

The Feeding Strategies of Two Freshwater Gastropods, *Ancylus fluviatilis* Müll. and *Planorbis contortus* Linn. (Pulmonata), in Terms of Ingestion Rates and Absorption Efficiencies

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Summary. Radiotracer and gravimetric techniques were used to investigate the effects of starvation, temperature, body size and food quality on both the ingestion rates and absorption efficiencies of *A. fluviatilis* (an algal grazer) and *P. contortus* (a detritivore which utilises the bacterial fraction of its food). In the face of food supply disturbance snails showed a considerable potential for adaptation. Both ingestion rates and absorption efficiencies increased with starvation, and ingestion rate increased with reductions in food quality. Absorption efficiencies were independent of temperature and Q_{10} values for absorption rates suggested that snails showed some acclimation to temperature disturbance. Food absorption was linearly related to body surface area but absorption efficiencies were to a large extent independent of age and size.

The above homeostases are discussed in terms of their contribution to fitness and also in terms of the possible underlying causal mechanisms. The implications of physiological homeostases for ecological efficiencies are also discussed.

Introduction

Survival and reproduction both require energy. Therefore fitness is dependent on energy intake and because food is generally limiting selection should favour maximum efficiency in feeding. Emlen (1973) has pointed to 3 avenues along which this process may occur, viz.:

1. increased ability to recognise food needs and to feed or cease feeding in response to some optimal (with respect to fitness) strategy,
2. increased ability to choose the best foods,
3. increased ability to locate, acquire and ingest foods.

However, this schedule emphasises the behavioural aspects of consumption and ignores the possibility of physiological adaptation. Thus, avenue 1 as well as focusing attention on, a) ingestion, could also be construed to incorporate, b) digestive and absorptive adjustments, c) defaecatory adjustments, and d) adjustments in the apportionment of absorbed energy between respiration, reproduction and growth. Whereas the behavioural strategies aim at long term solutions to given feeding problems the physiological strategies provide immediate but temporary solutions in that they are strictly limited by the amount of food eaten at any given time.

This paper examines feeding strategies in terms of 1a and 1b above for 2 species of freshwater snails, *Ancylus fluviatilis* Müll. and *Planorbis contortus* Linn. Food selection (2) by these species has been dealt with in previous publications and these investigations have shown that *A. fluviatilis* is a herbivore which ingests periphytic algae and prefers diatoms (Calow, 1973a) whereas *P. contortus* is a detritivore which appears able to make use of the bacterial fraction of its food (Calow, 1974a). Consequently, observations on these 2 related species provide an opportunity to compare feeding strategies in two different trophic groups. Throughout the text absorption will be used to describe the passage of digested food across the gut wall, whereas the term absorption efficiency will refer to the extent to which ingested material is absorbed.

The strategies associated with 1c and 3 have been discussed elsewhere (Calow, 1974b, 1975a, respectively) and some general remarks regarding 1d have been made in Calow (1973b)

Materials and Methods

a) Snails

Snails for the study were obtained from a small calcareous lake (Malham Tarn, Yorks., England), where both species are found on submerged rocks in the littoral region. The physico-chemical characteristics of the Tarn, together with associated details on the ecology of populations of *P. contortus* and *A. fluviatilis* have been described elsewhere (Calow, 1972). Unless otherwise stated animals were used within 5 days of collection. Standard, linear, size categories have been employed and these are defined in Table 1 in terms of maximum diameter (MD) for *P. contortus* and aperture length (AL) for *A. fluviatilis* (terminology after Hunter, 1961).

Table 1. Standard size categories (defined in terms of maximum diameter (MD) for *P. contortus* and aperture length (AL) for *A. fluviatilis*) for snails used in the experiments

	<i>P. contortus</i> (MD)	<i>A. fluviatilis</i> (AL)
Spat	0.8 mm	1.0 mm
Small	1.5 mm	2.0 mm
Medium	2.5 mm	4.5 mm
Large	3.5 mm	6.0 mm

b) Estimating Ingestion Rates and Absorption Efficiencies

Materials used as food are listed in Table 2. All algae except *Achnanthes*, both species of bacteria, and the lignin were isolated directly from submerged stones in the littoral region of Malham Tarn (for methods of extraction, and where appropriate, cultivation see respectively: Calow, 1972, 1974a, 1975b). Cultures of *Achnanthes* were supplied by the F. B. A. (Windermere laboratory) and preparation of the cellulose will be discussed below. All algal cultures were 2 weeks old on use whereas bacterial cultures were 1 week old. It was assumed that bacteria and diatomaceous algae contain 12% and 40% ash per unit dry weight respectively (Calow, 1972).

Methods used for estimating ingestion and absorption of the live materials followed those of Calow and Fletcher (1972) and involved the simultaneous use of ^{14}C and ^{51}Cr . More usual gravimetric and indicator methods are not strictly applicable to freshwater pulmonates because it cannot be assumed that all the materials contained within the faeces are derived directly from the food. For example, as much as 20% of the faecal, ash-free dry weight in

Table 2. Materials used in the feeding experiments

For <i>A. fluviatilis</i>	For <i>P. contortus</i>
Bacillarophyceae	Bacteria
<i>Gomphonema</i> ^b	Species D ^a
<i>Achnanthes</i> ^b	Species E ^a
<i>Navicula</i> ^b	Dead organic materials
Chlorophyceae	Lignin
<i>Scenedesmus</i> ^b	Cellulose
<i>Cladophora</i> ^c	
Cyanophyta	
<i>Rivularia</i> ^c	

^a Defined in Calow (1974a); species D is a small Gram positive coccus whereas species E is a small Gram negative rod.

