BULLETIN OF MARINE SCIENCE, 35(3): 510–521, 1984

DUAL-GRADIENT CONCEPT OF DETRITUS TRANSPORT AND PROCESSING IN ESTUARIES

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ABSTRACT

The concept is presented that organic detritus is not uniformly distributed in estuaries, but occurs principally along two gradients, the salinity axis gradient and the marsh stream order gradient. Preliminary evidence is reviewed suggesting that DOC and POC are distributed along these gradients in generally decreasing concentrations from the sources, river carbon in the first case and tidal marsh carbon in the second. Processing of detritus along the salinity axis gradient is proposed to be due principally to physical processes such as floculation while biological processes play a more important role along the marsh stream order gradient. Finally, the potential carbon sources for primary consumers along the marsh stream order gradient should demonstrate a shift from predominantly vascular plant detritus, benthic microalgae, and, possibly, carbon from terrestrial sources in the low order streams to phytoplankton and phytoplankton detritus in the larger streams and embayments. Large beds of submerged macrophytes such as seagrasses can introduce considerable variation in these trends in DOC and POC concentrations. All of these phenomenon are important in considerations of the relative importance of organic detritus as an energy source for estuarine consumers.

The relative importance of organic detritus as an energy source for coastal and estuarine animal consumers has been an actively debated topic for the past two decades. The basic concept states that marshgrasses, seagrasses, mangroves, macroalgae, and terrestrial plants provide a significant input of organic carbon to shallow coastal areas and that either directly, or indirectly through microbial conversion, this material provides a significant food source for a variety of primary consumers. An alternate concept suggests that organic detritus is not quantitatively of much importance to coastal consumers and that phytoplankton and other sources of microalgae probably provide most of the energetic base for coastal foodwebs.

Many attempts have been made to test these alternate concepts. These attempts have included estimates of organic carbon flux from marshes (summarized by Odum et al., 1979; Nixon, 1980), monitoring of nutritional quality during detrital decay (reviewed by Tenore and Rice, 1980), observations of significant quantities of detritus in the digestive tract of primary consumers (Darnell, 1958; Odum and Heald, 1972; 1975), correlations of wetland area with fisheries catches (Turner, 1977), calculations of community plankton respiration (Turner, 1978), simulations using systems models (Wiegert et al., 1980), and the use of isotopic ratios to trace the origin of consumer carbon (Haines and Montague, 1979; Fry, 1981).

Unfortunately, the evidence has been contradictory and the debate remains unresolved. Part of the confusion results from the complex nature of the topic under consideration, part results from the indirect nature of most of the scientific evidence, but much of the disparity in results and conclusions can be traced directly to the tendency of many of the various investigators to ignore details of space, location, and scale. For example, transport and processing of organic detritus at low salinities may differ fundamentally from what occurs at higher salinities. Patterns of detritus utilization in small tidal creeks may not be the same as in deep embayments. Consideration of these differences may help reconcile the con-

