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Literature Review of Organic Matter Transport From Marshes

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16. ABSTRACT

A conceptual model is presented to estimate a transport coefficient for the movement of nonliving organic matter from wetlands to the adjacent embayments. The transport coefficient is developed in a manner that makes it compatible with the Earth Resources Laboratory's Productive Capacity Model. The Transport Coefficient Model in its present form envisages detritus movement from wetland pixels to the nearest land-water boundary followed by movement within the water column from tidal creeks to the adjacent embayment. This conceptual model can be transposed to deal with only the interaction between tidal water and the marsh or to estimate the transport from embayments to the adjacent coastal waters.

The outwelling hypothesis postulated wetlands as supporting coastal fisheries either by exporting nutrients, such as inorganic nitrogen, which stimulated the plankton-based grazing food chain in the water column, or through the export of dissolved and particulate organic carbon which provided a driving force for a benthic, detritus-based food web which provides the food source for the grazing food chain in a more indirect fashion. Recent research has emphasized the fact that coastal nekton may move up into the wetlands during high tide to feed and that wetlands may provide an important habitat to support critical life history stages of coastal fisheries. The most important organic carbon sources emanating from wetlands may be living organisms and labile particulate detritus, while refractory dissolved or particulate organic carbon may have to be converted to microbial biomass before it can be used.

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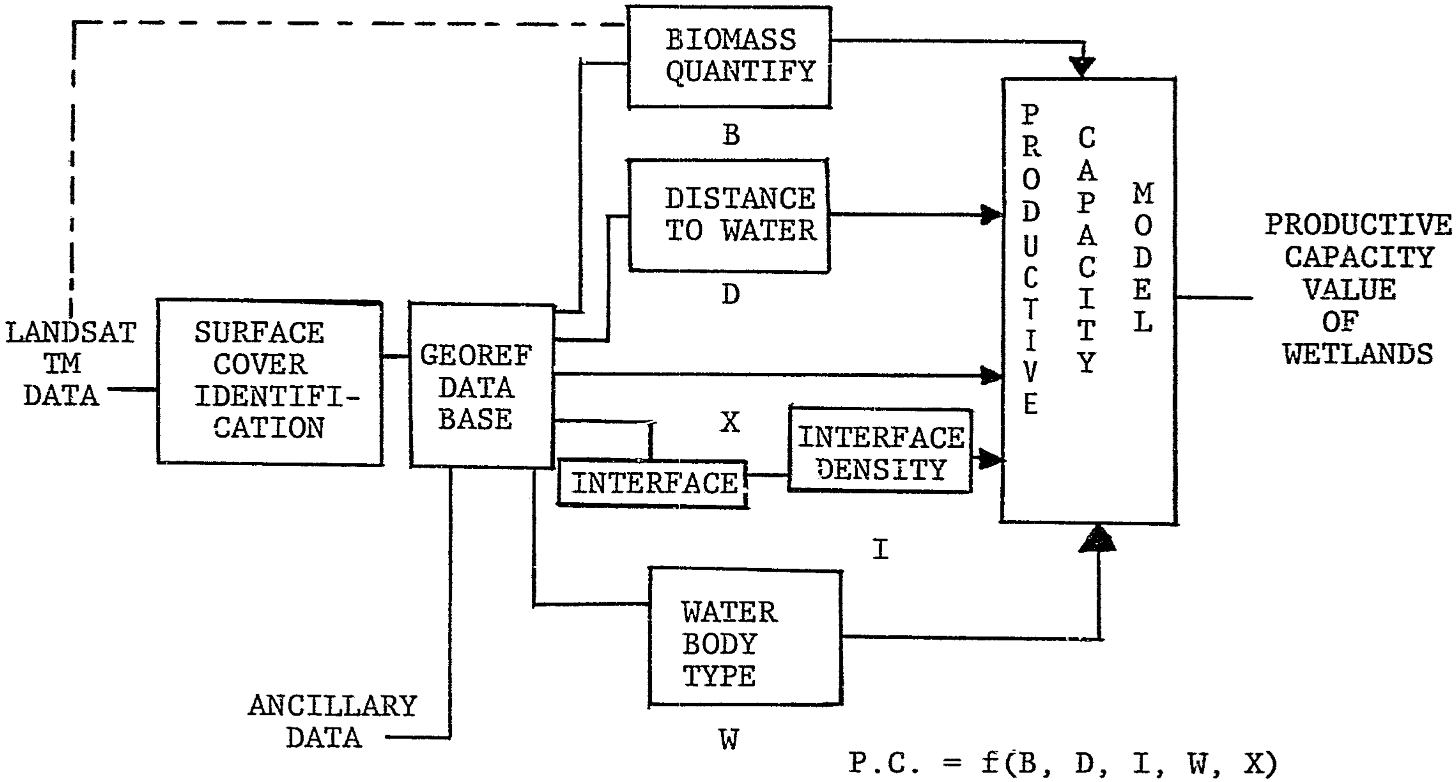
I. INTRODUCTION

This project has been conducted in support of the productive capacity modeling activity of research personnel at the Earth Resources Laboratory (ERL) located at the National Space Technology Laboratories in Mississippi. The productive capacity model assumes that the biomass of macrophytes in the marsh is a significant food source for estuarine-dependent fisheries. The model in its broadest sense relates marsh biomass to the export of nonliving organic matter, nutrients and trace elements, and organisms from the wetlands to the estuary. Any marsh pixel (0.45 ha or 1.1 ac unit area on ground) has associated with it a productive capacity value which is a function of the inherent plant productivity at that location and a transport coefficient which couples the spatial and temporal components of exchange between the wetlands and the estuary. In order to simplify the discussion, this report will focus on the transport of nonliving organic matter.

Figure 1 presents a diagrammatic overview of the steps involved in producing the first generation version of the Productive Capacity Model. The productive capacity model makes use of Landsat Multispectral Scanner (MSS) data to estimate the plant production levels in the marsh, ERL-developed software programs which use satellite and ground-based data to estimate parameters involved in transport, and the ultimate construction of a geographically referenced data base for manipulating and storing the data (Butera, 1979; Butera and Seyfarth, 1981). Successful implementation of this model will enable coastal zone planners to associate an importance value to different regions of wetlands, thus facilitating developmental decisions based on a regional scale data base.

Preliminary versions (Figure 1) of the productive capacity model have proposed the following parameters as being important in transport: distance from marsh pixel to the nearest water, type of water body involved in transport, complexity of the land-water boundary (interface density), length of land-water boundary (interface length), and type of plant involved. The focus of the preliminary model was transport from an interior marsh pixel to the land-water boundary. This report will consider additional factors, such as the effect of decomposition of organic matter on the marsh and hydrologic factors related to marsh inundation and current speed. A recent paper describing the implementation of some parts of the preliminary model considered the additional factors implicitly by assuming that transport is exponentially related to distance (Butera and Seyfarth, 1981). This paper represented water body type through importance values based on the concept that ponds and lakes are sinks for organic matter, and hence have lower importance values, while rivers and canals represent effective transport channels. Water body type represents the second stage in transport from water bodies in the wetlands to the estuaries containing commercial fish and shellfish. This study will consider additional factors, such as hydrology and geomorphology, in characterizing this transport.

This study assumes that each wetland is characterized by a unique set of hydrological and geomorphological parameters, while the underlying ecological processes operating in different systems are similar. An independent study at



P.C. = f(B, D, I, W, X)

E.G., 1. FIELD GROWTH DATA
2. SURFACE WATER SALINITY
3. VEGETATION NUTRIENT VALUES

Figure 1. Productive Capacity Model Diagram (M.K. Butera, Pers. Commun.)

the Earth Resources Laboratory related interface length and interface density to shrimp production in Louisiana (Faller, 1979). These two factors remain to be quantitatively incorporated into the productive capacity model. The type of plant in a wetland is directly related to the expected primary production values and rate of decomposition of dead plant material.

A caveat that accompanies any literature review investigation is that the compiler is limited by the accuracy of the data reported by the original authors. Where possible the original articles have been consulted in order to avoid the perpetuation of scientific myths sometimes incorporated in review articles. Space limitations prevent the incorporation of all the assumptions incorporated by the authors in their calculations to support a given hypothesis, but an attempt is made to list critical assumptions. In addition, for areas in which comparative research has been conducted, such as methods employed to estimate primary production in marsh macrophytes, techniques employed to measure sediment respiration, or uncertainties associated with water transport in wetlands, the comparative studies are referenced and the results summarized. Scientific studies on wetlands collect intensive information on small areas for short periods of time, while satellite data provide integrated information for large areas over longer periods of time. This creates certain limitations on the extrapolations of scientific data to remote sensing applications due to the difference in spatial and temporal scales.

II. OUTWELLING HYPOTHESIS

The basic assumption of the productive capacity model is based on the outwelling hypothesis popularized by Eugene Odum (Odum, 1980; Nixon, 1980). The outwelling hypothesis proposed that fertile coastal fisheries are the consequence of either "upwelling" of nutrients from deepwater which stimulate the phytoplankton production-based grazing food chain or by "outwelling" of nutrients or organic matter from productive inshore intertidal (salt marshes, mangrove swamps, or rocky shore attached algae) or subtidal (seagrass beds, coral reefs, or macroscopic algal beds) communities. Nonliving organic matter from salt marshes was presumed to support an extensive detritus food web which in turn provided a food resource for coastal fisheries. In those cases where the outwelling exported nutrients, the phytoplankton-based grazing food chain provided the food resource for coastal fisheries. Two excellent reviews have described the historical development of the outwelling hypothesis and the current data base which either supports or refutes this hypothesis (Gardner and Kitchens, 1978; Nixon, 1980). The highlights of this evidence for or against the outwelling hypothesis will be discussed. Odum has recently modified his original concept to permit a variety of forms of organic matter (dissolved, small particulate, large particulate or wrack, and living organisms ranging in size from bacteria to fish) to serve as the major component exported and to appreciate the dominant role of high spring tides and storms in transporting the bulk of the organic material exported (Odum, 1980). The sources and transport paths of dissolved (passes through a 0.20-micron filter) and particulate (retained on 0.20-micron filter) organic carbon from different aquatic angiosperm communities have been reviewed by Gallagher (1978). This paper points out that much of our knowledge of salt marshes stems from work done on the Atlantic and Gulf Coasts, while studies on the West Coast of the United States are in their infancy because of the importance of upwelling in supporting coastal fisheries in this region.

A. Evidence Supporting Outwelling Hypothesis

Table 1 presents the commercial landings of fish and shellfish for the Eastern and Gulf Coasts of the United States. There is an apparent relationship between the ratio of marsh area to open water area and the percentage of estuarine-dependent fish and shellfish in the total catch. The Northeast fishery is supported by productive subtidal areas like Georges Bank, while the North Pacific fishery is supported by coastal upwelling (marsh area/open water area = 0.02). For penaeid shrimp there is a significant correlation in different regions of the Gulf of Mexico between the area of subtidal and intertidal vegetation in an estuary and the catch of inshore shrimp (Turner, 1977). There is also a relationship between the marsh area/open water area and the relative contribution of detritus exported from marshes to in situ phytoplankton production in the estuarine carbon budget (Nixon, 1980). The marsh contribution is proportionately greater in regions such as coastal wetlands in Georgia and Louisiana or wetersheds such as the Upper Patuxent River in Maryland which feature a high ratio of marsh area to open water area (Nixon, 1980).

