Ann. Zool. Fennici 35: 231–240 ISSN 0003-455X
Helsinki 17 December 1998

The energy budget: a useful tool?

Mark S. Davies & Alison M. Hatcher

Davies, M. S. & Hatcher, A. M., Ecology Centre, University of Sunderland, Sunderland, SR1 3SD, UK.

Received 23 September 1998, accepted 9 November 1998

Studies of energy flow and allocation in biological systems often result in the production of energy budgets. Our aim is to describe the potential mis-representations that energy budgets can produce and draw together the various criticisms levied at energy budgets. While such budgets purport to represent accurately energy allocation we, by discussing the literature, propose that many offer little. This is because in practice they rarely reflect actual energy relationships due to problems with their empirical derivation. These problems include both the omission of some energy budget terms (such as dissolved organic matter, non-lethal predation and metabolic faecal loss) and their underestimation (e.g. mucus production). Recalculation of budgets to account for these terms often results in new conclusions being drawn. Moreover, problems of extrapolation of measurements made in the laboratory to the field, coupled with misconceptions over the expression of temporal and spatial variation in budget terms, produce budgets that are both approximate and specific to an individual or population at the time each budget is constructed. In addition, the set of assumptions that are used in the construction of one budget are rarely the same as those for another and so budgets should be used with extreme care in comparative studies. We suggest that energy budgets have little value in the context of other studies and are of interest and value only as descriptors under a set of what should be well-defined assumptions. We urge caution in their use and propose that more modest studies of energy allocation with precise goals are more appropriate.

1. Introduction

Studies of the flow and allocation of energy in biological systems often have as their ultimate goal the construction of a budget describing the partitioning of energy within an individual, population or community. Such budgets are then used to make inferences about physiology or ecology, in particular explaining why an organism or population does what it is observed to do, assuming that energy allocation is the overriding concern. Here we intend not to decry the use of energy budgets — indeed they often have much to offer — nor to suggest that energy flow and allocation are unimportant in our understanding of the functioning of biological systems. Rather, we will propose that in practice — as a result of empiricism — the construction of a *complete* energy budget can offer very little. Where budgets have been discussed in the literature, too little emphasis has been placed on the mechanics and pitfalls of data acquisition. The classic work of Odum (1963) for example, offered an excellent introduction to ecological energetics, but the methods for ensuring that useful data are collected was not an issue. Similarly Lucas (1996) gave a more practically-oriented account of energy flow, but the limitations of the techniques described were not fully addressed.

Like most scientific topics, the empirical attention paid by biologists to energy budgets has fluctuated markedly over time. In the 1960s energy budgets were thought of as a valuable approach (Slobodkin 1962, Odum 1963) and were widely used in descriptive studies. This use continued in the 1970s and early 1980s, but waned in the mid to late 1980s (Science Citation Index). In the 1990s there has been a dramatic increase in the use of energy budgets and perhaps this is linked with their use in applied studies, such as the determination of 'scope for growth' (*see* below) and attempts to increase the yield of commercially valuable biological products. However, the resurgence of interest in studies of energy flow has thus far failed to appreciate some of the fundamental ways in which energy budgets can misrepresent and can produce information that may be misunderstood and taken out of context. The aim here is to describe these potential mis-representations and to draw together the numerous criticisms of energy budgets. We are not suggesting that authors have failed to point out potential shortcomings in their work, but we present a synthesis of ideas urging caution and improvements in technique. We hope that this paper will have points to make that are relevant and applicable to any habitat, but as our backgrounds are in coastal and marine biology, most references and illustrations are from this field and we will use mucus production as an example component of energy budgets.

The end-product of energy flow studies is often a budget from which numerous conclusions are usually drawn. These budgets may describe energy partitioning within a single organism (individual energy budgets), energy flow through a population of a single species (population energy budgets), or energy transfer between trophic levels (community/ecosystem energy budgets). The first two types of budget describe physiological energetics, the third type, ecological energetics (Grodzinski *et al.* 1975). The animal/population/community is usually considered for the purposes of measurement as a steady-state system through which potential energy passes (Slobodkin 1962). Energy is measured as chemical potential energy by calorimetry: thus the addition of energy to an organism by heating, for example by the sun, would not in itself affect the energy budget. A typical energy budget might be,

$$C = P + R + F + U \qquad (1),$$

where C is energy consumed, P is energy allocated to production (often split into P_r: reproductive production, the energy of shed gametes or offspring, and P_g: tissue growth, including that of the gonads), R is energy required for metabolic purposes, e.g., respiration (released eventually as heat), F is energy as faeces and U is energy as waste materials, typically nitrogenous in nature. Clearly, energy budgets should balance: the magnitude of the term on the left-hand side of the equation equalling the sum of those on the right-hand side. But all too often energy budgets, even the simplest — those for a single organism — fail to balance (e.g., Wright & Hartnoll 1981, Horn 1986, Peck *et al.* 1987, Davies *et al.* 1990a, *see* Carefoot 1988). Sometimes balance is forced by omitting to measure a term then obtaining its value by interpolation from the other terms (e.g., Wright & Hartnoll 1981, Blandenier & Perrin 1989, Plaut *et al.* 1996) — clearly an unsatisfactory situation. The reasons for lack of balance fall into two broad categories which we will discuss in turn: the omission or underestimation of the value of some energy budget terms; and that energy budgets can be inaccurate or imprecise. The conclusions drawn from energy budgets may have limited value because of a lack of balance and because of the unique nature of each constructed budget. This we will also address.