^b Unicellular.

^c Filamentous.

these animals may be mucus and of an excretory nature (Calow, 1975a). However, the applicability of the ¹⁴C-⁵¹Cr technique to both *P. contortus* and *A. fluviatilis* has previously been demonstrated by Calow and Fletcher (*ibid*) and their methods of labelling the food, offering it to snails on membrane filters in polythene chambers (2.5 cm dia.) and sensing labelled samples (G.M. tube for ¹⁴C; crystal scintillator for ⁵¹Cr) have been strictly followed in the present study.

Cellulose was prepared from cultures of the green alga, *Scenedesmus*. Two 500 cm³ cultures were used and were incubated with NaH¹⁴CO₃ (1 μ Ci/10 cm³) for 7 days at 18° C and under natural light conditions. The isotope was initially admitted when cultures were 7 days old. After a further 7 days cultures were filtered (Whatmans No. 1) and the residues were washed 3 times in distilled water. The filter was air dried and the cellulose, extracted according to the technique of Norman and Jenkins (1933)¹, was soaked in distilled water (12 hrs), air dried, and ground down to a fine powder (*ca.* yield 2.5 g; *ca.* specific activity 2000 counts g⁻¹ min⁻¹).

Ingestion and absorption rates of the ¹⁴C-cellulose were measured using a radiotracer technique similar to that used by Hargrave (1970). Suspensions (5 cm³) of finely divided ¹⁴C-cellulose in distilled water (2 g/L) were drawn through membrane filters (2.5 cm dia.; 0.8 μm pore size). These were offered to snails in feeding chambers as above and 3 control chambers were employed each containing food-laden, membrane filters but no snails. The latter were prepared in the same way as the experimental group but were used to estimate the initial weight of the food material added, the non-grazing losses which occurred during the experiment, and the specific activity of the food. After a 6 hr feeding period snails were removed to clean chambers for complete gut emptying. Faeces from the feeding and gut emptying chambers were bulked, dried, and estimated for ¹⁴C counts using an end window G.M. tube (see Calow and Fletcher, *ibid.*). Loss in weight of food on membrane filters (corrected for non-grazing loss, < 5%), estimated from ¹⁴C disintegration rate and specific activities, was assumed to be equivalent to food ingested, and the difference between this value and the cellulose recovered in the faeces (also estimated isotopically) was assumed to be due to absorption.

Ingestion and absorption of lignin was estimated gravimetrically. Suspensions (5 cm³) of finely divided lignin² in distilled water (400 mg lignin/L) were drawn onto membrane filters (2.5 cm dia.; 0.8 μm pore size) and offered to snails in feeding chambers over a 6 hr interval. As with the cellulose estimation, 3 controls were employed for each experiment and weight loss in experimental discs (corrected for non-grazing losses, < 2%) was assumed to be due to ingestion. Fed snails were transferred to clean chambers for complete gut emptying (5 days) and the faecal pellets collected over this time were bulked with those collected from the feeding

1 This yields Cross and Bevans (1911) cellulose.

2 Prepared by acid hydrolysis of natural detritus (Calow, 1975 b).

chambers and digested in conc. HCl (12 hrs). The residues were washed, re-attached to pre-weighed membrane filters (specifications as above), dried (40° C to constant weight) and weighed. The difference between lignin ingested and that recovered in the faeces after acid hydrolysis was assumed equivalent to absorption. Initial starvation of snails was necessary to prevent contamination of "experimental" with "natural" lignin already in the gut, and this manipulation may have resulted in increases in both ingestion and absorption rates (see p. 37).

c) Food Deprivation

The amount of food ingested after a particular starvation interval provides a good index of appetite (Holling, 1966) and has been used for this purpose here. Observations were made on 6 separate groups of 5 snails (medium-sized) for each species. Each group was subjected to a single deprivation interval of either 6, 24, 48, 72, 120 or 144 hrs before being offered labelled food. During starvation snails were individually isolated in aerated, filtered tap water. Faeces were removed frequently to prevent reingestion so that near-absolute deprivation could be assumed. Following this period *A. fluviatilis* was offered ¹⁴C-⁵¹Cr-*Achnanthes* and *P. contortus* ¹⁴C-⁵¹Cr-bacterium D. The food deprivation and feeding procedures were carried out at 10° C.

d) Absorption Efficiencies as Affected by Food Quality, Snail Size, and Environmental Temperature

The food used was as defined in Table 1 but in addition *A. fluviatilis* was tested against bacterium D and *P. contortus* was tested against both *Navicula* and *Scenedesmus*. Most of the experiments were carried out at 10° C using medium-sized snails.