Carbon budget studies of wetlands have provided evidence for the export of particulate organic carbon and dissolved organic carbon from wetlands to adjacent waters. One type of investigation of this export measures the production of plant material in the marsh and subtracts the carbon that sediments onto the marsh surface and that is consumed through the metabolic activities of microorganisms and animals on the marsh. Export is computed by difference (material produced that is not sedimented or metabolized). Most of these studies assume that the products of anaerobic metabolism in the deeper layers of the sediment diffuse to the surface of the sediment where they are metabolized aerobically. This implies that surface measurements of aerobic matabolism and chemical oxygen demand represent integrated values for the metabolism of the aerobic and anaerobic portions of sedimentary columns.

The validity of this assumption will be discussed at greater length in another section of this study, but studies in Massachusetts salt marshes suggest that aerobic and anaerobic metabolism may not be tightly coupled either spatially or temporally (Howarth and Teal, 1979 and 1980). The permeable marsh soil in Massachusetts allows extensive lateral movement of ground water emanating from land, which may explain the loose coupling of surface and subsurface events in the marsh.

Table 1. Commercial Fish and Shellfish Landings in 1966 for the Eastern and Gulf Coasts of the United States (After Nixon, 1980; Woodwell et al., 1973)

REGION	TOTAL LANDINGS[1] (MILLIONS OF POUNDS)	PERCENT OF TOTAL ESTUARINE DEPENDENT	MARSH AREA/ OPEN WATER AREA
Northeast	611	7	0.03
Middle Atlantic	241	53	0.12
Chesapeake Bay	502	98	--
Southeast	368	95	0.60
Gulf of Mexico	1196	86	0.17

[1] The total landings feature different species compositions in each geographical region and the catch per unit effort varies between different regions for the same species.

Table 2 presents the export results from some selected studies which have utilized this type of investigation. The values are reported in energy units (kilocalories) rather than carbon units, because in systems containing active aerobic and anaerobic metabolism the carbon cycling is not proportional to energy flow (Howarth and Teal, 1979). A rough conversion for aerobic respiration would be 10 Kcal/g carbon and for anaerobic sulfate reduction would be 2.6 Kcal/g carbon. The end products of sulfate reduction are inorganic sulfur compounds which contain stored energy which can be utilized by chemoautotrophic bacteria. The end products of aerobic respiration, carbon dioxide and water, do not contain additional energy.

The studies listed in Table 2 can be divided into those which focus primarily on the marsh (Great Sippewisset Marsh and Barataria Bay) and those which concentrate on the marsh-embayment complex (Sapelo Island, North Inlet, and Bissel Cove). The amount exported is largest in those studies which estimate the transfer of organic matter from the marsh to the nearest water, while the export is greatly reduced in the transfer from embayments to coastal waters. Studies that focus on embayments should incorporate phytoplankton production in the water column and respiration in the water column and on the bottom. The Sapelo Island study ignores phytoplankton production in the water, underestimates soil and water column respiration, and includes export of some motile organisms in the unexplained category. The importance of the organic matter transported from the wetlands in correcting the production-respiration imbalance in the embayments is a function of the ratio of the marsh area to open water area and the depth of the water. The allochthonous sources of organic matter become less important in the carbon budget of a watershed as one moves from the headwater to the tidal portions. For example, in the Barataria Basin of Louisiana the net community production (net daytime production minus nighttime respiration) ranges from - 171 $gC.m^{-2}yr^{-1}$ in Lac des Allemands to 0 to +20 $gC.m^{-2}yr^{-1}$ in Barataria Bay (Hopkinson and Day, 1979). Table 3 presents these data more fully.

The Barataria Bay study presented in Table 2 suggests that the plants and bacteria represent the major pathways for respiratory loss of carbon in the marsh itself. The Great Sippewisset Marsh study in Table 2 suggests that systems characterized by a large component of belowground production can support an anaerobic system based on sulfate reduction which is responsible for a greater fraction of the energy flow than is the carbon cycle in the marsh. Much of the energy-bearing reduced sulfur compounds produced in sulfate reduction are recycled in the peat as a result of chemical oxidation or the activities of chemoautotrophic bacteria. Of the energy exported from the Great Sippewisset Marsh, three times as much energy is exported as reduced sulfur compounds than as dissolved plus particulate carbon (Howarth and Teal, 1980). The Bissel Cove and North Inlet studies listed in Table 2 suggest that the heterotrophic embayments process much of the organic matter lost from the marshes and only a minor fraction of the marsh produced organic carbon is exported to coastal waters.

Table 2. Selected Studies of Export from Wetlands Utilizing the Energy Budget Technique (Units: Kcal/m^2 yr)[1]

System-Components	Marsh Area	Estuarine or Water Area
1. Sapelo Island, Georgia (Wiegert and Pomeroy, 1981)		
Spartina alterniflora		6,867
Microscopic Marsh Algae		499
Soil Respiration		- 1,620
Water Column Respiration		- 2,220
Air Respiration		- 680
Sedimentation		- 109
Unexplained		- 534
Tidal Export		- 2,203
2. Barataria Bay, Louisiana (Day et al., 1973)		
Spartina alterniflora		
Gross Production	40,406	
Respiration	-33,120	
Net Production	7,286	
Microscopic Epiphytes		
Gross Production	154	
Respiration	- 31	
Net Production	123	
Bacterial Respiration	- 2,933	
Meiofaunal Respiration	- 177	
Macroinvertebrate Respiration	- 568	
Vertebrate Respiration	- 6	
Export from Marsh	- 3,725	- 2,896

Table 2 (Continued)

System-Components	Marsh Area	Estuarine or Water Area
3. North Inlet, South Carolina (Summers et al., 1980)		
Spartina alterniflora and Marsh Algae		
Net Production	1,323[3]	
Animal Respiration in Systems	- 523[3]	
Export from Marsh	- 800[3]	
Particulate Organic Matter		91[2] [3]
Dissolved Organic Matter		- 280[2] [3]
Transfer to Marsh/Bottom Sediment		- 22[3]
Outward Migration of Nekton		- 0.8[2] [3]
Consumed by Heterotrophic (Oysters and Benthos) Communities within Embayment		- 588[3]
4. Bissel Cove, Rhode Island (Nixon and Oviatt, 1973)		
Benthic Plant and Phytoplankton Production in Embayment		9,600
Sediment, Plankton, and Nekton Respiration in Embayment		-9,800
Import of Stream Organic Matter		15
Net Immigration of Shrimp and Fish		3.5
Import from Tall *Spartina alterniflora* Marsh	2,800	240
Sediment Organic Matter Storage and Export to Narragansett Bay		- 60[2]

Table 2 (Continued)

System-Components	Marsh Area	Estuarine or Water Area
5. Great Sippewisset Marsh, Massachusetts (Howarth and Teal, 1980)		
Spartina alterniflora Net Production		
Above-ground	2,033	
Below-ground	16,790	
Microscopic Marsh Algae	376	
Respiration of Anaerobic Bacteria	- 2,334	
Respiration-Aerobic Bacteria and Invertebrates	- 1,280	
Recycling of Reduced Sulfur Compounds in Marsh Peat	- 8,432	
Transfer to Marsh/Bottom Sediments	- 1,205	
Export from Marsh		
Reduced Sulfur Compounds	- 4,292	
Organic Carbon	- 1,355	

[1] Conversion Factors Used: g. dry wt. organic matter x 0.48 = gC; carbon aerobic respiration: 10 Kcal/g.C; sulfate reduction: 2.6 Kcal/g.C; 1 Watt/m^2 = 7529 Kcal/m^2 yr; *Spartina alterniflora*: 4.36 Kcal/g. dry wt.; microscopic marsh algae: 3.81 Kcal/g. dry wt.; marsh detritus: 3.76 Kcal/g. dry wt.

[2] Represents export from marsh-embayment to coastal water.

[3] Negative values represent pathways that reduce preformed organic matter by respiration, export, or burial, while positive values indicate additions of organic matter to the system by primary production or import.

Table 3. Net Community Production Values Along a Headwater to Tidal Water Transect in the Barataria Basin, Louisiana (Hopkinson and Day, 1979)

Location of Watershed	Net Community Production[1] (Units: $gC/m^2\ yr^2$)
Lac des Allemands	-171[3]
Lake Cataouatche	-133
Lake Salvador	- 75
Little Lake	- 44
Airplane Lake	0 to +20

[1] Net Community Production = Net Daytime Production in Water Column Minus Nighttime Respiration

[2] Conversion made assuming 1 g O_2 = 0.38 gC

[3] Minus value implies system is heterotrophic and plus value indicates system is autotrophic

The second type of investigation utilized to quantify the carbon budget of marshes is the input-output approach. The input-output method measures the volume of water and concentration of organic matter moving in and out of a marsh between adjacent tidal cycles and then computes the flux of carbon and its net direction of movement. Some of the factors to be considered in studies of this type are discussed by Gardner and Kitchens (1978), Boon (1978), Kjerfve and McKellar (1980), and Kjerfve (1980). Since one has to sample both horizontally across the channel and vertically from the surface to the bottom of the cross-section, these studies are both labor and capital intensive, which limits the number of tidal cycles which can be monitored in order to estimate the seasonal or yearly flux of organic matter out of or into the marsh. This situation is complicated by the fact that the water level in a marsh responds to wind stress and meteorological pressure changes as well as to regular tidal forcing. Temporal variations during a tidal cycle in discharge rates and the concentration of dissolved and particulate carbon necessitate sampling at hourly intervals. Spatial heterogeneity in current velocity and concentration in a channel's cross-sectional profile require computations to be made for each section in the channel separately, with the results to be summed to provide a net flux estimate for organic matter for the whole channel. Since the net flux of organic matter is derived by difference from two much larger numbers (total influx minus total outflux), it is subject to considerable error, with a maximum precision of ± 20 percent (Pomeroy and Imberger, 1981).

At higher water levels the water can leave the creek bank and spread out over the surface of the marsh. This greatly increases the effective channel width and may result in the transfer of water from one marsh basin to another. This can cause a serious violation of the basic assumption underlying input-output studies that the changes in water chemistry are a result of uptake or release of organic matter from the sediments and biota within a well-defined water mass. The input-output studies have generally been conducted on systems which lack a significant freshwater input from streams or ground water, thus allowing a budget to be constructed from sampling at one location where all the water enters or leaves. If storm events or spring tides are not adequately sampled, the input-output studies can underestimate the flux of organic matter. When the system involves the marsh creeks and the associated wetlands, the organic matter transport from the marsh to water column depends on the area of marsh flushed during high water and the effective tidal prism. The tidal prism is the net volume of water transported out of or into the channel between adjacent tidal cycles. If significant portions of the ebb tide volume re-enter the creek on the following flood tide, then a remixing coefficient must be used to compute the effective tidal prism (Summers and McKellar, 1979).

A review of the results from eight input-output studies of marshes revealed an export of dissolved organic carbon in all five systems for which it was measured and a particulate organic carbon export in seven of the studies (Nixon, 1980). The export (gC/m^2marsh yr) for dissolved organic carbon ranged from -8 to -140, while particulate organic carbon ranged from -303 to 61 (Nixon, 1980). The export of total organic carbon (dissolved plus particulate carbon) ranged from -165 to +53 (Nixon, 1980). Hackney and de la Cruz (1979) reported a particulate carbon import of 10 gC/m^{2}marsh yr. for a *Juncus* marsh near Catfish Bayou in Mississippi. The Stroodorpe salt marsh in the Netherlands imports about 0.6 gC/m^{2}marsh yr. of particulate organic carbon during regular tidal exchanges, while storm tides export 36 gC/m^{2}marsh of wrack (Wolff et al., 1979).

