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DETRITIVORY

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DEFINITION

We choose to define detritivory operationally as the relatively frequent ingestion of particulate food whose bulk generally is not composed of animal, plant or bacterial protoplasm. Our definition does not preclude the possibility that a major fraction of a detritivore's requirements for specific nutrients may be met from bacterial, plant or animal constituents (e.g. Anderson, 1976). We consider it largely an open and exciting question whether particular detritivores or the majority of detritivores under our rather in-

clusive definition meet their metabolic needs by (1) digesting and assimilating non-living detritus directly, (2) employing bacteria in external "gardening" or internal "rumination" to digest detritus, (3) digesting the normal bacterial component of detritus, (4) digesting plant (e.g. benthic diatom or fragmented macroalgal) protoplasm, (5) digesting the living or recently dead faunal components of detritus, or (6) utilizing some combination of these food sources. Within this potential continuum, are there "adaptive peaks" that allow natural functional grouping of detritivores for further investigation and generalization?

Rapid progress can now be expected in the study of detritivory. With a few exceptions (e.g. those noted below with respect to the measurement of the rate of detrital supply), major advances in understanding the detritus feeding process appear to have been blocked by the lack of simple, if only provisional parameterization of the detritus feeding process and its major components. One example of the difficulty of working on detritivory without an explicit rate-process model is the fact that many more data have been published on the assimilation efficiencies of detritivores than on their rates of detrital throughput. Without the measurement of both parameters for the same species fed on the same detrital food source, it is impossible to calculate so basic a quantity as a rate of material or energy gain.

PARAMETERISATION

The need for an explicit rate-process parameterization of marine detritivory has been met only recently (Levinton and Lopez, 1977; Taghon et al., 1978; Taghon, 1981). To illustrate the power of such models in formulating well-poised questions that promise new insights into detritivory, we will extend (Figure.1), the simplified graphical procedure of Sibly (1981). Because we have perhaps over-simplified to make our point, one should consult Sibly (1981) and the other references cited above before carrying out any explicit tests of the detritivore model. We use, for example, the simplifying assumption (often true for detritivores) that the volume or mass of absorption through the gut wall is insignificant relative to the volume or mass of the throughput. Sibly (1981) gives an explicit correction to use when the approximation that ingested volume or mass equals egested volume or mass is a poor one.

Let G be the net gain (grams or energetic equivalent - not a rate) of a limiting nutrient per gram of food ingested. Retention time (t) in the gut begins with ingestion ($t = 0$). One can argue, without the need to specify an exact functional form for $G(t)$, that it must first be decreasing while mechanical (e.g. masticatory) and chemical (e.g. enzymatic) energy is expended in initial breakdown of the food. This net loss should be followed by a period of relatively

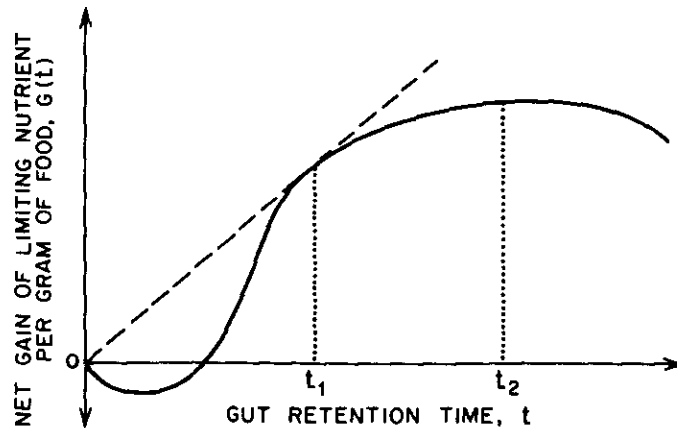


Fig. 1. Net gain of limiting nutrient per gram of food versus gut retention time (modified from Sibly, 1981). Time t_1 and t_2 respectively, optimal gut retention times for non-food-limited cases. (see text).

rapid absorption, with eventually diminishing returns as time proceeds. To these three regions of Sibly's, we would add a final downturn or net loss of energy as the basal catabolism of carrying the weight of gut contents exceeds any gross gain from further retention.