2. Unassessed and underassessed terms

As discussed above, the energy budget (Petrusewicz 1967) commonly fails to account for all forms of gain and loss of chemical potential energy. Some of these might be small and have no significant effect on the overall budget, but since diversity in form and function is great, many organisms have some overlooked term as a significant part of their energy budget.

Non-lethal predation is rarely accounted for. It would seem clear that the energy budget of a pasture should take into account the effects of grazing, yet although many animals themselves are 'grazed' (e.g., Duarte & Cebrian 1996), few budgets include this term where it is appropriate. An exception is the study by Trevallion (1971) on the bivalve *Angulus (Tellina) tenuis*, whose siphons are grazed by fish.

Consumed energy may be thought of as easy to measure, and in the majority of cases probably is. But many organisms (of at least eleven phyla, *see* Stephens 1967) can take up dissolved organic matter directly across the body surface. In some organisms (*see* e.g., Wright & Secomb 1986) this is the only mode of nutrition, but in others, where it forms a minor route of energy input (*see* e.g., Stephens 1983), it is routinely ignored. Likewise, dissolved organic matter may form a significant route for energy loss (e.g., Johannes & Satomi 1967, Thomas & Eaton 1998), and again is routinely ignored. Whether it is important to include dissolved organic matter in studies on energetics will depend on the stated aims, but it should at least be considered.

In measuring unassimilated material, or faeces (F), it is common practice to assume that material is only taken from, and not added to, the contents of the gut as they pass from mouth to anus. Yet faeces commonly contain digestive juices, sloughed-off intestinal cells, bacteria and lubricatory mucus. Indeed faeces are often surrounded by a 'faecal envelope' comprised largely of mucus. These additions to the gut (termed 'metabolic faecal losses') are rarely accounted for (but *see* Edwards & Welsh 1982) and are thought to represent as much as 20% of assimilated energy in bivalves (*see* Bayne *et al.* 1989).

In aquatic studies nitrogenous waste (U) is rarely measured and is often assumed to be negligible (e.g., Hughes 1970, 1971). Where it has been measured (e.g., Wright & Hartnoll 1981, for a limpet), it has been found to represent only a small proportion of the overall energy budget, but the omission of U will nevertheless contribute a small amount to the overall inaccuracy of the budget. For other groups the U term can be a significant sink for consumed energy, e.g., anemones (Zamer & Shick 1987). Another commonly overlooked component of energy balance is the energy partitioned into solid skeletal material. In terrestrial and marine environments, the energy required to form skeletons is often negligible as material (typically calcium salts) may be passively sequestered from food or water, respectively. In freshwater, a specific, energy-requiring mechanism may be necessary, but the energy involved will be measurable as the R term. Nevertheless, some metabolised energy will be stored in the skeleton (or perhaps lost as teeth or radular components) and this energy is usually unaccounted for, although Edwards and Welsh (1982) recorded energy stored in shell periostracum for the mud snail *Ilyanassa obsoleta*. Typical structures involved are the shells, opercula and byssus of molluscs, the carapaces of arthropods and bristles of annelids. Again, whether these components need to be assessed will depend on the nature of the study.

Secreted products are also commonly overlooked. These include cnidarian nematocysts, toxins, antifoulants, inks and other defensive or offensive substances and perhaps should include desquamation. Surprisingly, however, the substance whose omission has led to arguably the most serious errors in budget construction is one that is ubiquitous: mucus. Calow (1974), Richardson (1975), Edwards and Welsh (1982), Horn (1986), Peck *et al.* (1987), Davies *et al.* (1990a), Kideys and Hartnoll (1991), Scheu (1991), Riegl and Branch (1995), Navarro and Torrijos (1995) and Smith and Davies (1995) have demonstrated the important role of mucus in energy flow for those organisms which use mucus, mostly as a locomotory agent. In each case mucus production accounted for a considerable proportion of energy turnover (up to 68% of ingested energy, Horn 1986). Bayne and Newell (1983) included mucus as part of U; Richardson (1975), Branch (1981) and Horn (1986) thought of mucus as representing produced energy and so expressed it as P_{m} or P_{muc}; Deslous-Paoli *et al.* (1990) included bivalve pseudofaeces (which have a large mucus component) as part of F; Hawkins and Hartnoll (1983) advocated a secretions (S) term to cover urine (S_{u}), mucus (S_{m}), dissolved organic matter (S_{do}) and exuviae (S_{e}); whilst Peck *et al.* (1987) and Davies *et al.* (1990a) separated mucus to its own term, M. Despite these researches, the lack of incorporation of mucus in energy budgets is common (e.g., Barkai & Griffiths 1988, Carefoot 1989, Wilbur & Hilbish 1989, Grant 1996). This lack has resulted from both an underestimation of the role of mucus and to technical difficulties in its measurement (*see* Paine 1971, Bayne & Newell 1983), although the latter is clearly surmountable. Mucus production may have been ignored because of its typically steady, slow rate of release, which is not as apparent an energy drain as other energy budget components. Mucus is, of course, not limited in function to locomotion and such a ubiquitous substance may be important in other organisms which do not rely on it for locomotion (*see* Davies & Hawkins 1998 for review). In the Mollusca this would include those species which use mucus in food capture (often suspension feeders, *see* e.g., Fretter & Graham 1994), particularly the bivalves, in which much energy (unaccounted for in most energy budgets) is released to the environment as the mucus which forms pseudofaeces (*see* Bayne & Newell 1983); or those that use mucus as a defence (e.g., Reel & Fuhrman 1981). Fish commonly employ skin mucus both as a drag-reducing agent and as a defence (Shephard 1994), though we have been unable to find mucus included in the energy budget of a fish (e.g., Cui *et al.* 1992).

