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TOWARDS A SIMPLE INDEX BASED ON LIVE-WEIGHT AND BIOMASS TO PREDICT ASSIMILATION IN ANIMAL POPULATIONS

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SUMMARY

(1) Using published data on energy budgets a simple index is used to derive equations predicting assimilation or production in animal populations.

(2) The index is based on the commonly measured parameters of mean annual biomass (cal m^{-2}) and maximum live-weight (mg). The index (I_m) is: mean annual biomass (cal m^{-2})/maximum live-weight (mg)^{0.75}.

(3) The available data relating I_m to assimilation can be grouped into five taxonomic categories; homoiotherms (excluding mice and voles), mice and voles, fish, invertebrates (excluding ants), and ants.

(4) The invertebrates can be separated by both life-cycle duration (<2 years and >2 years) and habitat (aquatic and terrestrial) but too few data are available to analyse separately the combined effects of habitat and life cycle duration.

(5) Seven parallel regression lines are derived relating the index ($\log I_m$) to assimilation ($\log A \text{ cal m}^{-2} \text{ year}^{-1}$). These lines account for 93% of the variance in the data.

(6) The relationship between the index ($\log I_m$) and production ($\log P \text{ cal m}^{-2} \text{ year}^{-1}$) is used, with previously derived equations relating production and respiration, to predict assimilation. It accounts for 91% of the variation in the data.

INTRODUCTION

Determination of an energy budget for a natural population of animals is complex, protracted and expensive. It is possible to construct community energy budgets but it is only practicable for quite simple communities. Even in studies of single species the reliability of the data collected, when combined to produce an energy budget, is usually uncertain and the variability in different years and between different populations seldom determined. These problems result from the quantity of information required for the more sophisticated energy budgets, methodological differences between studies (Humphreys 1978), poor resolution in time for some of the parameters required (especially population changes and the seasonal characteristics of respiration) and from the extrapolation of laboratory determined measurements to natural populations.

To derive first order estimates of energy flow through different communities powerful predictive models are required to circumvent the need for energy budgets for all the component species. Some models have been derived (e.g. turnover rate; Zaika & Malovitskaya 1967; Mathias, personal communication in Mann 1969; Waters 1969) but most concentrate on the relationship between production and respiration (Engelmann

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1966; Golley 1968; Hughes 1970; McNeil & Lawton 1970; Shorthouse 1971; Lévêque 1973; Grodziński & French in Grodziński & Wunder 1975; Jensen 1978; Humphreys 1979). Using this relationship seven distinct metabolic groups have been derived (Humphreys 1979). The predictive power of these regressions accounted for between 71% and 95% (mean 86%) of the variance in the data. However, both production and respiration are difficult to determine in most natural populations and require a high level of information on growth rate, population structure and metabolic plasticity if they are to achieve an acceptable degree of accuracy.

There is clearly a need for predictive equations based on parameters more easily determined in natural populations and it is to this problem that the paper is addressed. The prediction of population respiration from mean biomass (Phillipson 1970), separation of different metabolic groups of animals with respect to production efficiency (P/A ; Humphreys 1979) and of different individual metabolic rates between taxa (Hemmingsen 1960) suggest that assimilation should be predictable from biomass information. I use here crude measurements, biomass and maximum live-weight, to derive equations predicting assimilation in natural populations: $\text{Index} = I_m = \text{mean annual biomass (cal m}^{-2}) / \text{maximum live-weight (mg)}^{0.75}$ which includes some measure of population density corrected for individual metabolic capacity. The dimensions of the index are strange ($\text{cal m}^{-2} \text{mg}^{-0.75}$) but if the caloric measurement is converted to a gravimetric measure the inverse dimensions ($\text{mg}^{-0.25} \text{m}^2$) take the familiar form of a weight specific metabolic allometric relationship.

As both live-weight and biomass are easily determined and are commonly collected in many field studies, if only for book-keeping purpose, any predictive power the index may show should be of widespread use.

MATERIALS AND METHODS

I follow the terminology of Petruszewicz & Macfadyen (1970) to depict the relevant components of energy budgets, namely R (respiration), P (production), \bar{B} (biomass) and A (assimilation; $A = P + R$) all in caloric units.

Energy budgets for natural populations were extracted from the literature. Biomass and live-weight data were included if they were explicit in the original paper or could be calculated from illustrations or from tables of the structure, biomass and duration of size classes. Of the 235 budgets used previously (Humphreys 1979) only 100 contained additional information on biomass and live weight and these form the data for this analysis (Appendix). The same conversion factors and exclusions were used as described elsewhere (Humphreys 1979).

The data were originally grouped for analysis according to the seven derived groups based on P and R (Humphreys 1979) except that there were no data for 'small mammal communities' and that fish were separated from social insects (ants in this case) as they were, on inspection, clearly different with respect to the relationship between I_m and A .

Least squares regressions were calculated for the relationship between $\log I_m$ and $\log A$ in each group taking assimilation as the dependent variable. The lines were compared using the analysis of variance procedure of Davies & Goldsmith (1972; Table 7.7). Analyses were conducted to test four relationships within and between the regression lines of the form $\log y = a + b \log x$. Firstly whether x and y were correlated and the slope (b) of the equation differed from zero. Analysis continued to test whether the two (or more) regression lines had similar slopes ($P > 0.05$); if the slopes were statistically

similar the lines were tested for a common intercept (a). If the intercepts were similar ($P > 0.05$) the data were pooled, otherwise ($P < 0.05$) they were treated as separate groups. In this manner all groups were tested against adjacent groups before pooling.

The data for the invertebrates only were subdivided according to habitat (aquatic *v.* terrestrial), trophic type (herbivore *v.* carnivore *v.* detritivore) and life-cycle duration (short-lived < 2 years and long-lived > 2 years) in a separate analysis to attempt to assess the effect of these factors on the relationship, as all have been suggested as groups by various workers (see Humphreys 1979).

A similar, though less extensive, analysis is made of the relationship between the index ($\log I_m$) and production ($\log P \text{ cal m}^{-2} \text{ year}^{-1}$).

While the original number of data pairs is 100 some analyses are on fewer data as information about production or life-style was unavailable.

The data are mostly presented as familiar least squares predictive regressions but in the final grouping the geometric mean estimate of the functional regression of y on x (the GM regression) is given, in addition to predictive equations, as this gives a better estimate of the slope for predictive purposes (Ricker 1973) and avoids having to decide on the relative accuracy of the x and y measurements. Where necessary the common slope (v) for the GM regression is approximated from the weighted mean correlation coefficient of the predictive equations.

