CHAPTER 9

Nitrogen in Benthic Food Chains

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9.1 INTRODUCTION

The potential cycling of nitrogen in benthic food chains is controlled by extrinsic hydrodynamic forces of water depth, currents and mixing that determine the extent to which pelagic phytoplankton can be exploited by suspension-feeding benthos, and the formation and sedimentation of particulate detritus into the sediment regime that supports a complex of trophic levels that comprise deposit-feeding benthic food chains. Intrinsic factors such as feeding types of benthos, nutritional needs and ecological energetics determine how nitrogen is exploited and incorporated by benthic organisms, and/or buried into sediment. Thus, to understand the role of benthos in cycling of nitrogen in marine environments it is necessary to understand: (1) the basic nutritional needs of benthos; (2) the food resources that can supply the needs of benthos; and (3) the feeding strategies by which benthos exploit available resources.

9.2 THE ROLE OF NITROGEN IN NUTRITION OF BENTHOS

Compared to the extensive literature available on fishes and, to a lesser extent, on commercially important invertebrates, much less is known about the nutritional requirements of organisms that comprise most benthic communities. The limiting nutritional role of nitrogen has been soundly documented for vertebrates, and some invertebrates, especially in animal husbandry and aquaculture studies (McDonald et al., 1973). Most ecological research of benthos, however, has focused on more gross measures of carbon or energy (caloric content) in attempting to study bioenergetics and production. Even in studies of detritivores, where the regulatory role on nitrogen has been at least surmised, only crude measures of '% N' or 'C/N ratios' have been used to characterize and to speculate on the relative nutritional value of various food resources. More attention has been given to documenting metabolic activity (e.g. oxygen consumption), energy flow and production of benthic communities or their dominant organisms (e.g. Teal, 1962; Pamatmat, 1968; Warwick, 1980; Wolff and de Wolf, 1977; Gerlach, 1971; Asmus, 1982).

To understand better the role that nitrogen plays in the nutrition of benthos, it is important to review the basic trophic dynamics that underlie the ecological energetics. Animals require: (1) substrate(s) that provide potential energy (calories) for organisms to carry out 'work', i.e. metabolic activities; and (2) substrate(s) that provide essential nutritional components such as fatty acids, amino acids and a variety of other organic compounds and trace elements needed to maintain cell structure and for metabolic processes. Of the basic food components—carbohydrates, lipids and proteins—protein essentially provides cellular structural materials that is not (necessarily) involved in supplying energy for metabolic activities. Two points are of interest: (1) nitrogen is a more conservative element in cellular structure than carbon and hydrogen components of organic compounds, and (2) high concentrations that are needed by animals, relative to concentrations in the plant and/or detritus food supply, result in organic nitrogen usually limiting production of heterotrophic growth. Thus, attempts to delineate the food potential of various food resources to benthos, based solely on energy needs, can overlook the potentially more regulatory role of food resources that supply the essential organic nitrogen compounds, e.g. essential, amino acids, needed by benthic heterotrophs.

Benthos display a variety of feeding types that can be arbitrarily divided into suspension, deposit and scavenging/carnivorous feeding. Suspension feeders filter, remove and ingest particulates from the surrounding water. This definition of suspension feeding is one of degree: the filtration results not just in herbivory, i.e. ingestion of phytoplankton, but can include suspended detritus and sediment bedload itself. Deposit feeders can be characterized as either non-selective bulk feeders that indiscriminately ingest and process large volumes of sediment, or as selective deposit feeders that selectively ingest food-rich particles from the sediment or scrape organics from inorganic particle substrate. Deposit feeders can feed on the sediment surface or at depth. The latter have been termed 'conveyor-belt species' (Rhoads, 1967) and the result is sediment bioturbation, i.e. vertical mixing of sediments to up to 20–30 cm.

9.3   NITROGEN SOURCES AVAILABLE TO BENTHOS

9.3.1   Suspension feeders

The nitrogen content of phytoplankton varies with species and physiological condition (Parsons *et al.*, 1961). Generally, nitrogen content increases with increased nutrient availability and growth rate. Nitrogen content can range from 4 to 9% (as percentage of dry weight) (Parsons *et al.*, 1961). Protein content can range from 10 to 70% of dry weight. Amino acid contents of 2 to 8 μg per 100 mg dry weight have been reported for natural phytoplankton populations. Amino acid composition can vary with species and growth conditions.

