

## Energetics of growth and reproduction in two species of chink shells (*Lacuna*, Mollusca : Prosobranchia)

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**Résumé** : Une évaluation quantitative de la croissance, de la production de pontes et de la respiration a été obtenue chez les prosobranches intertidaux *Lacuna pallidula* et *L. vineta*, à des températures de 5 °C et 10 °C. A 10 °C, la consommation d'oxygène s'abaisse chez les animaux ayant atteint la maturité sexuelle. La quantité d'œufs produits varie selon la température et l'espèce étudiée. Lorsque l'accouplement est empêché, les femelles des deux espèces ont des réponses différentes : *Lacuna pallidula* réduit son taux de croissance et pond des œufs non fécondés, tandis que *L. vineta* réduit peu son taux de croissance, mais ne donne aucune ponte.

**Abstract** : Growth, spawn production and respiration were quantified for the intertidal prosobranchs *Lacuna pallidula* and *Lacuna vineta* at 5 °C and 10 °C. At 10 °C respiratory demand became relatively low on sexual maturity. The behaviour of productivity depended on temperature and species. When prevented from mating, females of the two species behaved differently : *Lacuna pallidula* reduced their growth rates and commenced spawning infertile eggs ; *L. vineta* showed some reduction in growth rates and did not produce infertile spawn.

### INTRODUCTION

Marine ecologists have long shown interest in the diversity of reproductive modes among marine invertebrates and in seeking explanations for the observed patterns. One of their major preoccupations has concerned the putative costs and benefits of having planktonic larvae. The field has been reviewed several times, e.g. Grahame & Branch (1985). While many authors have considered the "choice" between planktotrophy or lecithotrophy in terms of energetics, this may be governed by demographic and not energetic constraints (Grahame, 1982).

Another area of interest is that in which organisms may be seen as performing functions (e.g. growth, reproduction) which have costs and benefits, with the organism representing an optimal solution to the problems of allocation of resources to these functions (Sibly & Calow, 1986). Here, reproduction is treated as a function that must compete with others for resources. Calow (1983) pointed out that conversion efficiencies involved in gamete production were usually better than those involved in somatic growth. This might be achieved in a variety of ways, including the relative depression of respiration when sexually mature so that during the reproductive phase respiratory losses were a reduced portion of the total energy budget. Even taxonomically related animals might, however, have different metabolic strategies, and Calow (1983) called for more studies of life-time energy budgets, especially in closely related species.

In the small prosobranch *Lacuna pallidula* (da Costa) females produce relatively few, large and well-protected eggs, which develop directly into juveniles. *Lacuna vineta* (Montagu) produces many more, smaller and less well protected eggs, hatching into plank-

trophic veligers. The relative proportions of energy devoted to growth, spawning and respiration were very similar in both species (Grahame, 1982) but *L. vincta* had a substantially higher energy turnover than did the larger *L. pallidula*. This was not simply a consequence of the allometric relationship between size and metabolism, because respiration rate was about 25 % higher in *L. vincta* than in *L. pallidula* of same size over much of the size range studied. Both species are short-lived, surviving for a year or less in the field (Grahame, 1985) and can be successfully reared in the laboratory.

The present paper reports on data for growth, respiration and reproduction (spawn output) of animals kept in the laboratory over a protracted period covering much of the life of the juvenile, until somatic growth had virtually ceased and spawning was well established. Comparison is made with data considered earlier (Grahame, 1982) which cover a much shorter time period.

## METHODS

The methods were the same as those used by Grahame (1982), but with the aim of studying the animals in the laboratory for a much longer period of time. Snails were collected on the shore at Robin Hood's Bay, Yorkshire, in autumn or winter and brought into the laboratory. They were reared in pairs in 'Toby Tea Boys' at either 5°C or 10°C, depending on which was nearer the ambient sea temperature at the time of collection. Shells were measured at about weekly intervals using a dissecting microscope with an eyepiece micrometer. The food supplied was *Fucus serratus* L., which both species fed on readily in the field and laboratory. Shell length measurements were converted into estimates of dry body mass using regression equations. The utility of the predictive allometric equations was checked by using females for weight determinations at the end of experiments, which in the main lasted for between four and six months. One experiment at 10°C lasted for only 11 weeks, and begun just before first spawning, therefore it did not take account of the pre-reproductive growth phase.