The iterative procedure used to separate the groups is suspect statistically and is retained only as an objective method of grouping the data. Consequently the probability levels cited are inexact and should be viewed with caution.

RESULTS

Relationship between I_m and A

In the seven initial groups assimilation (A) is significantly regressed against the index (I_m) with the regressions accounting for between 45% and 100% (mean 79%) of the variance in the data (Table 1). The regressions are parallel ($P = 0.70$) but not common ($P < 10^{-5}$). Pairwise comparison of these regressions shows that these seven lines can be arranged in four groups which are statistically internally consistent, with common slopes but separate intercepts (Tables 2 & 3). These groups are the homoiotherms, fish, ants and all other invertebrates.

Further analysis shows that voles and mice (Appendix and Table 3) have common lines and that after pooling the common regression for voles and mice differs from the

TABLE 1. Regression statistics relating the metabolic index ($\log I_m$) to assimilation [$\log A \text{ cal m}^{-2} \text{ year}^{-1}$] in various taxa of animal populations. The lines are parallel [$P = 0.70$] but not common [$P < 10^{-5}$]

Group	Regression equation	n	Standard error of slope	F_s	P	r	Intercept for common slope of $0.776 \pm 0.024 \dagger$
Birds	$A = 0.993I_m + 2.346$	7	0.194	26.25	0.0037	0.92	2.033
Other mammals	$A = 0.903I_m + 2.293$	42	0.093	94.25	$< 10^{-5}$	0.84	2.000
Shrews	$A = 1.201I_m + 2.803$	5	0.326	13.58	0.035	0.91	1.933
Fish	$A = 0.698I_m + 1.635$	8	0.117	35.75	0.001	0.93	1.650
Non-insect invertebrates*	$A = 0.669I_m - 0.059$	25	0.164	18.26	0.0003	0.67	-0.184
Non-social insects*	$A = 0.628I_m - 0.295$	9	0.123	37.33	0.0005	0.92	-0.727
Ants	$A = 1.016I_m - 1.653$	4	0.002	> 999	$< 10^{-5}$	1.00	-1.295

* Excluding ants; † Residual standard error of slope.

TABLE 2. Regression statistics relating the metabolic index ($\log I_m$) to assimilation [$\log A \text{ cal m}^{-2} \text{ year}^{-1}$] in the four separate groupings of animal populations. The lines are parallel [$P = 0.085$] but not common ($P < 10^{-5}$). Below each predictive equation the GM regression is given

Group	Regression equation	n	Standard error of slope	F_s	P	r	Intercept for common slope of $0.723 \pm 0.024^*$ and for $v = 0.881$
Homoiotherms	$A = 0.893I_m + 2.254$	54	0.076	139.01	$<10^{-5}$	0.85	1.882
	$A = 1.047I_m + 2.590$						2.228
Fish	$A = 0.698I_m + 1.635$	8	0.117	35.75	0.001	0.93	1.640
	$A = 0.754I_m + 1.646$						1.669
Invertebrates (-ants)	$A = 0.590I_m + 0.037$	34	0.100	35.14	$<10^{-5}$	0.72	-0.224
	$A = 0.816I_m - 0.405$						-0.533
Ants	$A = 1.016I_m - 1.653$	4	0.002	>999	$<10^{-5}$	1.00	-1.216
	$A = 1.016I_m - 1.653$						-1.452

* Residual standard error of slope.

TABLE 3. Synopsis of analyses of variance testing for common slopes and intercepts for some of the regressions relating the index ($\log I_m$) to assimilation ($\log A \text{ cal m}^{-2} \text{ year}^{-1}$) in animal populations

	Test for parallel lines			Test for common intercept			Comment
	F_s	d.f.	P	F_s	d.f.	P	
All mammals <i>v.</i> birds	0.01	1,50	0.931	0.13	1,51	0.722	parallel common
Shrews <i>v.</i> other mammals	0.19	1,43	0.663	0.21	1,44	0.652	parallel common
Fish <i>v.</i> ants	0.85	1,8	0.383	154.61	1,9	$<10^{-5}$	parallel separate
Non-social insects <i>v.</i> non-insect invertebrates	0.09	1,30	0.763	1.97	1,31	0.170	parallel common
Ants <i>v.</i> all other invertebrates	0.30	1,34	0.588	9.86	1,35	0.003	parallel separate
Homoiotherms <i>v.</i> fish	1.24	1,58	0.271	5.93	1,59	0.018	parallel separate
Voies + mice <i>v.</i> other mammals - shrews	1.52	1,38	0.225	20.30	1,39	0.00006	parallel separate
Voies + mice <i>v.</i> shrews	0.17	1,32	0.680	0.09	1,33	0.760	parallel common
Shrews <i>v.</i> mammals (-voies & mice)	0.18	1,12	0.680	2.50	1,13	0.138	parallel common
Aquatic <i>v.</i> terrestrial invertebrates (-ants)	0.19	1,30	0.665	6.84	1,31	0.0014	parallel separate
Long- <i>v.</i> short-lived invertebrates (-ants)	0.14	1,29	0.709	17.34	1,30	0.00024	parallel separate
Short-lived terrestrial <i>v.</i> short-lived aquatic invertebrates (-ants)	0.35	1,13	0.566	0.39	1,14	0.543	parallel common
Long-lived terrestrial <i>v.</i> short-lived terrestrial & long-lived aquatic invertebrates (-ants)	0.17	1,20	0.683	0.65	1,21	0.429	parallel common
Short-lived aquatic <i>v.</i> short-lived terrestrial & long-lived aquatic invertebrates (-ants)	0.05	1,21	0.831	1.87	1,22	0.185	parallel common
Long-lived terrestrial <i>v.</i> short-lived aquatic invertebrates (-ants)	0.35	1,13	0.566	0.39	1,14	0.543	parallel common

remaining mammals. The latter group are not distinguishable from either birds or shrews so the homoiotherms are separated into voles and mice, and the remaining homoiotherms.

Separation of invertebrates by life style

Sufficient information was available for the comparison of life-style only for the invertebrates (excluding ants).

Trophic type

Examination of the data for trophic type (herbivore, carnivore or detritivore) for the insects and the non-insect invertebrates showed that no trophic categories could be separated from either group or the two groups combined (Table 3).

