 kcal/ash-free g) = 122.6 kcal/m² are lost from the population.

No mortality estimate for the subpopulation of the upper intertidal is possible because of irregularities in size (age) structure, probable underestimation of the numbers of very small (<6.0 mm) individuals, and a general absence of the appropriate natural history information. For the purpose of completeness, I have assumed a relatively low rate of 10% per year and that these average 11.0-mm diam. This rate is difficult to justify except that the known predators of small gastropods (*Pisaster*, *Leptasterias*, and *Searlesia*) do not extend this high in the intertidal, and no mortality has been directly observed except that due to infrequent physical events (severe winter storms; coverage of the upper area by sand). Thus (80) × (0.042 g ash-free)(5.2 kcal/ash-free g) = 17.5 kcal m⁻² yr⁻¹ lost as mortality in the upper area.

Tissue growth

Accumulated growth, represented as potential increase in the mass or caloric value of the standing stock was obtained as follows. The size distributions for each area (Table 1) were assumed both to be representative and to be static; that is, all emigrations and immigrations were assumed to have occurred before the census. The annual growth increment then was determined from a growth curve for *Tegula* (Paine 1969) and the dry weight-shell diameter relationship (Table 2). The weight increase was summed for each

TABLE 4. Reproductive contribution (kcal m⁻² yr⁻¹) in *Tegula funebralis* by sex, degree of maturation, and tidal position

	High area	Low area
Immature male	0.440	4.247
Mature male	0.059	8.407
Total	0.499	12.654
Immature female	0.467	4.578
Mature female	0.064	9.532
Total	0.531	14.110
Grand total	1.030	26.764

area, corrected for ash content and converted to kcal/m² using the appropriate average values (Fig. 3) for immature and all reproductively capable *Tegula*. The difference between these average values probably relates to a significant energetic advantage of building a growing individual initially out of "cheap" material, and then, when the surviving individuals are becoming capable of making a genetic contribution, adding higher value tissues. Given the above conditions, the annual growth (new tissue) increment becomes 36.7 kcal/m² in the high area and 69.6 kcal lower down.

Organic matter of the shell

The gastropod shell is secreted by specialized tissues of the mantle and includes two regions of organic accumulation: an outer uncalcified area, the periostracum, which is believed to consist of a quinone-tanned protein, and inner layers of primary CaCO₃ secreted around a proteinaceous matrix (Wilbur 1964). Vinogradov (1953) has given the percent organic matter in the shell of another herbivorous marine gastropod, *Turbo* sp., as 1.1%. I have made rough measurements of the annual increment of new shell for average-size individuals in the upper and lower intertidal. In the upper area this is 0.051 g shell/yr and 0.545 g lower down. These values, multiplied by the respective population densities and the 1.1% organic matter and assuming shell

TABLE 5. *Energy budgets and their associated efficiencies for Tegula funebris. All units of the budget are expressed in kcal m⁻² yr⁻¹. The efficiencies are expressed as percentages. The ecological efficiency of predators is calculated as including both mortality and reproduction components*

	Population		
	High	Low	Com- posite
Egestion	237	560	318
Respiration	459	921	578
Reproduction	1	27	8
Tissue growth	37	70	45
Mortality	18	123	44
Mucus and urine	57	130	75
Shell growth	3	14	6
Ingestion	808	1,845	1,071
Assimilation efficiency	70.8	69.6	70.3
Gross efficiency of growth	14.3	19.7	16.5
Net efficiency of growth	20.2	28.3	23.5
Ecological efficiency of predators	2.3	8.1	4.0
Ecological efficiency of decomposers	7.4	7.8	7.6
Gross efficiency of tissue accumulation	4.6	3.8	4.2

protein has a value of 5.7 kcal/g, give estimates of 2.6 kcal m⁻² yr⁻¹ for the upper area and 14.1 for the lower. These numbers have been added to the energy budget in full recognition both of the nature of their derivation and their failure to include the unknown annual increments of organic matter incorporated into the operculum, shell repair, or callus formation around eroded portions.

