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Energetics of mucus production in the common whelk *Buccinum undatum* L.

Ahmet E. Kideys and Richard G. Hartnoll

Port Erin Marine Laboratory, University of Liverpool, Isle of Man, UK

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Abstract: Pedal and hypobranchial mucus production of the common whelk *Buccinum undatum* L. were measured at three different temperatures (8.2, 10.5 and 15 °C). Pedal mucus production at 8.2 °C was significantly lower from that at 10.5 °C, but similar to that at 15 °C. In contrast hypobranchial mucus production at 8.2 °C was significantly higher than that at 10.5 °C but again similar to that at 15 °C. At all temperatures whelks produced more hypobranchial than pedal mucus. Food consumption was measured, and from this it was determined that $\approx 27.5\%$ of the total energy intake appeared as mucus production (pedal + hypobranchial). Other studies on gastropod mucus energetics are reviewed, and possible sources of error in the determination of mucus energetics are discussed.

Key words: *Buccinum*; Energetics; Gastropod; Mucus; Temperature

INTRODUCTION

The energy consumed by a gastropod is partitioned in various ways, summarised by the equation:

$$C = P_g + P_r + R + F + U + M,$$

where C = consumption, P_g = somatic growth, P_r = reproductive investment, R = respiration, F = faeces (including faecal mucus which is used in compacting faeces), U = excretion, and M = hypobranchial and pedal mucus (after Branch, 1981). The last of these, mucus production, has been largely ignored in energy studies (Hughes, 1970, 1971; Huebner & Edwards, 1981; Davis & Wilson, 1985).

Investigations have shown that molluscan mucus is a protein-carbohydrate complex (Hunt, 1970; Grenon & Walker, 1980). In gastropods, hypobranchial and pedal mucus serve many purposes, including locomotion (Denny, 1980a,b), adhesion (Grenon & Walker, 1980), location of home position (Cook et al., 1969; Cook, 1971; McFarlane, 1980), a medium for microbial growth (Calow, 1974; Connor, 1986; Herndl & Peduzzi, 1989), reduction of desiccation when animals are exposed to air (Grenon & Walker, 1980), removal of sediment and faeces from the pallial space (Hunt, 1970; Peck et al., 1987), reproduction (Rollo & Wellington, 1977), reduction of exposure to environmental

Correspondence address: A. E. Kideys, Port Erin Marine Laboratory, Isle of Man, UK.

stress (Denny, 1983), as offensive or defensive agents (Branch, 1981), and in home scar formation (Lindberg & Dwyer, 1983). The existence of mucopolysaccharides in the shell composition indicates that mucus might also play a part in shell formation (Barnes, 1987). Thus, it is hardly surprising that in recent studies mucus production has been suggested as a major energy drain in molluscs (Edwards & Welsh, 1982; Horn, 1986; Peck et al., 1987; Davies et al., 1990).

In general, metabolic functions such as respiration, feeding, growth and reproduction in marine poikilotherms are temperature-dependent (Prosser, 1950; Connell, 1974). For any accurate energy budget determination, temperature-dependent changes in metabolic activities must therefore be taken into account, but there has been no study of the influence of temperature upon mucus production in aquatic gastropods. This study attempts to fill that gap by investigating mucus production in the common whelk *Buccinum undatum* L., which is a predator with a tendency for opportunistic feeding on carrion (Fretter & Graham, 1962). It is widely distributed in the North Atlantic from low water mark to depths > 1000 m (Nielsen, 1975).

We have investigated the effect of temperature on the hypobranchial (all slimy secretions from the pallial space) and pedal (mucus secreted from the foot which is in contact with the substratum during crawling) mucus production. The energy invested in mucus has been assessed in relation to the overall energy intake of *B. undatum*, and the results compared to those in the literature for other aquatic gastropods.