Life-cycle duration

The invertebrates as a whole could be separated into short- (<2 years) and long- (>2 years) lived species with the two regression lines being parallel but separate (Table 3). Long-lived invertebrates had greater assimilation rates (7.2 times) for a given level of I_m (Table 4).

Non-insect invertebrates alone could be separated by life-cycle duration (Table 3) with the long-lived species having greater (11.3 times) assimilation for a given I_m (Table 4).

Habitat

Separation of the invertebrates alone into aquatic and terrestrial species have parallel but separate regressions (Table 3) with aquatic species having greater (6.1 times) assimilation rates for a given I_m .

Habitat and life cycle duration are independent classifications (contingency $\chi^2_1 = 0.138$, NS) so we may be reasonably confident that both, independently, influence the regressions.

Separation of the invertebrates by habitat and life-cycle duration partitioned the same data in two ways. Attempts to separate these data using both life-style criteria together were frustrated by small sample size resulting in non-significant regressions for short-lived terrestrial and long-lived aquatic invertebrates. These groups were pooled and the remaining two groups also retained as separate lines giving three artificial groups (short-lived terrestrial plus long-lived aquatic, long-lived terrestrial and short-lived aquatic invertebrates excluding ants); these groups had relative assimilation rates (calculated for the common slope) respectively of 4.2:2.7:1.0 for a given level of I_m . These three groups are retained as an expedient to allow the analysis to continue, as comparison of the invertebrates as a whole with the other four derived groups results in non-parallel lines ($P = 0.023$). The reasons for this will be discussed later.

TABLE 4. Regression equations relating the index ($\log I_m$) to assimilation ($\log A$ cal m^{-2} year $^{-1}$) in invertebrate populations with differing life-cycle duration and habitat. All comparisons exclude ants

	Regression equation	n	Standard error of slope	F_s	P	r	Intercept for common slope
Short-lived invertebrates	$A = 0.771I_m - 0.816$	14	0.102	56.91	<10 $^{-5}$	0.91	-0.741
Long-lived invertebrates	$A = 0.702I_m + 0.178$	19	0.150	21.96	0.0002	0.75	0.118
	lines are parallel ($P = 0.709$) but not common ($P = 0.0002$). Common slope is $0.741 \pm 0.081^*$						
Aquatic invertebrates	$A = 0.399I_m + 0.730$	20	0.105	14.35	0.001	0.65	0.649
Terrestrial invertebrates	$A = 0.508I_m - 0.236$	13	0.177	8.20	0.015	0.65	-0.139
	lines are parallel ($P = 0.589$) but not common ($P = 0.001$). Common slope is $0.432 \pm 0.079^*$						
Non-insect invertebrates:							
Short-lived	$A = 1.026I_m - 1.362$	7	0.249	16.99	0.009	0.88	-0.930
Long-lived	$A = 0.739I_m + 0.200$	17	0.147	25.19	0.0002	0.79	0.122
	lines are parallel ($P = 0.396$) but not common ($P = 0.00037$). Common slope is $0.790 \pm 0.124^*$						

* Residual standard error.

TABLE 5. Predictive regression equations relating the metabolic index ($\log I_m$) to assimilation ($\log A$ cal m^{-2} year $^{-2}$) in seven derived groups of natural populations of animals. The geometric mean regression, which better estimates the slope, is given below each equation; statistics refer to the predictive equations. The intercept for the common slope ($b = 0.778 \pm 0.023$) of all groups is given in parentheses after each equation. The weighted mean correlation coefficient was used to approximate the common slope ($v = 0.941$) for the G M regressions

Group	Regression equation	Correlation coefficient	n	Mean A	Mean I_m	Standard error slope	F_s	P
Homoiotherms*	$A = 0.674I_m + 1.974(2.198)$ $A = 0.910I_m + 2.483(2.551)$	0.741	23	0.525	-2.152	0.133	25.62	0.0001
* Mice + voles	$A = 1.047I_m + 2.447(1.854)$ $A = 1.096I_m + 2.449(2.215)$	0.955	31	0.136	-2.209	0.060	303.67	<10 $^{-5}$
Fish	$A = 0.698I_m + 1.635(1.650)$ $A = 0.755I_m + 2.495(1.680)$	0.925	8	1.506	-0.185	0.117	35.75	0.001
Short-lived terrestrial and long-lived aquatic invertebrates†	$A = 0.739I_m - 0.032(-0.099)$ $A = 1.458I_m - 1.289(-0.385)$	0.507	16	1.261	1.749	0.336	4.84	0.045
Long-lived terrestrial invertebrates†	$A = 0.577I_m - 0.072(-0.301)$ $A = 0.665I_m - 0.172(-0.487)$	0.868	8	0.585	1.139	0.135	18.29	0.005
Short-lived aquatic invertebrates†	$A = 0.661I_m - 0.369(-0.727)$ $A = 0.682I_m - 0.433(-1.230)$	0.969	9	1.661	3.071	0.064	106.84	<10 $^{-5}$
Ants	$A = 1.016I_m - 1.653(-1.297)$ $A = 1.016I_m - 1.653(-1.540)$	1.000	4	-0.136	1.492	0.002	>999	<10 $^{-5}$

* Excluding mice and voles. † Excluding ants. The lines are parallel ($F_{s, 685} = 1.49, P = 0.191$) but not common ($F_{s, 6, 91} = 22.57, P < 10^{-5}$).

These groups together with those derived for the other taxa are presented in Table 5 and this represents the best current separation of the data for the relationship between I_m and A (Fig. 1). These parallel lines account for 93% of the variance in the data.

Potential accuracy of the index

To obtain some measure of the potential accuracy of the index (I_m) as a predictor of A when larger samples are available the regression lines in Table 5 were superimposed. This was achieved by subtracting the intercept for the common slope of the regression lines from each appropriate datum point for the dependent variable A . This results in a common regression line based on 99 points. The regression accounts for 92% of the variance in the data and has the values $\log A = 0.777 \log I_m - 0.015$ ($v = 0.811$; $SEb = 0.024$; $t_s = 32.86$, $P < 0.001$). The regression has fine confidence intervals but the predictive power for one new observation is low (Fig. 2).

