Energy Expended on Growth and Gonad Output in the Ribbed Mussel *Aulacomya ater*

C.L. Griffiths and J.A. King

Zoology Department, University of Cape Town; Rondebosch 7700, South Africa

Abstract

Length/weight relationships have been computed for shell, flesh and byssus of *Aulacomya ater* (Molina) and energy values used to convert the weights to energy equivalents. Shell accounts for some 26% of total body energy, while the contribution of the byssus declines from 15 to 8% during growth. Observations of juvenile growth rates have been used to generate a Gompertz growth equation which predicts attainment of maximum length (90 mm) after 11 years. Reproductive condition has been assessed by monitoring seasonal fluctuations in the flesh weight of standard-sized individuals, calculated from monthly length/weight regressions. There appear to be three spawnings, of variable date and intensity, each year. From the above data, annual energy expenditure on growth and gonad output has been calculated for individuals of various sizes. The ratio of total production to biomass (P:$\bar{\text{B}}$) is a declining function of shell length, dropping from 29.5 at 5 mm to 0.8 at 85 mm. The proportion of total production expended on gamete output increases steadily from 25% at attainment of maturity (15 mm) to 81% at 85 mm length. The considerable effects of changing size composition on the amount and type of production in natural populations are discussed.

Introduction

Although descriptive studies of the growth and reproductive cycles of marine bivalves abound in the literature (reviewed by Bayne, 1976) few attempts have been made to compare the energetic costs of these processes.

Growth can be relatively easily converted into energy units, providing that the changing weights and energy values of the various body components (shell, flesh and byssus) are known. Gonad production has been assessed by inducing spawning in the laboratory and measuring the output (Bayne *et al.*, 1975), but more commonly estimates are derived by comparison of gonad weight before and after spawning. Where the gonad is a discrete organ its weight may be determined directly, after dissecting it from the body (Dame, 1976). More frequently, however, it is inextricably bound into the visceral mass and indirect methods must be used. These normally involve recording fluctuations in body weight in standard-sized individuals derived from seasonal length (or height) to flesh-weight

regressions. This method has been used by Kuenzler (1961) and Hughes (1970), although both authors treated their data somewhat unconventionally, Kuenzler expressing weight loss as a function of body weight itself and Hughes standardizing the slopes of his regression lines. Hibbert (1977) used a similar technique, but calculated gonad output as the difference between a small decline in body energy upon spawning and a theoretical increase obtained by projecting the growth rate preceding spawning. The assumption was thus made that the rate of increase in body energy in the month(s) prior to spawning was maintained during the period of gamete release. A more conservative approach was taken by Griffiths (1977), who used actual slopes of monthly regression equations and included only real declines in body energy in calculating gonad output. Whatever methods are used, it is desirable to cross-check the estimates obtained. Kuenzler (1961), Hughes (1970) and Hibbert (1977) did this by completing energy budgets for their respective populations. In the present study, growth —

and hence total production — are calculated and compared with predicted values of scope for growth (Griffiths and King, 1979).

Materials, Methods and Results

The following analyses were undertaken on a population of *Aulacomya ater* (Molina) collected from a buoyed site at 13 m depth off Oudekraal on the Cape Peninsula, South Africa. Physical conditions at the site, described in detail by Velimirov *et al.* (1977), are profoundly affected by wind-induced upwelling. Temperatures show little seasonal variation, although minima (7° to 9°C), occur during the peak upwelling season in the southern summer and maxima (15° to 16°C) follow onshore wind conditions in winter (April-August).

The various steps in the calculations of production rates are treated separately below.

Length/Weight Relationships and Energy Equivalents

In order to assess the energy expended on growth, length/weight relationships must be computed for each body component (shell, flesh and byssus) and the energy content of each component evaluated.

