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Detritus: Mother Nature's Rice Cake

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Detritus has been studied since ancient times. Early man and ancient civilizations considered muds and slimes the source and sustenance of all aquatic life (Darnell 1967). Early civilizations which relied on the bounties of the sea for nutrition and commerce, and which worshipped elements within the oceans, highly revered detritus.

While today's popular opinion appears to simply discount the importance of detritus as "just plain mud," scientific evidence indicates that the ancient cultures may have been correct concerning the importance of detritus. Detritus is important on a global scale as well as locally; from its role in the world carbon cycle to supplying part of the nutritional requirements of a marsh periwinkle (Stumm & Morgan 1981, Baker & Allen 1977). It has even been suggested that man should devise ways to use detritus as food (Odum 1969).

The importance of detritus as the basis of ecosystem foodwebs has been researched extensively. In estuarine foodwebs particularly, scientific studies indicate that detritus serves as a food source for microscopic organisms, which in turn are consumed by larger organisms, forming the basis for the estuarine foodweb. As will be discussed in this paper, and a second, more detailed paper to follow, the estuarine detrital foodweb is fairly complex, yet fundamentally based on the decay of vegetative matter providing a growing substrate for microbes which are a food source for larger animals. In turn, these animals are prey for larger animals and eventually, recreationally and commercially important finfish, shellfish, crustaceans, waterfowl and wading birds.

What is Detritus?

Detritus, derived from the Latin root meaning to break down or wear away, is used to define ***organic*** muds, slimes and oozes. Early efforts by the scientific community to define detritus resulted in very general definitions. Darnell (1961) defined detritus as "all types of ***biogenic*** material in various stages of bacterial decomposition." Later, Darnell (1967) modified his definition to "all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species." However, further efforts by the scientific community to define detritus were hampered by the philosophical debate over the inclusion, or exclusion, of microorganisms. In one school of thought, detritus refers to "organic debris together with attendant microorganisms," while another school of thought defines the substance as "detritus plus attendant microorganisms" (Crosby 1985). In other words, is detritus the non-living organic debris (vegetative matter and feces) alone, or does it include the living microorganisms? Classically, the definition should be limited to the organic matter, the material which is being broken down, and should exclude the microorganisms which are the agents of "breaking down" the substrate. However, a more functional definition of detritus includes attendant microorganisms with the organic debris. As much of the current interest in detritus relates to the role it plays in marine foodwebs, and as microorganisms are a fundamental element of that role, we will use the functional definition which includes attendant microorganisms.

Using any definition, detritus is found in all ***biotopes***. This report will address the marine environment only, and specifically, the estuarine and marsh environment.

What is in Detritus: Composition

Detritus can be composed of a diverse suite of living and non-living constituents. The gross composition of marine detritus includes particulate vascular plant matter, Monerans (blue-green algae and bacteria), yeasts and other fungi, algae (benthic and phytoplankton), carcasses, feces, bacterial ***exopolymers***, protozoans (ciliates and zooflagellates), metazoans (nematodes, turbellarians, rotifers, ostracods, and harpacticoids), shed ***exoskeletons***, regurgitations, molecular aggregates (***colloidal*** lipids, carbohydrates and proteins), dissolved liquids (vitamins, amino acids, simple sugars, and urea), and dissolved gases (methane, ammonia, and hydrogen sulfide) (various authors).

Fecal matter is a relatively important component of detritus. Fecal pellets are a major marine food source which is high in protein, and ingestion and use of such is an important marine energy transfer mechanism (Frankenberg & Smith 1967, Johannes & Satomi 1967).

Where Does Detritus Come From: Sources

Natural sources of marine detritus include animals, phytoplankton, bacteria and blue green algae, ***periphyton***, submerged aquatic vegetation, intertidal ***macrophytes***, river borne detritus, beach and shore material, terrestrial detritus and atmospheric deposition (Darnell 1967 and others). Detritus is produced during all seasons and is available in three forms: particulate, micellar (organic material adsorbed onto

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inorganic particles), and dissolved (Darnell 1961, Odum & de la Cruz 1967). Particulate forms can either be suspended in the water column or precipitated. The sources of particulate detritus can be determined by chemical testing, as sources have distinct "signatures." The importance of each source varies with area, salinity and season.