Mucus production and excretion

Most authors continue to ignore these metabolic products, probably because of difficulty of separation and quantification. For instance, a recent authoritative review (Wilbur and Yonge 1966) has given little or no indication of rates of production or of energetic content of either mucus or "urine." These, especially the former, must account for a significant portion of the total energy budget in many aquatic animals. Teal (1957) estimated that the equivalent of 57% of a flatworm's assimilated energy eventually appeared as mucus. In my work on the opisthobranch

Navanax (Paine 1965), the difference between assimilation directly measured and obtained by difference is 7% of the ingested energy. This difference could be due to the unmeasured mucus and excretion factors. Mann (1965) assumed 20% of assimilated energy for the summation of these two products for fish, and Carfoot (1967b), working with three opisthobranchs, assumed them as 15% of assimilation. For *Tegula* I have estimated that they account for 7% of all energy ingested or about 10% of the assimilated energy.

DISCUSSION

The standard way of considering energy budgets is to write, and perhaps balance the following equation (Richman 1958; Welch 1968):

$$\text{Ingestion} = \text{egestion} + \text{respiration} + \text{production.}$$

Production here should be taken to mean net productivity in the sense of Kozlovsky (1968) and to include components of energy 1) transferred to the next higher trophic level, 2) passed to decomposer food chains, 3) accumulated as tissue, and 4) lost from the system, say through migration. Energy of reproduction should be allocated to either category 1 or 2. No assumption of steady-state conditions is made in the use of this equation. Table 5 gives the energy categories recognized for *Tegula* from both high and low areas of the intertidal and expressed as the rate, kcal m⁻² yr⁻¹. In addition I have composed a budget for a synthetic population representative of the entire area by assuming that the high area is three times as prevalent as the low. Although this composite group is a hypothetical entity unrecognizable in the field, the budget is of potential interest because it must approach one that is characteristic of all the Mukkaw Bay *Tegula* subpopulations. All three budgets in Table 5 are artificial to the extent that ingestion has been attained by summation rather than independently estimated. In the paragraphs below, the annual *Tegula*

TABLE 6. Benthic algal production ($\text{kcal m}^{-2} \text{yr}^{-1}$) as determined by harvesting intertidal stands of known age

Pool	Pool ht (m)	Date began and ended	Term (yr)	Weight harvested (g)	Pool area (m^2)	Annual production	
						(g wet wt/ m^2)	(kcal/m^2)
2	+0.6	May 1964–May 1967	3.0	1,654	0.27	2,042	988
3	+0.3	Sep 1964–Jun 1967	2.75	3,355	0.36	3,389	1,604
A	+0.3	Apr 1966–Jun 1967	1.17	1,051	0.34	2,642	1,279
B	+0.3	Apr 1966–Jun 1967	1.17	1,334	0.63	1,809	876
4	-0.3	Feb 1965–May 1967	2.25	796	0.33	1,072	519
4p	-0.3	Mar 1966–May 1967	1.17	657	0.16	3,509	1,698
						$\bar{x} = 2,411$	$\bar{x} = 1,167$

consumption is compared to a preliminary estimate of local net primary production, and the energy budget is evaluated in light of what it reveals about *Tegula's* distribution and ecological well-being.

Primary production and secondary consumption

In that portion of the environmental mosaic where this study was made, *T. funebris* is certainly the most abundant herbivore that attains a major body dimension greater than, say, 2.0 cm. It is by no means the only one, and it coexists with significant numbers of two chitons (*Mopalia muscosa* and *M. lignosa*), the limpet *Acmaea t. scutum*, the urchin *Strongylocentrotus purpuratus*, and such genera of small gastropods as *Homalopoma*, *Margarites*, *Lacuna*, and *Littorina*. Together these species would exert a significant grazing pressure on the benthic plant community if total consumption and production were approximately equivalent.

Tegula is known to browse on the diatom film and attached benthic algae (Best 1964); it also seems to consume, whenever possible, such detached macroscopic algae as *Nereocystis leutkeana*, *Macrocystis integrifolia*, *Costoria costata*, and *Gigartina corymbifera* that drift across the rocky intertidal. In fact, it is only when many individuals band together and, by their combined weight, anchor a piece of drift algae that they can clearly be observed feeding.