The effect of snail size and temperature on absorption efficiency was investigated in a separate series of experiments; 2 other temperature regimes were used (4 and 18° C) and 3 other size classes of snails (large, small and spat). All individuals, except those tested against lignin, were satiated and acclimated to laboratory conditions by keeping them on stones (density: ca. 4-5 individuals/stone of ca. 60 cm perimeter) for 5 days prior to experimentation. The stones were freshly collected from the field and cultures were held at the relevant temperature in aerated tap water under natural illumination. In contrast, the "lignin group", was starved (see above) for 3 days prior to use. Each experiment involved groups of 10 individuals (or 50 spat) which were treated together in determining absorption efficiencies, and all groups were replicated 3 times.

e) Effect of Lignin on the Ingestion and Digestion of Bacteria by *P. contortus*

Bacteria were obtained from a single culture (250 cm³) of ¹⁴C-⁵¹Cr-bacterium D. Three, 25 cm³ aliquots were transferred into separate, sterile, conical flasks. A further 25 cm³ aliquot was removed, filtered (membrane filters: 0.8 μm dia.), dried and weighed to estimate the approximate concentration of bacteria per unit volume of culture. On this basis sufficient sterilised lignin powder³ was added to the 3 other sub-cultures (held at 4° C to suspend growth) to provide solutions containing 100, 300 and 500% dry weight lignin to dry weight of bacteria. Filtrates of 5 cm³ aliquots of the resultant solutions were fed to snails in the usual manner. Groups of 5 snails (large and starved) were used at each lignin concentration and were allowed to feed over 6 hr intervals. Estimations were also carried out on bacterial filtrates not mixed with lignin.

Two control filters carrying food but not subjected to grazing were used for each solution. These, together with sub-samples from other solutions from the above "parent" culture but containing 100, 50, and 0% dry weight lignin to bacteria enabled investigation of the self-absorption effect due to lignin during G. M. tube measurements. This was found to be negligible (Fig. 1) so that specific activities applicable to the "parent" culture could be used to estimate the weights of bacteria offered (from controls) and subsequently eaten (from experimental discs). Gravimetric measurements on control and experimental discs after feeding allowed an estimation of total food ingested, and ingestion and absorption of the bacterial component were estimated isotopically.

³ See footnote 2 on p. 35.

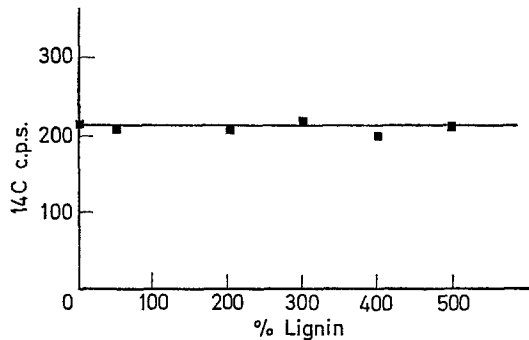


Fig. 1. An estimation of the self-absorption effect of lignin during G. M. tube measurements of ¹⁴C

f) Effect of Snail Size and Environmental Temperature on Rate of Absorption

Ingestion and absorption rates of *P. contortus* and *A. fluviatilis* were measured at 3 different temperatures (4, 10, and 18° C). At least 30 individuals of varying lengths were used in each case. All groups were satiated prior to use and the feeding experiments were carried out over 12 and 6 hr intervals for *A. fluviatilis* and *P. contortus* respectively. Measurements were made in the summer of 1971.

Snail dry weights were estimated from the following equations (see Calow, 1975c):

$$\text{for } A. \textit{fluviatilis} \quad y = 3.0 x - 3.762 \quad (1)$$

$$\text{for } P. \textit{contortus} \quad y = 2.0 x - 2.331 \quad (2)$$

where: $y = \log_{10} (10 \times \text{dry weight in mg})$ and $x = \log_{10} (10 \times \text{length in mm})$. It was assumed that 10% of adult and 20% of spat tissue dry weight was ash (Calow, *ibid*).

Six hr feeding intervals were used for *P. contortus* and 12 hr intervals for *A. fluviatilis*. In both cases the rate of absorption was expressed as μg ash-free dry weight (food) per 12 hrs so that time corrections were only necessary for the former species.

g) Time of Day

Both laboratory and field techniques were used to investigate the possibility of differences in feeding rate with time of day. In the laboratory 2 groups of medium-sized snails were fed ¹⁴C-⁵¹Cr labelled food; one beginning at 12 noon and one at 12 midnight. Pre-treatment of snails and estimation of consumption and absorption was as previously described. *P. contortus* was given bacterium D and *A. fluviatilis*, *Navicula*. Thirty individuals were considered in each group and measurements were made at 10° C under natural light conditions.

In the field, 30 individuals of both species were collected from Malham Tarn in a non-selective fashion at 6 hr intervals over a 24 hr period. These were allowed to defaecate for a 6 hr period into white enamel dishes on the bank. Faecal pellets so obtained were collected and their lengths were measured using an ocular micrometer.

Results

a) Food Deprivation

The effects of varying periods of food deprivation on appetite (ingestion rate) and absorption efficiency are summarised in Figs. 2 and 3 for *A. fluviatilis* and *P. contortus*, respectively. In both species these parameters (and thus absorption rate) increased with starvation time but at a progressively reducing rate. After

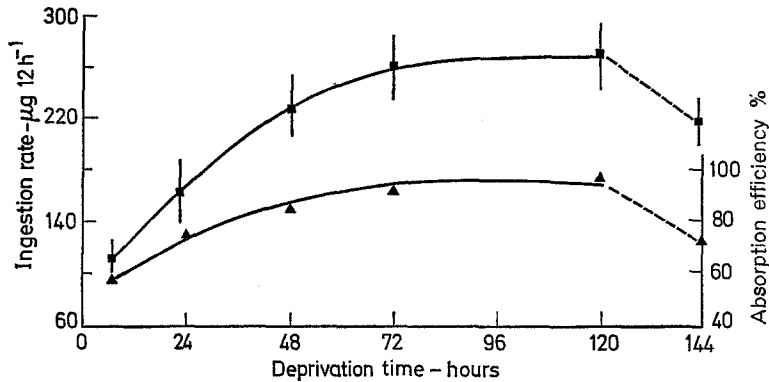


Fig. 2. The effect of food deprivation on the ingestion rate (■) and absorption efficiency (▲) of *A. fluviatilis* fed on *Achnanthes*. Vertical bars represent 95% confidence limits