The largest import of particulate organic carbon (61 gC/m^{2}marsh yr) occurs at Flax Pond on Long Island, which has a sill at its mouth leading to a deep pond which may act as a sediment trap (Woodwell et al., 1977; Valiela et al., 1978). At Flax Pond the dissolved organic carbon export is 8.4 gC/m^2 which, when combined with the particulate organic carbon import, suggests that tidal exchange imports roughly 50 gC/m^2 yr. to the marsh. Litter bag studies of the decay of *Spartina* stems in windrows on the marsh estimated an export of dead grasses from the marsh by spring and storm tides of 150 gC/m^2 yr (Woodwell et al., 1979; Houghton and Woodwell, 1980). This suggests the net export from the system is approximately 100 gC/m^2 yr to coastal waters. Of the annual above and below-ground vascular plant production (400 gC/m^2 yr) in Flax Pond, the atmosphere provides 3/4 of the CO_2 fixed photosynthetically and the remaining 1/4 comes from sediment respiration (CO_2 recycling between heterotrophic and autotrophic components of the marsh). Of the 300 gC/m^2 yr. of CO_2 fixed by the *Spartina* from the atmosphere, 2/3 of this is stored as organic carbon in the sediments of Flax Pond and 1/3 is exported to Long Island Sound (Houghton and Woodwell, 1980). These studies suggest that even systems which import organic carbon to marshes, based on a sampling of selected tidal cycles, can become net exporters when catastrophic events are considered. Catastrophic transport is a difficult process to quantify through regular sampling and it may be necessary to model selected marsh-embayment ecosystems in order to appreciate its significance (Wiegert, 1979).

B. Evidence Inconsistent with the Outwelling Hypothesis

Some wetland ecologists feel that even though the marsh/water area is correlated to the predominance of estuarine finfish and shellfish in the commercial catch, the marshes are not the cause of this relationship (Nixon, 1980). The large landings in the Northeast (see Table 1) with a negligible amount of marsh is cited as an exception to this postulated relationship. The relationship of intertidal marsh to shrimp yield discussed earlier may be a consequence of the marsh functioning as a critical habitat for shrimp, rather than functioning as an essential food source via the outwelling mechanism (Turner, 1977). The salt marsh investigations on the Fraser River Estuary in British Columbia were stimulated by the hypothesis that marshes provide a habitat for juvenile salmon and thus were critical in the life history of the salmon (Kistritz and Yesaki, 1979). The quantitative impact of salt marshes as a critical habitat for finfish and shellfish is not well understood, even though some of the experimental studies on subtidal epibenthic communities suggest possible experimental approaches to this problem (Nelson, 1981; Dean, 1981). The critical habitat hypothesis simply offers a different mechanism for relating wetland extent and fish production.

Studies of carbon-13: carbon-12 isotope discrimination attempt to infer an animal's food from its isotopic composition. The basic concept is that an organism's isotopic composition reflects what it eats and is not greatly influenced by an organism's metabolism or excretions (DeNiro and Epstein, 1978). Isotopic discrimination is expressed by σ^{13} values which represent:

$$\{ \frac{^{13}C/\ ^{12}C \text{ sample}}{^{13}C/\ ^{12}C \text{ standard}} - 1 \} \text{ X } 1000$$

The two major inorganic carbon sources for aquatic plants are the dissolved bicarbonate-carbonate system (σ^{13} C = 0) and atmospheric carbon dioxide (σ^{13} C = 7). The σ^{13} C values for vascular plants vary with the biochemical pathway used to fix inorganic carbon, with isotopic ratios of -9 to -19^{o}/oo characteristic of the C_4 Hatch-Slack pathway and values of -24 to -34^{o}/oo for C_3 Calvin pathway plants. Algae have σ^{13} values between -12 to -23^{o}/oo. Table 4 presents σ^{13} C values for different potential food sources for estuarine finfish or shellfish. The σ^{13} C values for particulate organic detritus in the water column suggest that its origin is not from the C_4 vascular plants which dominate many salt marshes, but instead is contributed by photoplankton, C_3 vascular plants of terrestrial origin, or C_3 plants in the wetlands. The soil organic carbon in the salt marsh generally have σ^{13} C values intermediate between those of the vascular plants and benthic algae in the marsh and those found in the phytoplankton and particulate organic carbon in the water column. A study of particulate organic detritus σ^{13} values in the water column in Georgia reported similar values (-22^{o}/oo) in the estuary and in the coastal water up to 20 km offshore (Haines, 1976). This suggests that organic detritus has a similar origin in the estuary and in the coastal waters.

Haines (1978) presents arguments to support her hypothesis that particulate organic detritus in the water column comes from phytoplankton production. The peak in phytoplankton production in a zone 10 to 15 km off the Georgia coast is maintained by relatively high nutrient concentrations in the water and an increasing depth of the euphotic zone resulting from a loss of suspended sediments from the water column. This pulse of plankton productivity can be carried into the estuary by tidal forces and can be retained in the salt marsh through sedimentation (Haines, 1978).

An alternative explanation for the origins of particulate organic detritus in the estuary is that it is a mixture of carbon from C_4 plants and bacterial carbon (σ^{13}C = -19 to -36^{o}/oo) from the sediments. Chemoautotrophic bacteria which utilize the energy stored in the reduced sulfur compounds produced by anaerobic sulfate reduction are thought to occupy a pivotal spot in this scheme (Peterson et al., 1980). This scheme may be characteristic of marshes in which ground water supplies a source of nitrogen which stimulates the rate of sulfate reduction, while the water movement carries the reduced sulfur compounds to the creek banks where they are utilized by the

Table 4. Carbon-13: Carbon-12 Isotopic Discrimination Ratios for Potential Food Sources for Estuarine Animals

Source of Organic Carbon	$\sigma^{13}C^{o}/oo$ (PDB Chicago)
1. Water Column	
Particulate Organic Detritus	-19.8 to -26.7
Phytoplankton Blooms	-20.0 to -26.3
2. Marsh Surface	
Benthic Diatoms	-16.2 to -17.9
Soil Organic Matter	-18.2 to -23.2
C_4 Plants: *Spartina alterniflora* *S. cynosuroides* *Distichlis spicata* *Sporobolis virginicus*	-12.1 to -13.6
C_3 Plants: *Juncus roemerianus* *Salicornia virginica* *Batis maritima* *Swamp forest leaves*	-22.8 to -29.0
3. Subtidal Systems	
Seagrasses: *Zostera marina* *Thalassia testudinum* *Halodule wrightii* *Syringodium filliformis*	-5.4 to -12.7
Seagrass Epiphytes	-14.0 to -16.3
Sediment Organic Carbon	-12.6 to -18.7

Sources: Haines, 1976 a. and b.
Fry et al., 1977
Thayer et al., 1978
Haines and Montague, 1979
Fry and Parker, 1979
Hackney and Haines, 1980

resident chemoautotrophic bacteria. The particulate organic detritus in the estuary might also represent a mixture of sources from C-4 and C-3 plants which occur either intertidally or subtidally.

Measurements of the σ^{13}C values in animals and the relationship of this information to potential food sources must consider the following factors:

1. Due to the metabolism of food, whole animal σ^{13}C values are 0.5 to $1^{o}/oo$ less negative then their dietary sources (DeNiro and Esptein, 1978).

2. Different chemical fractions within an animal have different σ^{13}C values (DeNiro and Esptein, 1978; Fry and Parker, 1979) and this may influence the σ^{13}C values of predators if differential assimilation occurs in their intestinal tracts.

3. Different carbon pools within an organism turn over at different rates and a measurement of a static σ^{13}C value for the groundup tissues of an organism could reflect the dominance of carbon pools of large size, but with a slow turnover rate.

4. Intraspecific variability of σ^{13}C values are in the range of 1.8 to $2.0^{o}/oo$ (Fry and Parker, 1979).

5. The initial stages of aerobic decomposition of marsh detritus does not appear to alter the σ^{13}C values (Haines, 1977), but this may change during anaerobic decomposition (Peterson et al., 1980).

6. Most nekton (fish and shrimp) are very mobile and exhibit either seasonal or diurnal movements within an estuary (or between estuarine and coastal waters) Thus an organism caught in the marsh may not feed there extensively. The results of gut content analysis are influenced by organisms that leave parts resistant to digestion and may not be a true indicator of the quantity of various food items consumed.

7. Few animals contain the cellulase enzymes necessary to consume detritus directly, so they feed on the microorganisms which degrade the detritus or have symbiotic bacteria in their intestinal tracts which degrade the detritus (Fenchel and Jorgensen, 1977).

Table 5 presents the σ^{13}C values of selected estuarine animals which feature either different modes of feeding or characteristically occupy different habitats. Marsh detritovores, such as fiddler crabs and periwinkle snail, appear to reflect the σ^{13}C values of the vascular plants in the marsh. The grasshopper <u>Orchelium sp</u>. and square back crab <u>Sesarma reticulatum</u> have σ^{13}C values which reflect that they feed on the vascular plants in the marsh. Filter feeding bivalves, such as <u>Geukensia demissus</u> and <u>Crassostrea virginica</u>, have σ^{13}C values characteristics of the phytoplankton and particulate organic detritus in the water column. The grass shrimp, <u>Palaemonetes pugio</u>, has σ^{13}C values characteristic of the vascular plants in the system,

Table 5. Carbon-13: Carbon-12 Isotopic Discrimination Ratios for Selected Estuarine Animals

Type of Animal	Mode of Feeding	Habitat	$\sigma^{13}C^{o}/_{oo}$ (PDB Chicago)
Uca pugnax (fiddler crab)	Detritovore	Marsh	-14.6 to -18.9
Uca minax (fiddler crab)	Detritovore	*Spartina* Marsh	-14.7
		Zinaneopsis Marsh	-24.8
		River Swamp	-24.0 to -25.3
Sesarma reticulatum (square back crab)	Omnivore	Marsh-Georgia	-13.0 to 13.5
Orchelium sp. (grasshopper)	Herbivore	Marsh-Georgia	-13.1
		Marsh-Mississippi	-16.9
Littorina irrorata (periwinkle snail)	Detritovore	Marsh-Georgia	-11.8 to -20.2
		Marsh-Mississippi	-19.5
Geukensia demissus (ribbed mussel)	Filter Feeder	Marsh-Georgia	-17.5
		Marsh-Mississippi	-25.9 to -27.5
Crassostrea virginica (oyster)	Filter Feeder	Mudflat-Epibenthic	-21.0
Palaemonetes pugio (grass shrimp)	Omnivore	Seagrass Beds-TX	-10.4 to -11.9
		Creeks in Marsh-GA	-13.6 to -14.9
Penaeus aztecus (brown shrimp)	Omnivore	Estuarine Water-MS	-23.6 to -25.8
		Estuarine Water-TX	-11.1 to -15.4
Mugil cephalus (mullet)	Detritovore	C_4 Marsh Creek-MS	-19.0
		Seagrass Bed-Texas	-11.2 to -12.3
Callinectes sapidus (blue crab)	Omnivore	Estuarine Water-MS	-19.3 to -22.0
		Estuarine Water-TX	-9.8 to -13.0
Archosargus probatocephalus (sheepshead)	Carnivore	Estuarine Water-MS	-22.4
Lutjanus campechanus (red snapper)	Carnivore	Offshore Water-Texas	-14.9 to -16.3

Sources: Haines, 1976 a. and b.
Haines and Montague, 1979
Fry and Parker, 1979
Hackney and Haines, 1980

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while the brown shrimp, Penaeus aztecus, appear to feed on a mixture of vascular plant detritus and phytoplankton. Open water fish detritovores, such as the mullet, have $\sigma^{13}C$ values which reflect the local source of vascular plant detritus. Carnivorous fish, such as the sheepshead in Mississippi and red snapper in Texas, have $\sigma^{13}C$ values less negative than potential prey like the mullet. The geographic variations in the $\sigma^{13}C$ values for the same species reflect differences in the dominant vascular plant communities. The Georgia marsh is dominated by Spartina, while the Mississippi marsh contains a mixture of Spartina (C_4 plant), Juncus (C_3 plant), and terrestrially derived carbon. The system in Texas is dominated by subtidal seagrass beds. The fauna in the Mississippi marsh reflect the $\sigma^{13}C$ value of the dominant vascular plant less well than in the Georgia marsh (Hackney and Haines, 1980). In reviewing this literature, Haines (1979) suggested that the true value of salt marshes in to act as a nursery ground which results in an export of living organisms rather than particulate organic detritus.