A preliminary estimate of the primary

production potentially available to all the grazing herbivores has been obtained as follows. I have assumed that annual production estimates of two of the dominant benthic algae, when averaged, will suggest rates approximating that of the total mixed algal assemblage, exclusive of diatoms. Glynn (1965) has measured by cropping the production of *Endocladia muricata*, a characteristic midintertidal species at Mukkaw Bay, as equivalent to $1.2 \text{ g dry wt m}^{-2} \text{ day}^{-1}$. Assuming 9 months of production and applying the caloric value given in Paine and Vadas (1969a), this species contributes $1,347 \text{ kcal m}^{-2} \text{ yr}^{-1}$. The net annual production of low areas of the intertidal has been determined by harvesting shallow tide pools (Paine and Vadas 1969b). These pools, although containing a mixed crop of algae, were dominated by *Hedophyllum sessile* and had been subjected to minimal grazing pressure once sea urchins had been removed. The net annual production, based on the pool's principal component (*Hedophyllum*) and using the conversion factors in Paine and Vadas (1969a), is $1,167 \text{ kcal m}^{-2} \text{ yr}^{-1}$ (Table 6).

The averaged *Endocladia* and *Hedophyllum* production estimates come to about $1,250 \text{ kcal m}^{-2} \text{ yr}^{-1}$, a value close to the total annual consumption of a composite *Tegula* population of $1,071 \text{ kcal}$ (Table 5). This consumption figure is minimal, because a variety of other browsers have not been included. However, the production figure is also certainly an un-

derestimate in that all diatom growth has been excluded, and no way has been found to determine satisfactorily the contribution of drift algae, which are certainly important. Scagel (1947) estimated the annual production of a subtidal stand of *Macrocystis* to be 509 lb/400 sq ft (6,218 g wet wt/m² or 3,233 kcal m⁻² yr⁻¹ making the appropriate conversions). Under natural conditions most of this would be washed shoreward, and thus made available to the resident browsers. At Mukkaw Bay, algae drift ashore in a bimodal annual pattern with a spring peak dominated by *Nereocystis* and a major fall accumulation composed of most of the annual species. Thus it seems likely that the quantities of plant material derived from the highly productive shallow subtidal that are deposited onto the intertidal or traverse it are a major energy source for the grazing invertebrates, as they are in some other shallow-water marine communities (MacGinitie 1935; Fager 1968). In the absence of allochthonous production, preliminary measures suggest that *in situ* macroscopic algal production would be insufficient to maintain the herbivore density.

Efficiency values

I have calculated six efficiency values based on the data given in Table 5. Assimilation efficiency defined as (ingestion - egestion) ÷ ingestion is about 70%. Intuitively, this value appears high because *Tegula* are presumably consuming the entire spectrum of foods available or attractive to them. The observed value would be reduced if significant quantities of food energy derived from dissolved organic material—a possibility strongly enhanced by the recent work of Stephens (1968)—could be accounted for. On the other hand, the relatively high assimilation value could reflect the great variety of digestive enzymes characterizing the species (Galli and Giese 1959). Further, Carefoot (1967a) found that assimilation efficiency ranged from 45–75% in the herbivorous opisthobranch *Aplysia*, and

higher values are not at all uncommon in the literature.

The gross efficiency of growth (Richman 1958), defined here as net productivity/ingestion, averages 16.6%. Net productivity is ingestion minus both egestion and respiration. Carefoot (1967a) reported values from 15–61% in *Aplysia* feeding on a variety of food, although the range of values is not strictly comparable with my results because his animals were maintained for an even briefer portion of their life span. The gross efficiency of *Littorina* is 6.3% (Odum and Smalley 1959). Net efficiency of growth in *Tegula*, defined as net productivity/assimilation, ranges from 20–28% and falls close to the relationship between assimilation efficiency and net growth efficiency plotted by Welch (1968) for 15 species of aquatic consumer.