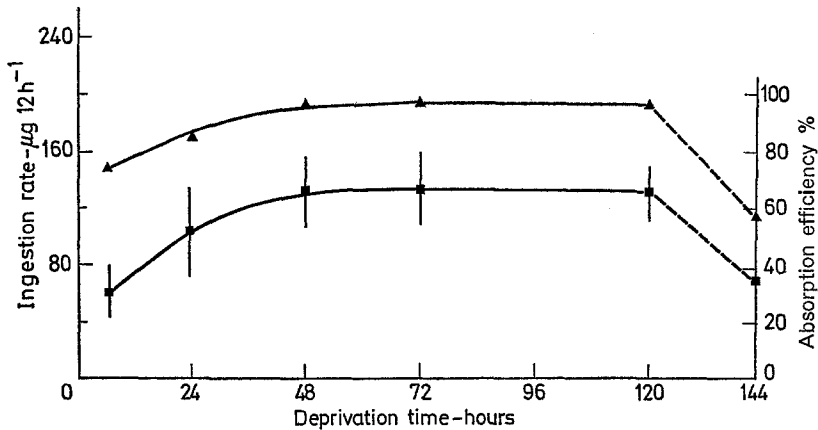


Fig. 3. The effect of food deprivation on the ingestion rate (■) and absorption efficiency (▲) of *P. contortus* fed on bacterium D. Vertical bars represent 95% confidence limits

144 hr starvation, however, both appetite and absorption efficiencies became reduced and this probably reflects the onset of some pathological state.

b) Absorption Efficiencies as Affected by Food Quality, Snail Size, and Environmental Temperature

Table 3 shows the effect of food quality on the absorption efficiencies of *A. fluviatilis* and *P. contortus* respectively. Efficiencies for *A. fluviatilis* ranged from 10–60% ; the higher value being associated with the most preferred food (*i.e.* diatoms; Calow, 1973 a). There was no significant ingestion of bacterium D.

Efficiencies for *P. contortus* ranged from 1–75% and again there was a positive correlation between food preference and assimilation efficiency; the preference sequence of *P. contortus* being: bacterium D > bacterium E > crude, sterile detritus \equiv cellulose + lignin (Calow, 1974 a). However, associations of bacterial

Table 3. The effect of food quality on the absorption efficiencies (AE) of medium sized snails at 10° C

<i>A. fluviatilis</i>		<i>P. contortus</i>	
Food	AE (%) ^a	Food	AE (%) ^a
<i>Achnanthes</i>	60.0 ± 3.4	Bacterium D	76.0 ± 2.9
<i>Navicula</i>	56.3 ± 3.2	Bacterium E	74.8 ± 3.4
<i>Gomphonema</i>	59.5 ± 2.7	Bacteria D & E	75.3 ± 3.5
<i>Scenedemus</i>	13.9 ± 3.6	<i>Navicula</i>	21.3 ^b
<i>Cladophora</i>	10.3 ± 5.0	<i>Scenedesmus</i>	9.0 ^b
<i>Rivularia</i>	10.7 ± 5.0	Lignin	1.0 ^b
Bacterium D	^c	Cellulose	5.3 ^b

^a Confidence limits = $t.s/\sqrt{n}$, where $t = 4.303$ for $2(n-1)$ degrees of freedom at the 95% level.

^b One replicate only.

^c Quantity ingested too small for estimation.

Table 4. The effect of temperature and body size on the absorption efficiency of *A. fluviatilis* fed on *Navicula* and *P. contortus* fed on Bacterium D. Confidence limits represent $t.s./\sqrt{n}$, when $t = 4.303$ for $2(n-1)$ degrees of freedom at the 95% level

Size	Temperature (° C)		
	4	10	18
<i>A. fluviatilis</i>			
Large	—	56.6 ± 5.0	—
Medium	60.0 ± 5.3	56.3 ± 3.2	59.0 ± 4.6
Small	—	55.6 ± 3.9	—
Spat	—	74.7 ± 4.8	—
<i>P. contortus</i>			
Large	—	74.0 ± 3.0	—
Medium	76.3 ± 3.2	76.0 ± 2.9	78.3 ± 2.62
Small	—	76.9 ± 4.0	—
Spat	—	94.0 ± 2.1	—

species (D + E) were not digested any better than when each was offered in isolation (see also Calow, 1974a) and although diatoms and green algae were ingested, digestion was not as efficient as in *A. fluviatilis*.

P. contortus digested the non-living detrital fractions with efficiencies of less than 10%, and Hargrave (1970) has obtained similar values for the benthic amphibod, *Hyalella azteca* Saussure. This result suggests that though *P. contortus* is a detritophage it is only able to make efficient use of the bacterial fraction of its food (see also Calow, 1974a).

Both environmental temperature and snail size appeared to have little effect on absorption efficiency, (Table 4) but the efficiencies of the spat were significantly higher than those of the adults ($P < 0.05$).