A large sample of *Aulacomya ater* was collected for this purpose in July 1975, care being taken to retain the byssus intact. The dry weights (3 days at 60°C) of shell, flesh and byssus were determined for individuals of different shell lengths, following which the shell, flesh (males and females separately), and byssal thread portions from each 10 mm length class (0 to 90 mm) were pooled. Flesh and byssus portions were each homogenized, and replicate subsamples were fired in a ballistic bomb calorimeter. Calcium carbonate from the shell fractions was dissolved in 13N HCl for 1 to 3 days (until chemical reaction ceased), and the remaining matrix was rinsed twice with distilled water, dried, reweighed, and then fired in the calorimeter. From these results, energy values per unit whole dry shell could be calculated. Further flesh samples were analysed in February 1976 to test for variation in energy content with reproductive condition.

The relationships recorded between shell length and the dry weights of shell, flesh and byssus are depicted in Fig. 1 and are described by the equations:-

$$\log_{10} (\text{shell weight}) = -5.58 + 3.04 \log_{10} (\text{shell length})$$
$$(r = 0.98) \qquad (1)$$

$$\log_{10} (\text{flesh weight}) = -6.43 + 3.12 \log_{10} (\text{shell length})$$
$$(r = 0.98) \qquad (2)$$

$$\log_{10} (\text{byssus weight}) = -6.81 + 2.49 \log_{10} (\text{shell length})$$
$$(r = 0.77) \qquad (3)$$

Table 1 gives energy values of whole dry shell, flesh and byssus for individuals of the various size classes. No
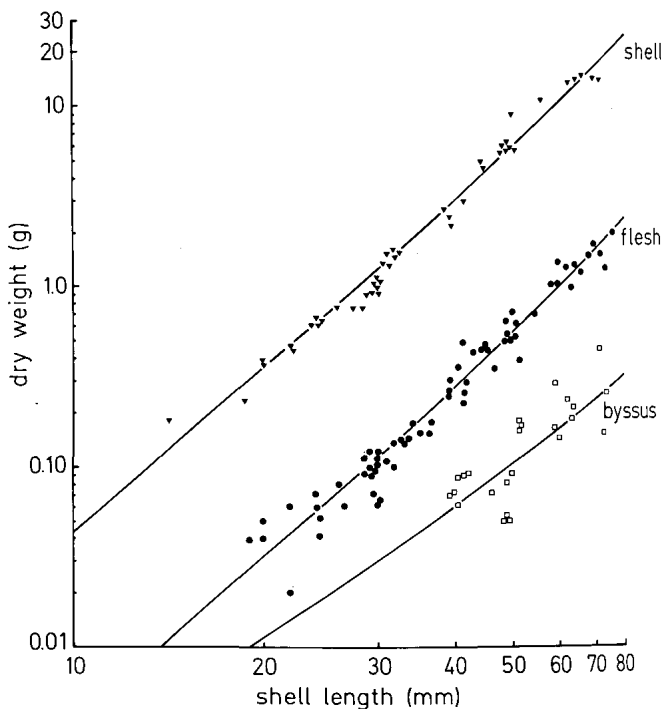

Fig. 1. *Aulacomya ater*. Dry weights of shell, flesh and byssus as a function of shell length (July, 1975)

Table 1. *Aulacomya ater*. Energy content (kJ g^{-1} dry weight) of whole dry shell, flesh and byssus for different size classes (flesh values mean of 4 readings, shell and byssus values mean of 2 readings). SD: standard deviation

Length class (mm)	Energy content (kJ g^{-1} dry weight)		
	Shell	Flesh	Byssus
0-10	0.6	17.1	17.3
10-20	1.0	20.6	19.2
20-30	0.9	20.3	17.3
30-40	0.9	22.2	18.1
40-50	1.0	22.5	21.7
50-60	1.0	24.8	22.9
60-70	1.0	25.8	22.4
70-80	1.0	23.6	21.9
80-90	0.9	22.2	22.5
Mean	0.92	22.1	20.4
SD	0.13	2.60	2.36