Table 5 shows three other efficiencies which represent a gross efficiency of growth partitioned into biologically distinct categories. Ecological efficiency of predators, as defined by Slobodkin (1962), is the caloric value of a prey species ingested by a predator divided by the total calories ingested by that prey. The majority of the reproductive products of *Tegula* are probably consumed during their planktonic existence, so I have summed both the reproduction and mortality figures to calculate this efficiency. The composite value for *Tegula* is 4.9%. In the low-area subpopulation, where a heavy mortality is attributable to *Pisaster*, it is 8.1%—a value similar to that obtained by Slobodkin (1962) for heavily exploited *Daphnia* and *Hydra* populations. In addition, many products of *Tegula* are passed not to higher levels but to decomposers. In this category would be mucus, urine, the shell's organic matrix, etc. The ecological efficiency of decomposers in the composite population is 7.6%, suggesting that about 60% of the total energy transfer of *Tegula* is to lower (decomposer) food chains. The final column represents a tissue growth efficiency, tissue increment/ingestion. It is not immediately transferred to other levels but rather offsets the tissue loss at

all ages to predation or physiological death. That this efficiency and the ecological efficiency of predators are approximately equivalent in the composite population suggests that these *Tegula* may be at or near an ecological steady state. Decomposer efficiency is functionally different because the categories considered in it represent the byproducts of molluscan metabolism or life rather than those that directly serve to replace or increase population mass. Thus it would be incorrect to compare a summed ecological efficiency of predators and decomposers with tissue growth efficiency.

Distribution

Like many gastropods *Tegula* is characterized by striking differences in mean individual size throughout its range; though such differences are found locally in *Tegula* (Wara and Wright 1964; Paine 1969), their causes and significance are difficult to infer. In the low zone at Mukkaw the larger *Tegula* grow more rapidly than their counterparts of similar size higher in the intertidal (Paine 1969). The absence of small animals in the low zone (Table 1) indicates that this population can only be maintained by immigration. The energy flux substantiates this, for mortality ($123 \text{ kcal m}^{-2} \text{ yr}^{-1}$) greatly exceeds tissue growth (69 kcal), indicating that without the input of new individuals, this population would rapidly dwindle.

The caloric analysis of individuals suggests two proximate reasons for the migration from high to low. As a population, *Tegula* produce more kilocalories of gametes in the lower than in the higher intertidal ($27 \text{ vs. } 1 \text{ kcal m}^{-2} \text{ yr}^{-1}$). In part this is due to the much higher proportion of sexually mature individuals in the low-zone population. Also contributing to the difference is the reduced gonadal size, and hence caloric value, in females of the high intertidal when compared with individuals of equivalent size lower down (Fig. 2). And the comparison indicates that some aspect of the high intertidal is inimical to large *Tegula* and that the re-

sultant physiological stress or relative food shortage is directly reflected in a reduced reproductive output and individual growth rate. These factors either do not or cannot influence small *Tegula*, leaving the basic causes of the great population density in the upper intertidal unexplained.

REFERENCES

- ANRAKU, M. 1964. Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. *Limnol. Oceanogr.* **9**: 195-206.
- BEST, B. 1964. Feeding activities of *Tegula funebris*. *Veliger* **6**(Suppl.): 42-45.
- CAREFOOT, T. H. 1967a. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. Mar. Biol. Ass. U.K.* **47**: 565-590.
- . 1967b. Growth and nutrition of three species of opisthobranch molluscs. *Comp. Biochem. Physiol.* **21**: 627-652.
- ENGELMANN, M. D. 1961. The role of soil arthropods in the energetics of an old field community. *Ecol. Monogr.* **31**: 221-238.
- . 1966. Energetics, terrestrial field studies and animal productivity. *Advan. Ecol. Res.* **3**: 73-115.
- FAGER, E. W. 1968. A sand-bottom epifaunal community of invertebrates in shallow water. *Limnol. Oceanogr.* **13**: 448-464.
- GALLI, D. R., AND A. C. GIESE. 1959. Carbohydrate digestion in a herbivorous snail, *Tegula funebris*. *J. Exp. Zool.* **140**: 415-440.
- GHIRETTI, F. 1966. Respiration, p. 175-208. In K. M. Wilbur and C. M. Yonge [eds.], *Physiology of Mollusca*, v. 2. Academic.
- GLYNN, P. W. 1965. Community composition, structure, and interrelationships in the marine intertidal *Endocladia muricata*-*Balanus glandula* association in Monterey Bay, California. *Beaufortia* **12**: 1-198.
- JOLANNES, R. E., S. J. COWARD, AND K. L. WEBB. 1969. Are dissolved amino acids an energy source for marine invertebrates? *Comp. Biochem. Physiol.* **29**: 283-288.
- KHAILOV, K. M., AND Z. P. BURLAKOVA. 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. *Limnol. Oceanogr.* **14**: 521-527.
- KOZLOVSKY, D. G. 1968. A critical evaluation of the trophic level concept. *Ecology* **49**: 48-60.
- KUENZLER, E. J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oceanogr.* **6**: 191-204.
- MACGINITIE, G. E. 1935. Ecological aspects of