*Lacuna pallidula* males are markedly smaller than females; at the start of the experiment this dimorphism was just beginning to appear, making their discrimination very easy. Shell banding patterns were used to sort sexed *L. vincta* into pairs of recognisable individuals. As well as pairs of males and females, some snails were maintained as pairs of females or of males. This allowed data to be obtained for animals prevented from normal mating and spawning when sexual maturity was reached.

Spawning egg masses were carefully removed from the alga on which they were deposited, rinsed quickly in distilled water, and dried for 24 h under vacuum at 60°C. They were weighed to the nearest 5 µg on a Cahn 4400 micro-balance, a precision of the order of 0.1 %.

Measurements of oxygen uptake were made on individuals collected from the field and acclimated in the laboratory for a least 2 days at the experimental temperature. Oxygen consumption was measured using a Radiometer oxygen electrode in a stirred plastic chamber 10 ml in volume, the medium was sea water aged for several years before use. "Blank" experiments showed a constant very small oxygen depletion due to the electrode with no evidence of bacterial activity. From the data the relationship between oxygen uptake and body mass was obtained for each species at 5°C and 10°C.

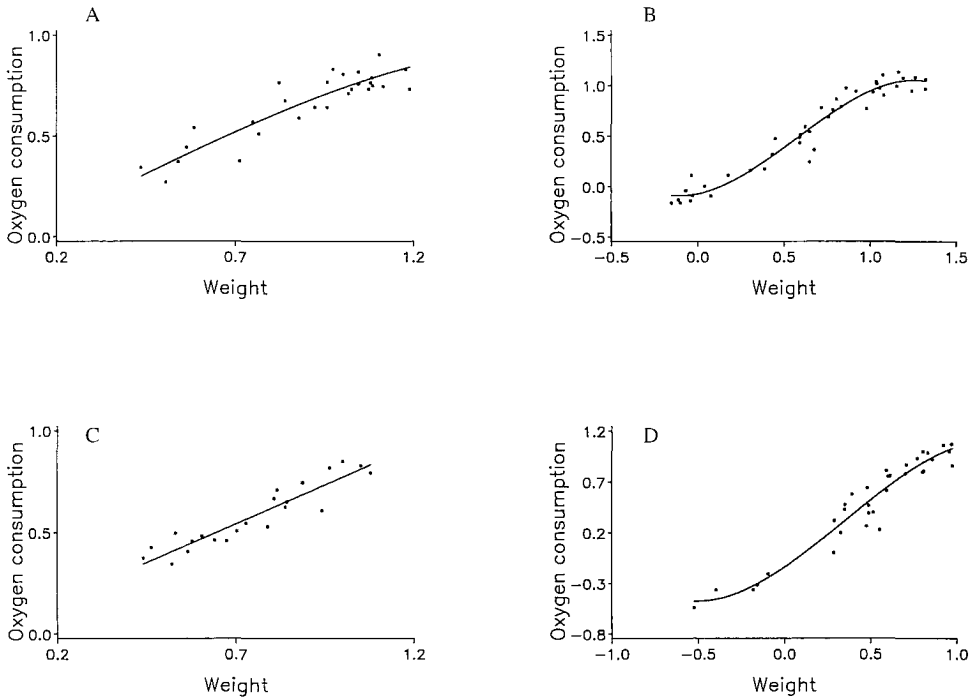


Fig. 1 : Logarithm (to base 10) of oxygen consumption ( $\mu\text{l.snail.h}^{-1}$ ) plotted on logarithm of body dry weight (mg) for *Lacuna pallidula* at 5 °C (A) and 10 °C (B), and *L. vincta* at 5 °C (C) and 10 °C (D).