The great bulk of organic detritus is derived from vegetation. The majority of vegetative material in salt marshes is of macrophyte origin. *Spartina alterniflora* and algal species are the two major sources of primary production in salt marshes, but algal production is estimated to be only 20-25% of marsh grass production. Estimates of aerial production for *Spartina alterniflora* range from 550-2,000 grams per meter square per year (g $m^{-2}y^{-1}$) dry weight with below-ground production up to 7 times aerial production (Marinucci 1982). This far exceeds marsh phytoplankton or benthic algae production. However, there is an increase in benthic algae production during winter months when the ***senescence*** of the marsh grasses allows light to penetrate a greater area of the marsh surface (Gallagher & Daiber 1974, Peterson & Howarth 1987, Van Raalte et al. 1976, Benner et al. 1988).

Mann (1976) estimates that a maximum of 10% of marine macrophyte (both emergent and submerged aquatic) production is directly consumed by primary consumers and the remaining 90%, or more, enters detritus food chains. Studies in a Georgia estuary estimate that of the total detrital pool, approximately 86% of the detritus was decaying *Spartina alterniflora* (Odum & de la Cruz 1967). Hodson et al. (1984) showed annual detrital production from *Spartina alterniflora* to be approximately 1,200 g $m^{-2}y^{-1}$. Haines (1977), however, found *Spartina alterniflora* detritus (780-1,660 g $m^{-2}y^{-1}$) approximately equal to phytoplankton (770 g $m^{2}y^{1}$) and terrestrial (600 g $m^{-2}y^{-1}$) sources for a Georgia salt marsh.

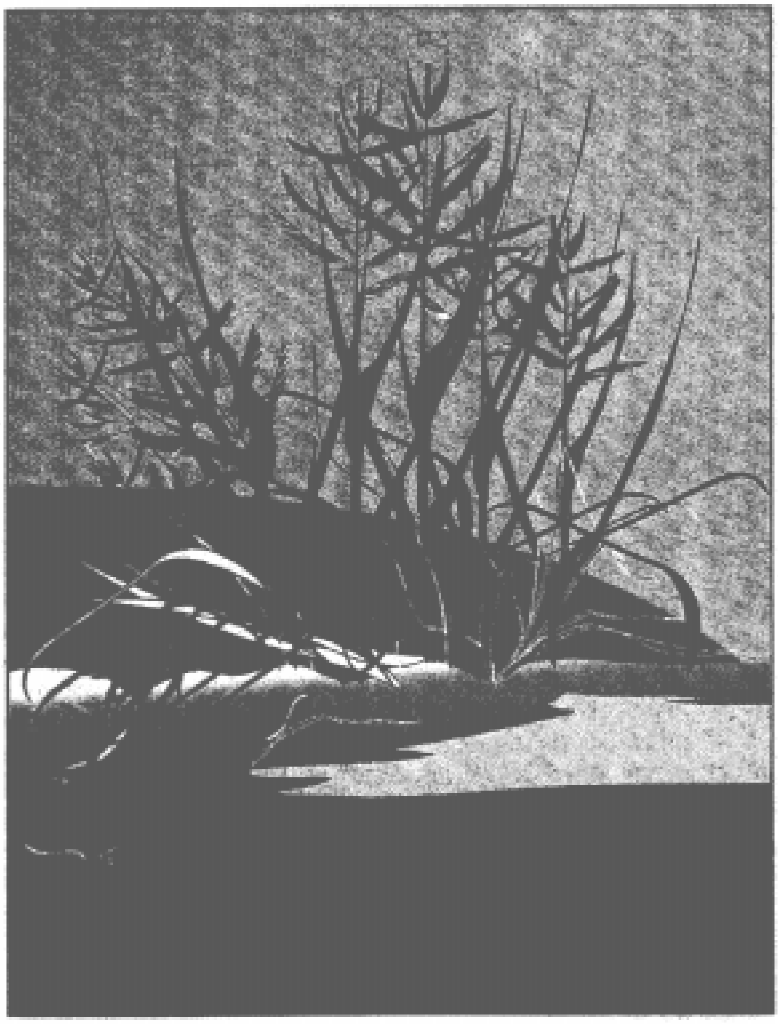
How is Detritus Produced?

There is little scientific information on the decay rate of salt marsh vegetation. However, some research has been undertaken to study the production of detritus from *Spartina alterniflora*. Since approximately 2/3 of the primary production of east coast intertidal marshes is derived from *Spartina alterniflora* (Pomeroy et al. 1981), a discussion of these processes is particularly relevant.