The actual exploitation of water column phytoplankton (and suspended

detritus) by suspension feeders is controlled by phytoplankton density, vertical mixing of the water column from the surface photic zones to the benthic regime, and currents that regulate the potential total amount the organisms can filter. Suspension feeders can, in fact, compete with planktonic herbivores where the water column is shallow enough and vertical mixing is strong enough to transport water-containing plankton production to the bottom (for an excellent discussion of such hydrographic effects on food supply to the benthos, see Riley, 1972).

9.3.2   Deposit feeders and detritus-based food chains

A detritus pool is composed of dead organic matter derived from various sources that can have variable nutritional nitrogen content and food value; it is essentially a food resource (except for microbiota components) not immediately responding to intrinsic population dynamics, such as phytoplankton food in herbivores; it is continually modified biochemically in time by microbial transformations, and physically modified by physical and biological (meio- and macrofaunal) activity. The variability in nutritional composition of detritus, at a point source and in time, affects the bioenergetics (assimilation and growth efficiencies, and reproductive activity) and resultant production of benthos, and thus food chain transfer (i.e. how much of the nitrogen of the detritus ends up in net production).

To illustrate the implications of the heterogeneous nature of a detritus pool, and to appreciate the work over the past 20 years on the role of coprophagy, microbial decomposition and particle size effects of detritus, a simplified model presents potential food resources and potential regulatory mechanisms of detritus food chains (Figure 9.1). (See Christian and Wetzel, 1978; Lee, 1980; Tenore *et al.*, 1982, for more detailed review.) Potential food sources to benthic deposit feeders include: benthic microalgae (I); sedimenting detritus from various sources (II); fecal pellets (III); whether in the sedimenting detritus (C) or recycled via coprophagy (D); and microbenthos (bacteria, fungi, protozoa) (IV). Micro-algae are produced in the sediment and can be affected by grazing activity of the deposit feeders (E). Detritus is more or less continually settling to the bottom and is a major pathway in benthic–pelagic coupling. If the detritus is refractory, e.g. mostly of vascular plant material, it must be depolymerized by microbial decomposition (F), and the resultant microbial biomass (G) or transformation products (H) can be utilized by the deposit feeder. The added trophic level interposed between resource and consumer imposes a metabolic 'cost' in the microbial energetics required to achieve these transformations. If the detritus is directly assimilable to the deposit feeder, e.g. seaweed-derived, then microbes and deposit feeders might well compete for the resource (F and I). The fecal material produced by the deposit feeder (and other deposit-feeding or deposit-modifying organisms) can itself be further degraded into available substrates or can serve as
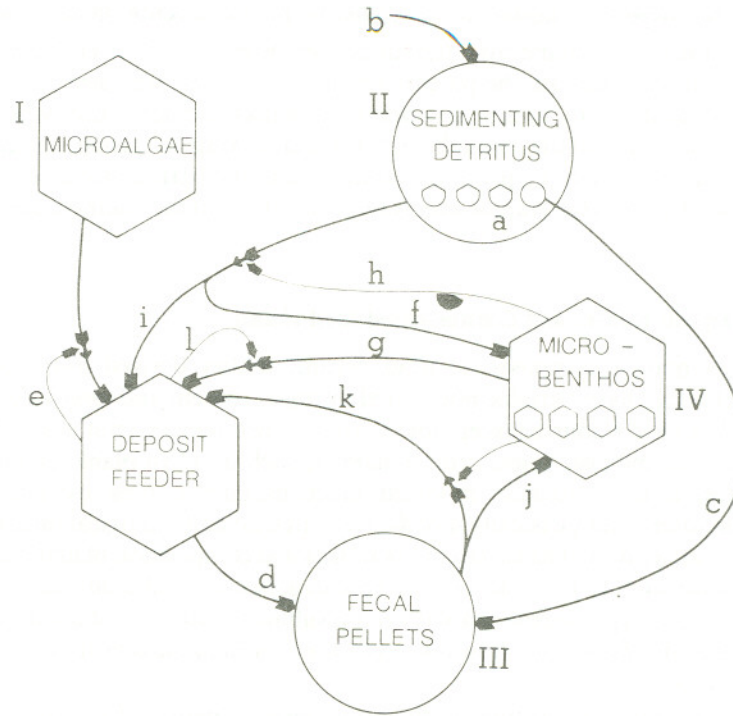
Figure 9.1. Diagram illustrating different potential food resources and mechanisms regulating pathways to detritivores