When a mucus term is inserted into an otherwise unaltered energy budget, the information the budget presents, and hence the conclusions reached by empiricists, change. Taking the revision (Davies *et al.* 1990a) of an energy budget compiled for the limpet *Patella vulgata* (Wright & Hartnoll 1981), the assimilation efficiency increases from 41% to 45% and the animal is thus regarded as more efficient at extracting energy from food. A smaller amount of consumption is perceived to be allocated to those energy losses other than mucus. This means, for example, that the animal appears not to channel as much of consumption into growth and gamete production (10% to 3%), but also appears to operate more efficiently than was previously thought by utilising a smaller proportion of assimilated energy in respiration (31% to 10%). Changes such as these upon simple recalculation can have major effects on the way animals are thought to operate, depending on whether the magnitude of each change is considered as important. This scenario may suggest that other energy budgets are in need of similar revision. However, such may not lead to meaningful results since it would also seem apparent that small errors in budget construction could easily lead to grossly aberrant conclusions. Thus conclusions drawn from budgets, not least for this reason, should be treated as speculative. For example, mucus is clearly a complex multifunctional product which should be incorporated into individual, population and community energy flow studies (Branch 1981, Hawkins & Hartnoll 1983) with due regard to the seasonal variation in its composition and production. Before such incorporation, however, the validity and usefulness of the energy flow study should be critically assessed.

3. Approximations

The quantification of the total metabolic processes of animals *in situ* is a very difficult task, yet this is the goal of physiological energetics. Direct measurement in the animal's environment is the preferable approach (Petrusewicz & Macfadyen 1970), but this is rarely possible because of the number of confounding factors present and the technical difficulties of obtaining data, e.g., during flight or swimming. Extrapolation from the laboratory to field situations may then be necessary, but may not be accurate for two reasons: stress and an inaccurate mimicking of field conditions in the laboratory (which may induce stress). For example, problems in extrapolation of laboratory-assessed pedal mucus production by intertidal grazers lie in differential animal behaviour (since mucus is produced as these animals locomote) and in the simulation of shore conditions. Also, the act of moving animals from field to laboratory may cause stress that persists through the experimental procedure. Unfortunately, in many cases there is a lack of information enabling experimenters to assess the degree of such stress and its effects on the parameter under investigation. Likewise, it is difficult to assess *from the test organism's perspective* how different the simulated environment is from the real one and how this affects the measurements made. For example, Davies *et al.* (1990a), Davies (1993) and Niu *et al.* (1998) measured mucus production from intertidal limpets adhering to, or moving on, glass.

It is likely that the intertidal substratum will be a good deal rougher than glass and mucus production may have been underestimated since it has been shown to increase with substratum particle size (Culley & Sherman 1985), the mucus perhaps filling troughs between the particles. Such problems will be a factor in almost all laboratory experiments, but are particularly important where the results obtained are used in energy budget calculations.

Consumption has been measured in the laboratory under '*ad libitum*' conditions of food supply (e.g., Blandenier & Perrin 1989, Cui & Liu 1990, Cui *et al.* 1996, Niu *et al.* 1998), though this may not result in an over-consumption of food in such circumstances because of the effects of stress on laboratory subjects. In measuring the R term, experimenters may fail to realise that a respirometer (or telemetric devices) may not be conducive to normal activity; and where they do, a guessed correction factor may be applied (e.g., Trevallion 1971, Wright & Hartnoll 1981). Furthermore, even those methods of assessing energy flow which rely on a time-budget technique, estimating the energy cost of, and time spent doing, each activity (e.g., Chew & Chew 1970, *see* Nagy 1989) suffer from the same constraints. Time-budgeting also relies on accurate recording of time spent in each activity (which is difficult to estimate for individuals, let alone a population or community) and can be very difficult to apply to poikilotherms (Phillipson 1963) where metabolic activity is dependent on environmental temperature. Thus energy budgets tend to be crude approximations of energy allocation.