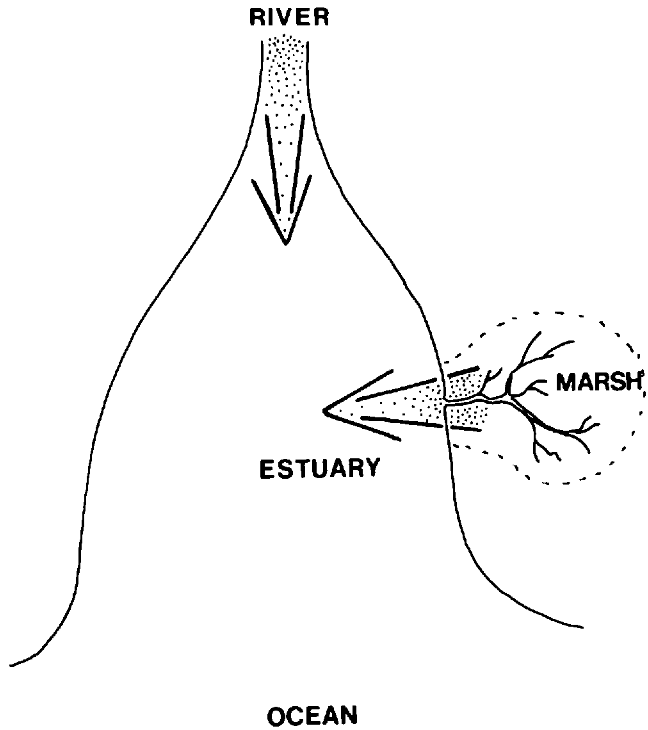


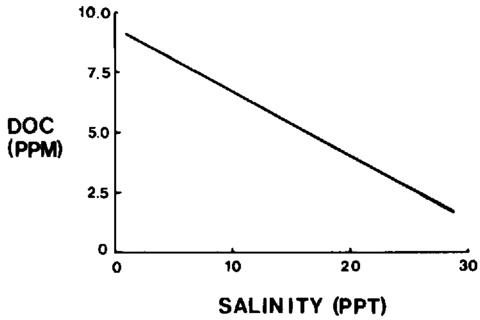
Figure 1. Conceptual model of organic detritus gradients in estuaries showing (a) the salinity axis gradient with inputs of terrestrial and river organic detritus and (b) the marsh stream order gradient with inputs of marsh or mangrove swamp organic detritus.

flicting observations which have been made concerning the importance of vascular plant detritus as an energy source for estuarine consumers.

Dual Gradient Concept

It is the basic tennet of this paper that there are two fundamental gradients of detritus transport and processing in most estuaries (Fig. 1). Furthermore, these detritus gradients appear to be closely linked to two basic gradients in estuarine physical conditions: (1) the salinity gradient from freshwater to marine conditions sometimes called the "salinity axis gradient" and (2) the gradient from small tidal marsh creeks to large bodies of water, which I will refer to as the "marsh stream order gradient." An important corollary to this concept is that detrital material associated with the salinity axis gradient comes primarily from riverine and terrestrial sources along with phytoplankton while detrital material associated with the "marsh stream order gradient" comes principally from marshes, mangrove swamps, and other wetland sources.

In the conceptualization of these gradients, the work of Horton (1945), Cummins (1974), and Vannote et al. (1980) in freshwater streams plays an obvious role. While theories of changes in detrital processing and utilization with increasing stream order in freshwater streams seem to apply, at least partially, to estuaries, it is also necessary to include considerations of salinity change down the axis of the estuary.



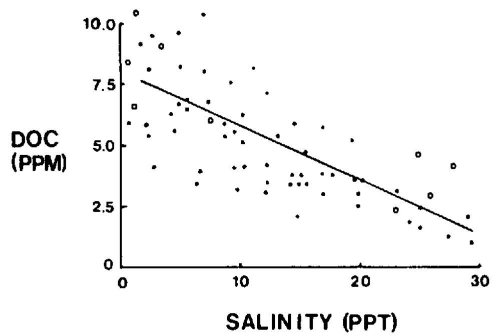


Figure 2. (Left) Hypothetical relationship of DOC and salinity along the salinity axis gradient.

Figure 2. (Right) Field data relating DOC concentration and salinity. Data recalculated from Fox, 1983 (closed circles) and Odum et al., m.s. in prep. (open circles).

Salinity Axis Gradient

Recent research (Morris et al., 1978; Sharp et al., 1982) has shown that a number of chemical and biological processes are closely linked to the estuarine salinity gradient. For example, concentrations of both dissolved and suspended particulate organic carbon appear to follow predictable patterns in response to relative position along the salinity gradient.