MATERIALS AND METHODS

B. undatum was collected by traps in December 1989 and April 1990 from a population off Douglas, southeast of the Isle of Man. Mucus production was measured at three different temperatures, at 8.2 °C using the April 1990 sample, and at 10.5 °C and 15 °C using the December 1989 sample. All specimens were acclimated at the appropriate experimental temperature for ≈ 15 days. The experimental temperatures approximate to the minimum, average and maximum seasonal bottom seawater temperatures in the areas where these animals occur around the Isle of Man (Slinn & Eastham, 1984). Animals were maintained on a diet of queen scallops *Chlamys opercularis* prior to the experiments. All shell surfaces were gently scraped clean of a few sedentary organisms (e.g., tube worms, barnacles, etc.) at the start of acclimation. Three whelks from six representative size groups (30–39, 40–49, 50–59, 60–69, 70–79 and 80–90 mm shell length) were selected. Each group of three was carefully transferred to a rectangular glass tank (≈ 7 l) filled with filtered (1- μ m) seawater (34‰). Whelks withdrew into their shells on removal from stock tanks to experimental tanks, but after a variable period resumed pedal activity. The start of this active period was recorded for each individual. Sometimes whelks remained inactive for the duration of the experimental period. In a few cases whelks produced totally aberrant amounts of hypobranchial mucus which

completely covered the animal. This was presumably a severe stress reaction, and these animals were not included in the analysis.

Experiments were terminated after 20–30 min, depending upon when activity had commenced. After removal of the animals, the seawater in each tank was filtered through a preweighed glass-fibre filter (GF/C, Whatman) to retain the hypobranchial (suspended) mucus. If any defaecation had occurred during the experiment, the faeces were removed before filtration. Each tank was rinsed with distilled water to remove seawater and this rinsing water was also passed through the filter. There was no obvious detachment of pedal mucus during rinsing (see Discussion). Each filter was washed twice with distilled water and reweighed after drying at 60 °C for 48 h. After rinsing the pedal mucus adhering to the inner wall of the tank was scraped off with a razor onto a preweighed watch glass. After scraping the glass surface no longer felt slippery. The watch glass was dried at 60 °C for 48 h, then reweighed to determine the dry weight of pedal mucus. For each experiment two controls without animals were run to determine whether any weight increase occurred during either filtration or scraping. The entire experiment was repeated three times.

A portion of dried hypobranchial mucus obtained from several whelks was analysed for its energy content using a Phillipson microbomb calorimeter calibrated against benzoic acid (Phillipson, 1964). Initially the dried mucus pellet did not burn well (probably because of its high inorganic content), so it was ignited together with a known amount of benzoic acid. A second portion of hypobranchial mucus was divided into three, rinsed with distilled water on a GF/C filter, and ashed at 550 °C for 5 h to determine its ash-free dry weight.

The consumption rate of *B. undatum* at 10.5 °C was determined in November 1989. 12 whelks from six representative size groups (30–39, 40–49, 50–59, 60–69, 70–79 and ≥ 80 mm shell length) were selected. Each group of 12 were allowed to feed on preweighed dogfish *Scyliorhinus canicula* flesh (of which the energy content was measured calorimetrically) for 24 h in a rectangular plastic tank (≈ 15 l) with flowing seawater. At the end of this period the remaining dogfish flesh was weighed, the difference from the initial weight giving the consumption. Some dogfish flesh was kept under the same conditions in whelk-free tanks to determine whether any change in weight of the flesh occurred.

At the end of each experiment the shell length of each individual was measured with vernier calipers to the nearest 0.1 mm. The complete animal, lightly blotted dry, was first weighed, and the tissue then removed from the shell after breaking it in a vice. The soft tissues (with the operculum) were placed in a weighed Al foil dish and dried in an oven at 100 °C until constant weight. The ash content was obtained by incinerating the dry samples in a muffle furnace at 550 °C for 4–6 h.

Regression analysis and ANCOVA of the data were carried out. Comparisons of slopes and intercepts of the regression equations were made according to the methods given by Zar (1984).