III. ELEMENTS REQUIRED TO MODEL NONLIVING ORGANIC MATTER EXPORT FROM WETLANDS

A. Production of Vascular Plants in Marshes

The best estimate of primary production would be a measurement of gross production which includes the net production of the plant as well as its respiration. Sophisticated systems for measuring gas exchange (carbon dioxide or oxygen) associated with intact plants have proven too costly and cumbersome for many measurement of gross production to have been made. Table 6 presents some representative values for the gross production of vascular plants in the marsh. For the North Carolina marshes, plant respiration accounts for 35% of gross photosynthesis, while soil respiration accounts for 36% (Blum et al., 1978). At Sapelo Island, Georgia plant respiration accounts for 77% of gross photosynthesis in the marsh, while soil respiration accounts for 11% (Teal, 1962). Gross photosynthesis measures both above and below-ground production, because the below-ground carbon used for growth, storage, morality, or exudates has as its source carbon from photosynthesis in the above-ground parts of the plant. The below-ground carbon follows a different seasonal cycle than that above-ground, which necessitates numerous measurements of gross photosynthesis throughout the year if one hopes to obtain a good estimate of above and below-ground production (Lytle and Hull, 1980 a., b., and c.; Livingstone and Patriquin, 1981).

Measurements of the respiration of intact Spartina alterniflora and of the marsh surface with the top of the plants removed suggested that root respiration was 73% of the respiration of the surface portions of the plant (Teal and Kanwisher, 1961). The quantity referred to as soil respiration in Table 6 represents the oxygen consumption of intact surfaces without Spartina minus the estimated root respiration (Teal and Kanwisher, 1961). This interpretation is somewhat ambiguous(Pamatmat and Skjoldal, 1979). Despite this uncertainty, it is important to note that the combined respiration of roots and soils exceeds that of above-ground Spartina (Teal and

Table 6. Gross Production of Some Vascular Plant Species in Coastal Marshes (gC/m^2 day)

Location	Plant Species and Height	Gross Production	Plant Production	Soil Production
Sapelo Island, Georgia (Teal, 1962)	*Spartina alterniflora* -tall form	11.6[1]	9.0[1]	0.9[1]
	S. alterniflora - short form	3.4[1]	2.6[1]	0.9[1]
Southport, North Carolina (Blum et al., 1978)	*Spartina alterniflora* - tall form	4.2	1.7	1.3
	S. alterniflora - medium form	3.3	1.1	1.1
	S. alterniflora - short form	1.6	0.3	0.8
	Juncus roemerianus	2.5	1.2	0.9

[1] Conversion Factors:

Spartina alterniflora: 9.3 Kcal/g Carbon

Respiratory Loss: 12 Kcal/g Carbon

Kanwisher, 1961). The respiratory quotients measured in this study were close to one, which supports the generalization that surface measurements of gas exchange represent an integrated metabolism value for a whole soil column. Extensive anaerobic production of carbon dioxide would increase the respiratory quotient (exchange ratio of CO_2 to O_2) significantly above one.

Most of the literature values for marsh primary production have employed the harvest method in which above-ground plant material (living and dead) is periodically removed and weighed. The change in the biomass of the live and dead standing crop between sampling periods is used to estimate production. In some methods the loss of dead material between sampling periods is estimated using litter bags or paired plots. Harvest method derived production values have been reviewed by Keefe (1972) and Turner (1976). Table 7 presents marsh plant primary production values for the same species using different harvesting methods and one phenometric technique.

The peak standing crop method equates the largets quantity of live biomass during the year with the annual production. It does not account for mortality, decomposition, or growth occurring subsequent to the peak biomass. It yields an underestimate of net primary production, but the magnitude of this error decreases at northern latitudes. The Milner and Hughes methods (Shew et al., 1981) measures the positive changes in live standing crop and then accumulates these to estimate production. The Smalley method (Shew et al., 1981) measures changes in live and dead standing crop. Positive changes in live or dead biomass are summed to estimate production. The Wiegert and Evans method (1964) uses paired plots to estimate the instantaneous rate of disapperance of dead material which, when combined with the change in standing crop of dead material, can be used to estimate the mortality of live biomass. Production equals the change in standing crop of live biomass between sampling intervals plus the mortality loss from live biomass.

A variation of the Wiegert-Evans approach suggested by Lominicki et al., (1968) employs paired plots to measure mortality directly, but does not include the decomposition of dead material between sampling intervals (instantaneous rate of disapperance in Wiegert-Evans technique). The technique of Williams and Murdoch (1969) estimates the ratio of growth to average standing crop, the ratio of growth to mean life span of culms, and the ratio of stem mass to stem height. These ratios are combined to estimate annual primary production. A variation of this phenometric approach would be applicable in the use of Landsat remote sensing-derived standing crop biomass estimates to be combined with estimates of plant turnover rate from the literature to estimate annual production.

The units in Table 7 are in g dry wt/m^2yr which can roughly be converted to gC/m^2yr by multiplying by 0.45. The turnover rates (crops per year) for the species are: <u>Spartina alterniflora</u> - 1.5 (North Carolina) and 2.9

Table 7. Comparison of the Primary Production of Wetland Vascular Plants Estimated from Different Harvest Techniques (g dry wt./m^2 yr)

System Species	Peak Standing Crop	Milner -Hughes	Smalley	Wiegert -Evans	Lominicki	Williams-Murdoch
Brunswick County, North Carolina-*Spartina alterniflora*	242	214	225	689 to 1038	454 to 1028	---
Barataria Drainage Basin, Louisiana *Distichlis spicata*	991	---	800	3237	---	1967
Juncus roemerianus	1240	---	1200	3416	---	3295
Sagittaria falcata	648	---	750	1501	---	2310
Spartina alterniflora	754	---	1000	2658	---	1381
S. cynosuroides	808	---	1150	1355	---	1134
S. patens	1376	---	2000	6043	---	4159

Sources: Shew et al., 1981
Hopkinson et al., 1980
Hopkinson et al., 1978

(Louisiana); Spartina patens = 4.2; Spartina cynosuroides = 2.6; Juncus roemerianus = 3.5; Sagittaria falcata = 9.1; and Distichlis spicata - 3.9. Based on the turnover rates (measured independently), the best estimates of the "true" net production was the lowest value provided by the Lominicki method in North Carolina (Shew et al., 1981) and the Wiegert-Evans values in Louisiana (Hopkinson et al., 1980). An intensive study is needed to compare the gross photosynthesis estimates provided by the gas exchange techniques with the net production estimates provided by the various harvest methods. Most harvest methods fail to measure the following organic carbon flows in marsh primary production: benthic algal production, material translocated to below-ground plant parts, material lost through leaching of above or below-ground parts, material consumed by herbivores, and material lost through decomposition or tidal action between sampling intervals (Pomeroy et al., 1981).

The state of knowledge regarding the below-ground production of vascular plants in the marsh is even more fragmentary than that for above-ground production. The fact that below-ground standing crop biomass values are fairly constant from year to year implies that below-ground production is consumed by microbial respiration or exported as dissolved material (de la Cruz and Hackney, 1977). The problems in the methods employed to estimate below-ground production have been discussed by Livingstone and Patriquin (1981). One of the difficulties is separating metabolically active underground tissue from inactive tissue (Pamatmat and Skjoldal, 1979; Valiela et al., 1976; de la Cruz and Hackney, 1977). No adequate solution for this problem has been developed to data. The technique of Livingstone and Patriquin (1981) for measuring living, functional biomass below ground was used to estimate net seasonal production, but this technique may not be adaptable to mature salt marsh systems.

The Spartina alterniflora stand near Halifax, Nova Scotia, had a ratio of below-ground production to above-ground production of 1.5 to 3.2, while the Great Sippiwisset Marsh in Massachusetts had a ratio of 4.0 to 8.3 (Livingstone and Patriquin, 1981; Valiela et al., 1976) and the Manahawkin Marsh in New Jersey had a ratio of 5.1 (Smith et al., 1979). A Juncus roemerianus marsh in Mississippi had a below/above-ground production ratio equal to 0.8 (de la Cruz and Hackney, 1977). The lack of comparability of the methods for measuring below-ground production and the paucity of data make it difficult to draw general conclusions. It it an area in need of further work.

B. Respiration of Organic Matter by Marsh Sediments

1. Background

Examination of the energy assimilated by consumer organisms, such as bacteria and animals, from the organic matter produced by plants would show that the energy is utilized mainly for respiration and growth (secondary

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B. Respiration of Organic Matter by Marsh Sediments

1. Background

Examination of the energy assimilated by consumer organisms, such as bacteria and animals, from the organic matter produced by plants would show that the energy is utilized mainly for respiration and growth (secondary production). Examining the fate of plant production at the ecosystem level would show that the energy is utilized by respiration (mineralization), chemical oxidation, or sedimentation. Material sedimented in the past forms the basis of present-day fossil fuel extraction. The basis of biological oxidations are paired electron donors and electron acceptors. Figure 2 presents a generalized scheme of the important redox pairs (electron donor-acceptor) in aquatic sediments and the oxidation-reduction potentials characteristic of these reactions. In such a system microorganisms catalyze reactions that are thermodynamically possible by abiotic chemical oxidations alone (Zimmerman, 1981). Electron acceptors in the sediments such as oxygen, nitrate, sulfate, and carbon dioxide are reduced to end products such as water, nitrogen, sulfide ions, and methane at progressively deeper layers in the sediment. In the absence of oxygen, organic compounds serve as both electron donors and electron acceptors in the process of fermentation. The end products of fermentation, such as hydrogen, acetate, formate, pyruvate, and ethanol, can serve as the electron donors for anaerobic sulfate reduction and methane reduction (Poole, 1979). Nitrate reduction can employ a broader range of dissolved organic carbon electron donors than either sulfate or methane reduction (Poole, 1979). The idealized scheme presented in Figure 2 ignores the fact that much of the microbial activity in the sediments occurs in microenvironments, so that anaerobic processes can occur in what is normally defined as the aerobic zone in the sediments. Generally the aerobic zone has a brown coloration due to ferric and manganic hydroxides, while the anaerobic zone is either black due to ferrous sulfides or a light gray due to pyrite (FeS_2).