That several carefully selected parameters should be measured in concert to provide new information on detritivory is shown by so simple a question as "How fast should a detritivore feed in order to maximize its average net rate of gain $G(t)$?" If food is available in unlimited supply (the case treated by Taghon *et al.*, 1978, and Taghon, 1981), as may be true for detritivores more frequently than for members of other feeding guilds, the retention time (t_1) providing maximal net rate of gain is found easily and graphically by drawing the tangent to $G(t)$ that also passes through the origin (figure.1). If food supply is limiting (the case treated by Levinton and Lopez, 1977), however, then food should be held so long (t_2) as any net gain occurs. Without the explicit model, the desirability of measuring rate of supply of detritus and detritivore gut retention time together might not be obvious.

DETRITAL SUPPLY

Although we thus must recommend consideration of detrital supply and utilization in concert, we will continue our report and recommendations by discussing, in turn, supply and the sequential steps involved in detrital utilization. Considering all the factors involved in determining gross and net rates of detrital supply (figure 2), input and export of detrital material to and from a system can

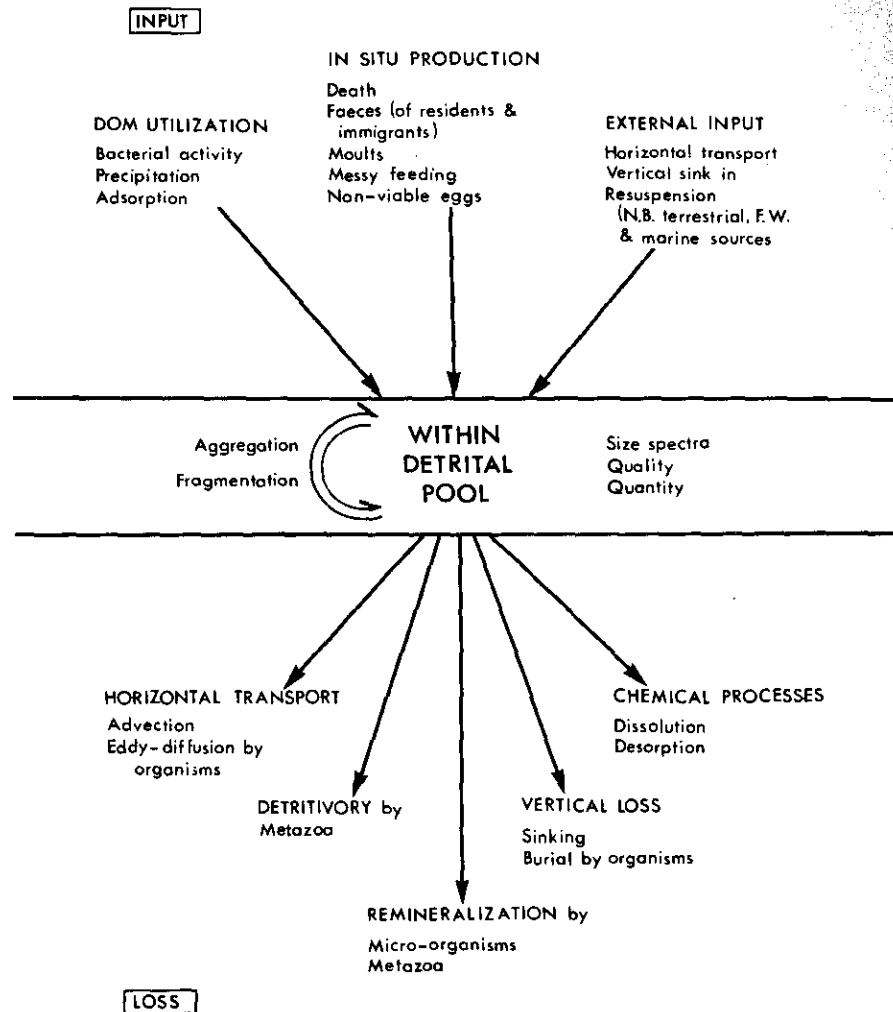


Fig. 2. Outline of detrital sources and sinks that require description and quantification. Spatial and temporal scales of measurement must be selected for the problem at hand, and predictability of detrital pool size and composition will have a major impact on detritivory.

rarely be treated as a constant. Even the deep sea is no exception to this generalization. For some purposes, the time-averaged value of detrital flux will be useful parameter. However, most detritivores are likely to have adaptations in their behavioural repertoires, feeding activities and life cycles in response to

variations in detrital availability. Quantities, chemical qualities and size spectra of detrital particles may fluctuate in predictable cycles (e.g. related to ripple-patterns of sand, tidal cycles of resuspension or seasonal variations in production). The more predictable the cycles, the more likely are organisms to be tuned to them. Conversely, large, irregular inputs may pass through the system without causing major functional or numerical responses in the organisms, or they may swamp the processing ability of the community entirely and cause major perturbations in its function (e.g. an episode of anoxia). In such circumstances, a "mean" estimate as provided, for example, by a long-term sediment trap deployment, may be totally misleading.

