



Fig. 1a, Model of the relationship between rate of feeding and food intake, and efficiency of assimilation, under conditions of high or low food availability. b, Hypothetical effect of feeding rate on gain of energy and on cost of feeding. The arrowed dotted lines show the maximum 'profit' that can be made at high or low food availability. Feeding rate should lie close to these points if maximum energy is to be gained.

ed up kelp. Coupled with this are striking metabolic rhythms.⁵ Throughout the day a low 'basal' rate is maintained, but during the nocturnal low tide respiration increases fifteen-fold. This rhythm ensures minimal energy expenditure while the animals cannot feed. Furthermore, the energy saving is increased by the rhythmicity of emergence, which keeps the animal's body temperature low.

4) Comparison of four *Patella* spp. also throws light on the conservation of metabolic energy. Two species (*P. cochlear* and *P. granularis*) suffer from food shortage. *P. cochlear* occurs low on the shore where temperatures are seldom high, so that its metabolism is kept low. *P. granularis* suffers from food shortage, a short feeding time and prolonged high temperatures during low tide because it occurs high on the shore, and it has several adaptations to minimise energy loss. These include: nocturnal activity; low metabolic levels; low temperature coefficients (Q_{10}); and differential rates of respiration in air and water, which are size dependent and related to zonation patterns. *P. granularis* migrates up the shore, small animals occurring lower on the shore and respiring slower in water than in air, while larger animals occur high on the shore but respire slower in air. This size-dependent response to respiration in air and water also keeps metabolic rates low. Both these species are 'conservationist' with low rates of energy turnover.⁶ By contrast *P. granatina* and *P. oculus*, which occur in the midshore, have abundant food and an 'exploitative' strategy of high turnover, with very high growth and reproductive output. Both have high metabolic levels, maintained by a high Q_{10} in *P. oculus* and by different rates in air and water which are the reverse of those found in *P. granularis*.^{6,7}

In all these examples, food availability and predictability are some of the key features in determining whether conservation or exploitation of energy is the most suitable strategy. The metabolic 'strategy' is probably just a symptom of the general 'rate' at which an animal lives, including its rate of growth and reproduction. One should ask why these rates often differ so strikingly in different (but often closely related) species. The answer may lie in the predictability and amount of food each animal can rely on. The question can be rephrased to ask why animals

should feed at different rates when it is seemingly best to feed at maximal rates.⁹

The principle of whether it pays to feed at a high rate or a low one can be illustrated in the following model (Fig. 1). As feeding rate increases, food intake should rise (although probably at a decreasing rate). On the other hand efficiency of assimilation will decline. If food levels vary, this may change both intake and assimilation. Decreased food levels will reduce intake, although compensatory increases in assimilation are likely (Fig. 1a). The actual assimilated energy (Gain) is the product of intake and assimilation efficiency, and will be affected by the rate of feeding and the amount of food available. Gain must be offset by the amount of energy put into the act of feeding and digestion (Cost). In Fig. 1b this is shown as increasing linearly with the rate of feeding. (This is of course a simplifying assumption, but curvilinearity does not alter the argument.) The difference between Gain and Cost will determine whether a high or low rate of feeding will be most profitable. If food supply is high, it may pay to be seemingly profligate with a high rate of feeding even if efficiency is low. This is the exploitative strategy⁹ with a high growth rate and a high reproductive output, bringing with it the symptomatic high metabolic rate and devices described above to maintain metabolism at a high level. Conversely, if food is short it is most profitable to feed at a low but efficient rate. If the input of energy is low, then conservation of energy is important, including all the mechanisms described above to restrict losses of metabolic energy.

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Energetics of Locomotion in the Sandy-beach Whelk *Bullia digitalis* (Dillwyn)

A. C. Brown

Zoology Department, University of Cape Town, Rondebosch 7700.

Bullia digitalis is the common intertidal sandy-beach gastropod of the west coast of South Africa, extending round the coast to beyond Port Elizabeth.¹ It spends much of its time buried beneath the sand of the foreshore but may emerge as the tide recedes towards low, spreading its foot and surfing up and down the shore in the waves. On being washed ashore, it crawls in search of food, this activity being frequently interrupted by phases of burrowing. A knowledge of the time spent and the energy expended in each of its activities would allow the construction of an activity budget for the first time in any marine invertebrate. An assessment of the energy required for some of these activities has already been completed.^{2–5} The present paper is concerned with the energetics of burrowing and crawling, the data on burrowing being published in full elsewhere.⁶

The oxygen consumption of large, female animals from Ou Skip was measured individually in the laboratory at 15°C, each whelk being placed in a small container of sea water over a layer of sand, and tethered by the apex of its shell by means of a thread attached to a force transducer. These conditions give rise to repeated digging cycles. The water, covered with a layer of paraffin, was sampled both before and after for oxygen

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analysis in a Radiometer unit. Results were compared with the oxygen uptake of the same animals while untethered and immobile. The oxygen consumption per burrowing step could then be calculated.