Concentrations of DOC.—Any discussion of so-called dissolved organic carbon (DOC) is confounded by the heterogeneous nature of the material which is lumped into this category. Various researchers have defined DOC as material which passed through filters with effective particle retention sizes ranging from 0.2 to 1.2 μm. Sharp (1973) has demonstrated that much of the material in seawater in the size range of 0.1 to 1.0 μm is colloidal rather than dissolved. Therefore, whenever the term DOC is used in this paper it includes both colloidal and true dissolved organic carbon, two types of materials which may have different chemical and biological properties.

Examination of the literature dealing with DOC in estuaries suggests a theoretical inverse relationship with salinity (Fig. 2a). Field data from several sources (Fig. 2b) tends to confirm this hypothetical relationship.

Several factors are probably responsible for this trend. (1) River water generally has a higher DOC concentration than seawater. Sholkovitz (1976) estimated that the average concentration of DOC for the world's rivers is 10 mg C/liter compared to 2 mg C/liter or less for seawater. This means that the DOC concentration should be higher at the upstream, low salinity end of the estuary and lower toward the estuary mouth where seawater has been advected into the estuary. (2) Further, "dissolved" high-molecular-weight organic compounds may be removed along the salinity gradient (Kalle, 1966; Brown, 1977), perhaps through precipitation of dissolved humic substances (Hair and Bassett, 1973; Sholkovitz, 1976). (3) Finally, biological processes such as microbial activity along the salinity gradient may remove DOC from the water column.

There is some evidence (Odum et al., m.s. in prep.[1]) that the inverse relationship between DOC concentration and salinity does not exist in the mid-Atlantic states

[1] W. E. Odum, D. E. Smith and T. S. Wolover. Flux of organic carbon from tidal freshwater and salt marsh surfaces.

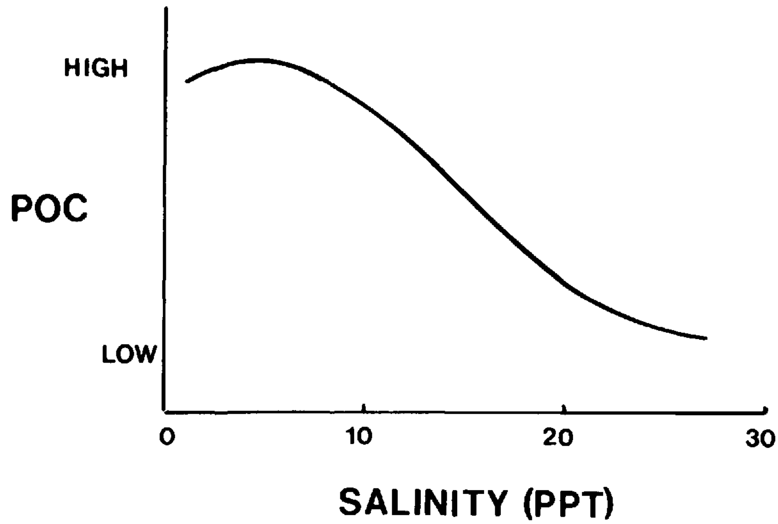


Figure 3. Hypothetical relationship of POC (suspended) and salinity along the salinity axis gradient. The rise in POC concentrations at low salinities corresponds with the turbidity maximum.

during the late summer and autumn and that concentrations may be relatively uniform along the salinity gradient at that time of year. This constancy may reflect the general lack of significant freshwater river inflow at that season.

Although most estuarine DOC is probably in a relatively refractive state (Sottile, 1974; Pomeroy et al., 1976; Gallagher et al., 1976), much of it can still be slowly metabolized by microorganisms. Material freshly leached from marshplants has been shown to be metabolized rapidly by the plankton community (Turner, 1978). Therefore, the DOC pool, no matter how refractory some of its constituents may be, should be considered a potential energy source for estuarine and coastal food-webs.

Distribution of POC.—Meaningful hypotheses about benthic POC concentrations along the salinity axis gradient are not possible at this time because of insufficient published data. Moreover, as discussed later in this paper, there is a complex relationship between suspended and deposited POC in many estuaries depending upon tide, current, wind, and wave conditions.