TABLE I

B. undatum: mucus production averaged for three replicates each of three animals. Values are given as mg dry mucus \cdot animal $^{-1} \cdot$ active h $^{-1}$ and in parentheses as weight-specific mucus production, mg dry mucus \cdot g $^{-1}$ dry animal wt \cdot active h $^{-1}$.

T (°C)	Mucus type								
	Pedal			Hypobranchial			Total		
	8.2	10.5	15.0	8.2	10.5	15.0	8.2	10.5	15.0
Size (mm)									
30-40	1.2 (2.5)	1.4 (2.0)	1.8 (2.6)	11.8 (24.6)	2.1 (3.0)	7.5 (10.9)	13.0 (27.1)	3.5 (5.1)	9.3 (13.5)
40-50	1.2 (0.8)	2.6 (1.5)	1.2 (0.7)	6.3 (4.4)	2.0 (1.2)	5.0 (3.0)	7.5 (5.2)	4.6 (2.7)	6.2 (3.7)
50-60	0.7 (0.3)	1.3 (0.6)	2.6 (1.2)	9.5 (4.5)	2.9 (1.3)	10.4 (4.8)	10.2 (4.8)	4.2 (1.9)	13.0 (6.0)
60-70	1.9 (0.5)	7.8 (1.6)	2.2 (0.4)	11.0 (2.8)	16.3 (3.2)	9.9 (2.0)	12.9 (3.3)	24.1 (4.8)	12.1 (2.4)
70-80	2.3 (0.2)	6.9 (1.0)	3.7 (0.6)	12.0 (1.7)	9.1 (1.4)	10.6 (1.6)	14.3 (2.0)	16.0 (2.4)	14.3 (2.1)
>80	1.8 (0.2)	12.3 (1.3)	6.9 (0.7)	14.8 (1.8)	14.0 (1.4)	55.1 (5.6)	16.6 (2.0)	26.3 (2.7)	62.0 (6.3)
\bar{x}	1.5 (0.8)	5.4 (1.3)	3.1 (1.0)	10.9 (6.6)	7.7 (1.9)	16.4 (4.6)	12.4 (7.4)	13.1 (3.2)	19.5 (5.6)

RESULTS

MUCUS PRODUCTION

The mean values for mucus production (mg dry wt mucus \cdot h $^{-1}$) at the three experimental temperatures are presented in Table I both as production per animal, and as weight specific production. At every temperature substantially more hypobranchial than pedal mucus was produced — the overall mean values for all size classes are, respec

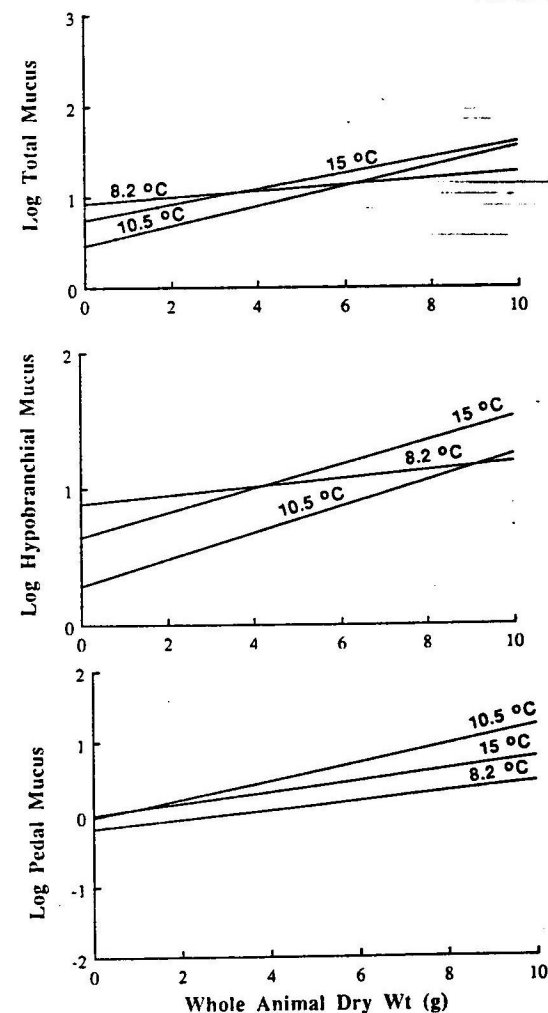


Fig. 1. *B. undatum*: logarithmic mucus production (mg dry wt \cdot h $^{-1}$) plotted against flesh dry wt (regression equations given in Table II).