- a California marine estuary. *Amer. Midl. Natur.* **16**: 629-765.
- MCLEAN, J. H. 1962. Manometric measurements of respiratory activity in *Tegula funebris*. *Veliger* **4**: 191-193.
- MANN, K. H. 1965. Energy transformations by a population of fish in the River Thames. *J. Anim. Ecol.* **34**: 253-275.
- NICOL, J. A. C. 1967. The biology of marine animals, 2nd ed. Pitman. 699 p.
- ODUM, E. P., C. E. CONNELL, AND L. B. DAVENPORT. 1962. Population energy flow of three primary consumer components of old-field ecosystems. *Ecology* **43**: 88-96.
- , AND A. E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and deposit feeding invertebrate in a salt marsh ecosystem. *Proc. Nat. Acad. Sci.* **45**: 617-622.
- PAINE, R. T. 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology* **46**: 603-619.
- . 1966. Endothermy in bomb calorimetry. *Limnol. Oceanogr.* **11**: 126-129.
- . 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. *Ecology* **50**: 950-961.
- , AND R. L. VADAS. 1969a. Caloric values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar. Biol.* **4**: 79-86.
- , AND ———. 1969b. The effect of grazing in the sea urchin *Strongylocentrotus* on benthic algal populations. *Limnol. Oceanogr.* **14**: 710-719.
- RICHMAN, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.* **28**: 273-291.
- RICKETTS, E. F., AND J. CALVIN. 1952. Between Pacific tides [3rd ed., revised by J. W. Hedgpeth.] Stanford. 502 p.
- RIGG, G., AND R. MILLER. 1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. *Proc. Calif. Acad. Sci.* **26**: 323-351.
- SCAGEL, R. F. 1947. An investigation on marine plants near Hardy Bay, B.C. *Prov. Dep. Fish.* **1**, Victoria, B.C. 70 p.
- SLOBODKIN, L. B. 1962. Energy in animal ecology. *Advan. Ecol. Res.* **1**: 69-101.
- SNEDECOR, G. W. 1959. *Statistical methods*, 5th ed. Iowa State. 534 p.
- STEPHENS, G. C. 1968. Dissolved organic matter as a potential source of nutrition for marine organisms. *Amer. Zool.* **8**: 95-106.
- TEAL, J. M. 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.* **23**: 41-78.
- U.S. COAST AND GEODETIC SURVEY. 1952. Surface water temperatures at tide stations. Pacific coast North and South America. USCGS Spec. Publ. 208. 59 p.
- VINOGRADOV, A. P. 1953. The elementary chemical composition of marine organisms. *Mem. Sears Found. Mar. Res.* **2**. 647 p.
- WARA, W. M., AND B. B. WRIGHT. 1964. The distribution and movement of *Tegula funebris* in the intertidal region of Monterey Bay, California. *Veliger* **6**(Suppl.): 30-37.
- WELCH, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology* **49**: 755-759.
- WILBUR, K. M. 1964. Shell formation and regeneration, p. 243-282. *In* K. M. Wilbur and C. M. Yonge [eds.], *Physiology of Mollusca*, v. 1. Academic.
- WILBUR, K. M., AND C. M. YONGE [Eds.]. 1966. *Physiology of Mollusca*, v. 2. Academic. 645 p.