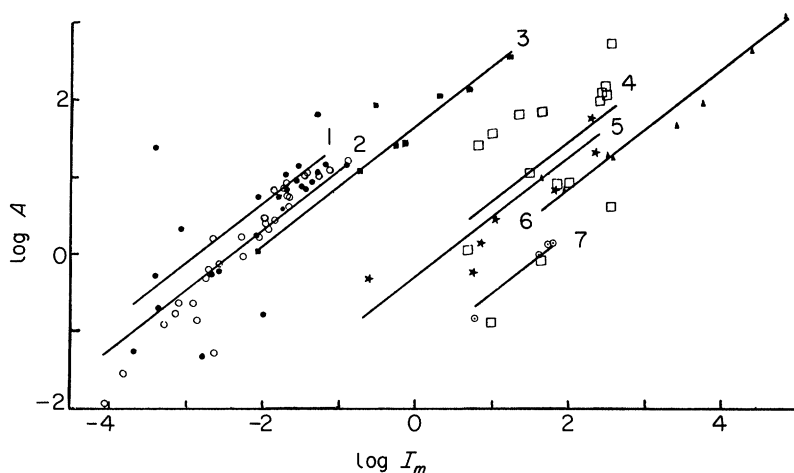


FIG. 1. Regression lines relating $\log I_m$ to $\log A$ ($\text{cal m}^{-2} \text{ year}^{-1}$), adjusted for the common slope of 0.788 ± 0.023 , for the seven derived groups of animal populations. The numbers on the lines refer to the following groups of animals: 1, Homoiotherms excluding mice and voles (\bullet); 2, mice and voles (\circ); 3, fish (\blacksquare); 4, short-lived terrestrial and long-lived aquatic invertebrates ($-$ ants) (\square); 5, long-lived terrestrial invertebrates ($-$ ants) (\star); 6, short-lived aquatic invertebrates (\blacktriangle); 7, ants (\odot).

The relationship between I_m and P

An alternative approach to this problem is to use the index (I_m) to predict P and then estimate R from the appropriate equations relating P and R (Humphreys 1979). A is then determined by adding the estimates for P and R .

Using the same procedure as before seven groups can be separated from the data set with respect to the relationship between P and I_m (Table 6) but the rank order of the intercepts for the common slope (Fig. 3) differs from that in Table 1 or 5 as would be expected from the rank order of the relationship between P and R (Humphreys 1979). The appropriate analyses are given in Table 7. No attempt was made to separate the invertebrates by life-style.

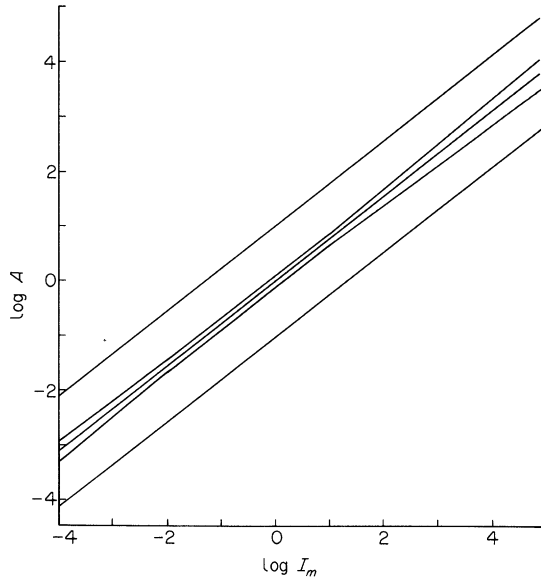


FIG. 2. Common regression line, derived as described in the text, relating the index ($\log I_m$) to assimilation ($\log A$ cal m^{-2} year $^{-1}$) in animal populations. The 95% confidence intervals are shown together with the 95% prediction intervals for one new observation.

TABLE 6. Regression equations relating production ($\log P$ cal m^{-2} year $^{-1}$) to the index ($\log I_m$) in the derived groups of natural population. The predictive equations are followed by the GM regression

Group	Regression equation	n	Standard error of slope	F_s	P	r	Intercept for common slope of $0.782 \pm 0.034^*$ and for $v = 0.972$
Other mammals	$P = 0.746I_m + 0.833$	11	0.231	10.24	0.011	0.730	0.928
	$P = 1.014I_m + 1.543$						1.431
Fish	$P = 0.614I_m + 0.573$	8	0.125	24.13	0.0027	0.895	0.604
	$P = 0.686I_m + 0.586$						0.639
Mice and voles	$P = 1.061I_m + 0.952$	31	0.083	165.19	$<10^{-5}$	0.922	0.334
	$P = 1.151I_m + 1.150$						0.754
Birds	$P = 1.214I_m + 0.821$	7	0.301	16.29	0.010	0.875	0.199
	$P = 1.388I_m + 1.071$						0.472
Shrews	$P = 0.989I_m + 0.169$	5	0.187	27.93	0.013	0.950	-0.255
	$P = 1.041I_m + 0.276$						0.134
Invertebrates†	$P = 0.677I_m - 0.758$	34	0.144	22.23	0.00005	0.640	-0.964
	$P = 1.057I_m - 1.502$						-1.336
Ants	$P = 1.035I_m - 2.669$	4	0.013	>999	0.0002	1.00	-2.291
	$P = 1.035I_m - 2.669$						-2.575

* Residual standard error; † Excluding ants.

Equations for the above relationship were used to estimate R from the appropriate equation for the relationship between P and R in Humphreys (1979) using the equations for the common slope in each case. The calculated R was added to P (estimated from I_m) to give a further estimate of A (A_I) derived indirectly from the index I_m . The actual

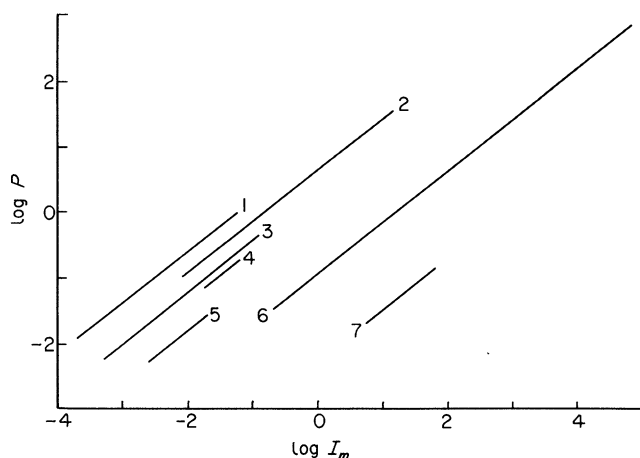


FIG. 3. Regression lines, adjusted for the common slope of 0.782, relating the index ($\log I_m$) to production ($\log P$ cal m^{-2} year $^{-1}$) in the seven derived groups of natural populations of animals. Various taxa are distinguished: 1, mammals (excluding shrews, mice and voles); 2, fish; 3, mice and voles; 4, birds; 5, shrews; 6, invertebrates excluding ants; 7, ants.