TABLE II

B. undatum: equations for logarithmic and semilogarithmic linear regressions of mucus production (mg dry wt \cdot h⁻¹) on animal dry wt (g) (30–90 mm in length).

T (°C)	df	Mucus type	Log mucus on animal dry wt			Log mucus on log animal dry wt		
			Equation	S _y (slope)	P _F test	Equation	S _y (slope)	P _F test
8.2	17	Hypobranchial	Log M = 0.880 + 0.031 DW	0.013	0.032	Log M = 0.932 + 0.164 log DW	0.096	0.107
8.2	16	Pedal	Log M = -0.207 + 0.063 DW	0.030	0.055	Log M = -0.153 + 0.439 log DW	0.222	0.074
8.2	16	Total	Log M = 0.923 + 0.034 DW	0.013	0.021	Log M = 0.971 + 0.195 log DW	0.102	0.074
10.5	16	Hypobranchial	Log M = 0.277 + 0.096 DW	0.023	<0.001	Log M = 0.259 + 0.868 log DW	0.179	<0.001
10.5	16	Pedal	Log M = -0.063 + 0.128 DW	0.027	<0.001	Log M = -0.065 + 1.116 log DW	0.225	<0.001
10.5	17	Total	Log M = 0.457 + 0.110 DW	0.019	<0.001	Log M = 0.492 + 0.906 log DW	0.152	<0.001
15.0	17	Hypobranchial	Log M = 0.629 + 0.094 DW	0.021	<0.001	Log M = 0.719 + 0.660 log DW	0.200	0.004
15.0	17	Pedal	Log M = -0.150 + 0.090 DW	0.031	0.011	Log M = 0.050 + 0.670 log DW	0.266	0.022
15.0	17	Total	Log M = 0.741 + 0.092 DW	0.021	<0.001	Log M = 0.825 + 0.652 log DW	0.194	0.004

Following are significantly different in semilogarithmic regressions:

Pedal mucus : slope 8.2 vs. 10.5 °C ($p < 0.01$).

Hypobranchial mucus : slope 8.2 vs. 10.5 °C ($p < 0.01$); elevation 10.5 vs. 15 °C ($p < 0.025$).

Total mucus : slope 8.2 vs. 10.5 °C ($p < 0.005$).

TABLE III

Calorimetrically determined energy values and composition of mucus in various aquatic gastropods (sample sizes in parentheses).

	Type of mucus	% water content	% AFDW of dry wt	Energy content (J \cdot mg ⁻¹) per		
				Dry wt	AFDW	
<i>Buccinum undatum</i>	Hypobranchial	99.7*	42.1 (3)	8.8 (2)	20.8 (2)	Present study
<i>Patella vulgata</i> (large)	Pedal	91.9 (88)	50.7 (65)	9.7 (53)	19.2 (53)	Davies et al. (1991)
<i>Patella vulgata</i> (small)	Pedal	91.6 (77)	52.4 (53)	10.8 (47)	20.7 (47)	Davies et al. (1991)
<i>Patella vulgata</i>	Pedal	90.1	68.1	-	-	Grenon & Walker (1980)
<i>Lottia gigantea</i>	Pedal	93.5 (5)	57.0 (3)	-	-	Connor (1986)
<i>Collisella scabra</i>	Pedal	89.3 (3)	53.0 (3)	-	-	Connor (1986)
<i>Collisella digitalis</i>	Pedal	90.6 (3)	55.0 (3)	-	-	Connor (1986)
<i>Nucella emarginata</i>	Pedal	81.4 (3)	24.3 (3)	-	-	Connor (1986)
<i>Haliotis tuberculata</i>	Pedal	-	-	22.8 (10)	-	Peck et al. (1987)
<i>Lymnaea stagnalis</i> **	Pedal	-	-	24.0 (1)	-	Calow (1974)