a substrate for microbial growth (J). The particles may be subsequently reingested, and associated microbial biomass and transformation products (K) utilized by the deposit feeder. The grazing pressure by the deposit feeder can stimulate microbial production (L). The relative importance of these various sources of detritus to benthic nutrition depends in great part on the feeding types found in deposit feeders. Surface deposit feeders can immediately exploit newly settling detritus. Benthos feeding 'at-depth' ingest materials that have been vertically transported into the sediment and are thus subjected to a greater degree of microbial activity. Benthos that scrap materials from surface inorganic particles are, to a greater degree, affected by biogeochemical processes of sediment particles.

In early research on detritus, two characteristics of detritus food chains attracted the attention of researchers: microbial recycling of fecal pellets (coprophagy) and the refractory nature of detritus derived from vascular plant, marsh and seagrasses that necessitates microbial decomposition before available to macroconsumers. Both processes were viewed as increasing nutritional value, especially nitrogen content, of the detritus.

Work in the 1960s documented the role of coprophagy by deposit feeders (Newell, 1965; Frankenberg and Smith, 1967; Frankenberg *et al.*, 1967; Hargrave, 1976). Microbes were shown to colonize fresh fecal pellets that were then reingested by the deposit feeders. The associated microbes were utilized while the refractive fecal pellets *per se* passed the gut undigested. As microorganisms recolonized the fresh fecal pellets, the nitrogen content (percentage of dw) of the pellets would increase. This early work led to a series of reports by Levinton and Lopez on the effect of grazing on the microbes associated with fecal pellets, and to models suggesting that deposit feeders were limited by such renewable resources (Levinton and Lopez, 1977; Lopez *et al.*, 1977; Lopez and Levinton, 1978; Levinton, 1980). Selective feeding by deposit feeders can actually enhance potential food quality of fecal pellets relative to surrounding sediment particles. Thus fecal pellets may be the foci of relatively high organic content, not because of microbial biomass, but because of feeding strategies by macroconsumers (Hylleberg, 1976; Hylleberg and Galluci, 1975; Lopez and Levinton, 1978; Whitlach, 1974). For example *Hydrobia* can feed by scraping sand grains, thus producing pellets potentially richer in organic matter than the sediment habitat (Lopez and Kofoed, 1980). These models of deposit feeder food limitation were generalized by Jumars *et al.*, 1981, who pointed out that the steady state established between particle selection by the animals, pellet breakdown, transportation and burial determines the residence time of material in superficial sediments.

Past research also emphasized the refractory nature of detritus derived from marsh and seagrasses, stressing the role of microbes in increasing nitrogen content of the aging detritus (Fell and Masters, 1973; Fenchel, 1972; Godshalk and Wetzel, 1977; Gosselink and Kirby, 1974; Harrison and Mann, 1975; Haines and Hanson, 1979). Though large amounts of detrital organic matter are present in coastal marine environments, most is not available at a given time for assimilation by macrobenthic deposit feeders (Bader, 1954; Degens and Reuter, 1964; Fenchel, 1972; George, 1964; Hargrave, 1970; Mare, 1942; Newell, 1965). Detritus derived from vascular plants (e.g. seagrasses and marshgrasses) is typically low in nitrogen and composed of structural materials not directly assimilable by detritivores. These substrates (at least the decay-resistant portions) are available to macroconsumers only after long periods (e.g. months) of 'aging' that allow microbial decomposition (Boling *et al.*, 1975; de la Cruz, 1975; Gosselink and Kirby, 1974; Gunnison and Alexander, 1975; Harrison and Mann, 1975; Kostalos and Seymour, 1976; Tenore, 1977; Tenore and Hanson, 1980; Rossi and Fano, 1979; Seki *et al.*, 1968).