It is possible to draw preliminary conclusions about average suspended POC concentrations along the salinity axis gradient. Studies of suspended sediment loads (Morton, 1972; Nichols, 1972; Duinker and Nolting, 1976; Sharp et al., 1982) suggest an inverse relationship between suspended POC and salinity (Fig. 3), except for a slight increase in POC concentration in the turbidity maximum zone of some estuaries (Schubel, 1968). This pattern is a general relationship and subject to variation from lateral inputs from the sides of the estuary, inputs from phytoplankton, inputs from beds of submerged aquatic vegetation, and the formation of flocs (see the following paragraph). In some cases the rise in suspended POC in the low salinity section of the estuary is probably related to high phytoplankton production (Spiker and Schemel, 1979).

Portions of the pools of refractive DOC and POC appear to become coalesced into flocculent particles as the material moves from the river into the relatively

Table 1. Approximate characteristics of marsh creeks by stream order. Stream order classification originally proposed by Horton (1945) based on the number of tributaries (i.e., first order streams = no tributaries, second order streams = two first order streams combined, etc.)

Stream size	Drainage basin (ha)	Stream width (m)	Comments
First order	0.25	1	Located on marsh surface, drains completely at low tide
Second order	5.0	3	Approximately 75% of volume drains at low tide leaving extensive creek banks
Third order	100's	10	Relatively deep channel, 50% or less of volume drains at low tide
Fourth order (and higher)	1,000's	50+	Deep channels, 25% or less of volume drains at low tide
Embayments	10–100,000's		

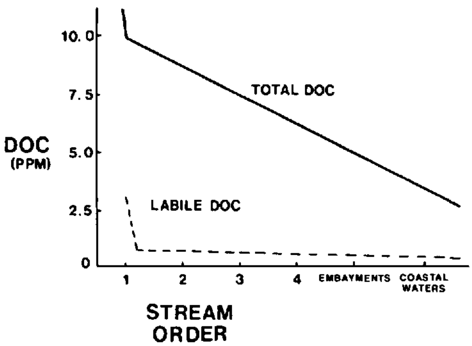
low salinities of the upper estuary. These "flocs" have been described by Krank (1974, and pers. comm.) as combinations of organic and inorganic particles which may reach diameters as great as several hundred micrometers ("macroflocs"). As a result of these flocs, the mean particle size of the suspended material increases slightly in the low salinity zone of the estuary before declining in size further down the estuary in higher salinities.

The general decline in suspended POC concentration down the axis of the estuary is probably related to (a) dilution with saltier water with lower suspended POC concentrations and (b) deposition of riverine and terrestrial detritus. There is some evidence (Folger, 1972; Nichols, 1972) which suggests that the sediments at the low salinity end of the estuary are much higher in organic content than near the mouth. Presumably, this change results, in part, from precipitation and deposition of river and terrestrial POC and DOC from upstream sources.

Distribution of Colloidal Material.—The finest fraction of the suspended load, the colloidal fraction (0.4–1.2 μm), is composed of small polymers which are not in true solution (Sharp, 1973). As pointed-out earlier, much of this material may pass through filters in the range of 0.2–1.2 μm and be included in the "DOC" fraction. Unfortunately, information concerning estuarine colloidal material is too limited to draw definite conclusions about its distribution in relation to the salinity gradient. Sigleo et al. (1982) have shown a gradual decline in colloidal concentrations with increasing salinity in the Chesapeake Bay system. They further showed within the low salinity section of the Patuxent River estuary that the colloidal fraction contained no lignin derivatives or other constituents suggesting a terrestrial origin. They concluded that the source for colloidal material in both the small estuary and other stations in Chesapeake Bay was autochthonous (aquatic microorganisms).