* From Hunt (1970). ** Freshwater gastropod.

tively, 11.7 and 3.3 mg dry wt mucus \cdot animal $^{-1} \cdot$ h $^{-1}$, and 3.8 and 1.0 mg dry wt mucus \cdot g $^{-1}$ dry animal wt \cdot h $^{-1}$. Total mucus production per animal increased with temperature — averaging 12.4 mg \cdot h $^{-1}$ at 8.2 °C, 13.1 mg \cdot h $^{-1}$ at 10.5 °C, and 19.5 mg \cdot h $^{-1}$ at 15 °C. However, taken independently, neither pedal nor hypobranchial mucus showed consistent temperature responses.

Table I indicates that at each temperature mucus production tends to increase with animal size, though in a less than consistent fashion. At each temperature the generally better correlations were obtained when log mucus production was plotted against flesh dry weight (Fig. 1), as opposed to a double logarithmic plot (Table II). The correlation was appreciably poorer at the lowest temperature than at the upper two indicating smaller effect of animal size on the mucus production at 8.2 °C (slopes were significantly different only at 90% confidence interval; regression analysis). ANCOVA (Zar, 1984) demonstrated that temperature had a significant effect on the slope of production for hypobranchial and total mucus, but not for pedal mucus (Table II). However, there was a significant effect of temperature on the elevation of the regression for pedal mucus. Multiple range tests indicated that the effects were predominantly due to differences between production at 8.2 and 10.5 °C.

ENERGY VALUES

Calorimetrically determined energy values for mucus from the hypobranchial gland of *B. undatum* are given in Table III, which also shows that organic matter (AFDW) made up only 42% of the total dry weight of this mucus. Consequently energy values based on dry weight and AFDW were very different at 8.8 and 20.8 J \cdot mg $^{-1}$, respectively. The energy value of the dogfish flesh used in the feeding experiments was also determined calorimetrically as 19.80 (SE = 0.66, $n = 3$) J \cdot mg $^{-1}$ dry wt.

An attempt was made to determine the importance of mucus in the individual energy budget. The total food consumption (in the presence of excess food) of different size groups of whelks was determined (Table IV). The regression of food consumption on

TABLE IV

B. undatum: consumption rate at 10.5 °C (log $C = 0.763 + 0.637 \log$ dry wt; $df = 5$, S_y (slope) 0.139, $P_{Ftest} < 0.02$).

Mean animal dry wt (g)	Food consumed (mg dry wt \cdot h $^{-1}$)
0.50	2.75
1.37	11.17
3.39	11.42
5.31	19.17
7.08	23.75
9.31	16.83

Consumption corrected for weight change of control dogfish flesh.

animal weight obtained from these data, and the regression equations of mucus production (Table II), were together used to estimate the importance of hypobranchial, pedal and total mucus production in the energy budget (Table V). The energy allocated to mucus (pedal + hypobranchial) was almost 30% of the total energy uptake. Energy loss via hypobranchial mucus secretions was appreciably higher than that of pedal mucus in all size groups (Table V).

TABLE V

B. undatum: estimated percentage of total energy intake at 10.5 °C invested in mucus by various sizes (shell length 30–90 mm) of whelk. Based on equations for mucus production in Table II and for food consumption in Table IV.

Animal dry wt (g)	Mucus type		
	Hypobranchial	Pedal	Total
1	18.1	8.9	27.0
3	14.0	8.0	22.0
5	15.7	10.4	26.1
7	19.7	15.1	34.8
\bar{x}	16.9	10.6	27.5

DISCUSSION

The experiments were subject to two potential errors.