The energy produced from the aerobic respiration of one gram of carbon is 9.4 Kilocalories, while sulfate reduction yields 1.9 Kcal/gC (Howarth and Teal, 1979). The reduced sulfur compounds produced as a result of sulfate reduction yield 7.3 Kcal/gC when they are oxidized in the aerobic zone of the sediments. It can be seen in Figure 2 that the products from the reactions catalyzed by certain physiological groups of bacteria can serve as reactants for the chemical reactions carried out by other classes of bacteria. The bacteria in the sediments are involved in a complex series of interactions which make it difficult to quantify the rates of aerobic and anaerobic respiration in intact sediment cores. The approach of measuring the activities of individual physiological groups of bacteria (fermenters, nitrate reducers, and sulfate reducers) in the laboratory from sediment cores gathered in the field may underestimate the true rate of these processes in nature because of the absence of critical interactions. It is common practice to homogenize the sediments from a core and to place the sample into a liquid buffer prior to making rate measurements in the laboratory. This ignores the possible role of the diffusion of carbon sources or electron donors-acceptors in the interstitial water on controlling the rates of reaction in the sediments. The values reported here represent potential reaction rates for various respiration processes that occur in the sediments.

Surface	Electron Donor	Electron Acceptor	Products
Aerobic Zone:	1. $(CH_2O)_{106}(NH_4)_{16}H_3PO_4$	$106\ O_2$	$106\ CO_2 + 16\ NH_3 + H_3PO_4 + 106\ H_2O$
R.P. = +400mV	2. NH_4+	$1.5\ O_2$	$NO_2^- + H_2O + 2H^+$
	3. CH_4	$2\ O_2$	$H_2O + HCO_3^- + H^+$
Anaerobic Zone:			
Fermentation	Varied Organic Compounds	Varied Organic Compounds	hydrogen, pyruvate, lactate, ethanol formate, malate, acetate, methanol
Nitrate Reduction and	1. $(CH_2O)_{106}(NH_3)_{16}H_3PO_4$	$84.8\ NO_3^-$	$106\ CO_2 + 42.4\ N_2 + 16\ NH_3 + H_3PO_4 + 106\ H_2O$
Denitrification R.P. < -100 mV	$5NH_4+$	$3NO_3^-$	$4\ N_2 + 9H_2O + 2H^+$
Sulfate Reduction	1. $(CH_2O)_{106}(NH_3)_{16}H_3PO_4$	$53\ SO_4$	$106\ CO_2 + 53\ S^{-2} +16\ NH_3 + H_3PO_4 + 106\ H_2O$
R.P. = -160 to -200 mV	2. CH_4	SO_4^{-2}	$HCO_3^- + HS^- + H_2O$
	3. $2\ CH_3CHOHCOOH$	SO_4^{-2}	$2CH_3COOH + 2HCO_3 + H_2S$
Methanogensis	1. CH_3COOH	CO_2	CH_4
R.P. = < -300 mV	2. $4H_2$	CO_2	$CH_4 + 2H_2O$
At Depth			

R.P.: redox potential

Figure 2. Vertical Distribution of Important Oxidation - Reduction Pairs in Aquatic Sediments (Poole, 1979; Martens, 1979)

Biological organisms require a source of carbon to use as building blocks for their cellular organic matter. This carbon source may be separate from the biochemical reactions required to produce the energy required for growth and metabolism. Autotrophs obtain their cellular carbon from inorganic carbon in their environment. A vascular plant is a photoautotroph which obtains its energy from light, utilizes an inorganic chemical as an electron donor, and uses carbon dioxide as its carbon source. Certain bacteria are chemoautotrophs which obtain their energy from the oxidation of reduced inorganic chemicals and use carbon dioxide as their carbon source. A heterotroph is an organism which obtains its carbon and energy from preformed organic matter and which releases carbon dioxide as a waste product. The interactions between bacteria in the sediments may involve their energy generating reactions or their carbon source for building cellular protoplasm.

2. Aerobic Respiration

The measurement of aerobic respiration involves following the changes in the oxygen or carbon dioxide concentrations over time for communities held in the dark (this eliminates photosynthesis). Table 8 presents the results measured for selected marine and estuarine communities (Dow, 1971). Polluted systems have higher respiration rates than non-polluted systems because of the subsidy of organic matter or nutrients from land introduced into the estuarine food chain. Intertidal systems have relatively high respiration rates compared to seagrass beds, subtidal sediments, subtidal epibenthic associations, and non-polluted water.

Table 9 presents the results of two studies of aerobic respiration in a salt marsh (Hopkinson et al., 1978 b., Christian et al., 1981). The data presented in Table 9 prorate the respiration based on the relative area occupied by different vascular plants in the marsh and the ratio of water to marsh area in the embayment. The organic matter produced in the water column is not included in these calculations and much of the subtidal sediment and water column respiration are utilized to mineralize this source of microscopic plant production. The ratio of marsh to open water area in the Duplin River watershed is 3.76, while the ratio at Airplane Lake is 0.78 (Christian et al., 1981; Hopkinson et al., 1978 b). The difference in the marsh to open water area between the two locations explains the dominance of marsh respiration in Georgia and of water respiration in Louisiana. The marsh/open water ratio also explains the fact that only 41% of the above-ground vascular plant production in the marsh would be mineralized in the marsh-embayment system in the Duplin River watershed, while 113% would be mineralized at Airplane Lake. The percentage of the vascular plant production mineralized in the marsh-embayment system is an overestimate, since it ignores production in the water column. These percentages would be reduced if below-ground production of marsh plants were included. In the Duplin River watershed in Georgia, only 22% of the above and below-ground production is estimated to be mineralized by respiration in the marsh-embayment system (Christian et al., 1981).

Table 8. Aerobic Respiration in Selected Aquatic Ecosystems (Dow, 1971)

System	Respiration: Mean ; Standard Deviation (gC/m^2 day)[1]	Number of Observations
Intertidal Vegetation and Substrate	5.9; 1.3	8
Benthic Sediments	1.8; 0.6	26
Turtle Grass Beds	4.7; 0.8	11
Coral Reefs	8.4; 2.6	14
Epibenthic Communities	4.0; 2.0	6
Coastal and Oceanic Water	1.2; 0.3	15
Estuarine Water - Polluted	7.4; 2.0	9
Estuarine Water - Nonpolluted	3.1; 0.5	25

[1] Conversion: 1 gO_2 = 0.38 gC

Table 9. Aerobic Respiration of the Subtidal and Intertidal Portions of Two Salt Marshes

LOCATION	COMMUNITY	RESPIRATION RATE: MEAN AND % TOTAL (gC/m^2 yr)	PERCENT OF ABOVE-GROUND PLANT PRODUCTION (NET)
Duplin River Watershed, Georgia (Christian et al., 1981)	Standing Dead *Spartina*	180; 52	22
	Marsh Soil Surface	90; 26	11
	Subtidal Sediment Surface	20; 6	2
	Water Column	50; 15	6
Airplane Lake, Louisiana[1] (Hopkinson et al., 1978b; Day et al., 1973)	Live and Dead *Spartina*	221; 28	32
	Marsh Soil Surface	43; 6	6
	Subtidal Sediment Surface	254; 33	37
	Water Column	258; 33	38

[1] Conversion Factors: Relative Areas of Marsh: 30% streamside and 70% inland

Airplane Lake Embayment: 56% water and 44% marsh

g dry wt = 0.45 gC

g O_2 = 0.38 gC

The respiration values for subtidal sediments and marsh soils presented in Tables 8 and 9 assume that surface measurements represent integrated values of the aerobic and anaerobic respiration in a column of sediments with an area of 1 m^2. This assumption rests on the concept of tight spatial and temporal coupling of the aerobic and anaerobic subsystems in the sediment. A study of the potential respiration rate of the sediments and water column based on measurements of the activity of the enzymes in the electron transport system suggested that in the Dutch Wadden Sea the respiration rate per m^2 in a 35-cm-deep column of sediments is about 47 times greater than the rate in the overlying 300-cm-deep water column (Vosjan and Olanczuk-Neyman, 1977). This is a much larger difference than that found in the studies reported in Table 9, which measured the surface respiration rates in intact sediments. As will be discussed more fully later, the enzymatically-derived respiration rate may measure biological and chemical oxidation in the sediments (Zimmerman, 1981) and the potential rate may not be realized in nature due to limitations in the concentration of the dissolved organic carbon sources utilizable by sulfate or methane reducing bacteria (Vosjan and Olanczuk-Neyman, 1977). It should be realized that the sediment and marsh soil respiration rates reported in Tables 8 and 9 may be underestimates of the mineralization rates that occur in nature.

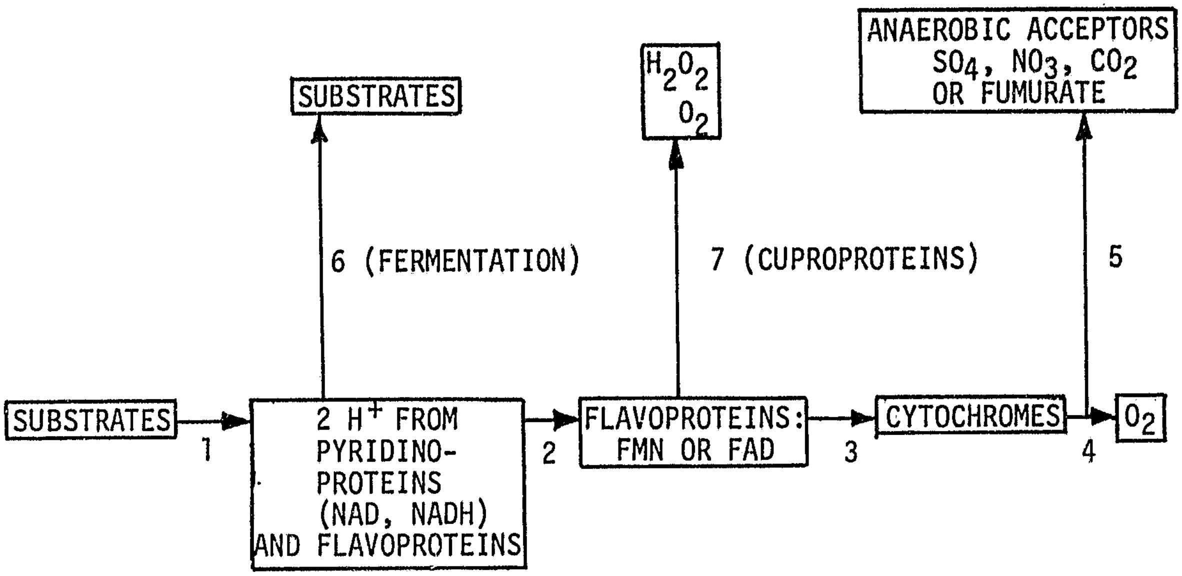
The respiration rates measured in the dark are normally extrapolated to daily values by multiplying the hourly rate by 24. This procedure assumes that the nighttime and daylight respiration rates are equal. This ignores the phenomenon of photorespiration in plants in which an accelerated rate of carbon dioxide release occurs in the light. The rate of photorespiration is generally higher in C-3 plants than in C-4 plants. Studies in the Duplin River marshes in Georgia reported ratios of photorespiration to dark respiration of 1.7 to 3.4 for the tall and short forms of *Spartina alterniflora*, 4.3 for *Juncus roemerianus*, 3.8 for *Batis maritima*, 6.7 for *Borrichia frutescens*, and 9.7 for *Salicornia virginica* (Pomeroy et al., 1981). *Spartina alterniflora* is a C-4 plant, while the others are C-3 plants. *Salicornia virginica* is a succulent plant which grows in the high marsh. Any communities which involve macroscopic vascular plants as a significant contributor to the community repsiration rates will have a serious underestimate of the metabolism per unit area if the process of photorespiration is ignored.