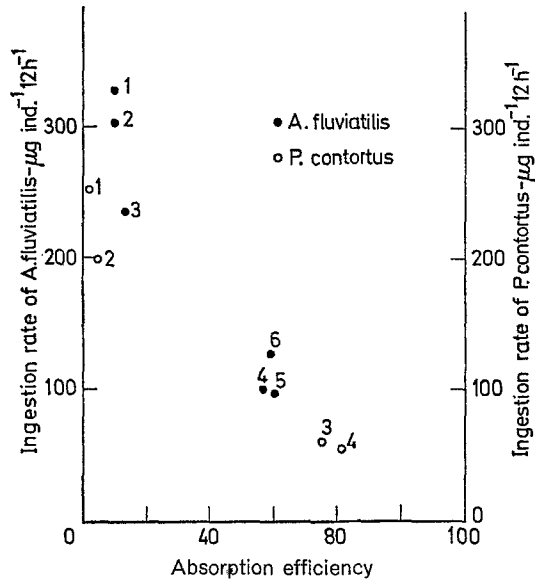


Fig. 4. The relationship between ingestion rate and absorption efficiency in *P. contortus* and *A. fluviatilis* fed on various foods; for *A. fluviatilis*: 1 *Rivularia*, 2 *Cladophora*, 3 *Scenedesmus*, 4 *Navicula*, 5 *Achmanthes*, 6 *Gomphonema*; for *P. contortus*: 1 Lignin, 2 Cellulose, 3 bacterium E, 4 bacterium D

c) Ingestion Rate and Absorption Efficiency

Fig. 4 shows the relationship between ingestion rate and absorption efficiency in medium-sized *P. contortus* and *A. fluviatilis* fed on various types of food (defined in the figure) at 10° C. There was an obvious, though not necessarily linear, negative relationship between these two parameters. This means that snails eat more of the least well digested food materials.

d) Effect of Lignin on the Ingestion and Digestion of Bacteria by *P. contortus*

Results from this series of experiments are summarised in Table 5. Column 2 gives the average ash-free dry weight of the total food consumed (estimated gravimetrically), column 3 gives the average ash-free dry weight of bacteria consumed (estimated isotopically) and column 4 the average ash-free dry weight of lignin consumed (estimated by difference). Absorption efficiencies of bacteria (estimated isotopically) are given in column 5.

Addition of lignin did not appear to affect the actual input of bacteria. Furthermore, the amount of lignin eaten remained relatively constant and independent of the amount offered. The simplest explanation of these results is that snails compensate for the addition of lignin by preventing interference between bacteria and lignin in the gut and also by selectively ingesting bacteria.

Apparent discrimination by *P. contortus* between bacteria and lignin is surprising in view of the intimate association of these 2 components. The question therefore arises as to whether bacterial selection is an experimental artefact, and

Table 5. The effect of lignin on the ingestion rate and absorption efficiency (AE) of *P. contortus* (large) at 10° C over a 6 hr interval. The results are expressed in terms of a single individual. Confidence limits represent $t.s/\sqrt{n}$, when $t=2.776$ for 4 ($n-1$) degrees of freedom at the 95% level

1	2	3	4	5
% Lignin to bacteria	Total food eaten (μg ash-free dry weight)	Bacteria eaten (μg ash-free dry weight)	Lignin eaten (μg ash-free dry weight)	AE (%)
500	58.0 \pm 4.9	24.2 \pm 2.3	23.8	76.3
300	57.8 \pm 5.1	24.3 \pm 2.1	23.5	75.7
100	52.5 \pm 3.3	26.0 \pm 2.5	26.5	75.9
0	—	25.9 \pm 2.9	—	76.7

Table 6. Comparison of the relative proportions of bacteria and detritus in gut extracts and samples from stones

Source	Fields with bacteria	Fields with detritus
Stones	62	91
Guts	97	33

this possibility was investigated further by comparing the ratio of bacteria to detritus found on the natural substratum at Malham Tarn with that found in snails' guts. If selection occurs, the ratio should increase in the gut samples and although this does not offer sufficient proof (since endemic gut flora may shift the value of the ratio anyway), it is a necessary condition for a "selection hypothesis".

Detritus was scraped from 5 randomly chosen stones into 50 cm³ of distilled water (Calow, 1975b) and the gut contents of snails taken from these stones were emptied into 10 cm³ of sterile distilled water. The latter, and also a 10 cm³ aliquot of the "stone sample" were subjected to automatic stirring for 12 hrs to dislodge bacteria and to provide some consistency in detrital particle sizes. Three smears were made for each sample and these were heat fixed and Gram stained (Cruikshank, 1965). Twenty randomly chosen, non-repeated fields were observed and given a bacterial score of 1 if bacteria were present and similarly a detritus score of 1 if detrital particles were present; refractive, calcareous particles were ignored. Table 6 summarises the results in terms of summed scores and indicates, as required for the "selection hypothesis", that the ratio, bacteria/detritus increases in the snails' guts.

e) Effect of Snail Size and Environmental Temperature on Rate of Absorption

There was a significant linear relationship between absorption rate and individual size (mg ash-free, dry weight) when each of these parameters was plotted on logarithmic coordinates (*e.g.*, see Fig. 5). The equations specifying these relationships are:

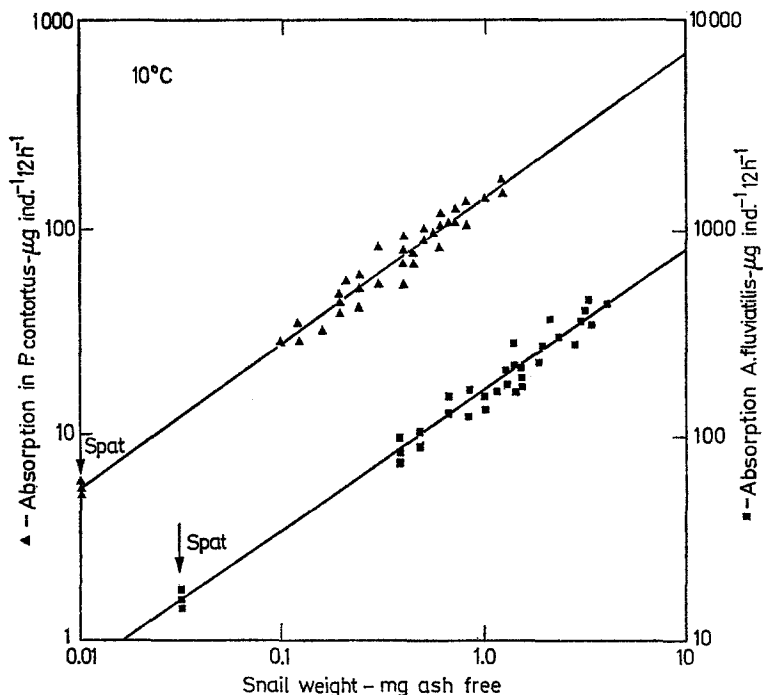


Fig. 5. The relationship between absorption rate and soft body weight (ash-free) at 10°C

for *A. fluviatilis*

$$\begin{array}{l} \text{at } 4^{\circ}\text{C} \quad y = 1.26 + 0.71 (\pm 0.18) x \\ \text{at } 10^{\circ}\text{C} \quad y = 1.89 + 0.67 (\pm 0.10) x \\ \text{at } 18^{\circ}\text{C} \quad y = 2.15 + 0.70 (\pm 0.12) x \end{array}$$

for *P. contortus*

$$\begin{array}{l} \text{at } 4^{\circ}\text{C} \quad y = 1.20 + 0.72 (\pm 0.09) x \\ \text{at } 10^{\circ}\text{C} \quad y = 1.74 + 0.71 (\pm 0.10) x \\ \text{at } 18^{\circ}\text{C} \quad y = 2.80 + 0.72 (\pm 0.09) x \end{array}$$

where $y = \log_{10} (\mu\text{g absorption } 12 \text{ hrs}^{-1} \times 10)$ and $x = \log_{10} (\text{tissue dry weight of snails in mg} \times 100)$.

All the regression coefficients are significant at the 95% level ($b > 1.96$). However, none is significantly different from the hypothetical value of 0.67 ($b < 1.96 \times 0.67$) so that all regression coefficients are assumed equal to 0.67 and the "a" coefficients have been suitably modified to provide the following equations:

for *A. fluviatilis*

$$\begin{array}{l} \text{at } 4^{\circ}\text{C} \quad y = 1.56 + 0.67 x \\ \text{at } 10^{\circ}\text{C} \quad y = 1.89 + 0.67 x \end{array}$$

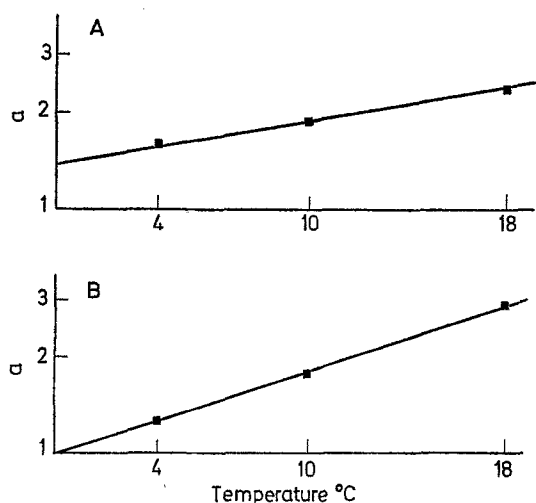


Fig. 6A and B. The relationship between coefficient "a" (in the regression equations relating absorption rate to snail weight) and temperature for *A. fluviatilis* (A) and *P. contortus* (B)

$$\begin{aligned} & \text{at } 18^\circ \text{ C } \quad y = 2.45 + 0.67 x \\ \text{for } P. \textit{contortus} & \\ & \qquad \qquad \qquad a \quad b \\ & \text{at } 4^\circ \text{ C } \quad y = 1.25 + 0.67 x \\ & \text{at } 10^\circ \text{ C } \quad y = 1.78 + 0.67 x \\ & \text{at } 18^\circ \text{ C } \quad y = 2.85 + 0.67 x \end{aligned}$$

The logarithms of the above "a" coefficients are linearly related to temperature over the range considered (see Fig. 6) and this is summarised by:

for *A. fluviatilis*

$$\log_{10} a = 0.014 T + 0.135$$

for *P. contortus*

$$\log_{10} a = 0.026 T + 0.005$$

Hence Q_{10} values for *A. fluviatilis* and *P. contortus* are 1.38 and 1.82 respectively. Both values are less than two suggesting that both snail species are able to effect partial compensation (Precht, 1958) of their absorption rates in terms of temperature disturbance. However, compensating abilities appear to be more effective in *A. fluviatilis*.

f) Time of Day

Laboratory feeding experiments suggested that there was no significant difference between snail feeding rates and absorption efficiencies at various times of the day (Table 7). This conclusion was also confirmed by field observation (Table 8). Here the constancy in faecal output over a 24 hr period suggested constancy in ingestion rate, and constancy in the ratio between gizzard and liver string fractions of the faeces suggested constancy in absorption efficiency (see Calow, 1970).