significant difference was found between the flesh of males and females, nor were there any seasonal fluctuations in the
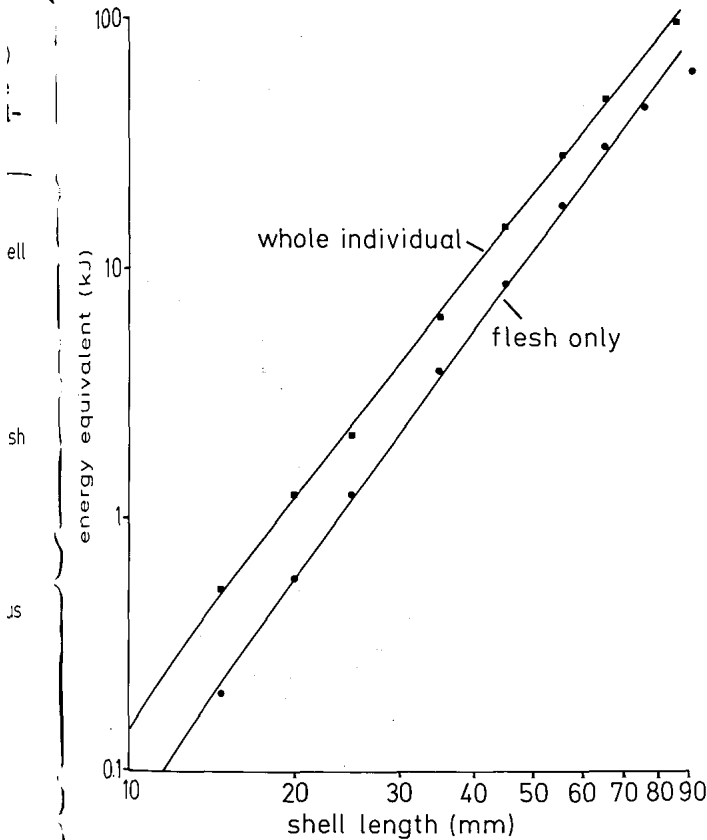

Fig. 2. *Aulacomya ater*. Energy equivalents of whole individual and of flesh alone as a function of shell length (July, 1975)
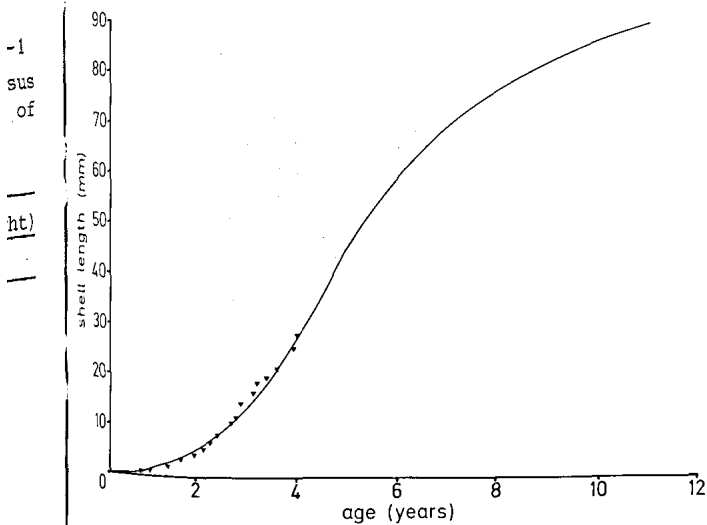

Fig. 3. *Aulacomya ater*. Composite growth data and calculated Gompertz growth curve for mussels collected at Oudekraal, on the Cape Peninsula, South Africa

energy value of flesh; the values given are therefore means of all readings.

The increase in energy content of each body component during growth may be obtained from the product of component weight (Eqs. 1-3) and energy value (Table 1). The results of such calculations (using the appropriate energy values for each size class), for flesh alone and for the whole individual, are illustrated in Fig. 2. The equations relating energy content to shell length are:

$$\log_{10} \text{(flesh kJ)} = -4.57 + 3.33 \log_{10} \text{(shell length)} \quad (4)$$

$$\log_{10} \text{(total kJ)} = -3.90 + 3.07 \log_{10} \text{(shell length)} \quad (5)$$