Marsh Stream Order Gradient

The second hypothetical gradient of detritus transport and processing in estuaries consists of the series of increasingly larger tidal streams and rivers which drain the wetlands on the edges of the estuary. This gradient is an application of Horton's (1945) concept of stream order, originally applied to freshwater stream networks. The approximate characteristics of each increasing marsh stream order are outlined in Table 1. Most coastal marsh systems do not appear to have streams



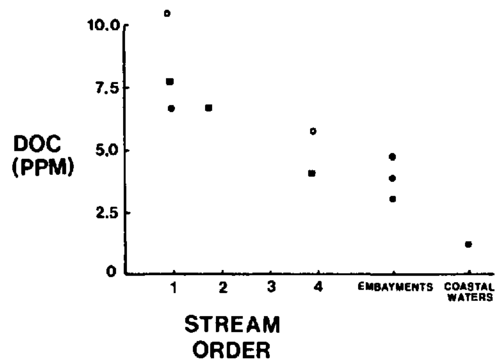


Figure 4. (Left) Hypothetical relationship between labile (easily metabolized) DOC, total DOC, and marsh stream order. Rapid decreases in concentration at stream order one represents changes in crossing the marsh surface. Local increases in DOC may occur anywhere along the gradient in the vicinity of large beds of submerged macrophytes.

Figure 4. (Right) Field data relating DOC concentration and marsh stream order. Open circles represent data from Sotille (1974), closed circles are from Happ et al. (1977), and squares are from Odum et al. (m.s. in prep.).

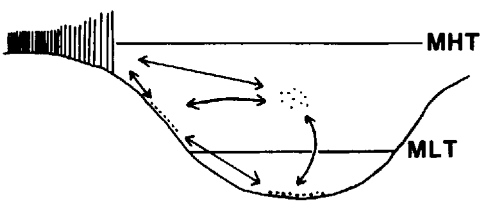
exceeding order five or six. Although there is little information linking changes in detritus concentrations and transport with marsh stream order, it is possible to propose several hypothetical trends.

Concentrations of DOC.—Typically, concentrations of DOC in marsh creek water gradually decrease with increasing stream order (Fig. 4a, b), presumably in response to dilution with seawater (Pomeroy and Imberger, 1980). Similar to earlier discussions of DOC concentrations (Fig. 2a), local increases in DOC may occur throughout the stream order gradient (Fig. 4a) in response to inputs of DOC from small-scale features such as phytoplankton blooms or beds of underwater vegetation (Robert Wissmar, pers. comm.).

Concentrations appear to be highest in water flooding the marsh surface, and particularly in the rear of the marsh, as compared to even the smallest tidal creeks. This preliminary observation is based upon limited information from flume studies in which the same volume of water is monitored as it floods and moves across the marsh surface within the confines of a fiberglass flume approximately 1.5 m in width (Odum et al., m.s. in prep.[1]). The increase in total DOC in the water flooding the rear of the marsh does not appear to be great, typically averaging less than a 25% increase above the concentration in the tidal creek.

Due to a lack of suitable data, it is difficult to hypothesize concerning the relative concentrations of labile DOC along the estuarine stream gradient. The more labile components of the DOC pool appear to remain in the water column for an extremely short period of time before being metabolized by microorganisms (Gallagher et al., 1976). Preliminary experiments utilizing microcosms to test the relative degree of metabolizable DOC suggest that water overlying the center and rear of the marsh contains a higher concentration of labile DOC (Fig. 4a) than water at various points down the tidal creek gradient (Odum et al., m.s. in prep.[1]), except, perhaps, at points where phytoplankton blooms are occurring in the larger creeks.