Table 7. Comparison of ingestion rates and absorption efficiencies (AE) of snails (medium sized) fed at different times of the day and at 10° C. Confidence limits represent $2.s/\sqrt{n}$, when $n = 30$

Time	<i>A. fluviatilis</i>		<i>P. contortus</i>	
	Ingestion (μg , ash-free dry wt./individual/ 12 hrs)	AE (%)	Ingestion (μg , ash-free dry wt./individual/ 12 hrs)	AE (%)
12 noon	110.7 \pm 6.7	61.1	61.0 \pm 4.1	75.9
12 midnight	108.9 \pm 7.2	59.8	59.2 \pm 3.8	76.3

Table 8. Total faecal production (length) of snails (30) collected from Malham Tarn at various times through the day. G = gizzard string length, L = liver string length and F = total length of faeces

Time	<i>A. fluviatilis</i>		<i>P. contortus</i>	
	F (mm)	G/L	F (mm)	G/L
6 a.m.	120.8	0.27	218.1	0.32
12 noon	117.7	0.23	222.3	0.33
6 p.m.	122.5	0.29	220.8	0.35
12 midnight	124.3	0.27	217.9	0.31

Discussion

This discussion considers in turn the general aspects of ingestion and absorption and then the specific responses of these parameters to absolute food shortage, brought about by complete starvation, and relative food shortage (*i.e.* relative to the species concerned) brought about by food materials of inferior quality.

Absorption (ingestion rate \times absorption efficiency) was dependent on temperature and body size. The temperature dependence was, however, less than expected for physicochemical processes ($Q_{10} < 2$) suggesting acclimation and in this context *A. fluviatilis* was a better regulator than *P. contortus*. The size dependence of absorption was allometric and of a form to be expected when absorption is functionally related to body surface area (regression coefficient, $b \approx 0.67$). Similar results have been obtained by Van der Drift (1951), Gere (1956), Dunger (1958) and Reichle (1968) although Phillipson (1960) has shown that the value of the regression coefficient may change with age and Tsikhon-Lukanina (1967) found it to be significantly less than 0.67 in terrestrial isopods.

Neither temperature nor individual size appeared to have any significant effect on absorption efficiency but spat efficiencies were significantly higher than those of the adults. Temperature independence, though surprising in view of the *in vitro* sensitivity of digestive enzymes, has also been recorded in *Calanus* (Conover, 1966), *Daphnia* (Schindler, 1968) and *Pyrrhosoma* (Lawton, 1970) but

Widdows and Bayne (1971) have found reverse temperature dependence in *Mytilus*. A similar inconsistency occurs with regard to size dependence in poikilothermic absorption efficiencies and although Sorokin and Panov (1968) have recorded independence other relationships have been found (*e.g.* Schindler, 1968; Chlodny *et al.*, 1967). It is interesting to note, however, that Soldatova *et al.* (1969), in their studies on aquatic crustaceans, found that absorption efficiencies in *Idothea baltica*, and algal herbivore, were independent of temperature and body size but that in the young there was a 20–30% increase in efficiency over the adults. These results are completely analogous to those for the snails.

The absorption efficiencies of both *A. fluviatilis* and *P. contortus* on the preferred foods exceeded the value of 30%, which was the upper limit set by Engelman (1966) for poikilotherms. In general the range of values recorded for *P. contortus* feeding on bacteria (74–78% adults; 94% spat) is consistent with the range of values recorded by Hargrave (1970) for *H. azteca* (60–80%) and the low values recorded on lignin and cellulose (1–5%) are also consistent with Hargrave's finding that *H. azteca* could not digest these materials to any appreciable extent. Lignin and cellulose are the most important components of aquatic detritus and low efficiencies in animals feeding on this material are typical (Newell, 1965). The range of efficiencies recorded for *A. fluviatilis* feeding on algae (10–94%) is slightly greater than that recorded for littoral, marine, algal herbivores (35–84%, Carefoot, 1973) but the fact that *A. fluviatilis* digests blue-green algae with least efficiency is typical (Kajak and Warda, 1968; Hargrave, 1970; Schindler, 1971).

When food was made available after varying periods of starvation, both ingestion rate and absorption efficiency (and therefore absorption rate) increased but at a progressively reducing rate with starvation time. A similar response of ingestion (appetite) to starvation has been recorded in a variety of vertebrate and invertebrate animals (Miner, 1955; Holling, 1966; Beukema, 1968; Brett, 1971; Hubbell, 1971) and one model accounts for this behaviour by relating appetite to the unfilled volume of the gut (Holling, *ibid.*). However, evidence like that of Barnett (1953), which showed that rats ate less when sugar was added to their water supply, suggests that at least some animals are able to regulate their ingestion rate in terms of the energy content of food eaten rather than in terms of its mass (see also Avery, 1973). This will be discussed further below.

The increased efficiency of digestion found in starved snails has also been noted for other species (Brett, 1971; Windell, 1966) and could result from passive or active control mechanisms. Thus a greater gut space could result in more effective trituration of the ingested materials, when control would be passive, or there could be an increase in the level of activity and rate of secretion of digestive juices as the gut empties, when control would be active. Histochemical evidence indicates that in another freshwater pulmonate, *Lymnaea truncatula* (Müll.), the concentration of enzymes in the hepatopancreas rises during starvation (Moore, 1971) so that at least part of the regulatory mechanism is under active endogenous control in this species. Also, Moore (*ibid.*) observed the same phenomenon in snails parasitised with trematode larvae so that the effects of parasitisation and starvation are similar and probably represent a homeostatic attempt at maintaining constant food energy input in the face of different forms of food supply, disturbance. The final effect of enzyme accumulation in the hepatopancreas is

cell autolysis which impairs the digestive processes (Moore, *ibid.*) and which could, therefore, account for the pathological state noted in *P. contortus* and *A. fluviatilis* after 144 hr starvation.