(1) The suspension of pedal mucus adhering to the tank walls, either during the experiment or when rinsing the tanks. During preliminary experiments it was observed that some surfaces (e.g., Al foil) were less efficient than glass surfaces at retaining pedal mucus during rinsing. In order to retain mucus (visible mucus in particular), such containers had to be rinsed less thoroughly than others. This resulted in a heavy inorganic salt layer (from seawater) remaining after drying. In the present work only glass containers were used, so this problem did not arise. However, variable removal of salts might account for the very high correlation between the log mucus production of the ormer *Haliotis tuberculata* and particle size of crawling surface (which was silicon carbide coated crystallizing dishes) in Culley & Sherman's (1985) work, where they used the same washing technique.

In this experiment the glass tanks used were rinsed twice with distilled water, which was then filtered. If any pedal mucus from the glass surfaces was suspended, this should have been retained during filtration and supplemented the hypobranchial and total mucus values. However, Calow (1974) noted that carmine-stained mucus trails of two freshwater gastropods, *Ancylus fluviatilis* and *Planorbis contortus*, retained their integrity for up to 3 days whilst immersed in water, and he concluded that mucus suspension was not a serious problem.

(2) The loss of some hypobranchial (suspended) and/or pedal (adherent) mucus as a result of solution. However, Grenon & Walker (1980), working with the pedal mucus of *Patella vulgata*, concluded that mucus was always insoluble in distilled and seawater. Additionally, Denny (1980a) indicated that mucus possessing a glycoprotein structure formed a gel network and was not readily soluble in water. The GF/C filters used in the present study were highly efficient in retaining hypobranchial mucus. Evidence of this was that hypobranchial mucus often contained minute air bubbles, but none were evident in the GF/C filtrate.

Previously the relationship between mucus production and animal size (generally, dry weight) has been calculated using the logarithms of both. In this study, however, better results were obtained when the logarithm of mucus production was regressed on untransformed animal dry weight. A basis for such a relationship could follow from the importance of mucus for locomotion (Denny, 1980b). Pedal mucus production is assumed to be a function of pedal area (Davies et al., 1991), but a two-fold increase in pedal area would be accompanied by an increase in body mass by a factor of 2.8. This relatively greater increase in body mass could be compensated by producing proportionately more mucus, which may explain the exponential relationship found in this study.

Mean pedal mucus production ranged from 0.8 to 1.3 mg dry mucus \cdot g⁻¹ dry tissue \cdot h⁻¹. These are higher values than those found by Culley & Sherman (1985), 0.01–0.58 mg dry mucus \cdot g⁻¹ dry tissue \cdot h⁻¹, but comparable to those of Peck (1983), 0.04–2.00 mg dry mucus \cdot g⁻¹ dry tissue \cdot h⁻¹ — both for *H. tuberculata*. Culley & Sherman (1985) suggested that the reduction by a factor of 10 of pedal mucus production in *Patella longicosta* (Branch, 1981) compared to *H. tuberculata* was due to lower activity of the former. *B. undatum* was always observed to be very active (from underwater camera, diving and laboratory observations), and so comparable pedal mucus production to *H. tuberculata* might be expected.

The literature provides no direct measurements of hypobranchial mucus production in other gastropods, making interspecific comparisons impossible. In *B. undatum* hypobranchial mucus production was higher than pedal production at all temperatures. This may result partly from the experimental situation, with increased hypobranchial mucus production a result of laboratory stress, and inhibition of movement reducing pedal production. Alternatively higher hypobranchial mucus production in this species might genuinely reflect its importance in removing sediment from the pallial space, as suggested by Hunt (1970). There is the possibility that some of the pedal mucus became detached during rinsing, and was added to the hypobranchial sample, but the earlier discussion suggests that this effect was minimal.

The regression slopes for pedal mucus production on animal dry weight did not differ significantly with temperature, but the elevation at 8.2 °C was significantly lower than at higher temperatures. Low growth rates for this species in lower winter temperatures have been recorded (Hancock, 1963; Santarelli & Gros, 1985), attributed to decreased feeding, and this reduced foraging will involve less pedal mucus secretion. In the present

study it was observed that whelks consumed less food with decreasing temperature (Kideys, unpubl. data).