Distribution of POC.—Field observations of POC concentrations along the estuarine stream order gradient are scarce, usually address only one section of the



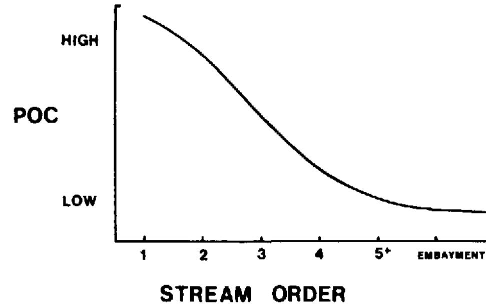


Figure 5. (Left) Conceptual model of POC movement between several micro-locations in response to current, precipitation runoff, and wave action.

Figure 6. (Right) Hypothetical relationship between POC (suspended and bedload combined) and marsh stream order.

gradient, and have often ignored deposited material on the stream bed. It is important to remember that detritus particles associated with marsh/tidal creek systems can either be in suspension or on the stream bed (Fig. 5) depending upon the current velocity (Odum et al., 1979). If the current is much below 20 cm/sec, most of the particles larger than 5–10 μm will settle rapidly out onto the stream bed or marsh surface. Above 30–40 cm/sec the larger detrital particles are either temporarily in suspension or rolling along the bottom as bedload. This makes the accurate estimation of the concentrations and fluxes of POC extremely difficult in tidal creeks.

Because of these difficulties, the hypothetical behavior of POC with increasing estuarine stream order shown in Figure 6 represents combined suspended and deposited POC. In discussing POC changes along the salinity gradient (Fig. 3), it is possible to differentiate to some extent between suspended and deposited material because of the extremely small size of the particles and their relatively slow sinking velocity. However, even along that gradient there is a tendency for bedload particles to become resuspended under increased current velocity conditions (e.g., at the turbidity maximum section of highly stratified estuaries).

The hypothetical trend of decreasing POC with increasing estuarine stream order (Fig. 6) probably results from a decreasing ratio of wetland to water surface and an increase in oceanic water volume. Furthermore, much of the particulate marshplant material is decomposed on the marsh surface and in the first and second order stream networks. In certain locations seagrass or kelp beds may be sufficiently widespread to increase POC concentrations in higher order streams and embayments.

Potential Carbon Sources for Primary Consumers.—Accompanying the hypothesized stream order/POC relationship is an apparent series of changes in the organic carbon sources available to the primary consumers (Fig. 7). Primary consumers are the functional group of invertebrates and fishes which are able to assimilate living plant material and plant detritus along with associated microorganisms (Odum and Heald, 1975).

According to the hypothesized trends shown in Figure 7, the principal carbon sources for primary consumers in small order streams originates from either marshplant or mangrove communities, depending upon the latitude. There may also be quantities of benthic microalgae and, in certain locations, significant inputs

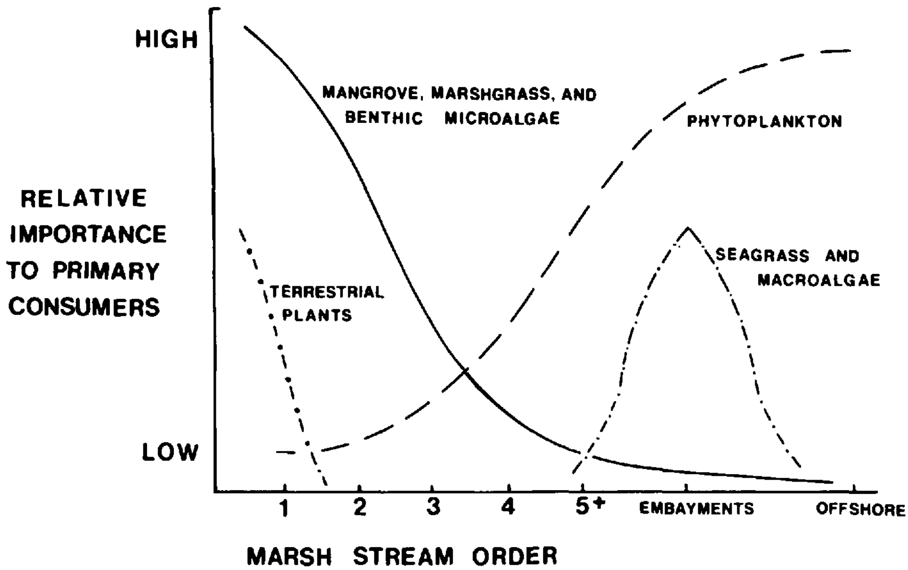


Figure 7. Conceptual diagram of the principal sources of organic carbon available to primary consumers along the marsh stream order gradient. Relative importance values are hypothetical.