Where fluxes are large, sampling on temporal and spatial scales appropriate to individual and community responses may not be a major problem, even with extant sampling techniques. Where the fluxes are small, however, such as in many parts of the deep sea, present methodology may not be adequate to discriminate functionally relevant short-term or small-scale spatial variations adequately, especially where analysis of size spectra or chemical composition of detritus is concerned. Once again this problem becomes explicit by attention to the model of Figure. 1; the spatial scale of interest is the foraging area of a single individual and the temporal scale of attention is the gut retention period.

A second technical problem is the estimation of detrital fluxes where fluid motions cause appreciable (gross or net) particle fluxes either vertically upward or horizontally. Here severe bias can be expected in collections by conventional sediment traps. Prominent examples of such regions are surface mixed layers or bottom boundary layers during their respective episodes of active turbulent mixing. To provide even crude estimates of detrital supply rates in these situations, the expert advice of physicists concerned with fluid dynamics and sediment transport will be required; their approach generally is to couple suspended load measurements with models of particle and fluid motion in order to yield the desired vector quantities of net or gross particulate fluxes.

While biologists may benefit directly from measurements made in other disciplines, they run the risk of receiving data on biologically inappropriate parameters or on unsuitable temporal and spatial scales. For example, stratigraphers employing radio-isotopic measures of sedimentation obtain a net rate and generally average over periods well in excess of organism life-spans, and geochemists studying diagenesis generally do not measure the chemical components of detritus that biologists require. Interdisciplinary coordination clearly would benefit all concerned. Besides the obvious benefit to biologists, stratigraphers stand to gain insights into the component processes of bioturbation, and geochemists stand to increase their grasp of biochemical transformations involved in diagenesis.

DETRITAL UTILIZATION

For the study of detritivory itself, rates of detrital supply should be scaled against detrital feeding rates, and estimates of food quality should be scaled against deposit feeder nutritional requirements and assimilative capabilities. Nutritive quality of detritus thus must be determined both by the chemical composition of the detrital supply and by the ability of detritus feeders to utilize the material during its period of gut passage. With few exceptions, little is known of the biochemistry or even bulk organic chemistry of detritus and its associated microbiota or of the extent to which digestive enzymes of consumers can degrade detrital components. Both kinds of data are required to specify more precisely and accurately the shape of the curve in Figure. 1. More subtly, increasing food quality or digestive ability in the food-limited case means a higher plateau in the curve, while in the non-food-limited case it means a more rapid initial rate of assimilation.

It seems likely that in some nearshore systems where freshly produced and fragmented plant debris is available for consumption, detritivores may obtain their daily ration from the detritus itself. For example, the style enzymes of some bivalves have been shown to be fully capable of digesting algal fragments from the kelp beds in which they live (Seiderer *et al.*, 1982; Stuart *et al.*, 1982; Newell and Field, 1983). Insufficient information is available on the gut retention time and digestive physiology of most other detritivores, however, to assess whether the detrital carbon supply meets the consumer's nutritional needs. Nitrogen requirements and, above all, trace requirements for such substances as vitamins and essential fatty acids are also largely unknown and represent areas which require detailed investigation. There is especially great difficulty in obtaining realistic estimates of food quality from hydrolysates of detrital material unless the details of the biochemistry of the intact components and their ease of degradation by consumer organisms is known.

Although some information is available on the carbon and nitrogen content of detrital sources in certain nearshore systems, the chemistry of decomposition, including the formation of humic substances, is in general poorly understood in marine systems. More information is required on the significance of detritus not merely as a possible carbon resource, but as a source of protein and trace nutrients as well. Sufficient information now exists to show that bulk carbon and nitrogen contents alone are not sufficient to characterize food quality.