TABLE 7. Synopsis of analyses of variance testing for common slope and intercept for some of the regressions relating $\log I_m$ to $\log P$ (cal m^{-2} year $^{-1}$) in animal populations

	Test for parallel lines			Test for common intercept			Comment
	F_s	d.f.	P	F_s	d.f.	P	
Homoiotherms <i>v.</i> fish <i>v.</i> ants <i>v.</i> invertebrates	0.36	3,92	0.781	14.79	3,95	$<10^{-5}$	parallel separate
Birds <i>v.</i> shrews <i>v.</i> other mammals	0.05	2,48	0.949	6.58	2,50	0.0029	parallel separate
Fish <i>v.</i> social insects	1.30	1,8	0.287	112.19	1,9	0.000002	parallel separate
Insects <i>v.</i> other invertebrates*	0.46	1,30	0.501	1.01	1,31	0.322	parallel common
Birds <i>v.</i> shrews	0.40	1,8	0.544	5.99	1,9	0.037	parallel separate
Mice and voles <i>v.</i> other mammals	2.85	1,38	0.099	17.28	1,39	0.00017	parallel separate

* Excluding ants.

budget $\log A$ was regressed against $\log A_I$ yielding the common equation $\log A = 0.917 \log A_I + 0.115$ ($v = 1.004$) which slope differs from zero ($P < 0.001$) but not from a slope of 1.0 ($t_s = 1.07$, NS) and accounts for 91.3% of the variance in the data. This equation, with the 95% confidence intervals and 95% prediction intervals for one new observation, is presented in Fig. 4.

DISCUSSION

Analysis of the relationship between A and I_m and between P and I_m has resulted in separation of a number of metabolic categories of animals which is similar to those derived for the relationship between P and R (Humphreys 1979). Homoiothermic animals separate into two groups (mice + voles, and other homoiotherms) compared with three and possibly four groups for the relationship between P and R (Humphreys 1979). The

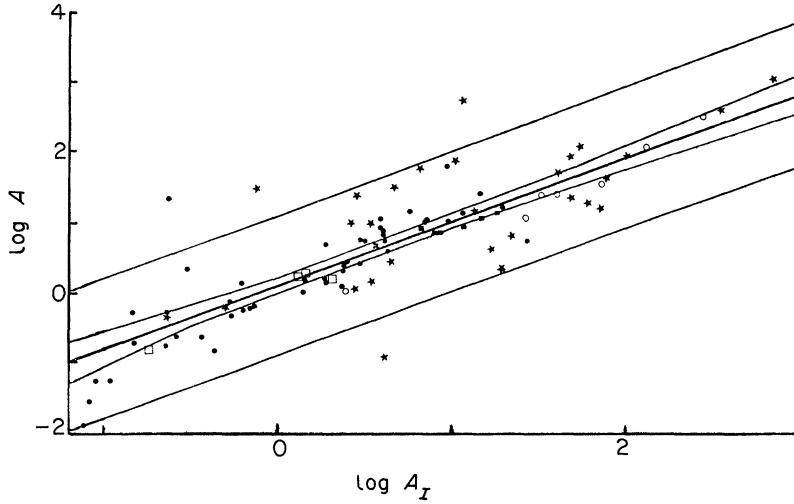


FIG. 4. The relationship between estimated assimilation ($\log A_T$) and budget assimilation ($\log A$ $\text{cal m}^{-2} \text{ year}^{-1}$). A_T was calculated from the relationship between the index ($\log I_m$) and production ($\log P$ $\text{cal m}^{-2} \text{ year}^{-1}$). Production was used to estimate respiration ($\text{cal m}^{-2} \text{ year}^{-1}$) from the equations relating production to respiration in animal populations (Humphreys 1979). Assimilation was then the sum of the estimated P and the estimated R . The geometric mean slope (ψ) = 1.004. Several taxa are distinguished; mammals (●), birds (■), fish (○), invertebrates excluding ants (★) and ants (□).

poikilothermic animals separate into three taxonomic groups (fish, invertebrates (–ants) and ants) as they did for the relationship between P and R (Humphreys 1979). The categories are, however, not the same because non-insect invertebrates were not separable from the non-social insects in this study and fish separate clearly from the social insects (Table 1).

The P and R relationship permitted the separation of trophic categories within the invertebrates (Humphreys 1979; Table 7) but not of habitat or life-cycle duration. For the relationship between A and I_m no trophic categories were separable within the invertebrates but separation was possible for both habitat and life-cycle duration (Table 4).

In the relationship between P and R shrews could be separated from other mammals and non-social insects from non-insect invertebrates (Humphreys 1979). Both these comparisons for the relationship between I_m and A have significance levels which suggest that a larger data set may result in separation of these taxa (Table 3). Due to the clear and wide separation of the invertebrates by both life-cycle duration and by habitat it is not satisfactory to group the invertebrates as a whole but no sensible subdivision can be offered at present. Due to the wide, though non-significant, separation of the non-social insects and the non-insect invertebrate lines (Table 1) use of these regressions adjusted to the common slope of 0.78 would be more satisfactory than lumping the invertebrate data. Alternatively, where there are sufficient data for minor taxa, calculation of the relationship between A and I_m from the Appendix, with adjustment for common slope, should prove satisfactory because of the presence of clear relationships between A and I_m for the other major taxa. This is a temporary expedient and there is need for further data and analysis if satisfactory subdivisions are to be obtained for the invertebrates, a group showing considerable energetic variability and which is so important in community studies.

Analysis of the relationship between P and I_m resulted in the separation of more taxonomic groups than did that for the relationship between I_m and A . The finer resolution was to be expected as P is a more direct measurement in energy budgets while A is the sum of two estimates each with their own error. However, separation of the invertebrates (excluding ants) was not possible although they were clearly separated in the analysis of the relationship between P and R (Humphreys 1979).