The pattern of hypobranchial mucus production with size was not consistent at all temperatures — small animals produced considerably more hypobranchial mucus at 8.2 °C than at higher temperatures (Fig. 1). Denny (1983) observed that gastropods were able to produce extra mucus to reduce exposure to environmental stresses, and in the present programme small animals may have been more susceptible to stress than larger ones. However, there is no reason why a temperature of 8.2 °C should be unduly stressful to this species.

The regressions for total mucus production showed little significant effect of temperature on elevation or slope. The total energy allocated to mucus was affected by temperature surprisingly little (Fig. 1), though differential partitioning may occur between pedal and hypobranchial (and possibly faecal) mucus through the year. Davies et al. (1991) suggested a similar variable allocation of assimilated energy between mucus and gonads in *P. vulgata*. The lack of a consistent effect of temperature on mucus production was surprising, suggesting that a complex of factors control production, possibly both environmental and intrinsic.

Confusion may arise from different ways of expressing the calorific value of mucus (per dry weight or AFDW) in the energy budget studies cited. There is a high percentage of ash in the mucus of marine gastropods (Table III), arising from a large content of seawater. The one record for a freshwater gastropod in Table III (Calow, 1974) gives a high calorific value per dry weight compared to marine species, but this is to be expected because of the low salt content of freshwater compared to seawater. The value per dry weight for the pedal mucus of *Halotis* (Peck et al., 1987) is much higher than for other marine species, but in the absence of data on the chemical composition this cannot be explained.

The limited number of calorimetrically determined energy values for mucus can be supplemented by calculating energy content on the basis of known biochemical composition (Table VI). Several authors have pointed out the difficulties of igniting mucus samples in calorimetry (Davies et al., 1990, 1991; Calow, 1974; Horn, 1986). The range of energy values is wide when expressed in dry wt (4.9–12.3 J \cdot mg⁻¹), but less variable in AFDW (18.3–23.2 J \cdot mg⁻¹). The range of calorific values of mucus lies between the mean calorific values of carbohydrate and protein [17.2 and 23.7 J \cdot mg⁻¹, respectively (Crisp, 1984)], the main constituents of mucus (Table VI). For purposes of comparison the energy value of mucus is best expressed in AFDW. The big difference between this value, and that per dry weight, must be taken into account or serious errors in energy budget computation will result. Thus Horn (1986) used Calow's mucus energy value based on dry wt in a freshwater gastropod for an intertidal polyplacophoran, *Chiton pelliserpentis*, and suggested that 66–74% of the assimilated energy was lost as mucus. However, if Davies et al.'s (1991) energy values (based on dry wt) are used (which was for an intertidal species), this loss would decrease to 30–33% of the assimilated energy.

The importance of mucus in energy budget studies has often been neglected (for

TABLE VI

Energy value of mucus calculated from chemical composition. Energy values taken as: protein, 23.7 J · mg⁻¹; lipid, 39.6 J · mg⁻¹; carbohydrate, 17.2 J · mg⁻¹ (from Crisp, 1984). Sample sizes in parentheses.

	Percentage of dry wt				Energy (J · mg ⁻¹) per		
	Ash	Protein**	Carbohydrate	Lipids*	Dry wt	AFDW	
<i>Patella vulgata</i> (large)	49.3 (65)	31.7 (39)	14.4 (39)	4.6*	11.8	23.2	Davies et al. (1991)
<i>Patella vulgata</i> (small)	47.6 (53)	32.5 (39)	18.8 (39)	1.1*	11.4	21.7	Davies et al. (1991)
<i>Lotia gigantea</i>	43.0 (3)	37.9 (3)	18.4 (3)	0.3	12.3	21.6	Connor (1986)
<i>Collisella scabra</i>	47.0 (3)	36.7 (3)	17.1 (3)	0.4	11.8	22.0	Connor (1986)
<i>Collisella digitalis</i> ***	45.0 (3)	29.9 (3)	8.1 (3)	0.8	8.8	19.0	Connor (1986)
<i>Nucella emarginata</i>	75.7 (3)	1.8 (3)	25.4 (3)	0.2	4.9	18.3	Connor (1986)