A source of information that would be useful in evaluating the carbon mineralized on the surface of the marsh is how the respiration rate varies along a transect from the streamside marsh to the inland marsh. This would be an important component in evaluating a transport coefficient to be incorporated into the productive capacity model. The 50 by 50-meter cell size of current Landsat data would require this information along a transect that was 500 to 1,500 meters long. It was not possible to find any data in the literature that provided this type of information. A study of sediment core respiration from samples gathered in the Duplin River watershed in Georgia reported comparable oxygen metabolism rates in the subtidal mud and the tall *Spartina alterniflora* at the streamside marsh, while the short *Spartina* in the inland marsh had a rate approximately 26% lower than that found at the streamside marsh (Christian et al., 1981).

A study of plankton respiration along a transect from a marsh creek to the mouth of the Wassau Estuary in Georgia showed the following values (gO_2/m^2 yr): 234, 513, 978, and 658 (Turner, 1978). The decrease in the community plankton respiration rate in the coastal waters off the Wassau Estuary was quite pronounced in the summer and early fall. The estuarine plankton respiration exceeded the primary production of the net plankton by 0.415 gC/m^2 day; Turner (1978) hypothesized that this excess respiration was supported by dissolved organic carbon leached from living and dead *Spartina* in the marshes. Leachate loss of dissolved organic carbon from *Spartina* blades is most rapid immediately after submersion, while the rate is 20-fold lower when the plant is not submerged (Turner, 1978). A study of experimental dissolved organic carbon leaching from *Spartina alterniflora* leaves in the field reported peak leaching rates in March and June and minimum values in July and August (Gallagher et al., 1976). Gallagher (1978) reported that as the marsh elevation increased, the respiration rate of the plants decreased and the dissolved organic carbon leaching rates increased. It appears that the dissolved organic carbon leached from *Spartina* leaves is utilized by microscopic plants and bacteria attached to the leaves and by microplankton in the water column (Turner, 1978; Gallagher et al., 1976). The activity of the microbial community in the sediments does not appear to be directly coupled to above-ground plant production or to organic carbon or nutrients leached from above-ground plant parts (Christian et al., 1978). The rate of leachate production, its transport, and fate is an area of research that deserves much more work.

There are a number of approaches for estimating the respiration rate in the sediments other than the gas exchange method (Pamatmat, 1975; Pamatmat et al., 1981). One approach that appears feasible to employ in support of the productive capacity model is an enzymatic assay of the potential activity of the electron transport system (ETS). This enzymatic activity can be related to the maximum potential respiratory activity. In deep oceanic waters the ETS-derived oxygen consumption rates may be an order of magnitude greater than rates measured by other methods (Suess, 1980). Procedures for conducting the ETS analysis in sediments are described in Olanczuk-Neyman and Vosjan (1977) and Christensen and Packard (1977). The ETS method involves the *in vitro* reduction of the tetrazolium salt, INT, by electrons flowing through the cytochrome-based electron transport system. The electron donors, NADH, NADPH, and succinate, are added to the assay at saturating levels, so that the amount of INT reduced is a function of the activity of the electron transport system at its presumed limiting step (coenzyme Q - cytochrome B site).

Figure 3 presents an overview of the key steps in the electron transport system (which generates the majority of the energy utilized by both aerobic and anaerobic organisms). Normally INT is reduced at step 3, which couples the flavoproteins to the cytochrome system, but if the detergent, Triton-X, is added the INT reduction occurs at step 2 (Zimmerman, 1975). As can be seen from Figure 3, all cytochrome-mediated aerobic and anaerobic metabolism goes through step 3 in the electron transport pathway, while some types of anaerobic metabolism not mediated by the cytochrome system bypass both steps 2 and 3.



PHYSIOLOGICAL CLASS OF ORGANISM	ELECTRON TRANSPORT PATHWAY	CYTOCHROME INVOLVEMENT
1. OBLIGATE AEROBES	1,2,3,4	YES
2. FACULTATIVE ANAEROBES		
AEROBIC METABOLISM	1,2,3,4	YES
	1,2,7	NO
ANAEROBIC METABOLISM	1,2,3,5	YES
	1,6	NO
3. OBLIGATE ANAEROBES	1,2,3,5	YES
	1,6	NO

NOTE: INT may be reduced after step 3 at the coenzyme Q-Cytochrome B site.

Figure 3. Overview of the Biochemical Pathways Involved in the Electron Transport System of Aerobic and Anaerobic Microorganisms (After Zimmerman, 1975).

The ETS assay would not measure respiratory activities which bypass steps 2 or 3. In aquatic sediments humic acids act like a "flavoprotein" external to the cells, which couples the oxidation of reduced inorganic compounds (iron, manganese, sulfide) to the reduction of INT (Zimmerman, 1981). Thus the ETS analysis can measure components of both biological and chemical oxygen demand in the sediments. In the gas exchange method for estimating sediment respiration, the cores are poisoned with formalin in order to separate chemical and biological oxygen consumption (Christian et al., 1981).

To measure the ETS activity, cores could be collected in the field along a transect from the streamside to interior marsh pixels and the cores could be subsampled back in the laboratory to measure the ETS activity associated with different depths in the sediments. Such an approach in the Dutch Wadden Sea estimated an oxygen consumption of 2100 ml O_2/m^2hr for a 35-cm-deep sediment core, which greatly exceeded the 45 ml O_2/m^2hr potential respiration rate in the overlying 300 cm of water (Vosjan and Olanczuk-Neyman, 1977). The ETS method should also provide an opportunity to estimate the difference in the respiration rate when the marsh is covered with water versus the rate when it is exposed to air. There appears to be a dearth of data in this area for the gas exchange method, even though Pomeroy (1959) reported that in the winter sediment respiration under air exposure exceeded that under water in a Georgia salt marsh. In any application of the ETS method to aquatic sediments, it is important to calibrate the activity of the INT (Zimmerman, 1975) and to compare the results occasionally to other methods of measuring respiration (Pamatmat et al., 1981).

An enzymatic assay for alcohol dehydrogenase activity (ADH) has been utilized to examine the influence of aerobic versus anaerobic respiration in the roots of Spartina alterniflora on its distribution in Louisiana salt marshes (Mendelssohn et al., 1981). The ADH enzyme catalyzes the conversion of acetaldehyde to ethanol during alcoholic fermentation. This process produces adenosine triphoshate (ATP) energy through anaerobic processes. In streamside Spartina root metabolism is primarily aerobic, with most ATP produced by oxidative phosphorylation using the electron transport system. In inland Spartina ADH activity produces ATP anaerobically, which results in healthy, but less productive, plants (toxic ethanol is lost by diffusion from the roots). The movement of pore water in the soil decreases as the transect runs from streamside to inland locations and this leads to the redox (oxidation-reduction) potential going from positive to negative values. Thus the gradient in redox potentials influences the type of root respiration occurring in the Spartina. The pore water movement and soil water percentage have a profound influence on the aerobic and anaerobic mineralization processes in the soil (Wiebe et al., 1981).

The aerobic respiration rate in benthic sediments is influenced by temperature, organic matter content and chemical nature, and the density and composition of the organisms. Temperature appears to be the dominant environmental factor as indicated by the following regression equation (Hargrave, 1959):

$$\log_e(SOD) = 1.74 \log_e (T) - 1.30$$

where SOD = sediment oxygen demand
T = temperature in °C
R = 0.85 (correlation coefficient)

This regression analysis involved the annual rate of sediment oxygen consumption versus the average temperature, thus ignoring seasonal effects. Sediment oxygen consumption gave no significant correlation with the total organic matter, protein, and carbohydrate content of the sediments (Hargrave, 1969). The lack of a relationship between sediment oxygen consumption and sediment organic carbon concentration may reflect an imbalance between the rate of sedimentation and rate of aerobic respiration in which organic matter is buried at depth before aerobic oxidation is complete (Hargrave and Phillips, 1981). The interpretational difficulties involved in estimating the relative rates of aerobic and anaerobic respiration in the sediments from simultaneous measurements of oxygen and carbon dioxide exchange (Hargrave and Phillips, 1981) make it difficult to estimate the coupling between the rate of sedimentation and total rate of mineralization (aerobic and anaerobic respiration plus chemical oxygen consumption). The turnover time of organic carbon in the sediments is uncertain because the depth in the sediments to which respiration contributes carbon dioxide to the measured flux at the water-sediment surface is unknown. It is likely that the particulate organic carbon turnover rate varies with depth in the sediment (Hargrave and Phillips, 1981).

3. Decomposition Rates of Particulate Organic Carbon: Field and Laboratory Measurements

A number of approaches have been developed for measuring the decomposition rate of particulate organic carbon based upon field observations or laboratory measurements. The paired plot technique for measuring net primary production of vascular plants in the marsh removes all of the dead material and litter from one plot and all of the live material is removed from the second plot without disturbing the dead organic matter. After a suitable period of time the dead organic matter in the second plot is harvested and utilized to compute a rate of disappearance for dead material (r). The first plot harvested at two points in time measures changes in the standing crop of dead material on a plot which can be combined with the "r" value to compute a value for the mortality of living biomass. Plant production is equal to the change in live biomass between sampling intervals plus the estimated mortality loss (Shew et al., 1981). The first plot is used to measure the change in living biomass between sampling intervals. The litter bag method encloses a known weight of live or dried plant tissue in a nylon or fiberglass bag with a 2-5-mm mesh, suspends the bags in the marsh, and measures the weight loss through time by a sequential removal procedure. In the laboratory, samples of detritus of different particle size are placed in flasks and an innoculum of bacteria is added. The weight loss or change in the chemical composition of the detritus in the flask is followed over time under varying redox or chemical regimes (de la Cruz, 1978).

Table 10 presents data on the decomposition rate of selected vascular plants characteristic of marshes of the South Atlantic and Gulf coasts of the United States using the litter bag technique. The data on decomposition rates between sites is not comparable due to differences in the mesh size of the litter bags, environmental conditions at each location (temperature, sedimentation rate, salinity, duration and frequency of inundation, and oxygen concentration) and differences in the periods during which the litter bags were exposed (de la Cruz, 1978; Montagna and Ruber, 1980). Comparison at different marsh zones at the same location support the generalization that decomposition is greatest under complete submersion and decreases in moving from low to high marsh zones. Succulent plants, such as Scirpus and Salicornia, decompose faster than grasses (Spartina) or rushes (Juncus). A study of the below-ground decomposition of roots and rhizomes in Mississippi has demonstrated higher rates of decomposition occur in above-ground stems and leaves (Hackney and de la Cruz, 1980). Most of the below-ground decomposition of roots and rhizomes occurs in the top 10 cm of the sediment. The decomposition rate of vascular plant tissue is a function of the fiber (lignin, cellulose, and hemicellulose) content, nitrogen concentration, and ultrastructure of cells in plant tissue (Godshalk and Wetzel, 1978).