The predictive power of the index is unexpectedly high and the seven parallel lines account for 93% of the variance in the data for the relationship between I_m and A and 91% of that for the indirectly derived relationship between A and A_I . These compare with equations relating P and R which accounted for 89% of the variance in the data (Humphreys 1979). The common line derived for the relationship between I_m and A is used here to discuss the confidence intervals as it accounts for the same amount of the variance and is a better indicator of the potential accuracy of the index. The 95% confidence intervals for the regression (Fig. 2) are narrow and over the range of values for $\log I_m$ between -3 and 5 vary between ± 0.1 and ± 0.27 log units ($A = \pm 1.26$ to ± 1.86). These confidence intervals compare favourably to those presented for the relationship between P and R by McNeill & Lawton (1970) which had ranges in log units as follows; homiotherms (± 0.32 to ± 0.39), all poikilotherms (± 0.8 to ± 0.97) and short-lived poikilotherms (± 0.43 to ± 0.55).

The predictive power of the equation, despite the fine confidence intervals, is still low as new observations are likely to be based on one set of data. The 95% prediction intervals for one new observation vary, over the range of I_m , between ± 0.955 and ± 0.985 . These compare with the 95% prediction intervals for one new observation for the relationship between P and R in terrestrial and aquatic poikilotherms between ± 0.65 and ± 1.07 log units (Shorthouse 1971; cited in Humphreys 1978).

The relationship between $\log A$ and $\log A_I$ has wider confidence limits, as would be expected from the method of calculation. The 95% confidence intervals vary between ± 0.03 and ± 0.11 log units (1.06 to 1.29 times) and the 95% prediction intervals for one new observation vary from ± 1.0 to ± 1.06 log units over a range of A_I between -1 and 3 .

One can also examine the predictive power of the two relationships by calculating production efficiency (P/A) from the intercepts for the common slopes in the two relationships (I_m against A and I_m against P). This is a sensitive way of examining the data as it includes two estimates derived from the index (I_m). These are presented in Table 8 together with the actual P/A for the data used and P/A for the large data set analysed elsewhere (Humphreys 1979). This table identifies the main area of uncertainty as the invertebrates. There is need to subdivide the invertebrate data into both taxonomic and life-style categories. This has been done partially for the relationship between P and R (Humphreys 1979) but is frustrated here by lack of sufficient data. The mean value of

TABLE 8. Production efficiency ($P/A\%$) of various taxa calculated from the intercept for a common slope for both predictive and GM regressions for the relationships between I_m and A and between I_m and P

Group	Mean $P/A\%$ of the			
	Equations used: predictive	GM	data used in this study	From Humphreys (1979)
Homiotherms	3.9	4.0	3.1	2.6
Fish	9.2	9.3	9.9	10.7
Invertebrates	18.2	15.7	34.4	32.2
Social insects	8.4	7.5	10.3	10.3

P/A (30.6%) for all invertebrates (except ants), derived as above from I_m , agrees with those for the means of both the data presented in the Appendix ($P/A = 34.4\%$) and those in Humphreys (1979; $P/A = 32.2\%$). Clearly further analysis and data are required to elucidate the energetics relationship within the invertebrates.

It is perhaps surprising that such a simple index based on crude parameters has the degree of predictive power achieved and the ability to resolve between various groups of animals. Whether this is a comment on the lack of resolution in published energy budgets or some underlying principle, only further analysis will resolve. This crude index could be improved by correcting the weight by a power function appropriate to the allometric relationship between respiration and body weight for each species, by using the caloric equivalent of body weight and by taking a more appropriate measurement of weight dependent on the size-class structure of the population. However, in the published literature these types of information are too rarely given to extract a data set sufficient for analysis.

Within their predictive power the general utility of these equations is great due to the simplicity of the information required. Biomass data can be reduced to their caloric equivalent with reasonable accuracy from the caloric data for a wide range of species presented by Cummins & Wuycheck (1971).

A plea

One of the prime functions of energy budget determinations for single populations must be to gather a set of data to enable the derivation of generalized predictive equations to facilitate studies on communities. Only about 43% of the 234 energy budgets considered for this analysis had appropriate information on live-weight and biomass, although these parameters must have been measured to create budgets. This is a consequence, I think, of the attitude of 'yet another energy budget' which has made all concerned loath to devote much space to energy budgets in the literature. Clearly the way budgets are being published is inadequate if they are to fulfil one of their prime purposes. There is a need for authors, referees and editors alike to be aware of the shortcomings of energy budgets. In many cases more detailed presentation is required if they are to be useful for prediction. The excessive disenchantment with energetics generalizations (May 1980) will only be dispelled if they can be erected on a firm base of empirical data.

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NOTE ADDED IN PROOF

Banse, K. & Mosher, S. (1980). Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs*, **50**, 355–379.

This extensive analysis of log mass specific production rate in relation to log mature body weight, mainly in aquatic invertebrates, appeared after my manuscript had gone to press. Mostly the method used in each paper is more suited to the data for which it was derived.

APPENDIX

The values of the parameters used to analyse the relationship between I_m and both production and respiration. The categories relate to those described in Fig. 1.

Species or taxa	Group or common name	Category	Maximum live weight (log g ⁻⁶)	Mean annual biomass (kcal m ⁻²)	Assimilation (kcal m ⁻² year ⁻¹)	Production (kcal m ⁻² year ⁻¹)	Authority
Mammalia							
<i>Peromyscus polionotus</i>	Old field mouse	2	7.12	0.024	6.7	0.12	Odum, Connel & Davenport 1962
<i>Peromyscus osgoodi</i>	Deer mouse	2	7.30	0.002	0.204	0.014	Chew & Chew 1970
<i>Peromyscus eremicus maniculatus</i>	Cactus mouse	2	7.30	0.003	0.468	0.035	Chew & Chew 1970
<i>Peromyscus leucopus</i> (Rafinesque)	White footed mouse	2	7.1	0.066	10.07	0.194	Baar & Fiehart 1976
<i>Perognathus penicillatus</i>	Desert pocket mouse	2	7.11	0.00013	0.0121	0.0001	Chew & Chew 1970
<i>Perognathus baileyi</i>	Bailey's pocket mouse	2	7.20	0.0002	0.0287	0.0001	Chew & Chew 1970
<i>Perognathus flavus</i>	Silky pocket mouse	2	6.81	0.001	0.134	0.009	Chew & Chew 1970
<i>Neotoma albigula</i>	White throated wood mouse	2	8.05	0.0027	0.12	0.008	Chew & Chew 1970
<i>Glaucomys sabrinus yukonensis</i> Osgood	Flying squirrel	1	8.21	0.013	0.73	0.01	Grodzinski 1971
<i>Dipodomys merriami</i>	Merriam's kangaroo rat	2	7.60	0.055	5.788	0.30	Chew & Chew 1970
<i>Reithrodontomys megalotis</i>	Western harvest mouse	2	7.09	0.0003	0.048	0.0035	Chew & Chew 1970
<i>Onychomys torridus</i>	Southern grasshopper mouse	2	7.38	0.005	0.69	0.037	Chew & Chew 1970
<i>Proechimys semispinosus</i> (Tomes)	Cavimorpha	1	8.70	0.355	12.58	0.602	Gliwicz 1973
<i>Apodemus flavicollis</i>	Yellow necked field mouse	2	7.25	0.021	2.604	0.086	Bobek 1971
<i>Apodemus flavicollis</i>	Yellow necked field mouse	2	7.314	0.014	1.614	0.054	Bobek 1971
<i>Apodemus flavicollis</i>	Yellow necked field mouse	2	7.30	0.0036	0.56	0.025	Hansson 1971
<i>Apodemus flavicollis</i>	Yellow necked field mouse	2	7.36	0.0015	0.22	0.006	Hansson 1971
<i>Apodemus sylvaticus</i> (L.)	Wood mouse	2	7.08	0.0066	1.01	0.058	Hansson 1971
<i>Apodemus sylvaticus</i>	Wood mouse	2	7.20	0.0147	2.18	0.063	Hansson 1971
<i>Chelithriomys glareolus</i>	Bank vole	2	7.12	0.087	12.783	0.287	Bobek 1971