The equations relating oxygen due to body mass have been used together with estimates of body mass and measurements of spawn mass, to estimate daily fluxes of energy to the functions of growth, reproduction and respiration. Mass was converted to joules using equivalents determined using a microbomb calorimeter (Grahame, 1977). Oxygen uptake was expressed in joule equivalents using the coefficient of  $14.14 \text{ J mg}^{-1} \text{ O}_2$  (Elliott & Davison, 1975). Symbols for energy fluxes are  $P_g$  (growth),  $P_r$  (spawn production) and  $R$  (respiration). Statistical analyses of the estimates were carried out using the Statistical Analysis System (SAS) package (SAS Institute Inc., 1990).

## RESULTS

Regression parameters for the allometric relationship between weight and shell length are shown in Table I. The straight line fit is a very good one, explaining at least 96 % of the variation of log weight in terms of log length. After some experiments females were killed for shell length and body dry weight measurements. These determinations included the largest females from the experiments, and allow an independent test of the utility of the prediction of weight from length. Using back-transformed arithmetic values, the mean devia-

tion of observed from predicted weights was 0.528 (3.67 % of mean observed weight) for *Lacuna pallidula* and - 0.591 (6.05 % of mean observed weight) for *L. vincta*. To test for overall bias the deviations were ranked and a Wilcoxon matched-pairs signed-ranks test performed for each species. For *L. pallidula*  $T = 83$ ,  $P = 0.6292$ ; for *L. vincta*  $T = 149$ ,  $P = 0.9772$ . Therefore, in both cases the null hypothesis is sustained and there appears to be no bias in the deviations - they are equally likely to be positive or negative, taking into account both the direction and magnitude of the deviations (Siegel, 1956). Thus, there is no evidence that the use of the equations in Table I introduces bias into the weight estimates from shell length measurements. There is no evidence of 'degrowth' as occurs in nudibranchs (Havenhand & Todd, 1988 b).

TABLE I

Parameters for the logarithmic regressions of body dry weight on shell length.

Species	n	Intercept	Slope	R
<i>Lacuna pallidula</i>	73	- 1.5763	2.9346	0.982
<i>Lacuna vincta</i>	56	- 1.4204	2.6503	0.979

Oxygen uptake for both species at 5 °C and 10°C is shown in Fig. 1. For *L. vincta* at 5 °C the relationship between oxygen uptake and weight was a linear allometric one, however for *L. pallidula* at 5 °C and for both species at 10 °C, the graphs show evidence of non-linearity. In these cases, stepwise regression was used to determine the best polynomial model for predicting oxygen uptake from weight. The appropriate regression equations are shown in Table II. As the object was to obtain the best predictive model, terms were sometimes included despite the fact that they did not individually have significant sums of squares ( $P = 0.05$ ).

Fig. 2 shows the estimated outputs in  $J d^{-1}$  plotted on soma size in  $J$  for *Lacuna pallidula* and *Lacuna vincta* at 5°C and 10°C. Both species show similar patterns of behaviour in the spawning snails, with  $P_g$  declining when  $P_r$  commences. In both species, the decline in  $P_g$  is more pronounced at 10 °C than at 5 °C. As would be expected energy fluxes are lower at 5 °C than at 10 °C, but the relative patterns is much the same in both species and at both temperatures.

Fig. 2 suggests that the relationship of either total production ( $P_g + P_r$ ) or total energy flux ( $P_g + P_r + R$ ) to soma may be adequately modelled by a logarithmic regression. Fig. 3 shows the data for total energy flux of both species at 5 °C and 10 °C. Once spawning commenced the scatter of the data was greatly increased due to the comparatively discontinuous nature of spawn deposition. Table III gives regression coefficients and associated significance tests for the allometric equation

$$y = a.x^b$$

where  $y$  is energy flow, either as production or total energy flux, and  $x$  is the body size estimated in joules.

TABLE II

Parameters for the logarithmic regressions of oxygen consumption ( $\mu\text{l mg}^{-1} \text{h}^{-1}$ ) on body mass (mg).