Energy budgets for individuals are usually expressed as energy per unit time and population energy budgets as energy per unit area (or volume) per unit time. The latter presents difficulties involving the calculation of recruitment, mortality, immigration and emigration, and in selecting a suitably-sized area over which to conduct the study. In many cases energy budgets constructed for individuals are merely multiplied by the population density to arrive at population budgets (e.g., Deslous-Paoli *et al.* 1990), although typically some regression is computed between each budget component and size of organism in an attempt to take into account the size-structure of the population (e.g., Wright & Hartnoll 1981, Khalil *et al.* 1995). Aside from errors of scaling (*see* below), this, and any population-based approach, may be difficult to apply if within the population there are variations in density and the population boundaries, such as those found along a long stretch of rocky shore or those for mobile or planktonic species, are not clearly demarked by physical or biological barriers. Hence, in effect, the population budget may only refer to the very small area whose population was sampled and not the population the study aimed to investigate (*see* e.g., Hughes 1970). Furthermore, populations tend to be studied within their zone of maximum abundance, hence extrapolations over wider areas are prone to overestimation. Should a series of such studies be combined to obtain estimates of community energy flow, a gross overestimation may result since it is unlikely that all species will have convergent zones of maximum abundance.

The time period over which a budget is expressed should be the period over which the budget is calculated. Most budgets are expressed per year (although this may not be sufficient for mammals with a gestation period that is greater than 12 months), but few budgets embody annual variation in all their terms and so are approximate (e.g., Hughes 1971, Wright & Hartnoll 1981, Barkai & Griffiths 1988), although most embody seasonal variation in P_r with the reproductive cycle. Wright and Hartnoll (1981), for example, found considerable variation in C depending on time of year, yet in many budgets year-round variation in energy intake is not addressed (e.g., Barkai & Griffiths 1988). Returning to mucus, both the calorific value of gastropod pedal mucus (Davies *et al.* 1990b) and its production rate (Davies, 1993) vary temporally and again these have not been addressed in energy budgets. Clearly, not only can the magnitude of budget terms change, but so too can their calorific value. Most budget terms are converted from carbon or weight values to calorific values based on a single set of calorific determinations, without temporal replication (e.g., Edwards & Welsh 1982). Presumably all energy budget terms will vary temporally, making accurate energy flow calculation very difficult.

Energy budget terms may also vary spatially, presumably with differences in habitat, and with the incidence of pollution. Spatial variation in limpet mucus production occurs with shore height and exposure (Davies 1993). Spatial variation in consumption will depend on the availability of food, which may often be spatially and temporally patchy (e.g., Hawkins & Hartnoll 1983). Exposure to heavy metal pollution has been shown to have considerable effects on energy balance (e.g., Davies 1992, Khalil *et al.* 1995, Wicklum & Davies 1996), typically reducing P_g. Turbidity can have dramatic effects on the energy balance of corals (Riegl & Branch 1995). Energy budgets will be very sensitive to pollution because of the effect of pollutants on metabolic processes (*see* Ruivo 1972, Cole 1979, Vernberg *et al.* 1979). Locomotory mucus production will also vary with foraging behaviour which varies with habitat (*see* Little 1989) and perhaps microhabitat (Davies 1991). Thus energy budgets are specific to an individual or population at the time the budget is compiled and should only be used with extreme caution in comparative studies. Of course, the accuracy required in energy budgets will depend on the aims of any study and the use to which the data will be put. Clearly then some budgets are not designed to be comparable to others. Nevertheless it is hence very important that experimentalists give indications of error to facilitate the utility of their studies.

4. Uniqueness

It should be clear from the above that energy budgets are dynamic. Any energy budget, therefore, should be expressed as specific to a particular time: a ‘snapshot’ of energy flow. Unfortunately, during the time required to accurately compile a budget there is likely to be some shift in the values of terms, resulting in measurements over a period that could not be described as steady-state. Thus the suggestion of Slobodkin (1962) that the biological system under investigation “is considered as steady-state” results in an oversimplification both because these systems are not energetically stable, and because measurements cannot be made quickly enough before the system shifts.

Population energy budgets are, of course, uniquely dependent on the structure of the population they describe (e.g., Workman 1983, *see* Bayne & Newell 1983). For example, because of the allometry of the area of the pedal sole with animal size, larger gastropods will produce proportionately less locomotory mucus than will smaller conspecifics. Similar variations with size are likely to occur for other energy budget terms. Thus equal density — or biomass — between populations may not indicate equal population energy budgets, even though the populations are in similar habitats. For similar reasons, long-term changes in the structure of a population may be accompanied by changes in its energy budget. In addition, density itself can affect the magnitude of budget terms. For example, terrestrial and marine snails have been shown to have different movement patterns (*R* terms) and mucus production rates when kept at differing densities (Dan & Bailey 1982, Siddall 1984). Thus, the structure of populations renders each population energy budget difficult to compare with other budgets, and simply scaling budget terms to take into account population size might not be sensible.

Energy budgets for individuals avoid many of the above problems and could, to avoid scaling problems, be standardised to a hypothetical mature animal of a given size. This, however, leads to nonsense when, for example, comparing a 1 g mouse with a 1 g elephant. Differences between more closely related species, such as two intertidal molluscs, may be better expressed (especially if one animal is naturally mature at 1 g while the other has had maturity imposed upon it at this size) in other terms that do not require as much effort to determine, such as morphometrics or direct observation on behaviour. Similarly, single populations might be better described by models involving energetic constraints with due regard to behaviour (e.g., Santini *et al.* 1995). Thus individual energy budgets, which also take much time and effort to construct, may also be of limited value.