* Balance assumed to be lipids. ** Including free amino acids. *** Values as in Connor (1986); not explained why total so far from 100%.

review, see Davies et al., 1990), or consideration has been restricted to pedal (and rarely faecal) mucus, ignoring hypobranchial mucus (Paine, 1965; Calow, 1974; Edwards & Welsh, 1982; Peck et al., 1987; Davies et al., 1990). Estimates of energy investment in mucus are given in Table VII in which there seems a good correlation between pedal mucus production and lifestyle of gastropods. However, it is possible that some of these recent studies have overestimated this investment, as discussed above. Nevertheless, most of these values are <10% of the ingested energy. Exceptions are pedal mucus production of *H. tuberculata* (23–29% of energy intake) by Peck et al. (1987), though

TABLE VII

Percentage of total energy intake invested in mucus in various gastropods.

	Type of mucus	Percentage of ingested energy	
<i>Ilyanassa obsoleta</i>	Pedal	22.7	Edwards & Welsh (1982)
<i>Ilyanassa obsoleta</i>	Faecal	7.9	Edwards & Welsh (1982)
<i>Hydrobia ventrosa</i>	Pedal + faecal	9.0*	Kofoed (1975)
<i>Navanax inermis</i>	Pedal	7.0	Paine (1965)
<i>Ancylus fluviatilis</i>	Pedal	9.0	Calow (1974)
<i>Ancylus fluviatilis</i>	Faecal	4.0–6.0	Calow (1974)
<i>Haliotis tuberculata</i>	Pedal	23.3–29.1	Peck et al. (1987)
<i>Patella vulgata</i>	Pedal	23.0	Davies et al. (1990)
<i>Buccinum undatum</i>	Pedal	10.6	This study
<i>Buccinum undatum</i>	Hypobranchial	16.9	This study
<i>Buccinum undatum</i>	Total	27.5	This study

* Percentage of assimilated energy.

their calorific value for mucus was unusually high (22.8 J · mg⁻¹ dry mucus), and in *P. vulgata* (23% of energy intake) by Davies et al. (1990). Branch (1981), however, was unable to obtain measurable amounts of mucus from the trails of moving *Patella* spp. and surmised that relatively little energy was spent on mucus secretion during locomotion. Perhaps the method used (whereby the foot of *P. vulgata* was scraped of mucus) by Davies et al. (1990) induced the high values of energy loss reported in their study. Wright & Hartnoll (1981), working on the same population, suggested that 4% of the ingested energy was spent on mucus production, but only by analogy with studies on other species. It is not, however, surprising to find high values for pedal mucus production (22.7% of the ingested energy) for the deposit-feeding gastropod *Ilyanassa obsoleta* (Edwards & Welsh, 1982), since some of the energy lost in this way could be regained during feeding (probably after enrichment of mucus with microorganisms). Generally conclusions drawn from such budgets should at present be regarded with caution. The production of much less pedal (≈10%) than hypobranchial (≈17%) mucus by *B. undatum* is an adaptive feature for a subtidal carnivorous species. This reduces pedal mucus losses, and there is no possibility of regaining the energy lost in this way in contrast to deposit feeders and omnivores which may reingest it. The increased hypobranchial mucus production keeps the pallial space clear of sediment. Additionally the gastropods with operculae which close up on disturbance would need less pedal mucus for defensive purposes than clamping limpet forms. In this study the energy losses via total mucus secretion by *B. undatum* were ≈27.5% of the estimated energy intake, probably more taking into account mucus loss during faecal compaction. In the field when food supplies might be limiting mucus production could require a larger percentage of the intake. Expressed as a percentage of assimilated energy the value would be even greater, so mucus is certainly a major component of energy utilisation.

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