Litter bag studies provide an index of the relative rate of decomposition of particulate organic carbon in different zones within a salt marsh and as such could provide a useful input in estimating a transport coefficient to be utilized in the productive capacity model. The litter bag decomposition values integrate the interaction of environmental factors, refractibility of plant tissue to decay, and physical transport processes that remove dead material from the marsh surface (Kistritz and Yesaki, 1979). Decomposition rates in litter bags underestimate the influence of animals in converting large detritus particles to smaller particles and the role of hydrology in removing dead material during storm events. Litter bags can provide a surface of attachment for algae or animals which increases the organic content without becoming involved in the decomposition process (Kistritz and Yesaki, 1979). From a quantitative perspective, the measurement of sediment aerobic and anaerobic respiration, coupled with an estimate of the loss of dead organic matter above-ground using litter bags, should approximately balance the net above and below-ground plant production. This assumes that the loss of organic carbon through sedimentation is negligible.

The studies of particulate detritus degradation in the laboratory focus on the influence of the physical and chemical environment on the microbial yield (mg ash-free dry weight microbes/mg AFDW total particulate matter) and conversion efficiency ((g AFDW microbes/g AFDW plant material degraded) x 100). The ash-free dry weight gives a rough approximation of the carbon content of organic matter. An investigation of the mineralization of ^{14}C-labeled Spartina alterniflora leachate by bacteria, by fungi, and by a mixed community (bacteria, fungi, protozoa, and microcrustacea) found that the decomposition rate increased in going from fungi to bacteria to mixed community. The conversion efficiency and microbial yield increased in going

Table 10. Decomposition Rates of Selected Marsh Vascular Plants Based on Litter Bag Studies (Percent of Original Material Lost After One Year of *In Situ* Decomposition)

Species	Location	Marsh Zone	Decomposition Rate (%/yr)
Spartina alterniflora	Sapelo Is., GA	streamside & levee	60-65
		high	50
S. alterniflora	Barataria Bay, LA	creek	96
		streamside	89
		high	80
S. alterniflora	St. Marks, FL	creek	95
		low	89
		middle	84
		high	80
S. alterniflora	Black Bay, LA	stream mouth	100
Spartina patens	St. Louis Bay, MS	high	62
S. patens	Black Bay, LA	inland-low salinity	36
Spartina cynosuroides	St. Louis Bay, MS	high-leaves & stems	26
		high roots & rhizomes	20
Juncus roemerianus	St. Louis Bay, MS	brackish-leaves & stems	48
		brackish-roots & rhizomes	17
J. roemerianus	Sapelo Is., GA	brackish	35
J. roemerianus	St. Marks, FL	low-middle marsh	65
		high marsh	29
J. roemerianus	Black Bay, LA	brackish	80
Scirpus americanus	St. Louis Bay, MS	on marsh	53
		in creek	60
Distichlis spicata	St. Louis Bay, MS	on marsh	54
		in creek	73
D. spicata	Sapelo Is., GA	Saline zone of middle marsh	47

Table 10. (continued)

Species	Location	Marsh Zone	Decomposition Rate (%/yr)
D. Spicata	Black Bay, LA	on annually burned marsh	76
Salicornia bigelovii	Sapelo Is., GA	inland-high salinity	94

Sources: de la Cruz, 1978
Hackney and de la Cruz, 1980
Kruczynski et al., 1978
White et al., 1978

from the mixed community to bacteria to fungi (Fallon and Pfaender, 1976). In the first instance dissolved organic carbon (DOC) is converted to carbon dioxide and in the second case DOC is converted to microbial biomass which can serve as a food source for detritovores.

A study on vascular plant detritus from Georgia reported low microbial yields (0.0005 to 0.112) for flasks incubated for 28 days either anaerobically or incubated aerobically without nitrogen addition, while the microbial yield for flasks incubated aerobically with nitrogen additions were higher (0.155 to 0.290). In this investigation the aerobic conversion efficiency for *Spartina alterniflora* was 64%, for *Juncus roemerianus* it was 56%, and for *Salicornia virginica* it was 19% (Haines and Hanson, 1979). The microbial yields starting from live leaves of these three vascular plants was 0.033 to 0.121, which is less than the range (0.155 to 0.290) reported for dead leaves, numbers which suggests that live material is more resistant to degradation than dead organic matter.

A study of *Spartina alterniflora* detritus from Louisiana which was divided into size fractions reported conversion efficiencies of 66% for the 67-micron class, 46% for the 111-micron class, 42% for the 163-micron class, and 24% for the 213-micron class (Gosselink and Kirby, 1974). Some of the interpretational problems associated with microbial yield computations and the rate microbial activity per surface area for decreasing particle sizes are discussed by Christian and Wetzel (1978). These authors feel that 60% of the energy in an organic carbon substrate is converted to biomass and 40% is lost through respiration for bacteria and fungi growing aerobically.

The transport of large particulate organic matter out of a marsh through the action of storms or flood tides can be quite dramatic, and some of this debris is deposited in the marsh itself where it interferes with the growth of living plants. This larger-sized organic carbon fraction is referred to as wrack. As was mentioned earlier, the export of wrack by storm tides in the Stroodorpe salt marsh in the Netherlands exceeds the import of particulate organic matter accompanying the regular tidal cycle (Woff et al., 1979). The storm surge associated with Hurricane Bob exported as wrack an amount of organic matter from a Mississippi *Juncus* and *Spartina* marsh equal to 17% of the net annual above-ground vascular plant production (Hackney and Bishop, 1981). Most of this wrack was thought to emanate from debris on the marsh rather than the dead standing plant material.

Color infrared aerial photographs played a key role in assessing the negative influence of wrack on vascular plant growth in a salt marsh at Wallops Island, Virginia (Reidenbaugh and Banta, 1980). Each vegetative zone in the marsh and the *Spartina* wrack had a characteristic infrared spectral signature. The source of the tidal wrack was wave- or ice-scouring of the previous seasons' dead vegetation. Leaves and stalks from the tall growth form of *Spartina alterniflora* dominated the wrack. High tide moved the mats of wrack to higher zones in the salt marsh, where they were stranded at low tide. Little wrack appeared to be transported offshore. The result of the wrack deposition in the middle marsh was to devegetate 15% of the marsh area and to decrease net productivity by 15% (Reidenbaugh and Banta, 1980).

The instantaneous loss rates computed from the paired plot method of measuring net primary production of vascular plants provided another source of information for estimating decomposition rates of particulate organic detritus in wetlands. A study in the Barataria Basin of Louisiana reported instantaneous loss rates (mg/g · day) of 25.2 for Sagittaria falcata, 11.5 for Juncus roemerianus, 10.5 for Spartina patens, 7.7 for Distichlis spicata, 6.7 for Spartina alterniflora, 4.9 for Spartina cynosuroides, and 4.7 for Phragmites communis (Hopkinson et al., 1978 a.). In general, the summer (April to October) instantaneous loss rates are higher than those in winter (November to March), but the rates vary throughout the year due to inundation of the marshes by wind or tide-driven waters. The paired plot method shows changes in the loss rate from month to month, unlike the litter bag studies, but the average annual loss rate for Spartina alterniflora was similar for the paired plot and litter bag methods (Hopkinson et al., 1978 a.). The assumptions underlying the pair plot method and the validity of these in salt marshes are discussed by Linthurst and Reimold (1978) and Shew et al. (1981).

The first stage in the decomposition of particulate organic carbon (POC) is the release of dissolved organic carbon (DOC) through autolysis of plant cells. In the second stage microorganisms colonize the POC and microbial respiration degrades the POC until the activity is limited by environmental factors such as oxygen or nutrients. In the final stage of decomposition, the refractory nature of the remaining POC generally limits the degradation rate (Godshalk and Wetzel, 1978). A simplified model of this decomposition process is (Godshalk and Wetzel, 1978):

$$k = f \left(\frac{T \times O \times N}{R \times S} \right)$$

where k = decay rate
T = temperature
O = dissolved oxygen
N = limiting mineral nutrients for microbial growth
R = refractility of plant tissue
S = particle volume/surface area
f = constant to establish function

Not all of these factors may be independent, so further experiments will be needed to quantify the interaction terms. Also, the model may involve critical thresholds to activate different microbial groups involved in the decomposition process. It is important to realize that a succession of physiological types of bacteria is required to convert the POC to DOC, CO_2, or microbial biomass.

4. Anaerobic Metabolism in the Sediments

The vertical distribution of aerobic and anaerobic metabolism in the sediments presented in Figure 2 is a generalized picture which has ignored certain reactions which are either not well understood or thought to be unimportant quantitatively. The material presented in Figure 2 suggests a spatial localization of different oxidation-reduction reactions with depth that may in fact occur in reduced microzones in the aerobic region of natural sediments. The rate of anaerobic metabolism in the soils of wetlands is not well understood and many of the estimates to be discussed in this section represent potential rates. This potential may not be realized in nature due to limiting carbon sources and electron donors or acceptors; constraints imposed by salinity, temperature, or redox potential; and competition among different microorganisms (Wiebe et al., 1981; Fenchel and Jorgensen, 1977).

More work has been done on anaerobic processes in benthic sediments which receive their organic matter by sedimentation from the water column. Anaerobic processes in salt marsh soils are mainly fueled by particulate organic carbon and dissolved organic carbon within the soil with only indirect coupling to above-ground organic matter production (Wiebe et al., 1981; Howarth and Teal, 1980). Thus the work on benthic anaerobic metabolism is not extrapolative to the situation existing in salt marsh soils. For the Great Sippewisset Salt Marsh in Massachusetts, aerobic metabolism oxidizes 150 gC/m^2 yr, sulfate reduction respires 1,800 gC/m^2 yr, denitrification metabolizes 12 gC/m^2 yr, and methane export represents a loss of 8 gC/m^2 yr (Howarth and Teal, 1979). An interdisciplinary study of the Duplin River watershed in Georgia also found that sulfate reduction was the predominant anaerobic respiration process in salt marsh soils (Wiebe et al., 1981). This section will focus on the processes thought to control the anaerobic respiration in marsh soils in different vegetative zones in the marsh. Representative potential reaction rates will be discussed briefly.

Tidal inundation results in waterlogging of saltmarsh soils. Oxygen diffusion in these soils is greatly reduced by waterlogging. Reduced oxygen diffusion coupled with active respiration by soil microorganisms results in anaerobic conditions in the soil below a narrow (1 cm or less) surface zone. The tall zone in Spartina alterniflora marshes occurs along creek banks, which feature better drained soils and higher redox potentials at a given sediment depth. The tall plants can extend to 2 meters above ground and the fibrous roots penetrate to a depth of 1 meter in the sediment. The short Spartina alterniflora zone occurs in locations further inland, which have the water table closer to the surface and exhibit more reduced conditions at comparable depths in the sediment. The short plants are less than 1 meter in height and their roots from a compact mass to a depth of 15 to 20 centimeters (Wiebe, 1979; Howes et al., 1981). Fertilization of short Spartina alterniflora in the field with nitrogen results in a growth form typical of the tall plant, with the sediment becoming more oxidized (Howes et al., 1981). The sediment redox potential is similar in the tall and short Spartina zone at soil depths below those occupied by living roots (Howes et al., 1981).

A hypothesis advanced to explain these observations is that tall *Spartina* oxidizes the sediments by metabolic oxidation or passive oxygen release and that the critical nutrients limiting plant growth are more available under the slightly higher soil redox conditions (Howes et al., 1981). The activity of the anaerobic microbial community in the soil appears to be regulated by the balance between water movement and water availability (Christian and Hansen, 1980).