Energy budgets also tend to be unique since it is unlikely that the group of assumptions involved in forming one budget will be the same as those involved in forming another. These include those described above plus others such as, for example, assuming that there is a linear relationship between *R* and temperature. These assumptions further reduce the comparative usefulness of energy budgets, as do methodological errors which are common in budget construction. Such errors include the confusion of absorption with assimilation (e.g., Conover 1966, Grahame 1973, Blandenier & Perrin 1989); the misconception that P_r includes growth of gonad tissue (which should be included in P_g) (e.g., Davis & Wilson 1985); and the lack of accurate definition of terms, such as ignoring the role of dissolved organic matter and metabolic faecal losses.

In applied studies, particularly those of bivalves, (e.g., Bayne *et al.* 1987) a surrogate for growth ('scope for growth') is often determined as an index of physiological condition, since it gives an instantaneous measure of production that can be repeated on the same animal. Note that the way in which scope for growth is calculated (typically as $C - R + F + U$) implies it is an index of total production, not just P_g. The definition of scope for growth usually omits terms such as mucus, dissolved organic matter and metabolic faecal loss (e.g., Garton 1986, Magnusson *et al.* 1988), but its value can be affected by these terms (e.g., Navarro & Torrijos 1995) and is a reason why (Zamer & Shick 1987) large discrepancies have been found between actual growth and scope for growth (e.g., Hummel 1985). The labile factors already discussed rendering energy budgets open to question apply equally to the scope for growth, so this term must also be viewed with suspicion.

5. Conclusions

At its outset physiological energetics was thought to be a valuable approach with which to assess a species's contribution to community function and energy structure (Slobodkin 1962, Odum 1963), from which useful conclusions could be drawn. Whilst this is true, we have tried to show that while the accurate production of a complete energy budget is possible (just), its use is restricted. Slobodkin (1962) wrote: "no single measurement is intrinsically significant. All measurements derive their interest from their context and the richness of predictive generalization that can be produced from them", and suggested that energy budgets have little value in themselves and are of interest only in the context of other studies. Slobodkin's words are clearly true, yet here we suggest that energy budgets have little value in the context of other studies and are of interest only as descriptors under a set of what should be well-defined assumptions. Slobodkin (1962) also commented that experimentalists need to assess whether a study of energetics is worthwhile in terms of its ecological significance. Many excellent studies concerning energy flow have been performed whose methods are adequate for the stated aims and whose data, taken in context, are valid. Often the construction of an energy budget is unnecessary to accomplish a stated scientific goal and brings with it problems that experimentalists need not encounter. We have no doubt that an accurate description of energy flow in terms of a budget is useful; we are concerned that the arrival at that goal may not be worth the trouble as it very difficult to achieve in practice. This is not to say that all published studies are at fault — indeed many are exceptionally valuable, particularly in developing new insights and approaches — merely that they should be examined carefully. Schrödinger (1946) asked, ".... surely, any calorie is worth as much as any other calorie? One cannot see how a mere exchange could help." The point here is that it is possible that the majority of living systems are not limited by the availability of energy, but by the availability of some other quantity, such as carbon (perhaps some plants), nitrogen or calcium (perhaps some freshwater molluscs or arthropods) and that their metabolism is not structured to conserve and direct allocation of energy, but to conserve and direct allocation of the other limiting factor. If that limiting factor is one of those listed above, then it is probably much easier to measure than energy and perhaps it is here that attention should be directed. In any case, Ansell (1982), on observing imbalance in an energy budget he had constructed, suggested, with good reason, that metabolically useful energy yielded by physiological processes from ingested substances was considerably less than that yielded in calorimeters.

The consequences of ignoring mucus in physiological energetics also affect ecological energetics, the study of energy transfer between trophic levels (Crisp 1984). This may be one reason why energy budgets for 'large scale ecosystems' have 'not balanced at all closely' (Crisp 1984). Estimates of the energy available to trophic levels may have been miscalculated and the role of mucus in microtrophic energetics and ecology ignored. The loss of energy as mucus, perhaps at more than one trophic level, is a factor rarely considered which may contribute to the typically low ecological efficiencies and, perhaps, the shortness of food chains (Phillipson 1966, Pimm 1982).

Further work on energy flow could be directed towards modest yet thorough studies, including those that do not attempt to construct a full budget, but which ask precise questions about energy allocation. If a budget is desired, an approach may be to use an energy budget for a standardised individual consuming a particular diet to predict energy budgets for other sized individuals and even a whole population (assuming the same diet). Again this would embody many assumptions since Dan and Bailey (1982) have shown ingestion rate in *Helix aspersa* to vary with population density and Sutherland (1972) has shown individuals on the edge of the range of *Acmaea scabra* (limpet) to have faster growth rates than those in the centre of the range. Nevertheless, this may be at least as realistic a model of energy flow as that derived through many empirical assumptions. The rationale is as follows. Given the standardised energy budget of, for example, the limpet *Patella vulgata*, the magnitude of any term could be predicted for an animal of any size, providing the relationship between that term and size is known. R and U are dependent on the amount of tissue present and should vary with weight (or length^3). M in moving animals is a function of length (weight$^{1/3}$) and in stationary animals is a function of area (weight$^{2/3}$) and so M could be calculated from observations on time spent in activity. Preliminary data on how P_r and P_g increase with age in *P. vulgata* are given by Wright (1977) and Wright and Hartnoll (1981). The relationship between absorption efficiency (for F) and size would need to be determined, but F is probably proportional to weight. Of course, variations with environmental factors might need to be investigated too. This approach has the advantage that if it compares well with empirical studies it could lead to a faster and easier evaluation of energy allocation with less destructive sampling.