Increased absorption of food, as a result of increased ingestion rate and absorption efficiency following starvation, can be construed as a homeostatic attempt to make-good growth errors incurred during starvation. For example, Calow (1973c) was able to show that growth rates in cohorts of *P. contortus* fed either once every second, 3, 4, 6 or 8 days were greater over the first week after transference to a continuous, super-abundant food supply than in cohorts, of the same mean age, but which had been fed continuously throughout. This suggests that on a short-term basis *P. contortus* is able to remember its past nutritional history and compensate for it. Also, growth rates in the pulse-fed groups, over the period of pulse feeding, were greater than expected if growth were simply proportional to food availability. The implications are that growth is regulated to some "set-point" and that adjustments in ingestion rate and absorption efficiency with starvation (*i.e.* between pulse feeding) represent physiological mechanisms involved in this "set-point" regulation. Respiration may also reduce with starvation (Calow, 1974b) so that the resultant reduction in energy loss contributes to the regulation of growth as well. Significantly, the growth rates of cohorts of *P. contortus* fed every sixth and eighth day were similar and there was no significant difference in the growth rates of any of the cohorts over the second week after transference to a continuous food regime (Calow, 1973c). This suggests that after 7 days starvation further starvation cannot significantly increase a snail's compensation and may even retard it and this point corresponds to the time when starvation begins to have a deleterious effect on ingestion rate and absorption efficiency.

As already noted food quality influences absorption efficiency but this effect may be compensated for by adjustments in ingestion rate, suggesting, once again, that the mass of food in the gut may not be the only determinant of appetite. *A. fluviatilis*, for example, ingests more of the less well digestible components of the diet when these are fed in pure culture and Schindler (1971), finding the same phenomenon in *Diaptomus*, has attributed it to the maintenance of constant energy transmission across the gut wall in the face of variability in the quality of the food supply. This implies that there must be some real physiological link between the amount of energy absorbed (or rate of absorption) and the rate of consumption, and Gelperin (1971) gives experimental evidence for the presence of such a feed-back link in the insects. However, other components such as essential amino acids may also be important (Carefoot, 1973), and where absorption efficiencies are high anyway there may be no relationship between this parameter and ingestion rate (Conover, 1968). Similar conclusions follow from the strategy adopted by *P. contortus* in the face of increases in the ratio of lignin to bacteria in its food supply, except that searching efficiency also appears to be influenced in this instance. Lignin is a poor food source for *P. contortus*, but since it is intimately associated with bacteria in nature and since it forms a large fraction of the detrital food source of this species (Calow, 1974b) its consumption cannot be entirely avoided and it thereby assumes the twin roles of "food-carrier" and "food-diluent". However, unlike sheep and cattle (Dinius and Baumgardt, 1970), in-

creasing amounts of "diluent" in the diet of *P. contortus* do not impair digestion of the true food (bacteria) and interference from the former may be avoided in snails by the possibility of pre-digestive separation of these fractions at the level of the gizzard-stomach complex. Here ciliary sorting sends indigestible components direct to the intestine whereas digestible particles are diverted to the hepatopancreas (Carriker, 1946). Furthermore, increasing amounts of diluent are apparently detected and accounted for by an increase in ingestion rate and also by more effective selection of bacteria. The latter, although at first sight improbable with such a crude feeding mechanism as the radula may be facilitated by colonial aggregations of bacteria on natural substrates. This has been observed directly by Meadows and Anderson (1967) and Bott and Brock (1970), and Calow (1974a) has found evidence to suggest that *P. contortus* may be capable of sensing bacteria at a distance from their chemical exudates.

One of the most striking and recurrent features then of the "physiological" aspects of feeding in *P. contortus* and *A. fluviatilis* is their adaptive plasticity. During times of absolute food shortage the "urge to feed" (appetite) increases and when food again becomes available it is digested more efficiently. In consequence these strategies contribute to the metabolic repertoire involved in maintaining a "desired internal milieu", which becomes manifest as growth regulation (Calow, 1973c) and ultimately reproductive replacement (Calow, 1973b). Furthermore, if as these results suggest, animals are actively involved in maintaining a constant flow of energy across their gut wall then it may be possible, knowing absorption efficiencies, to obtain a reasonably accurate estimate of field ingestion rates by back calculation from "ideal" absorption rates. This suggestion will be investigated further in Calow (1975a).

Another important outcome which follows from these conclusions is that not only are there no *a-priori* grounds for believing ecological efficiencies to be constant (Slobodkin, 1962) but there are strong grounds for believing that they should alter with circumstances. This is also true for most of the other efficiencies employed in ecological energetics so that rather than searching for constant efficiencies, it would seem more interesting and of more value for a developing ecological theory to measure their variation, explain this in terms of fitness, and incorporate it into energy budget models as part of an adaptive repertoire (*e.g.* as in Hubbell, 1971). Certainly, homeostasis is an outstanding feature in biological systems and yet it appears to have been neglected by ecological energeticists.

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