Species or taxa	Group or common name	Category	Maximum live weight (log g ⁻⁶)	Mean annual biomass (kcal m ⁻²)	Assimilation (kcal m ⁻² year ⁻¹)	Production (kcal m ⁻² year ⁻¹)	Authority
<i>Chithrionomys glareolus</i>	Bank vole	2	7.16	0.028	4.004	0.112	Bobek 1971
<i>Chithrionomys glareolus</i>	Bank vole	2	7.20	0.015	2.34	0.063	Hansson 1971
<i>Chithrionomys glareolus</i>	Bank vole	2	7.28	0.018	2.77	0.051	Hansson 1971
<i>Chithrionomys glareolus</i>	Bank vole	2	7.41	0.074	11.012	0.207	Aulak 1973
<i>Chithrionomys rutilus dawsoni</i> Merriam	Red-backed vole	2	7.34	0.04	5.41	0.11	Grodziński 1971
<i>Microtus agrestis</i> (L.)	Field vole	2	7.48	0.083	10.89	0.172	Hansson 1971
<i>Microtus agrestis</i>	Field vole	2	7.48	0.203	26.73	0.423	Hansson 1971
<i>Microtus oeconomus macfarlanei</i> Merriam	Tundra vole	2	7.50	0.013	1.7	0.04	Grodziński 1971
<i>Microtus oeconomus</i>	Root vole	2	7.51	0.005	1.55	0.05	Hagen, Ostbye & Skar 1975
<i>Microtus pennsylvanicus</i> p. Ord.	Vole	2	7.46	0.286	17.52	0.517	Golley 1960
<i>Arvicola terrestris</i> (L.)	Vole	2	8.15	0.095	6.0	0.295	Pelikán 1974
<i>Arvicola terrestris</i>	Vole	2	8.15	0.139	8.3	0.39	Pelikán 1974
<i>Tamiasciurus hudsonicus preblei</i> Howell	Red squirrel	1	8.36	0.085	5.33	0.08	Grodziński 1971
<i>Spermophilus spilosoma</i>	Spotted ground squirrel	1	8.03	0.0012	0.055	0.0035	Chew & Chew 1970
<i>Amospermophilus harrisi</i>	Harris's antelope squirrel	1	8.09	0.0026	0.197	0.0105	Chew & Chew 1970
<i>Sciurus carolinensis</i>	Grey squirrel	1	8.81	1.25	67.59	0.77	Montgomery, Whelan & Mosby 1975
<i>Lepus californicus</i>	Jack rabbit	1	9.40	0.056	2.321	0.121	Chew & Chew 1970
<i>Sybilagus audubonii</i>	Desert cottontail	1	8.94	0.011	0.539	0.031	Chew & Chew 1970
<i>Cricetus cricetus</i> (L.)	Hamster	1	8.90	0.80	15.57	1.12	Gorecki 1977
<i>Loxodonta africana</i>	African elephant	1	12.7	7.10	23.3	0.34	Petrides & Swank 1965
<i>Mustela vison</i>	Least weasel	1	7.78	0.007	0.56	0.013	Golley 1960
<i>allegheensis</i> Rhoads	Shrew	1	6.58	0.005	1.22	0.01	Grodziński 1971
<i>Sorex cinereus hollisteri</i> Jackson	Shrew	1	6.65	0.0013	0.57	0.004	Hansson 1971
<i>Sorex minutus</i> (L.)	Shrew	1	6.60	0.0039	1.68	0.014	Hansson 1971
<i>Sorex minutus</i>	Shrew	1	6.60	0.0039	1.68	0.014	Hansson 1971