	Independent measure	Estimate of parameter	Fraction of sum of squares	P
<i>Lacuna pallidula</i> 5 °C intercept = - 0.078				
	Mass	0.881	98.8 %	0.0001
	Mass <sup>2</sup>	- 0.064	1.2 %	0.1845
<i>Lacuna pallidula</i> 10 °C intercept = - 0.073				
	Mass	0.357	98.2 %	0.0001
	Mass <sup>2</sup>	1.576	0.1 %	0.4110
	Mass <sup>3</sup>	- 0.913	1.7 %	0.0014
<i>Lacuna vineta</i> 5 °C intercept = 0.009				
	Mass	0.764	100 %	0.0001
<i>Lacuna vineta</i> 10°C Intercept = -0.142				
	Mass	1.154	99 %	0.0001
	Mass <sup>2</sup>	0.651	0.2 %	0.4550
	Mass <sup>3</sup>	- 0.626	0.8 %	0.0963

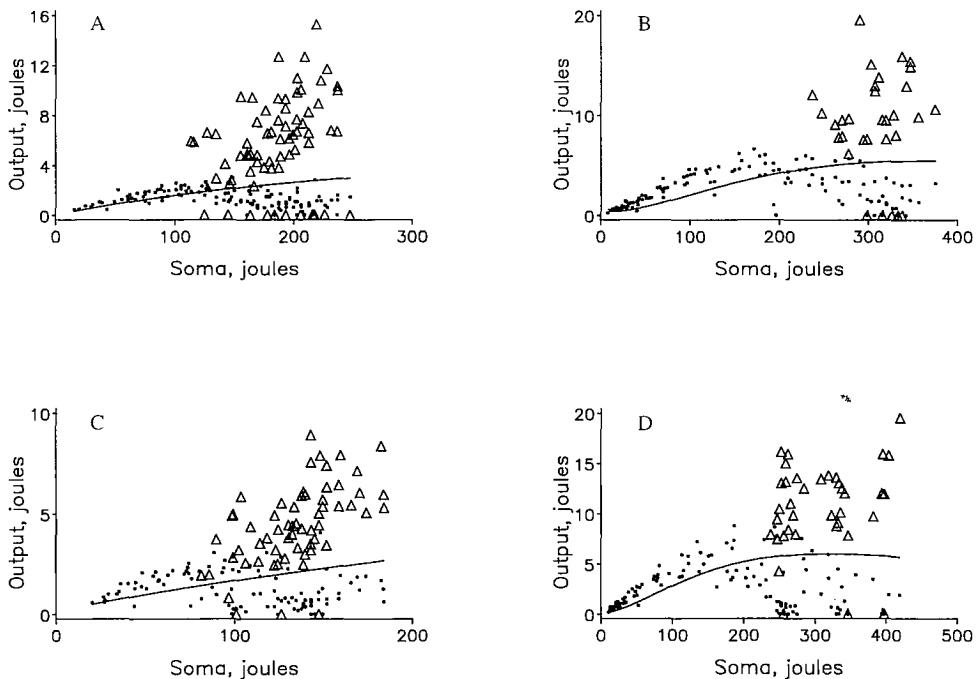


Fig. 2: Energy output as joules per day related to body size in joules for *Lacuna pallidula* at 5 °C (A) and 10 °C (B), and *L. vineta* at 5 °C (C) and 10 °C (D). The components of energy flow shown are somatic growth (dots), spawn production (triangles) and respiration (solid line).

Table III shows that for total energy flux ( $P_g + P_f + R$ ), the allometric exponent (estimated by  $b$  in the logarithmic regression equation) is high for both species. It is greater than 0.75, and at 5 °C is statistically indistinguishable from 1.0 for both species. For total production ( $P_g + P_f$ ) the situation is different, with coefficients statistically indistinguishable from 0.75 at 5 °C and < 0.75 at 10 °C. For spawn only ( $P_f$ ) the coefficients are not significantly different from 0 except in the case of *Lacuna vincta* at 5 °C. However for the short time series experiments (Table IIIB) there are very significant regression coefficients (indistinguishable from 1.0) for spawn only in the case of both species, suggesting that the lack of significance for the regression of  $P_f$  on soma in Table IIIA may be due to the relatively small sample sizes.