Most ***halophytes***, *Spartina alterniflora* included, are physiologically patterned much like terrestrial plants (Haines & Montague 1979). Therefore, marsh grass detritus is composed primarily of ***structural plant polymers*** such as ***cellulose***, ***hemicellulose*** and ***lignin***. These polymers are collectively referred to as lignocellulose (Benner et al. 1988, Hodson et al. 1984). Lignocellulose constitutes from 55-80% of the ash free dry weight of above-ground *Spartina alterniflora* biomass (Coston-Clements & Ferguson 1985, Benner et al. 1988). (See box above.) Lignin, starch and lipids make up the remaining percentage of the above-ground biomass, but can make up a greater percentage of ash free dry weight than either cellulose or hemicellulose in the below-ground portion of *Spartina alterniflora* (Coston-Clements & Ferguson 1985, Newell & Langdon 1986). *Spartina alterniflora* lignocellulose, by weight, is approximately 41% carbon and <1% nitrogen (Benner et al. 1988).

Valiela et al. (1985) showed decay rate to be directly related to internal nitrogen levels of the decaying material, generally the higher the nitrogen levels, the greater the decay rate. For instance, Odum & de la Cruz (1967) showed *Uca* spp. (fiddler crabs) to decompose much faster

Ash Free Dry Weight is the determination of mass after the removal of water and carbonaceous material. It is commonly used to determine the mass of the structural components of living matter, or the organic carbon content of soils. There are several techniques by which this determination may be made. In the most simple technique, a sample is ignited (burned) at high temperature. Prior to ignition, the material is placed in a low temperature oven, commonly referred to as a drying oven, to remove the water content of the material. The material is then weighed (dry weight) and placed in a high temperature (550° C) muffle furnace for a couple hours. At this temperature the organic material is burned off and the structural material remains. With vegetative samples, the ash residue is calculated, and in soils the loss-on-ignition (the difference between the dry weight and ash free dry weight) provides a rough estimate of organic carbon. (Allen et al. 1986)



than marsh vascular components. In *Spartina alterniflora*, and many other marsh plants with high lignocellulose component, decomposition rates are relatively slow (Tenore 1983). Salt grasses and *Juncus* spp. were found to decompose slower than *Spartina alterniflora*. *Spartina patens* may take up to twice as long as *Spartina alterniflora* to decompose (Valiela et al. 1985). Cellulose is ***mineralized*** at a higher rate than lignin (Hodson et al. 1984). *Salicornia* spp. (saltwort), a succulent plant high in water content, was found to decompose more rapidly than *Spartina alterniflora*.

Initial decomposition of *Spartina alterniflora* detritus is accomplished mechanically by either the movement of water or alteration by animals (Darnell 1967, May 1974, Valiela et al. 1985). Generally, chemical alterations follow mechanical alterations (Darnell 1967). For *Spartina alterniflora*, decomposition half-lives (the time in which the amount of original material is reduced by half) range from 18-350 days, dependent upon tide range and latitude (Marinucci 1982). It has been estimated that *Spartina alterniflora* looses only about 20% of its original ash free dry weight after 150 days of ageing.

Valiela et al. (1985) have identified a three phase decomposition process for above ground salt marsh grass. Phase one takes less than one month and is merely the leaching of the soluble component (also Hodson et al. 1984, Pomeroy et al. 1977). This component makes up 5-40% of the grass litter. Leaching has been estimated to release approximately 6 g Carbon $m^{-2}y^{-1}$ (Gallagher et al. 1976). Phase two takes up to one year and involves microbial degradation, which removes an additional 40-70% of the original material. Yeasts and bacteria are the major decomposing agents of salt marsh vascular plants (Meyers et al. 1975, Deegan et al. 1990, Benner et al. 1988, Pomeroy et al. 1981). The final phase takes up to an additional year. It is during this phase that the remaining structural material is decomposed. After phase three, as little as 10% of the original material may remain.

The contribution of below-ground material to detritus production is not well understood. Of the many common plant species, belowground decomposition has been explained only for *Juncus roemerianus* and *Spartina cynosuroides* (Hackney & de la Cruz 1980). Decomposition is restricted to the upper 20 cm of marsh sediment with greatest and most constant decomposition in the upper 10 cm. Due to greater diffusion of oxygen to root systems, *Spartina cynosuroides* decomposes faster than *Juncus roemerianus* for below-ground portions. Below-ground detritus is liberated by localized erosion and animal activities such as feeding, digging, burrowing and nesting.

Colonization

The process of breaking down the particulate vegetative material begins with the rapid and efficient colonization by bacteria, algae, blue-green algae and fungi (Odum & de la Cruz 1967, Gosselink & Kirby 1974, Fenchel & Harrison 1976, Marinucci et al. 1983). Shortly after bacterial colonization, bacteriovores, algivores and fungivores appear. These include ciliates, zooflagellates, rotifers, and later nematodes, turbellarians, ostracods and copepods (Fenchel & Harrison 1976, Benner et al. 1988). Bacterial colonization is the major link in colonization, but protozoan biomass can typically be of the same magnitude as bacterial biomass (Fenchel & Harrison 1976).