Oxygen consumption per step averaged $0.62 \mu\text{g}$ for a standard animal of 750 mg dry tissue mass. Assuming an oxy-caloric equivalent of 3.4 cal per mg O_2 this gives an energy cost per step of 5×10^{-4} J (or 2.1×10^{-3} cal). The total burrowing process, averaging 10 steps,⁷ must thus cost the animal about 5×10^{-3} J, over and above maintenance requirements.

Records made from the force transducer were used to calculate the actual work done by the burrowing animal, and this figure compared with the energy cost as calculated above. The mechanical work performed per step averaged 3.1×10^{-5} J. The gross efficiency of the burrowing process was thus calculated as 6.1% (S.D. ± 1.2).

It has not been possible to measure oxygen uptake during crawling. However, Trueman and Brown⁷ have shown that, as in other psammophilic gastropods, burrowing is essentially a continuation of crawling, using the same mechanisms but changing the angle of attack. It is therefore reasonable to assume that the efficiency of crawling is very similar to that achieved in burrowing. As the mechanical work done in crawling is only about one-tenth of the work performed in burrowing,⁷ the energy cost to the animal would be only about 5×10^{-5} J per step (in a standard animal).

The energy costs of crawling and burrowing are thus markedly different, the total energy required while crawling (including the maintenance costs) being only slightly higher than that for an immobile animal resting on the surface of the sand.⁵ In contrast, the total energy used while burrowing approaches closely the requirement for transport in the surf.⁴

An overall efficiency of about 6% may be unexpected in view of the 20% efficiency which is generally assumed for locomotory processes in vertebrates and invertebrates alike.⁸ However, the relative inefficiency of catabolic processes, coupled with mechanical losses, suggests, on purely theoretical grounds, that overall efficiencies might be less than 8%. It is postulated that an efficiency of some 6% is indicated in general for locomotion in benthic marine invertebrates.

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Sedimentation of Estuaries: Causes, Effects and Remedies

W. J. R. Alexander

Department of Water Affairs, Pretoria.

The major formative processes which control the location, shape, area and depth of an estuary vary from changes in sea level relative to the land on a geological time-scale measured in tens of thousands of years, to seasonal floods on an annual basis. The present concern is related to observed changes that have taken place during the past century.

It is shown that most coastal rivers have a sediment transport capacity in excess of the available sediment load generated in their catchments. The effects of accelerated soil erosion due to poor farming practices are evaluated and the conclusion is reached that this is unlikely to be the major cause of sedimentation of estuaries. An assessment of the factors which control the geometry of river channels and estuaries in alluvium, leads to the conclusion that changes in the morphology of the river channels and adjacent floodplains due to the denudation of the vegetation are the major causes of sedimentation of river estuaries. Possible remedial measures are described.

Seasonal Abundance, Distribution and Catch Per Unit Effort of Fishes in the Swartkops Estuary

J. F. K. Marais and D. Baird

Department of Zoology, University of Port Elizabeth,
P.O. Box 1600, Port Elizabeth.

Catch per unit effort was determined for the nekton of the Swartkops estuary near Port Elizabeth by means of gill netting. Fifty catches were made in which 1 269 fish were caught in areas representative of the mouth, middle and upper reaches of the estuary. *Pomadasys commersonni*, already known to be the most abundant angling species in the estuary, dominated these catches in terms of both mass (29%) and numbers (17%). The Mugilidae (5 species) comprised 25% of the mass and 42% of the numbers caught. Environmental factors and availability of food that might determine the distribution of fish in the estuary are discussed. The largest mean mass per individual was found in *Chanos chanos* (4.47 kg), *Elops machnata* (1.66 kg) and *Liza buechanani* (1.58 kg). Lowest mean masses were recorded for *Monodactylus falciformis* (63 g), *Rhabdosargus holubi* (88 g) and *Liza dumerili* (94 g).

Book Reviews

There was a Man. By Thelma Gutsche. Pp. 487. (Howard Timmins, Cape Town; 1979.) R28.60.

Diseases of animals have long been of interest to mankind. Ancient records from Assyria, Egypt and China describe epidemic diseases and disorders of animals. The code of Hammurabi (c. 2100 B.C.) spoke of doctors of oxen and asses, and an Egyptian papyrus (c. 1900 B.C.)—a fragment of a comprehensive report—indicates that the Egyptians had high regard for Veterinary

Medicine. Veterinarians of the Roman army are known to have conducted a high level of practice, especially on horses.

A tribute to Sir Arnold

Then, as with all science, veterinary practice disappeared in the Middle Ages to emerge later as that of a farrier. However, in 1598 with the publication of *Anatoma de Cavalho*, veterinary anatomy was created

and a series of changes occurred which ultimately led to the establishment of veterinary science as a serious discipline.

By the mid-seventeenth century, a distinction began to be made between farriers and veterinarians. Writing in 1646, Sir Thomas Browne, an English physician, reported that 'the second assertion that a horse has no gall is swallowed by the people, common farriers and also received by good veterinarians.' But it took more than semantics to bring home the value of veterinary science to