of carbon from upland, terrestrial sources. Phytoplankton, while apparently less important to consumers in low order streams, becomes increasingly important as a food source in larger order streams, embayments, and offshore. Finally, carbon from seagrasses and macroalgae, when present, may be important in higher order streams and embayments.

Tests of these hypothesized changes in consumer carbon sources are scarce. The best available evidence appears to come from isotopic ratio analyses of consumer tissues since these can give an indication of the original sources of organic carbon to the consumer. Unfortunately, only a few isotopic ratio studies have considered the relative position of samples in the marsh stream order gradient.

Zieman et al. (in press) found that the del ^{13}C value for pink shrimp, *Penaeus duorarum,* from low order streams and small embayments in a mangrove swamp closely approximated the del ^{13}C value of mangrove tissues. Pink shrimp from seagrass-dominated embayments showed del ^{13}C values 15 ppt lower and similar to seagrass del ^{13}C values.

Fry (1981) found del ^{13}C values for brown shrimp, *Penaeus aztecus,* in Texas seagrass beds (-12.8 to -15.4 ppt) to closely approximate the del ^{13}C of seagrasses. Brown shrimp from offshore waters had values (-16.2 to -16.8) closer to phytoplankton values.

Recently, Peterson et al. (m.s. in prep.)[2] utilized a dual tracer technique to investigate the apparent carbon source for the ribbed mussel, *Geukensia demissa.* They found that isotopic ratios for carbon and sulfur of mussels from first order marsh streams closely approximated values for the marshgrass, *Spartina alterniflora.* Isotopic ratios of mussels from larger order streams and embayments were

[2] B. J. Peterson, R. W. Howarth and R. H. Garritt, Sulfur and carbon isotopes as tracters of organic matter flow in thirteen salt marsh food webs.

more similar to phytoplankton; this suggested a shift in basic carbon source from margrass detritus to phytoplankton with increasing stream order.

While this consumer isotopic ratio evidence is preliminary, it tends to support the hypothesis of changes in carbon source and consumer utilization with increasing stream order. Further tests of this hypothesis should include (a) use of multiple isotopic ratios of consumer tissues (e.g., carbon and sulfur) and (b) inclusion of the marsh stream order gradient as an important variable in sampling primary consumers.

Qualifications

Spatial and Temporal Variability.—Seasonal variability probably exists even in estuaries with pronounced detrital gradients. Inputs of river and terrestrial detritus typically fluctuate in response to seasonal patterns of runoff. In the Chesapeake Bay region, the heaviest inputs of detritus along the salinity gradient occur in late winter, spring, and early summer (W. E. Odum, unpubl. data). The marsh stream order detritus gradient probably fluctuates in response to seasonal changes in wetland carbon release, although the detailed pattern of this release is not satisfactorily documented.

Both gradients have the potential to become greatly exaggerated during extreme weather events. A synoptic scale storm of long duration and heavy runoff can cause the salinity axis detrital gradient to carry heavy loads of DOC and POC from upriver and terrestrial sources. Even a modest cloudburst at low tide can increase the DOC and POC loadings in the smaller tidal channels by one or two orders of magnitude (W. E. Odum, unpubl. data).