Provision of food of known quality and composition at a known rate is no guarantee that the detritivore will ingest a representative sample. Several claims of chemical transformation are based on the tenuous assumption that a sample of detritus from the immediate

vicinity of a detritivore can be compared with its fecal composition as an estimate of digestive ability. That assumption is true only if (1) the animal is entirely non-selective in its choice of particles for ingestion and (2) the supply of detritus in its vicinity is in steady state. There is a shortage of critical data on the selective abilities of detritivores; note the strong effect that selection could have on the shape of the curve in Figure. 1 if the selected components proved to be highly digestible. An issue which demands attention is the degree to which particle selection is accomplished by purely mechanical means versus via chemosensory evaluation of individual food items. Some kinds of detritivores may process particles at a much greater rate (number of particles per unit time) than do members of other feeding guilds. At what feeding rates does it become uneconomical to reject unwanted items? Particle rejection criteria and costs in detritivores are virtually unknown.

Items selected for ingestion can be processed at varying rates. Details of digestion, absorption and assimilation may be relatively difficult to obtain in detritivores because such a small percentage (by total mass or volume) of ingested material is digested or absorbed. On the other hand, the frequent ability to roughly equate ingestion and defecation rates in detritivores eases some measurement problems inherent in the study of other trophic groups. Various tracer techniques employing both stable isotopes and natural and artificial radionuclides offer great promise in answering questions about detritus origin, age, digestion and assimilation. For example, examining radionuclide ratios in detritus and associated organisms can give useful information on the detrital component of the organism's diet as well as insight into the decompositional characteristics of the released detrital particles (e.g. fecal pellets and molts). Of particular interest is the recent availability of labeled inert plastic and glass microspheres which allow direct measurement of gut transit times under various ecological conditions.

In summary, a great deal can now be learned about detritivory from a few simple measurements, as we will highlight by presenting a few simple questions. Do most detritus feeders have short gut retention times, digesting only the most labile detrital components, or do they have long throughput times, refelcting the relatively refractory nature of detritus as compared with other foods? Will both digestive strategies work on the same food resource? One potential solution to maintaining a fixed rate of energy gain on food of lower quality is to increase the volume of material carried (processing more grams of food per time in the parameterization of Figure. 1), as has been found in some ruminants (Sibly, 1981, Table 5.5). Will a similar inverse relation be found between gut volume and food quality within marine detritivores? Due to the energetics of flight, birds that forage on food of low bulk value are under severe constraints in terms of the gut volume that they can carry - so severe that the gut volume (length) actually changes over periods of a few weeks in

response to changes in food quality (Sibly, 1981, Table 5.2). Will actively swimming or burrowing detritivores be similarly, if less severely, constrained in the marine realm?

In addressing these questions and others which by now will have occurred to the reader, we strongly recommend that the alternatives be made explicit by the use of figures (like that of Figure. 1, but showing the alternatives) or equations. Developing this habit will save work both by underscoring those parameters that must be measured very carefully and by pinpointing unnecessary measurements. Given the ease of posing important questions of detritivory in an easily understood graphic fashion and the existence of a wide spectrum of available methods for addressing them, we look forward enthusiastically to rapid progress in the study of this ubiquitous process.

SUMMARY

Understanding of marine detritivory and its component processes is in a primitive state. Until recently, progress appears to have been limited by the lack of simple, if only provisional, parameterizations. Now that such models are available, we recommend that they be used explicitly in designing experiments to investigate (sensu Pielou, 1981) marine detritivory. Given such use, we are confident of rapid progress.

Major gaps in available information are made apparent by our own provisional model, leading to the following recommendations:

1. detrital supply rates and detritivore utilization rates should be measured simultaneously on appropriate scales (e.g. within the foraging area of a detritivore over the time scale of its gut retention period);
2. conventional sediment trapping should be avoided in attempting to measure detrital supply in situations of substantial horizontal or vertically upward particulate fluxes;
3. interdisciplinary co-ordination should be sought in measuring detrital chemistry and supply rates;
4. food quality of detritus should be defined relative to detritivore nutritional requirements, necessitating new studies both of detrital chemistry and of detritivore digestive and assimilatory capacities;
5. nutritional requirements for both major and minor food components require study among detritivores until the limiting nutrients can be specified; and,

6. details of particle selection in detritivores should be elucidated, with particular attention to mechanical versus chemosensory selection and rejection mechanisms and costs.

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