Use of the energy budget as a tool in ecology appears to be on the increase and many useful and informative studies have been performed. But we urge caution lest it become a mis-representation of biological phenomena. If it is necessary to construct an energy budget then its derivation and hence its limitations should be explored in full.

Acknowledgements: We thank W.W. Arthur for comments on an early draft and S.J. Hawkins and H.D. Jones for comments on an extremely early draft.

References

Ansell, A. D. 1982: Experimental studies of a benthic predator-prey relationship. II. Energetics of growth and reproduction, and food-conversion efficiencies, in long-term cultures of the gastropod drill Polinices alderi (Forbes) feeding on the bivalve Tellina tenuis da Costa. — J. Exp. Mar. Biol. Ecol. 61:1–29.

Barkai, R. & Griffiths, C. L. 1988: An energy budget for the South African abalone Haliotis midae Linnaeus. — J. Moll. Stud. 54: 43–51.

Bayne, B. L., Hawkins, A. J. S. & Navarro, E. 1987: Feeding and digestion by the mussel Mytilus edulis L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. — J. Exp. Mar. Biol. Ecol. 111: 1–22.

Bayne, B. L., Hawkins, A. J. S., Navarro, E. & Iglesias, I. P. 1989: Effects of seston concentration on feeding, digestion and growth in the mussel Mytilus edulis. — Mar. Ecol. Prog. Ser. 5: 47–54.

Bayne, B. L. & Newell, R. C. 1983: Physiological energetics of marine molluscs. — In: Wilbur, K. M. (ed), The Mollusca, Volume IV: Physiology Part 1: 109–139.

Blandenier, P. & Perrin, N. 1989: A comparison of the energy budgets of two freshwater pulmonates: Lymnaea peregra (Müller) and Physa acuta (Drap.). — Rev. Suisse Zool. 96: 325–333.

Branch, G. M. 1981: The biology of limpets: physical factors, energy flow and ecological interactions. — Oceanogr. Mar. Biol. Ann. Rev. 19: 235–380.

Calow, P. 1974: Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods, Ancylus fluviatilis Müll. and Planorbis contortus Linn. — Oecologia 16: 149–161.

Carefoot, T. H. 1988: Gastropoda. — In: Pandian, T. J. & Vernberg, F. J. (eds), Animal energetics, Volume 2. Bivalvia through Reptilia: 89–172.

Carefoot, T. H. 1989: A comparison of time/energy budgeting in two species of tropical sea hares Aplysia. — J. Exp. Mar. Biol. Ecol. 131: 267–282.

Chew, R. M. & Chew, A. E. 1970: Energy relationships of the mammals of a desert shrub (Larrea tridentata) community. — Ecol. Monogr. 40: 1–21.

Cole, H. A. 1979: The assessment of sublethal effects of pollutants in the sea. A Royal Society Discussion. — The Royal Society, London.

Conover, R. J. 1966: Assimilation of organic matter by zooplankton. — Limnol. Oceanogr. 11: 338–345.

Crisp, D. J. 1984: Energy flow measurements. — In: Holme, N. A. & McIntyre, A. D. (eds), Methods for the study of marine benthos. 2 ed.: 284–372.

Cui, Y., Chen, S. & Wang, S. 1996: Effect of body size on the growth and energy budget of young grass carp (Ctenopharyngodon idella Val.). — Acta Hydrobiologica Sinica 20: 172–177.

Cui, Y. & Liu, J. 1990: Comparison of energy budget among six teleosts IV. Individual differences in growth and energy budget. — Comp. Biochem. Physiol. A: Comp. Physiol. 97: 551–554.

Cui, Y., Liu, X., Wang, S. & Chen, S. 1992: Growth and energy budget in young grass carp, Ctenopharyngodon idella Val., fed plant and animal diets. — J. Fish Biol. 41: 231–238.

Culley, M. & Sherman, K. 1985: The effect of substrate particle size on the production of mucus in Haliotis tuberculata L. and the importance of this in a culture system. — Aquaculture 47: 327–334.

Dan, N. & Bailey, S. E. R. 1982: Growth, mortality, and feeding rates of the snail Helix aspersa at different population densities in the laboratory, and the depression of activity of helicid snails by other individuals, or their mucus. — J. Moll. Stud. 48: 257–265.

Davies, M. S. 1991: Studies on mucus from intertidal gastropods with reference to energy budgets. — Ph.D. Thesis, University of Manchester, England.

Davies, M. S. 1992: Heavy metals in seawater: effects on limpet mucus production. — Wat. Res. 26: 1691–1693.

Davies, M. S. 1993: Energetic implications of variation in pedal mucus production by Patella vulgata L. — Veliger 36: 203–208.

Davies, M. S. & Hawkins, S. J. 1998: Mucus from marine molluscs. — Adv. Mar. Biol. 34: 1–71.