Universality of the Concept.—The preliminary evidence suggests that the concept of dual gradients of detritus concentrations may apply to many types of estuaries (e.g., evidence presented in this paper from Delaware Bay, Chesapeake Bay and tributaries, and estuaries in Georgia, south Florida, and Louisiana). Probably, detritus gradients are most pronounced in locations where detritus sources are highly defined rather than diffuse. An example of a highly defined source would be a tidal river system in which the headwaters are totally contained within coastal marshes such as the Duplin River system near Sapelo Island, Georgia. In contrast a more diffuse gradient might exist in an estuary consisting largely of a shallow embayment with scattered beds of seagrasses as occurs in Biscayne Bay, Florida.

Detritus-Based Foodweb Debate.—If estuarine detritus gradients are widespread, then it is important to consider the ramifications when debating the importance of plant detritus as an energy source for estuarine foodwebs. For example, evidence of detritus-based foodwebs will probably be most clear in the lowest order tidal creek communities. The del ^{13}C ratios of many of these organisms should more closely reflect wetland carbon in contrast to phytoplankton carbon. Evidence to test the "outwelling" hypothesis of Odum (1980) might best be tested in a location where extensive wetland/tidal creek systems lie in close proximity to the open ocean (i.e., the coast of Georgia).

Finally, the entire "importance of detritus" debate will probably be recognized as highly site specific. While some have questioned the importance of vascular plant detritus as an energy source for coastal foodwebs (Haines, 1976; Haines and Montague, 1979; Correll, 1978) others have emphasized the potential importance of plant detritus as an energy source (Darnell, 1958; Odum and Heald, 1975). In the future both groups may need to qualify their hypotheses and statements by including the location within the estuary and the relative position along the salinity axis and marsh stream order gradients.

Corollaries Based on the Detritus Gradient Concept

Although the basic concept of detritus gradients is difficult to investigate satisfactorily, there are a series of corollaries which can be tested, modified, or rejected with either field observations or experiments.

The Basic Concept.—Organic detritus is not uniformly distributed in estuaries, but occurs principally along two gradients, the salinity axis and marsh stream order gradients.

Corollary One. DOC and POC are distributed along these gradients in generally decreasing concentrations. Along the salinity axis gradient concentrations of DOC and POC are inversely related to salinity while along the marsh stream order gradient concentrations are inversely related to stream order.

Corollary Two. Isotopic ratios (e.g., del ^{13}C) of POC and consumer tissues along the salinity detrital gradient should indicate a shift from material of a predominantly terrestrial and river source to predominantly phytoplankton. Along the marsh stream order gradient, the shift should be from mangrove or marshgrass carbon, benthic microalgae, and possibly terrestrial carbon, to predominantly phytoplankton in the larger water bodies and offshore. In those estuaries which have significant macroalgal and seagrass beds, carbon from these sources should be important in larger order streams and embayments.

Corollary Three. Processing of detritus along the salinity gradient is primarily due to physical processes (flocculation, particle formation from DOC, sedimentation) and secondarily due to biological processes (removal of particles by filter feeders, slow microbial decomposition of deposited particles). This results from the highly refractory nature of most of the detrital material.

Corollary Four. Processing of particulate detritus along the stream order gradient is primarily due to biological processes (animals which shred or grind-up large particles, filter feeders, deposit feeders, microbial decomposition) and secondarily due to physical processes (deposition, some possible flocculation). This difference from the salinity gradient is because the detrital material originating from wetland sources contains significant amounts of easily metabolized carbon compounds, at least at the upper end of the gradient.

Corollary Five. The P/R ratio (the ratio of community gross primary production to community respiration) should increase along both gradients as the allochthonous carbon (terrestrial, river, and wetland sources) is gradually replaced by autochthonous sources such as phytoplankton. Turner's (1978) results from a Georgia estuary support this hypothesis, at least for the plankton community.

Acknowledgments

Most of the research which forms the basis for this paper was supported by the Ecosystems Division of the National Science Foundation (Grant No. DEB-8109674).

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DATE ACCEPTED: August 7, 1984.

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