TABLE III

Regression parameters for the allometric equations ( $y = ax^b$ ) relating total production, total output, and spawn production to body size ( $x$ ). The short time series experiments (B) lack information on pre-reproductive growth, and are analysed only for spawn production.

A - data for long time series experiments

	n	regression coefficient	significance tests, $H_0$		
			b = 0	b = 0.75	b = 1.0
<i>Lacuna pallidula</i> , 5 °C					
energy flux	126	1.043	0.0001	0.0001	0.4599
production	126	0.780	0.0001	0.7631	0.0139
spawn only	63	- 0.049	0.5100	-	-
<i>Lacuna pallidula</i> , 10 °C					
energy flux	125	0.895	0.0001	0.0001	0.0007
production	125	0.564	0.0001	0.0007	0.0001
spawn only	32	- 0.971	0.5433	-	-
<i>Lacuna vincta</i> , 5 °C					
energy flux	101	1.053	0.0001	0.0001	0.3406
production	101	0.839	0.0001	0.2007	0.0213
spawn only	55	0.387	0.0057	0.0093	0.0001
<i>Lacuna vincta</i> , 10 °C					
energy flux	120	0.925	0.0001	0.0001	0.0088
production	120	0.573	0.0001	0.0003	0.0001
spawn only	38	0.125	0.8598	-	-
B - data for short time series experiments					
<i>Lacuna pallidula</i> , 10 °C					
spawn only	160	1.030	0.0001	0.2307	0.8991
<i>Lacuna vincta</i> , 10 °C					
spawn only	223	1.049	0.0001	0.0001	0.3954

A straight line is fitted for the total energy flux on soma relation for *Lacuna pallidula*, since when the data were examined for non-linearity by including the term (body size<sup>2</sup>) in the regression equation, there was no significant increase in sums of squares (Table IV).

TABLE IV

Non-linear regression equation parameters relating total energy flux and total production to body size expressed in joules.

Total energy flux				
	Independent measure	Estimate of parameter	Fraction of sum of squares	P
<i>Lacuna pallidula</i> 5 °C	Size	- 0.146	99 %	0.0001
	Size <sup>2</sup>	0.308	1 %	0.1090
<i>Lacuna vincta</i> 5 °C	Size	- 0.707	98.8 %	0.0001
	Size <sup>2</sup>	0.473	1.2 %	0.0378
<i>Lacuna vincta</i> 10 °C	Size	2.036	98.7 %	0.0001
	Size <sup>2</sup>	- 0.290	1.3 %	0.0001
Total production				
	Independent measure	Estimate of parameter	Fraction of sum of squares	P
<i>Lacuna pallidula</i> 5 °C	Size	- 1.540	93.8 %	0.0001
	Size <sup>2</sup>	2.320	6.2 %	0.0219
<i>Lacuna vincta</i> 5 °C	Size	- 2.241	94.5 %	0.0001
	Size <sup>2</sup>	0.827	5.5 %	0.0029

The same treatment for *L. vincta* showed small but significant increases in sums of squares on inclusion of (body size<sup>2</sup>) in the regression, there is good reason for supposing that the relationship here is non-linear. Accordingly, the lines fitted in Fig. 3 are for the quadratic equations for this species at 5 °C and 10 °C. The effect appears to be opposite at the two temperatures, with increase in size there is an upturn in energy flux at 5 °C and a downturn at 10 °C.