Growth

Preliminary attempts to estimate growth rate using the standard technique of length-frequency analysis proved unsuccessful, due to the rapid merging of cohorts during development — a common feature in mussel populations (Seed, 1969). In the absence of annual disturbance rings, acceptable data were finally obtained by identifying patches in the mussel bed apparently composed of single cohorts, periodically sampling these patches to determine mean lengths, and finally combining the results into a composite growth series. Three such patches were followed for 12 or more months and the data fitted by computer to Gompertz and logistic growth curves, using the method of least-squares (having a sigmoid shape the data are unsuitable for a Von Bertalanffy fit). To do this it was necessary to specify L_{max}, the maximum shell length attained at the study site. This was fixed at 90 mm, the largest individual recorded in the area being 92.0 mm and the mean of the 10 largest mussels being 89.9 mm.

The best fit was obtained for the Gompertz curve, the growth equation obtained being given by:

$$Lt = 90(0.000184)^{0.604^t}, \quad (6)$$

where t is age in years and Lt the length (mm) at that time.

Although extrapolation procedures for growth curves should be treated with circumspection (Bayne, 1976), in the absence of better data the above equation has been used to predict growth to L_{max}. The results (Fig. 3), which suggest that maximum length is attained after 11 years, are consistent with data presented by Pollock (1978), who followed two cohorts, one of which grew from 12 to 30 mm in 25 months and the other from 1.6 to 2.5 mm in 4.4 months.

Gonad Output

Gonad production was estimated by a method similar to those of Hughes (1970) and Griffiths (1977). Monthly samples of *Aulacomya ater* were collected over a period of 2 years. From each sample, some 30 individuals were selected to cover the entire adult size range and were deep-frozen overnight (causing the shells to gape) before being preserved for 2 weeks in 5% formalin to harden the body tissues. Each individual was then measured with vernier calipers, sex noted and flesh removed, and then drained for 10 min and weighed. Regression equations of flesh weight against shell length were calculated for each month. Although the sexes were initially treated separately, no difference in weight was evident and the data were subsequently combined (Table 2). Individuals below 15 mm shell length could not be sexed and were excluded from the analysis.

It is evident from the equations in Table 2 that adult mussels synchronously undergo substantial changes in flesh weight. If the flesh weights of standard-sized individuals are calculated from these equations and plotted graphically, three periods of weight loss are evident in each annual cycle (Fig. 4), these declines being displaced by approximately 2 months in 1976-1977 compared with 1975-1976, when they occurred during August-October, December, and March-April.

It has been shown by Griffiths (1977), working at a nearby site, that these weight losses are the results of spawning bouts, each being paralleled by a marked decline in the percentage of mature oocytes in gonad smears. Each period of spawning is followed by deposition of small amounts of interfollicular material and subsequent rapid redevelopment of the gonad. These findings were confirmed by examination of the present material in which weight losses were accompanied by pronounced thinning (by up to 50%) and a gelatinous appearance of the mantle.

Production

The two components of production: growth (Pg) and reproductive output (Pr) were calculated for individuals of 9 initial shell lengths using the procedure outlined below:

Pg. Growth production was calculated by reading off the age of each standard individual (Fig. 3) and calculating the length 1 year later (Eq. 6). Both shell lengths were then converted to energy equivalents (Eq. 5), the difference between the two values being growth production over the year.

Table 2. *Aulacomya ater*. Monthly length/wet flesh weight regressions; $\log_{10}$ (wet flesh weight in g) = $\log a + b \log_{10}$ (shell length in mm)