<i>Sorex araneus</i> (L.)	Shrew	1	7-11	0-018	5-67	0-026	Hansson 1971
<i>Sorex araneus</i>	Shrew	1	7-11	0-0239	7-73	0-035	Hansson 1971
<i>Neomys fodiens</i> (Penn)	Water shrew	2	7-15	0-0009	0-16	0-004	Hansson 1971
Aves							
<i>Passerculus sandwichensis</i> (Gmelin)	Savannah sparrow	1	7-29	0-032	3-6	0-04	Odom, Connel & Davenport 1962
Avifauna							
<i>Rutilus rutilus</i> (L.)	Roach	3	7-80	21-2	129-1	10-7	Mann 1965
<i>Alburnus alburnus</i> (L.)	Bleak	3	7-40	34-3	344-7	30-5	Mann 1965
<i>Leuciscus leuciscus</i> (L.)	Dace	3	7-76	2-8	25-4	1-5	Mann 1965
<i>Perca fluviatilis</i> (L.)	Perch	3	8-0	3-1	25-0	1-8	Mann 1965
<i>Gobio gobio</i> (L.)	Gudgeon	3	7-46	4-5	39-6	2-6	Mann 1965
<i>Notothenia neglecta</i> Nybelin		3	9-44	19-39	86-75	6-12	Everson 1970
<i>Aspius aspius</i> L.	Platice	3	9-04	0-273	1-04	0-135	Backiel 1970
<i>Hippoglossoides platessoides</i> (Fabr.)		3	9-04	6-25	11-056	2-5	MacKinnon 1973
Insecta							
<i>Glyptotendipes barbipes</i> (Staeger)	Diptera: Chironomidae	6	2-82	19-43	428-0	165-0	Kimerle & Anderson 1971
<i>Glyptotendipes barbipes</i>	Diptera: Chironomidae	6	2-82	2-12	44-0	18-0	Kimerle & Anderson 1971
<i>Glyptotendipes barbipes</i>	Diptera: Chironomidae	6	2-82	54-06	1189-0	459-0	Kimerle & Anderson 1971
<i>Glyptotendipes barbipes</i>	Diptera: Chironomidae	6	2-82	4-36	95-0	37-0	Kimerle & Anderson 1971
<i>Tipula excisa</i> Schum.	Diptera: Tipulidae	4	5-38	1-838	10-581	4-765	Hofsvang 1973
<i>Pyrrhosoma nymphula</i> (Sulz.)	Odonata: Zygoptera	4	4-5	0-934	7-605	3-94	Lawton 1971
<i>Pyrrhosoma nymphula</i>	Odonata: Zygoptera	4	4-5	1-421	7-558	3-59	Lawton 1971
<i>Potamophylax cingulatus</i> Steph.	Trichoptera	6	4-75	0-87	10-03	4-53	Otto 1975
<i>Rhynchaenus fagi</i> L.	Coleoptera: Curculionidae	4	3-15	0-539	4-208	2-199	Grimm 1973
<i>Pogonomyrmex occidentalis</i> (Cresson)	Hymenoptera: Formicoidea	7	3-48	0-104	1-07	0-108	Rogers, Lavigne & Miller 1972

Species or taxa	Group or common name	Category	Maximum live weight (log g ⁻⁶)	Mean annual biomass (kcal m ⁻²)	Assimilation (kcal m ⁻² year ⁻¹)	Production (kcal m ⁻² year ⁻¹)	Authority
<i>Pogonomyrmex occidentalis</i>	Hymenoptera: Formicoidea	7	3-48	0-126	1-31	0-138	Rogers, Lavigne & Miller 1972
<i>Pogonomyrmex occidentalis</i>	Hymenoptera: Formicoidea	7	3-48	0-140	1-45	0-153	Rogers, Lavigne & Miller 1972
<i>Pogonomyrmex occidentalis</i>	Hymenoptera: Formicoidea	7	3-48	0-014	0-14	0-014	Rogers, Lavigne & Miller 1972
Arachnida							
<i>Pardosa lugubris</i> (Walckenaer)	Araneae: Lycosidae	4	5-0	0-175	1-101	0-298	Edgar 1971
<i>Pardosa palustris</i> (L.)	Araneae: Lycosidae	4	4-20	0-079	0-104	0-035	Steigen 1975
<i>Geolycosa godeffroyi</i> (Koch)	Araneae: Lycosidae	5	6-18	0-051	0-536	0-131	Humphreys 1978
<i>Urodacus yashenkoi</i> (Birula)	Scorpionida	5	6-54	0-26	0-605	0-224	Shorthouse 1971
Crustacea							
<i>Hyalella azteca</i> (Sanssure)	Amphipoda	6	3-68	1-051	18-07	4-535	Mathias 1971
<i>Crangonyx richmondensis occidentalis</i> (Hubricht & Harrison)	Amphipoda	6	4-2	0-705	6-523	1-363	Mathias 1971
<i>Ligidium japonica</i>	Isopoda	5	4-48	3-076	19-5	3-50	Saito 1965
<i>Tracheoniscus rathkei</i> Brandt	Isopoda	4	4-57	0-636	0-928	—	White 1968
Other invertebrates							
<i>Japonaria laminata armigera</i> Verhoeff	Diplopoda	5	5-7	19-39	57-8	26-9	Saito 1967
<i>Japonaria laminata armigera</i>	Diplopoda	5	5-7	1-117	3-01	1-50	Saito 1967
<i>Lithobius forficatus</i> (L.)	Chilopoda	5	4-16	0-536	2-083	0-085	Wignarajah 1968
<i>Lithobius crassipes</i> (L. Koch)	Chilopoda	5	5-20	0-322	1-341	0-074	Wignarajah 1968
<i>Neanthus virens</i> (Sars.)	Polychaeta	4	7-32	27-9	61-9	45-2	Kay & Braefield 1973
<i>Allophthora rosea</i> (Sav.)	Oligochaeta: Lumbricidae	5	5-54	3-548	15-444	2-717	Bolton 1969
<i>Sagittia elegans</i>	Chaetognatha	—	4-48	0-75	4-75	2-3	Sameoto 1972

Mollusca									
<i>Scrobicularia plana</i> (da Costa)	Pelecypoda	4	6-69	19-3	72-1	17-5	Hughes 1970		
<i>Scrobicularia plana</i>	Pelecypoda	4	6-69	204-2	600-0	124-0	Hughes 1970		
<i>Unio tumidus</i> Philipsson	Pelecypoda	4	7-16	6-60	25-06	1-684	Tudorancea & Florescu 1968a		
<i>Unio pictorum</i>	Pelecypoda	4	7-213	14-158	32-26	1-869	Tudorancea & Florescu 1968b		
<i>Acmaea scabra</i> (Gould)	Archaeogastropoda*	4	5-0	7-42	96-0	49-0	Sutherland 1972		
<i>Acmaea scabra</i>	Archaeogastropoda*	4	5-0	8-62	153-0	103-0	Sutherland 1972		
<i>Acmaea scabra</i>	Archaeogastropoda*	4	5-0	8-68	133-0	81-0	Sutherland 1972		
<i>Ancylus fluviatilis</i> O.F. Müll.	Gastropoda: Basommatophora	6	3-30	0-71	16-69	1-877	Streit 1976		
<i>Ancylus fluviatilis</i>	Gastropoda	6	3-30	0-421	21-16	2-516	Streit 1976		

* In the Appendix of Humphreys (1979) these were placed incorrectly in the Pelecypoda but were not used in the comparison of pelecypods and gastropods (p. 430).

ERRATUM

Humphreys, W. F. Towards a simple index based on live weight and biomass predicting assimilation in animal populations. Journal of Animal Ecology, 50, 543-561.

For 'cal $m^{-2}y^{-1}$ ', read 'Cal $m^{-2}y^{-1}$ ', throughout.