During aging there is a build-up on detrital particles of a heterogeneous group of microbes, bacteria, fungi, macroalgae that can enrich the protein content and decompose refractory plant material (de la Cruz and Poe, 1975; Fell and Masters, 1973; Fell *et al.*, 1980; Fenchel, 1969, 1972; Haines and Hanson, 1979; Harrison and Mann, 1975; Meyers and Reynolds, 1963; Odum and de la Cruz, 1967;

Parkinson, 1975; Zieman, 1975). Deposit feeders assimilate these microbiota associated with detritus at a high rate (Hargrave, 1970; Yingst, 1976) but biomass of microbiota is low compared to the detritus particles *per se* (Christian and Wetzel, 1978; Rublee, 1982, but see Rice and Hanson, 1984) and may not be sufficient, in themselves, to support detritivore food requirements (Cammen, 1980). Hobbie and Lee (1980) pointed out that the transformation products of bacteria may supply a portion of nutritional needs of deposit feeders.

Recently the concept that the role of microbes is basically one of 'protein enrichment', i.e. increasing the nitrogen nutritional quality of detritus, has been modified (see Tenore *et al.*, 1982, and Levinton *et al.*, 1984, for review). Initial nitrogen availability and the subsequent role of microbes depends on the detritus source. Briefly, seagrass-derived detritus is typically low both in available caloric and nitrogen content. The rate at which macroconsumers eventually exploit this vascular plant detritus may well be limited, not only by nitrogen content, but by the rate at which microbes degrade the complex polymers that comprise the structural components, and thus transform the detritus into substrates (breakdown products of microbial products) available for macroconsumer utilization. In contrast, seaweed-derived detritus is typically high (but variable) in both available caloric and nitrogen content that can be directly utilized by macroconsumers. Thus, microbes do not regulate availability but, in fact, may compete with macroconsumers for this detritus type. Depending on the initial detritus ingested, fecal pellets may be deficient in energy content, and thus act only as a substrate for microbial growth. Thus, fecal pelletization *per se* may be limiting availability of otherwise nutritious food sources. For example, disaggregated fecal pellets of *Capitella capitata* did not support growth of larval or adult worms (Phillips and Tenore, 1984). For fecal pellets that do contain undigested energy sources, rates of physical breakdown of pellets regulate microbial activity, and nitrogen enrichment can occur with microbial build-up.

Earlier work did not actually demonstrate, but inferred, nitrogen to be the nutrient limiting growth of detritivores, because of low nitrogen content of fecal pellets and vascular plant detritus. During the past decade investigators using classical growth studies, employing a wide variety of detritus types, have attempted to delineate the limiting role of nitrogen in the bioenergetics of detritivores (Tenore, 1981, 1983a, b). Nitrogen was the best overall indicator of nutritional value of a wide variety of detritus types for *C. capitata*; however, for detritus derived from vascular plant sources, low both in nitrogen and available energy content, available caloric content interacted in determining worm growth. That is, given the same nitrogen ration, there was no significant difference in growth with increasing caloric content, but rations with similar available caloric content, but higher nitrogen levels resulted in higher growth rates (Tenore, 1983a). Adding organic nitrogen supplement to easily assimilable seaweed detritus increased incorporation by worms, but had no affect on the utilization of refractory vascular plant detritus (Tenore *et al.*, 1982). Vascular plant detritus with higher available caloric content did show greater utilization by the worms

(Tenore, 1983a). Similar nitrogen limitations were found for the nematode, *Diploliamella chitwoodi* (Findlay, 1982) and the harpacticoid copepod, *Tisbe cucumariae* (Guidi, 1984) and, aside from particle size effects, for the gammarid amphipod, *Mucrogammarus mucronatus* (Phillips, 1984) and higher growth has been reported with increasing nitrogen content of aging detritus (Tenore *et al.*, 1984; Valiela *et al.*, 1984).

The question of the actual nitrogen source, whether detritus *per se* or microbial, being incorporated by the macroconsumer was studied using ^{15}N (Findlay and Tenore, 1982). *C. capitata* incorporated nitrogen overwhelmingly from the actual plant substrate when feeding on seaweed-derived detritus; microbial nitrogen was a significant nitrogen source when feeding on marshgrass-derived detritus.

9.3.3   Nitrogen changes in 'aging' detritus

Besides changes in nitrogen content associated with source, detritus, once it enters the detritus pool, undergoes decay that can result in biochemical transformations and loss to the particulate organic mass. Earliest work with aging fecal pellets showed that % N (of dry weight) increased as microbes colonized the particles and incorporated nitrogen from the surrounding water medium (Newell, 1965; Frankenberg and Smith, 1967). Subsequent reingestion (coprophagy) and formation of fresh fecal pellets results in a recycling, renewing nitrogen resource available to deposit feeders.