Davies, M. S., Hawkins, S. J. & Jones, H. D. 1990a: Mucus production and physiological energetics in Patella vulgata L. — J. Moll. Stud. 56: 499–503.

Davies, M. S., Jones, H. D. & Hawkins, S. J. 1990b: Seasonal variation in the composition of pedal mucus from Patella vulgata L. — J. Exp. Mar. Biol. Ecol. 144: 101–112.

Davis, J. P. & Wilson, J. G. 1985: The energy budget and population structure of Nucula turgida in Dublin Bay. — J. Anim. Ecol. 54: 557–571.

Deslous-Paoli, J.-M., Boromthanarat, S., Héral, M., Boromthanarat, W. & Razet, D. 1990: Energy budget of a Mytilus edulis population during its first year on bouchots in the bay of Marennes-Oléron. — Aquaculture 91: 49–63.

Duarte, C. M. & Cebrian, J. 1996: The fate of marine autotrophic production. — Limnol. Oceanogr. 41: 1758–1766.

Edwards, S. F. & Welsh, B. L. 1982: Trophic dynamics of a mud snail (Ilyanassa obtsoleta (Say)) population on an intertidal mudflat. — Estuar. Coast. Shelf Sci. 14: 663–686.

Fretter, V. & Graham, A. 1994: British prosobranch molluscs. — The Ray Society, London.

Garton, D. W. 1986: Effect of prey size on the energy budget of a predatory gastropod, Thais haemastoma canaliculata (Gray). — J. Exp. Mar. Biol. Ecol. 98: 21–33.

Grahame, J. 1973: Assimilation efficiency of Littorina littorea (L.) (Gastropoda: Prosobranchiata). — J. Anim. Ecol. 42: 383–389.

Grant, J. 1996: The relationship of bioenergetics and the environment to the field growth of cultured bivalves. — J. Exp. Mar. Biol. Ecol. 200: 239–256.

Grodzinski, W., Klekowski, R. Z. & Duncan, A. 1975: Methods for ecological energetics. — Blackwell Scientific, Oxford.

Hawkins, S. J. & Hartnoll, R. G. 1983: Grazing of intertidal algae by marine invertebrates. — Oceanogr. Mar. Biol. Ann. Rev. 21: 195–282.

Horn, P. L. 1986: Energetics of Chiton pelliserpentis (Quoy and Gaimard, 1835) (Mollusca: Polyplacophora) and the importance of mucus in its energy budget. — J. Exp. Mar. Biol. Ecol. 101: 119–141.

Hughes, R. N. 1970: An energy budget for a tidal-flat population of the bivalve Scrobicularia plana (Da Costa). — J. Anim. Ecol. 39: 357–381.

Hughes, R. N. 1971: Ecological energetics of the keyhole limpet Fissurella barbadensis Gmelin. — J. Exp. Mar. Biol. Ecol. 6: 167–178.

Hummel, H. 1985: An energy budget for a Macoma balthica (Mollusca) population living on a tidal flat in the Dutch Wadden Sea. — Netherl. J. Sea Res. 19: 84–92.

Johannes, R. E. & Satomi, M. 1967: Measuring aquatic matter retained by aquatic invertebrates. — J. Fish. Res. Bd. Can. 24: 2467–2471.

Khalil, M. A., Donker, M. H. & van Straalen, N. M. 1995: Long-term and short-tern changes in the energy budget of Porcellio scaber Latreille (Crustacea) exposed to cadmium polluted food. — Euro. J. Soil Biol. 31: 163–172.

Kideys, A. E. & Hartnoll, R. G. 1991: Energetics of mucus production in the common whelk Buccinum undatum L. — J. Exp. Mar. Biol. Ecol. 150: 91–105.

Little, C. 1989: Factors governing patterns of foraging activity in littoral marine herbivorous molluscs. — J. Moll. Stud. 55: 273–284.

Lucas, A. 1996: Bioenergetics of aquatic animals. — Taylor & Francis, London.

Magnusson, K., Berggren, M. & Granmo, A. 1988: Energy budget of caged common mussels (Mytilus edulis) in the vicinity of an industrial centre on the Swedish west coast. — Vatten 44: 59–64.

Nagy, K. A. 1989: Field bioenergetics: accuracy of models and methods. — Physiol. Zool. 62: 237–252.

Navarro, J. M. & Torrijos, R. A. 1995: Fisiología energética de Concholepas concholepas (Bruguière, 1789) (Gastropoda: Muriciae) en la bahia de Yaldad, sur de Chile. — Revista Chilena de Historia Natural 68: 61–77.

Niu, C.-J., Nakao, S. & Goshima, S. 1998: Energetics of the limpet Lottia kogamogai (Gastropoda: Acmaeidae) in an intertidal rocky shore in southern Hokkaido, Japan. — J. Exp. Mar. Biol. Ecol. 224: 167–181.

Odum, E. P. 1963: Ecology. — Holt, Rinehart and Winston, New York.

Paine, R. T. 1971: Energy flow in a natural population of the herbivorous gastropod Tegula funebralis. — Limnol. Oceanogr. 16: 86–98.

Peck, L. S., Culley, M. B. & Helm, M. M. 1987: A laboratory energy budget for the ormer Haliotis tuberculata L. — J. Exp. Mar. Biol. Ecol. 106: 103–123.