Considering total production ( $P_g + P_r$ ), for both *Lacuna pallidula* and *L. vincta* at 5 °C there was significant non-linearity, in both cases the slope of the line increased with size. Comparison were made of the growth of mated females with that of females denied access to males, and also with growth of males, all at 10 °C. The simplest possible approach was used, namely to model the daily growth rate as  $J d^{-1}$  (see Figs 1, 2) using the quadratic regression equation

$$\text{growth rate} = a + b_1 \cdot \text{soma} + b_2 \cdot \text{soma}^2$$

where the soma is expressed in joule equivalents. Fig. 4 shows the growth of small numbers of *L. pallidula* (Fig. 4A) and *L. vincta* (Fig. 4B) denied access to males as they matured. In

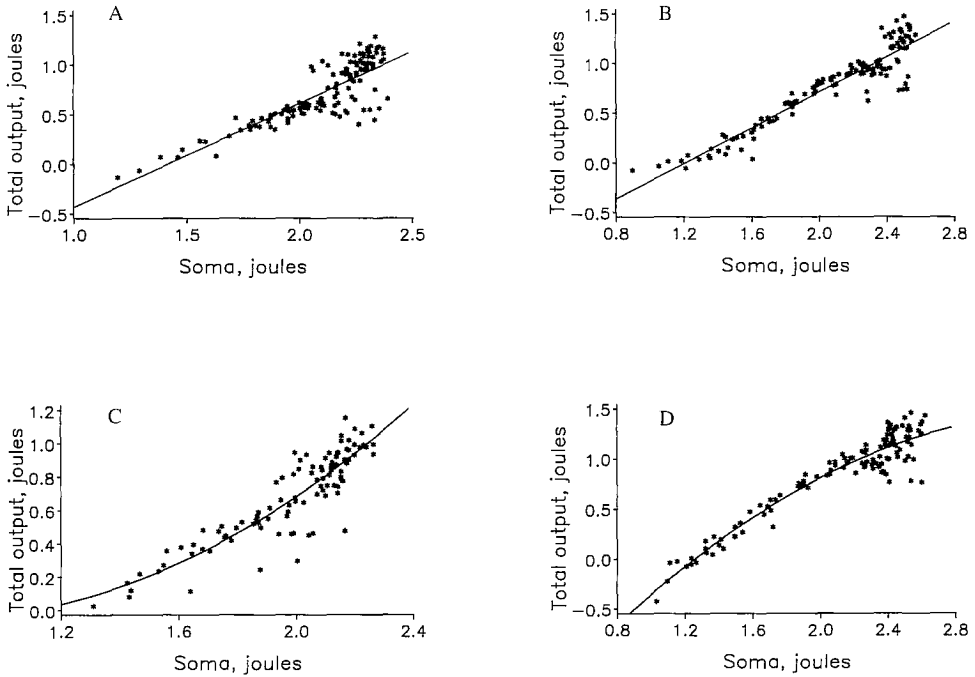


Fig. 3: Total energy output ( $P_g + P_r + R$ ) in joules per day related to body size in joules for *Lacuna pallidula* at 5 °C (A) and 10 °C (B), and *L. vincta* at 5 °C (C) and 10 °C (D).

the case of *L. pallidula* the curve fitted to the data is somewhat different from that calculated for the data for normally mated animals (Fig. 2B). Unmated females started spawning infertile eggs at an average soma size of 233.2 J, with an average first spawn size of 30.6 J. This is slightly less than the average soma size of 241.1 J at which normally mated females spawned at 10 °C, with an average first spawn size of 49.4 J. The soma sizes at first spawning in the two groups ( $n = 8$  in each) are not significantly different - Mann-Whitney  $U = 24$ ,  $P = 0.441$  (two tailed test). However the spawn sizes at first spawning in the two groups are different - Mann-Whitney  $U = 10$ ,  $P = 0.021$  (two tailed test). We may conclude that the *L. pallidula* females denied mates spawned at the normal body size but produced relatively small amounts of infertile spawn.