The break-up and transformation of plant materials into amorphous detritus particles, and related changes in nitrogen content, is more complex, involving initial biochemical composition of the detritus source, physical process and biological activity resulting in particle formations, and microbial decomposition and transformations.

Detritus source and related biochemical composition play an important role in the rate of changes in total mass and various biochemical pools, including nitrogen. In general, total mass of refractory types of detritus derived from vascular plants decompose slowly; whereas total mass of easily degraded detritus from seaweeds, typically high in nitrogen and available energy substrates, lose total mass quickly (Rice and Tenore, 1981; Marinucci *et al.*, 1983; Tenore *et al.*, 1984; Valiela *et al.*, 1984). Initially, there is a very rapid leaching phase of water-soluble components, followed by a slower decompositional phase where the more readily utilizable components, especially nitrogen, are mineralized, and finally a third slow stage of depolymerization of refractory (i.e. highly complexed polymers) components occur. The more readily utilizable components of both detritus types, including non-humic bound organic nitrogen and easily depoly-merized energy substrates, are more quickly lost from the total mass, leaving greater and greater concentrations of refractive lignins and organic-complexed unavailable nitrogen.

During the latter stages of the slow decay of refractory remains, microbial

biomass, but more importantly their nitrogen-rich exudation products, accumulate and can increase the absolute nitrogen mass of the detritus pool (Hobbie and Lee, 1980; Rice and Hanson, 1984).

Two points of caution are needed in evaluating data in the literature on changes in nitrogen content of aging detritus. Many studies only emphasize relative, i.e. % N of dry weight, changes that occur in the detritus mass, rather than absolute changes, i.e. total unit mass of nitrogen of the detritus. The conclusions as to flux of materials can be quite deceiving and, based on relative changes, the term 'nitrogen enrichment' can be erroneous. For example, a recent study of changes in nutrients in aging detritus (Tenore *et al.*, 1984) reported both relative and absolute changes in biochemical constituents of different detritus types. The data for nitrogen change of aging seaweed detritus illustrate the danger of considering only relative concentrations (Figure 9.2). Initially, during the period of rapid decomposition there was an actual loss of protein from the detritus pool that was not accurately reflected by the relative measure of percentage composition. The cause of this difference was that the mass of other biochemical components, i.e. easily oxidized energy substrates, were being lost at a faster rate than the nitrogen pool.

Another point of caution is that the various experimental approaches used to study detritus composition can produce artifacts or affect decomposition rates. Studies in stagnant flasks can result in decomposition being controlled by nutrient limitation of the culture medium (see Rice and Hanson, 1984) and/or build-up of metabolic products that reduce microbial activity. Studies in flow-through microcosms or with *in situ* litter bags will be affected by the intensity of
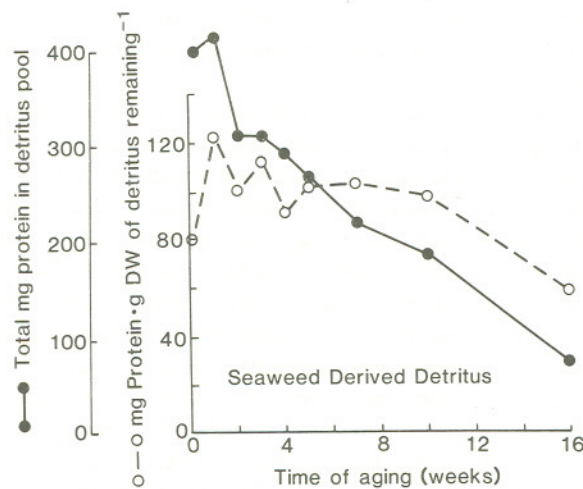

Figure 9.2.   Contrast of total nitrogen mass versus % N of total dry weight mass of an aging detritus pool

mixing. For example, in the microcosm studies by Tenore *et al.*, 1984, mixing was minimized so that these rates of decomposition probably represent minimal decompositional rates, e.g. for *Spartina*, a total mass loss of only about 20% in 280 days. In contrast, in the experimental design used by Rice and Hanson (1984), where the carboys were vigorously mixed, the total mass loss of *Spartina* detritus was about 14% for 26 days. In the *in situ* litter bag studies by Valiela *et al.*, 1984, the total weight loss was about 80% after about 300 days. The reported 'weight loss' of these last results using litter bags should be interpreted in the light that 'weight loss' is not only reflecting mineralization of mass, but loss of small particles through the litter bag mesh. It is obvious that mixing processes drastically affect microbial mineralization of detritus. Hanson and Tenore (1981) aged detritus anaerobically in a series of carboys, mixed with variable agitation by nitrogen gas, and found a positive correlation of increasing rate of loss of detritus mass with degree of mixing.