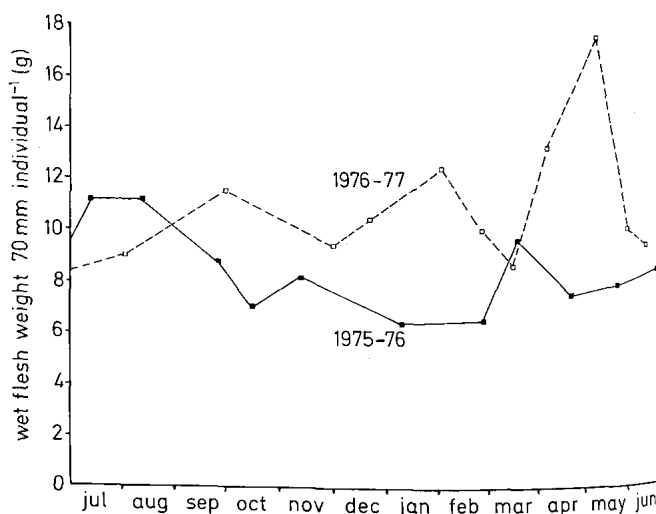| Date	Regression equation		r	n
	$\log a$	b		
1975				
May 5	-5.74	2.80	0.98	30
June 5	-4.63	2.25	0.91	30
July 12	-5.08	3.25	0.96	30
Aug. 12	-6.84	3.38	0.97	30
Sept. 25	-6.71	3.38	0.99	30
Oct. 16	-4.15	2.55	0.95	30
Nov. 12	-5.51	2.93	0.98	28
1976				
Jan. 9	-5.28	2.99	0.99	27
Feb. 27	-5.66	2.79	0.94	24
Mar. 18	-5.69	2.86	0.98	30
Apr. 22	-5.28	3.02	0.97	22
May 22	-5.91	2.70	0.97	21
June 24	-5.94	2.69	0.91	30
Aug. 2	-4.04	2.66	0.92	21
Sept. 30	-3.42	1.98	0.84	30
Dec. 1	-5.20	3.13	0.93	30
Dec. 20	-5.45	3.02	0.79	30
1977				
Feb. 2	-6.85	3.38	0.97	30
Feb. 25	-5.28	3.09	0.95	30
Mar. 15	-4.72	2.28	0.92	27
Apr. 7	-6.97	3.33	0.96	27
May 10	-5.40	3.17	0.95	30
June 1	-4.40	2.49	0.94	30
June 16	-4.11	2.63	0.97	30

Fig. 4. *Aulacomya ater*. Fluctuations in wet flesh weight of a 70 mm individual over 2 years, derived from monthly length/weight regression equations

Pr. Using the regression equations in Table 2, body weights of standard-sized individuals were calculated before and after each of the three annual spawning periods. The differences between these sets of values represents the gonad output over the three spawnings. Data for the 2 years of investigation (July 1975-June 1977) were averaged, and converted to energy equivalents assuming the energetic value of gametes to be the same as that of the flesh = 22.1 kJ g^{-1} dry weight (divided by a wet to dry flesh ratio of 7.1:1 = 3.1 kJ g^{-1} wet weight).

The total gonad output (kJ per year) so obtained may be related to shell length by the equation:

$$\log_{10} (\text{gonad output}) = -5.82 + 3.10 \log_{10} (\text{shell length}). \quad (7)$$

For calculation purposes, this was assumed to be in the form of three equal bouts taking place after 3, 6 and 10 months, respectively.

Since an individual of a particular length at the start of the year will have undergone varying amounts of growth by the times of the first, second and third spawnings, the calculated gonad outputs at each of these spawnings must be adjusted accordingly. This was done by calculating the size of each length class after 3, 6 and 10 months and computing the annual gonad output for individuals of each of these lengths from Eq. (7). The 3 values were then averaged to obtain total Pr over the year. Results are given in Table 3.

Discussion

The growth rate recorded in Fig. 3 is slow compared with that achieved by *Aula-comya ater* under culture conditions in South America (Lozada et al., 1974), but is well within the wide range of growth rates recorded for *Mytilus edulis* (Seed, 1969; Theisen, 1973), and is of the sigmoid type typical of their slower growing populations. The relationship between shell weight and dry flesh weight remains consistent during growth (10:1), with the shell component forming a steady 26% of total body energy. Byssus weight is more variable and relatively lower in larger individuals. The energy value of the byssus declines from 15% of the total at 25 mm to 8 to 10% in large adults. Over 35% of population production is thus tied up in the form of nondigestible body components and is probably eventually passed into the decomposer food chain.