Petrusewicz, K. 1967: Suggested list of more important concepts in productivity studies. — In: Petrusewicz, K. (ed.), Secondary productivity in terrestrial ecosystems Vol. I: 51–82.

Petrusewicz, K. & Macfadyen, A. 1970: Productivity of terrestrial animals, principles and methods. — Blackwell Scientific, Oxford.

Phillipson, J. 1963: The use of respiratory data in estimating annual respiratory metabolism, with particular reference to Leiobunum rotundum (Latr.) (Phalangida). — Oikos 14: 212–223.

Phillipson, J. 1966: Ecological energetics. — Edward Arnold, London.

Plaut, I., Borut, A. & Spira, M. E. 1996: Lifetime energy budget in the sea hare Aplysia oculifera. — Comp. Biochem. Physiol. 113A: 205–212.

Pimm, S. L. 1982: Food webs. — Chapman and Hall, London.

Reel, K. R. & Fuhrman, F. A. 1981: An acetylcholine antagonist from the mucous secretion of the dorid nudibranch, Doriopsilla albopunctata. — Comp. Biochem. Physiol. 68C: 49–53.

Richardson, A. M. M. 1975: Energy flux in a natural population of the land snail Cepaea nemoralis L. — Oecologia 19: 141–164.

Riegl, B. & Branch, G. M. 1995: Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. — J. Exp. Mar. Biol. Ecol. 186: 259–275.

Ruivo, M. 1972: Marine pollution and sea life. — Fishing News (Books) Ltd., West Byfleet, Surrey, England.

Santini, G., Chelazzi, G. & Della Santina, P. 1995: Size-related functional and energetic constraints in the foraging of the limpet Patella vulgata (Mollusca, Gastropoda). — Func. Ecol. 9: 551–558.

Scheu, S. 1991: Mucus excretion and carbon turnover of endogeic earthworms. — Biol. Fert. Soil. 12: 217–220.

Schrödinger, E. 1946: What is life? — Macmillan, New York.

Shephard, K. L. 1994: Functions for fish mucus. — Rev. Fish Biol. Fish. 4: 401–429.

Siddall, S.E. 1984: Density-dependent levels of activity of juveniles of the queen conch Strombus gigas Linné. — J. Shellfish Res. 4: 67–74.

Slobodkin, L. B. 1962: Energy in animal ecology. — Adv. Ecol. Res. 1: 69–101.

Smith, D. E. C. & Davies, R. W. 1995: Effects of feeding frequencies on energy partitioning and life history of the leech Nephelopsis obscura. — J. N. Am. Benthological Soc. 14: 563–576.

Stephens, G. C. 1967: Dissolved organic material as a nutritional source for marine and estuarine invertebrates. — In: Lauff, G. H. (ed.), Estuaries: 367–373. American Association for the Advancement of Science, Washington D.C.

Stephens, G. C. 1983: Dissolved organic material and the nutrition of marine bivalves. — In: Pruder, G. D. (ed.), Proceedings of the Second International Conference on Aquaculture: Nutrition: 338–357. Louisiana State University, Baton Rouge.

Sutherland, J. P. 1972: Energetics of high and low populations of the limpet, Acmaea scabra (Gould). — Ecology 53: 430–437.

Thomas, J. D. & Eaton, P. 1998: The origins, fate and ecological significance of free amino compounds released by freshwater pulmonate snails. — Comp. Biochem. Physiol. 119A: 341–349.

Trevallion, A. 1971: Studies on Tellina tenuis Da Costa. III. Aspects of general biology and energy flow. — J. Exp. Mar. Biol. Ecol. 7: 95–122.

Vernberg, W. B., Thurberg, F. P., Calabrese, A. & Vernberg, F. J. 1979: Marine pollution: functional responses. — Academic Press, London.

Wicklum, D. & Davies, R. W. 1996: The effects of chronic cadmium stress on energy acquisition and allocation in a freshwater benthic invertebrate predator. — Aquat. Toxicol. 35: 137–252.

Wilbur, A. E. & Hilbish, T. J. 1989: Physiological energetics of the ribbed mussel Geukensia demissa (Dillwyn) in response to increased temperature. — J. Exp. Mar. Biol. Ecol. 131: 161–170.

Workman, C. 1983: Comparisons of energy partitioning in contrasting age-structured populations of the limpet Patella vulgata L. — J. Exp. Mar. Biol. Ecol. 68: 81–103.

Wright, J. R. 1977: The construction of energy budgets for three intertidal rocky shore gastropods Patella vulgata, Littorina littorea and Nucella lapillus. — PhD thesis, University of Liverpool, England.

Wright, J. R. & Hartnoll, R. G. 1981: An energy budget for a population of the limpet Patella vulgata. — J. Mar. Biol Assoc. U.K. 61: 627–646.

Wright, S. R. & Secomb, T. W. 1986: Epithelial amino acid transport in marine mussels; role in net exchange of taurine between gills and seawater. — J. Exp. Biol. 121: 251–270.

Zamer, W. E. & Shick, J. M. 1987: Physiological energetics of the intertidal sea anemone Anthopleura elegantissima. — Mar. Biol. 93: 481–491.