As mentioned previously, all animals must obtain specific essential nutrients, as well as energy sources, in order to live. Most research into possible food value for both suspension- and deposit-feeding ecology, has focused on total caloric or total nitrogen needs. Regarding detritus food chains, the caloric carbon or nitrogen content of the standing amounts of various presumed food resources that comprise a detritus pool have been used to argue the question whether this or that particular resource can support the 'metabolic requirements' of detritivores. Little attention, at least in basic research, has been given to the potential limiting role of the more discrete biochemical constituents, such as amino acids, that can, in fact, be actually limiting heterotrophic growth. Moreover, the concept of 'limiting factor', i.e. that one nutritional factor limits the growth of an organism, has been unrealistically interpreted as to whether one component of a detritus pool, e.g. microbes, detritus particles *per se*, benthic diatoms, etc. supplies all the nutritional components of diet (Newell, 1965; Fenchel, 1970; Hargrave, 1970; Lopez *et al.*, 1977; Cammen, 1980). It is much more realistic to hypothesize that the total nutritional needs of a detritivore can be supplied from a variety of sources within a detritus pool.

In a recent extensive and well-documented review of the potential supplies of specific essential nutrients to marine detritivores, Phillips (1984) showed that the various components of a detritus pool have quite different concentrations of essential nutrients (available energy, essential fatty acids, sterols, and essential amino acids) (Table 9.1). For example, fungi and especially bacteria are poor sources of the long-chain polyunsaturate fatty acids (PUFA) essential to most marine metazoans. Algae, especially diatoms, are excellent direct sources of these fatty acids. Protozoans and meiofauna, because they can feed on bacteria and can themselves synthesize PUFA, are potentially important intermediaries in the detritus trophic complex. Similarly, bacteria lack sterols that are essential to growth of all crustaceans and many bivalves; whereas eucaryotic cells usually contain about 1% (dw) of sterols. Similar differences are found in the essential

Table 9.1. Differences in nutritional value of different sources of detritus

Detritus source	Nitrogen + amino acids	Essential long-chain polyunsaturated fatty acids (PUFA) of 18, 20, and 22 carbon length	Available energy content
Bacteria, yeast, fungi	Deficient in MET	Bacteria and secretions can have high lipid levels (up to 40% dw) but lack PUFA	High lipid content but much of cell wall not available; secretions readily available
	Fungi also deficient in arg, lys, his	Fungi and yeast contain up to 30% of 18C fatty acids but low amounts of 20C PUFA	
Marine vascular plants	Contain all essential amino acids but are usually low in total N (< 1% dw)	Low total lipid content (< 5% dw) fresh plants have some 18C fatty acids that quickly disappear during aging	High total caloric content but only 5–15% available
Seaweeds	Vary widely in total N (1 to 5% dw) and essential amino acid spectra	Total lipid levels about 10% dw, greens contain 18C and reds and browns have 18, 20, and 22C PUFA	Percentage of total calories that are available varies but is generally high (10–50%)
Phytoplankton	High in total N Diatoms contain well-balanced amino acid spectra	Generally high total lipid content (10–30% dw) especially diatoms (30% dw) High 18, 20, and 22C PUFA, greens generally have only 18C PUFA, diatoms contain 20C PUFA, phytoflagellates have high levels: 20–22 PUFA	High available caloric content
Protozoans	High in total N Well-balanced amino acid spectra	Little data available for marine forms Protozoans, but not rotifers, can synthesize PUFA	High available caloric content

amino acid total content and composition of the various components of a detritus pool. Marine invertebrates generally exhibit a consistent distribution of essential amino acids in their tissues, and need to extract from their ingested food the same relative proportions of essential amino acids. In nutritional studies a food resource is evaluated by comparing the essential amino acid profiles of the food relative to that of the animals; that acid most deficient relative to the composition of the animal is considered to be limiting. In general, methionine (met), histidine (his), lysine (lys), and arginine (arg) commonly limit metazoan growth. Most components of a detritus pool, with the exception of those derived from animal tissue, diatoms and some seaweeds, are to some extent deficient in one or more of these essential acids. Moreover, the idea that 'aging' results in a build-up of essential nutrients is unsubstantiated and, in fact, in error. Where the changes in the absolute pools of these constituents have been measured there is evidence that the more labile and nutritiously valuable a component is, the faster it disappears (i.e. is utilized) from the detritus pool (Tenore *et al.*, 1984).