The pattern of three variable spawnings which occurs each year is one observed in a number of other southern species, most of which show prolonged or repeated spawning bouts (see review in Bayne, 1976). The factors inducing spawning in such species are not fully understood, but a combination of longterm conditioning factors, particularly food availability, and short-term triggering factors, such as temperature shock, may account for the irregular patterns observed (Griffiths, 1977).

Annual growth production (Pg) of individual mussels (Table 3) increases with size up to 65 mm shell length, beyond which there is a decline brought about by the decelerating growth rate. Gonad production (Pr), however, continues to increase and hence forms a progressively larger proportion of total production (up to 81% at 85 mm). Despite increasing gonad output, there is an

Table 3. *Aulacomya ater*. Annual production (kJ) for individuals of various shell lengths. B is initial biomass. Pg: production as growth; Pr: reproductive output; *Lt*: length (mm) at time *t*; $L(t + 1)$: length 1 year later

Initial length Lt (mm)	$L(t + 1)$ (mm)	Pg	Pr	Total annual production (Pg + Pr)	Pr as % total production	P:$\bar{\text{B}}$ ratio
5	(+11) = 16	0.59	0	0.59	0	29.5
15	(+14) = 29	3.45	1.15	4.60	25	9.2
25	(+16) = 41	8.98	3.54	12.43	27	5.2
35	(+14) = 49	12.56	8.25	20.81	39	3.1
45	(+13) = 58	17.19	15.00	32.19	46	2.2
55	(+9) = 64	17.00	21.40	38.40	55	1.4
65	(+9) = 74	22.00	36.63	58.63	62	1.3
75	(+7) = 82	17.00	50.24	67.24	74	0.9
85	(+4) = 89	15.60	67.66	83.26	81	0.8

overall decline in annual $P:\bar{B}$ ratio with increasing size. A population consisting of small individuals (15 to 65 mm) will thus have both a larger gonad output and a higher flesh production, per unit biomass, than one comprised of very old individuals, and is hence to be preferred for culture purposes. The higher productivity of smaller individuals is a factor of the greater volume of water pumped per unit O_2 consumed, resulting in a greater percentage scope for growth (Griffiths and King, 1979).

It is of interest to compare the production rates recorded in nature with those obtained by Griffiths and King (1979) in short-term experimental studies. The production rates given in Table 3 are the equivalent of percentage increments in body energy of approximately 2.5% day^{-1} at 15 mm, 0.5% at 50 mm and 0.25% at 75 mm shell length. The relationships of these values to one another are similar to those recorded by Griffiths and King, who show that small mussels attain far higher percentage growth rates than do larger ones held at equivalent ration. Under laboratory conditions, the above growth rates would have been recorded under ration levels of between 0.7 and 1.8 mg dry weight *Dunaliella primolecta* l^{-1}. By comparison, 24 readings of suspended particulate organic matter taken 0.5 m above mussel beds at the study site gave values between 0.7 and 5.5 mg l^{-1}, with a mean of 3.3 mg l^{-1}. Although these values are considerably higher than predicted, the energetic value of natural detritus is probably well below that of pure *D. primolecta* culture, while some of the natural particles may also be too large for mussels to consume. Alternatively, mussels may be unable to maintain the production rates recorded in laboratory studies for extended periods and this may account for the low growth rates observed in nature.

Whatever the reasons for these discrepancies, it is evident that food levels in the field vary unpredictably over a wide range, with the result that production rates must also fluctuate. It is not clear how the available resources are allocated between somatic growth and gonad production, although the considerable variations in weight loss per spawning (Fig. 4) indicate that this factor is strongly influenced by environmental conditions. Successful spawnings may well follow periods of upwelling or of rough sea conditions which provide abundant food and allow for rapid gonad maturation, such conditions occurring at different times and with different intensities from year to year.

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Dr. D.J.W. Moriarty
CSIRO, Division of Fisheries and Oceanography
P.O. Box 120
Cleveland, Queensland 4163
Australia

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