Bacteria can either be attached to particulate detritus, or aggregated ***interstitially*** within the spaces of sediment and particulate matter. Microbial growth is commonly greatest in high marsh zones and areas with relatively small sediment and detritus particle size (Gosselink & Kirby 1974, Wilson & Stevenson 1980). It has been estimated that colonizing bacteria cover from 2-15% of the detritus surface (Fenchel & Harrison 1976). Wilson & Stevenson (1980) report from 13-52% of bacteria were attached to particulates; the remainder aggregated interstitially. Marsh & Odum (1979), however, found greater colonization on sediment particles than particulate detritus in Taskinas Creek, a tributary to the York River. Less than 2% coverage of the detrital particles surface area was found from Taskinas Creek samples. Marsh & Odum (1979) also found colonization greatest on larger diameter particles compared to colonization on smaller particles. These results seem to contradict other studies; perhaps due to the time of year sampling occurred. Marsh & Odum (1979) collected samples in late August. At this time of year, temperatures are highest and marsh primary production is low. It is possible that the sediment particles and larger detrital particles provided a more stable substrate and contained greater nutrients than small detrital particulates.

Avenues of Availability: Where Does Detritus Go

Early researchers adhered to the theory of a link between coastal marsh productivity and estuarine productivity, and promoted the theory as fact (Darnell 1961, Teal 1962, Odum & de la Cruz 1967, Heinle & Flemer 1976, Heinle et al. 1977, Pickral & Odum 1977). Odum (1968) suggested, as a parallel to the role of upwelling in nearshore productivity, that the term outwelling be applied to the interaction between the export of organic material from wetlands and estuarine productivity. The outwelling theory offered a tangible, and plausible explanation for the co-occurrence of high levels of primary production in coastal marshes and high levels of secondary production in coastal fisheries.

However, Haines' (1977) study of a Georgia salt marsh, and Nixon's (1980) critical review of early salt marsh plant detritus research, questioned the commonly accepted understanding of the role of detritus in estuarine foodwebs. Recent research reveals more complex processes than direct tidal transport of marsh plant detritus to the estuary. And dependent upon the size, morphology and hydrology of the marsh, phytoplankton, benthic algae and terrestrial sources of plant detritus may reach levels equal to that of marsh grass detritus (Haines 1977, Heinle et al. 1977).

More recent research has revealed geographic differences in both *Spartina alterniflora* detritus importance and transport to the estuary. Peterson & Howarth (1987) state *Spartina alterniflora*'s importance is geographically variable, with importance as a detrital food source increasing with increasing latitude. Southeastern United States salt marshes can act as a sink for particulate organic matter in the absence of stochastic events (Wolaver et al. 1988, Chalmers et al. 1985). However, in the Bay of Fundy, where outwelling appears to occur; *Spartina alterniflora* detritus is greater in suspension than in the sediment and only 10-24% of the detritus remains on the marsh surface (Cranford et al. 1987).

***(Authors note:** A more detailed discussion of the nutritive value and fate of detritus in the marine foodweb will follow this overview of the composition and production of detritus in a future technical report.)*

Glossary

Biogenic: Essential to the maintenance of life.

Biotope: An area of uniform environmental conditions and biota.

Cellulose: the main polysaccharide (carbohydrate) in living plants. Forms the skeletal structure of the plant cell wall.

Colloidal (system): An intimate mixture of two substances, one of which, called the dispersed phase (or colloid), is uniformly distributed in through a second substance, called the dispersion medium.

Exopolymer: A substance made of giant molecules external to the source of production.

Exoskeleton: The external supportive covering of certain invertebrates such as arthropods (i.e. insects, spiders and crabs).

Halophyte: A plant that grows well in soils having a high salt content.

Hemicellulose: A type of polysaccharide found in plant cell walls in association with cellulose and lignin.

Interstitial: Of, pertaining to, or situated in a space between two things.

Lignin: A substance, that together with cellulose, forms the woody cell walls of plants and cements them together.

Macrophyte: A plant large enough to be observed by the naked eye.

Mineralized: To convert to mineral material, the replacement of organic matter with inorganic materials.

Organic: Of chemical compounds, based on carbon chains and containing hydrogen (live matter, or of living origin).

Periphyton: Sessile biotic components of an aquatic ecosystem.

Senescence: Biological changes related to ageing (the breakdown of plant material with time).

Structural Plant Polymers: Those large molecules which form the skeletal structure of plant cell walls; cellulose, hemicellulose and lignin.

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