9.3.4 Temporal changes in nitrogen resources to detritus food chains

The total mass and individual nutrient components of a detritus pool in benthic marine coastal systems exhibit changes during the year that are related to

I. break up and decay of marsh and seagrasses contributing to detritus pool
II. "winter blooms" of seaweeds, e.g. *Ulva*
III. sedimenting material from water column production
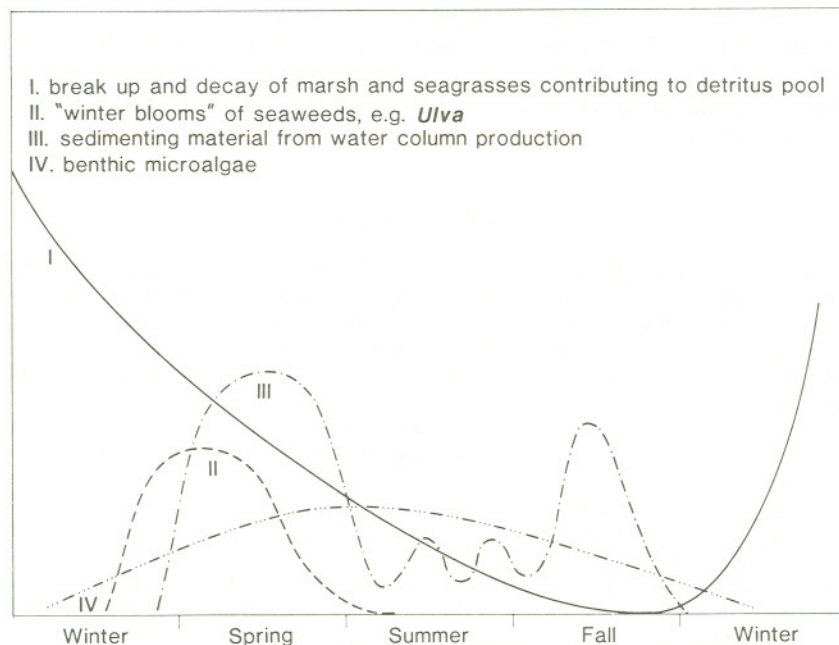IV. benthic microalgae

Figure 9.3.   Temporal changes in food sources to benthos

seasonal contributions and subsequent decomposition of various detritus sources. Figure 9.3 illustrates basic seasonal contributions and relative persistence with time of detritus derived from marine grasses, seaweeds, plankton production and benthic microalgae. There is strong evidence from field data that the early spring burst of benthic metabolism and production occurs in response to the eventual contribution of nitrogen-rich settling detritus derived from the spring phytoplankton bloom (e.g. Graf *et al.*, 1982; Cahet and Gadel, 1976). In shallow areas production of benthic diatoms (Admiraal *et al.*, 1984) probably supplies a significant food resource to benthos (Levinton and Bianchi, 1981; Bianchi and Levinton, 1984). Besides microalgal contribution to benthic food chains, most coastal temperate habitats in late winter and early spring blooms of sea lettuce, *Ulva* spp., occurs, which readily decomposed and provided an organic contribution to the sediments regime that is rich both in available energy substrate and nitrogen content. *Ulva* is, itself, low in the essential fatty acids necessary in marine invertebrate nutrition, but contributes a tremendous bulk for energy and amino acid needs. Thus the combination of these two organic sources to the detritus pool probably results in the bursts of opportunistic, fast-growing benthos characteristic of the spring. In contrast, the marine grasses that senesce in late autumn and winter eventually are broken up and enter the amorphous detritus pool. This fresh material, however, is of little direct nutritional value, and is slowly decomposed by microbial activity into microbial biomass and byproducts that are subsequently utilized by benthos as they become available. This more refractive component of a detritus pool is thus slowly made available to benthos over a long time period (years) and can provide a buffering food supply compared to the pulses of easily assimilated, quickly dissipated phytoplankton and seaweed components.

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