*L. vincta* behaved differently. The growth curve for these four animals (Fig. 4B) was markedly different from that of animals growing with access to males, and no infertile spawn was produced. In the case of males the growth curve for normally mated males (Fig. 5A) was different from that for females, showing slower growth later in life. It is very clear from the graph that the quadratic model is a poor fit to the data. Males growing



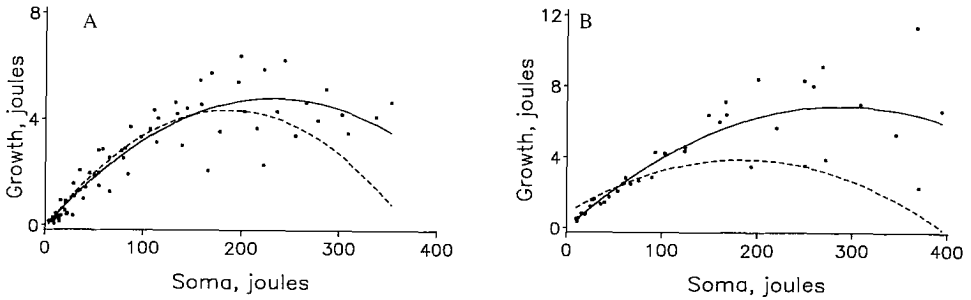


Fig. 4 Growth as joules per day related to body size in joules for female *Lacuna pallidula* (A) and *L. vincta* (B) denied access to males. In each case a growth curve has been fitted using a quadratic equation for these data (solid lines) and the data for females able to mate normally (broken lines).

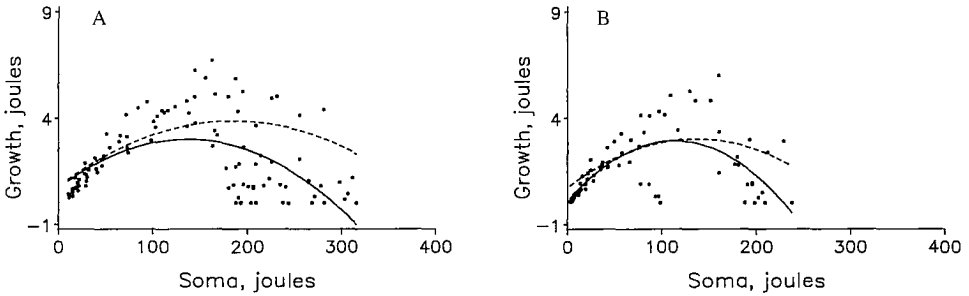


Fig. 5 Growth as joules per day related to body size in joules for male *Lacuna vincta* able to mate normally (A) and denied access to females (B). The solid line curves are quadratic equation fits to the data in the graph in each case, in (A) the broken line is for growth of mating female *L. vincta*, in (B) the broken line is for growth of mating male *L. vincta*.

without females with which to mate grew (if anything) even less rapidly in late life (Fig. 5B). In *L. pallidula* the male is markedly smaller than the female and by the time these snails were brought into the laboratory their growth was nearly complete, therefore comparable observations were not made for this species. *L. pallidula* represents a more extreme manifestation of the dimorphism apparent in *L. vincta* (Fig. 5B).

#### DISCUSSION

The amount of laboratory plant used to keep even these numbers of spawning pairs of snails was considerable, limiting the size of experimental design. Therefore of necessity the sample sizes used for these experiments were small, but very similar to those given by Havenhand & Todd (1989) for their work on nudibranchs. Fig. 2 shows a continuity of

organic production through the life of females. Early in life this production is devoted solely to growth, later to further slow growth but mainly to reproduction. At 10 °C, some time during the onset of sexual maturity, respiratory demand stops increasing with further increase in body size. Although a quadratic equation was used for predictive purposes in the case of *L. pallidula* at 5 °C, the relationship should not be taken to be non-linear in view of the very large value of  $P$  for the quadratic term (Table II). The phenomenon of a reduction in metabolic demand in maturity has often been observed (e.g. Zeuthen, 1953 ; Epp & Lewis, 1980 ; Calow, 1983) but has been relatively little discussed. It implies a greater efficiency of  $P_r$  than  $P_g$ , achieved in part by decreasing respiratory demand in sexual maturity.

The allometric relation between summed energy output ( $P_r + P_g + R$ ) and body size over the whole range of observations was significantly greater than 0.75 for both species, and in some instances indistinguishable from 1.0 (Table III). For *Lacuna vincta* this relationship was apparently non-linear, the slope increasing with body size at 5 °C and decreasing with body size at 10 °C. There was no good evidence of non-linearity of total energy output in *L. pallidula*, although at 5 °C inclusion of (body size<sup>2</sup>) resulted in a sum of squares term significant at  $P = 0.1090$ . When non-linear models were used in the case of the logarithmic regression of ( $P_g + P_r$ ) on soma, both species showed an increase in the slope of production on size at 5 °C but not at 10 °C.

Taken together, these observations indicate that at 5 °C rate of production (joules per unit of body) shows a tendency to increase with size (i.e. it is positively allometric), probably related to the change from growth to spawning. Thus, there is a tendency for production ( $P_g + P_r$ ) to be at a greater efficiency during the reproductive than the growth phase both because of a reduction in respiration (*L. pallidula*) and a relative increase in production (both species). In *Lacuna pallidula* the decrease in respiration rate largely cancels this out so that the total energy flux is linearly related to size in this species, with a slope of 1.043 (apparently isometric). A prominent feature is the sustained and sometimes increasing production throughout life, also noted by Havenhand & Todd (1988b) for the nudibranch molluscs *Adalaria proxima* and *Onchidoris muricata*.

At 10 °C production rate remains linear with a slope of  $< 0.75$  in both species (negative allometry), i.e. there is no longer evidence of increase in relative production with size. For total energy flow rate *L. vincta* shows evidence of a decrease with increase in size - this no doubt reflects the pronounced decrease in respiration rate with size in this species (Fig. 1). Thus, the precise natures of the curves of production and respiration through life seem to be temperature-dependent in *Lacuna*. Direct comparison with the situation in nudibranchs is difficult since the experiments of Havenhand & Todd (1988a, b) were carried out at temperatures that fluctuated according to those of the sea at the time of the work. It does not seem likely that 10 °C placed an undue physiological strain on *Lacuna* in the experiments reported above, since such temperatures (and greater) are regularly encountered in the field during times when the animals are growing (autumn) and spawning (late spring) (see Bowman, 1985).

The expectation of an exponent of  $\approx 0.75$  is implicit in much of the literature on these sorts of relationships (Peters, 1983 ; Bayne & Newell, 1983) ; it is apparent that is not always met here. Reiss (1987) contends that where a female reproduces several times over a range of body weights (as happens with *Lacuna*) the energy devoted to reproduction would be expected to scale with an exponent greater than 0.8 (the expected upper limit for species where weight increase in the reproductive phase is small). This is true for *Lacuna*, where there is evidence that the relationship has an exponent of  $\approx 1$  (Table IIIB), very close to the value suggested by Reiss (1987) based on studies of fish. Moreover, a major component of energy flow ( $R$ ) is markedly non-linearly related to size at 10 °C ; production is non-linearly related to size at 5 °C. Rather than there being simple linear relationships, we find complex ontogenetic changes in the levels of output to various functions.

The responses of snails of the two species, when denied mates, differed considerably (Figs 4, 5). In *Lacuna pallidula* females reduced their growth rate in the normal fashion and produced small batches of infertile spawn, commencing to do so at about the appropriate body size. In *L. vincta* growth rate of unmated females continued to be high, though showing some decrease after maturity was reached. No infertile spawn was produced. Of the two species, *L. vincta* was the more "active" in every sense, with higher respiration (Grahame, 1982) and higher exponents in the production : mass allometric relationships (this paper). An analysis of longevity has not been carried out, but there was no indication from the laboratory cultures that *L. vincta* is any less long-lived than *L. pallidula* - if anything, to the contrary (Grahame, 1977). Here there seems to be an absence of trade-off between life history variables, although the comparison is interspecific.

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