Fermentation is an anaerobic metabolic process which utilizes organic matter as both an electon donor and an electron acceptor. Bacteria and yeasts convert a broad range of substrates (simple sugars, cellulose, alcohols, amino acids, and pectin) into products such as short chain fatty acids, hydrogen, carbon dioxide, ammonia, and alcohol (Fenchel and Jorgensen, 1977; Wiebe et al., 1981). The end products of fermentation probably provide the substrates utilized by the anaerobic bacteria responsible for sulfate reduction and methanogenesis. The tremendous variety of substrates available for fermentation, and the diversity of microorganisms involved in this process, make it unlikely that a procedure will soon be developed to estimate the fermentative capacity of wetland soils. One approach to measuring potential fermentative capacity involves injecting ^{14}C-glusose into a sediment seawater slurry which is incubated from 5 to 30 minutes under anaerobic conditions. The labeled carbon in the CO_2, particulate "biomass", and ether-soluble fermentation end products is measured at the end of the experiment (Wiebe et al., 1981; Christian and Wiebe, 1978). The turnover time of glucose increased with depth in the marsh soil. The turnover times for the particulate (glucose to microbial biomass) and CO_2 (glucose mineralized) fractions were shorter at all depths in the tall *Spartina* zone than in the short *Spartina* regions.

The tall *Spartina* soil, when compared with the short zone plants, had a greater percentage of label in the particulate fraction and less in the ether-soluble fraction (Christian and Wiebe, 1978). The tall *Spartina* zone soil is hypothesized to utilize the end products of fermentation to support other types of anaerobic metabolism (Wiebe, 1978), while the fermentation activity in the tall *Spartina* soil is limited by the diffusion rates of substrates (Wiebe et *al.*, *1981*). The diffusion rate of substrates is probably limited by the soil water balance, even though experimental proof for this idea is lacking (Christian and Wiebe, 1978).

The anaerobic reduction of nitrogen is involved in respiration rather than the synthesis of new microbial protoplasm. Two types of processes occur: dissimilatory nitrate reduction (NO_3^- to NH_4^+) and denitrification (NO_3^- to N_2 or N_2O). Nitrate or some other nitrogenous oxide serves as the terminal electron acceptor of the electron transport system (which oxidizes organic carbon and traps the energy released as ATP). Organic matter is the electron donor and a wide variety of organic carbon substrates can be utilized. Dissimilatory nitrate reduction tends to predominate in permanently anaerobic sediments, while denitrification predominates in soils with a transient redox potential or in sediments with less reduced conditions

(Tiedje et al., 1981). The low nitrate concentrations in most marine waters make denitrification and dissimilatory nitrate reduction quantitatively unimportant, but these processes may be important in freshwater wetlands. For example, the reed swamp sediment in a Danish lake oxidized 290 gC/m^2 yr by aerobic respiration and 188 gC/m^2 yr by denitrification (Anderson, 1981).

At Sapelo Island, Georgia, denitrification potential was estimated by adding nitrous oxide to soil slurries and measuring the decrease in nitrous oxide concentration over time (nitrous oxide reductase method). The nitrous oxide reductase activity was greater in the short Spartina zone than in the tall zone (Wiebe et al, 1981). The denitrification potential was related to the quantity of large particulate organic matter in the upper 25 cm of the marsh soil. Due to the root and rhizome growth patterns characteristic of tall and short Spartina, this quantity is much greater in the short zone. The denitrification potential in the short zone appears to be coupled to the seasonal particulate organic matter production in the soil (Wiebe et al., 1981). Nitrate concentration appears to limit the denitrification rate in the tall Spartina zone soil, while denitrification in the short Spartina zone appears to be controlled by the concentration of available organic carbon (Wiebe et al., 1981).

As a consequence of the high sulfate concentration in seawater (20-30 mmol/liter), dissimilatory sulfate reduction is the most important anaerobic respiration process in marine and estuarine sediments (Fenchel and Jorgensen, 1977; Howarth and Teal, 1979). A limited number of organic carbon compounds (methane, acetate, lactate, pyruvate, and fatty acids) and dihydrogen (H_2) serve as electron donors in this process. Sulfate ions serve as terminal electron acceptors in a cytochrome-based transport chain. The end products of sulfate reduction are volatile sulfides (H_2S, S^{-2}, HS^-), acid-volatile sulfide ($FeS \cdot nH_2O$), and pyrite (FeS_2). The acid-volatile sulfide is less stable in the soil than pyrite, but the geochemical balance between iron, iron monosulfide, and pyrite in the soil determines the rate of formation and proportions of pyrite and acid-volatile sulfide in the soil (Wiebe et al., 1981; Howarth and Teal, 1979).

In the Great Sippewisset Marsh in Massachusetts, low soil pH (5.0 to 6.5) and fairly low total sulfide concentration result in an undersaturation of iron monosulfide (FeS) and a supersaturation of pyrite (FeS_2). Under these conditions, pyrite forms rapidly as an end product of sulfate reduction and is stored in the peat from fall through spring. Some researchers feel that this rapidly lost sulfide is organic sulfates rather than pyrite (Wiebe et al., 1981). Sulfide could also be lost as organic sulfide gases. In the summer the pyrite is oxidized either chemically or biologically in the aerobic zone of the marsh soil. Some of the reduced sulfur compounds move laterally through the pore water in the marsh soil and emerge directly into the marsh creeks (Howarth and Teal, 1979). Some of the hydrogen sulfide (H_2S) in marsh soil comes from the hydrolytic degradation of organic matter. Under anaerobic conditions this hydrolytic breakdown can result in free sulfur or methyl sulfides (Fenchel and Jorgensen, 1977).

Measurement of the sulfide reduction rate in marsh soils can utilize one of three methods:

1) Theoretical model of Berner (Jorgensen, 1978 a.), which estimates the rate of sulfate reduction from the sulfate concentration gradient in the sediment, the sedimentation rate, and the diffusion coefficient in the sediment (which is assumed to be insignificant).

2) The Sorokin approach (Jorgensen, 1978 b), which forms a sediment-seawater slurry to which $^{35}SO_4^{-2}$ is added and is then allowed to incubate under anaerobic conditions for 8 hours to 8 days. The relative amount of label in the sulfate and hydrogen sulfide at the end of the experiment estimates the sulfate reduction rate.

3) The core-injection method (Jorgensen, 1978 b), which injects $^{35}SO_4^{-2}$ into various depths of an undisturbed sediment core and incubates the core in situ for 1 hour to one day. The core is then frozen and returned to the laboratory, where each core segment is analyzed for labeled sulfate, labeled hydrogen sulfide, labeled acid-volatile sulfide, and the concentration of non-labeled sulfate in the soil. Labeled sulfide, which diffuses to the surface layer of the core and is oxidized, is not recovered in this method. The advantage of this method is the maintenance of the natural concentration gradients and diffusion processes (Jorgensen, 1978 b). Spatial microheterogeneity in the soil sulfate concentration could alter the specific activity of the labeled sulfur compounds, thereby causing the sulfate reduction rate to be overestimated if the specific activity is underestimated (Wiebe et al., 1981).

A comparison of these methods has been conducted by Jorgensen (1978 a. and c.). The theoretical model seriously underestimates the sulfate reduction rate because it does not take diffusion into account. The radiotracer methods give a better estimate of the sulfate reduction rate. In 8-hour incubations the core injection sulfate reduction rates exceed those from the sediment slurry method, but these results are reversed after 8-day incubations. The sediment slurry method overestimates the rate of sulfate reduction in the oxidized surface layer, while the core injection method underestimates the rate in the oxidized layer. The sediment slurry method eliminates bacterial heterogeneity, which results in less statistical variance when compared to the core injection method.

Table 11 presents data on the potential rate of dissimilatory sulfate reduction in marsh soils using variations of the core injection technique. The data are expressed in terms of the organic carbon that would be oxidized to support the measured rates of sulfate reduction. As was mentioned in the earlier discussion of Table 2, it is easy to convert the sulfate reduction rate to the energy consumed, since sulfate reduction is a form of anaerobic respiration. Table 11 points out the fact that the carbon equivalent of sulfate reduction depends upon whether the oxidation is complete or partial. The complete oxidation of carbon presumes that sulfate reduction is coupled to some other anaerobic fermentation processes or methanogenic bacteria

Table 11. Potential Rates of Dissimilatory Sulfate Reduction in *Spartina alterniflora* Marsh Sediments Using Variations of the Core Injection Technique

Location	Plant Type	Organic Carbon Required to Support Sulfate Reduction (gC/m^2 yr)[1]	Relative to Plant Net Photosynthesis[2]
Sapelo Island, Georgia	Tall	1764	12%
(Skyring et al., 1979)	Short	548	22%
Great Sippewisset Marsh, Massachuetts (Howarth and Teal, 1979)	Short	1800	96%

[1] Based on complete oxidation which yields a C:S ratio of 2:1. Partial oxidation yields a C:S ratio of 6:1, which would increase the carbon requirement threefold (Skyring et al., 1979).

Partial Oxidation: $2\ \text{lactate} + SO_4^{-2} \rightarrow 2\ \text{acetate} + 2\ CO_2 + S^{-2}$

Complete Oxidation: $\text{acetate} + SO_4^{-2} \rightarrow 2\ CO_2 + 2H_2O + S^{-2}$

[2] Based on gas exchange methods which include above and below-ground plant production.

(Skyring et al., 1979; Howarth and Teal, 1979). Complete oxidation was chosen as the basis for computing the organic carbon oxidized in Table 11 because it provides a conservative estimate.

An investigation of sulfate reduction in the Great Sippewisset Marsh in Massachusetts reported a peak rate between 4 and 18 cm in the sediment. On a seasonal basis the sulfate reduction rate (moles/m^2 day) in this short Spartina alterniflora zone peaked from July through October, with minimum values occurring from January to March. The seasonal trends in sulfate reduction were postulated to be controlled by temperature from winter to midsummer and by substrate availability in the late summer and fall (Howarth and Teal, 1979). A study of sulfate reduction in the tall and short Spartina alterniflora zones of a Georgia marsh reported maximum rates in the top 5 cm of the soil. It is apparent from Table 11 that the areal sulfate reduction rate in the tall Spartina zone in Georgia is threefold greater than that in the short zone. Active sulfate reduction was measured to a depth of 30 cm in the tall Spartina zone, but was difficult to detect below 10 to 15 cm in the short Spartina zone.

The total sulfide concentration in the tall Spartina zone soil was 20-fold that found over the same depth interval (20 cm) in the short Spartina soil (Skyring et al., 1979). The end products of sulfate reduction in the Georgia marsh soils were hypothesized to be controlled by the interstitial water exchange rate (2 to 3 days in the tall zone versus weeks to months in the short zone) and the rate of sedimentation (higher in tall zone). In the tall Spartina marsh soil, rapid interstitial water exchange and higher sedimentation rates favor the formation of acid-volatile sulfides ($FeS \cdot n H_2O$), while in the short Spartina zone low interstitial water exchange and lower sedimentation rates favor the accumulation of volatile sulfides (H_2S, S^{-2}, HS^-). Little evidence of pyrite (FeS_2) information was reported for Georgia marsh soils (Wiebe et al., 1981).

Experimental studies of sulfate reduction using the sediment slurry technique for the soils in an English salt marsh pan found that temperature variation was 2.6 times more effective than the electron donor (lactate) concentration and 6.5 times more effective than the electron acceptor (sulfate) concentration in controlling the reaction rate (Nedwell and Abram, 1979). There was no significant relation between the counts of the bacterium, Desulfovibrio, and the sulfate reduction rate. Problems associated with measuring the numbers of marine sulfate reducing bacteria are discussed by Jorgenson (1978 c). The importance of the electron donor concentration on the rates of sulfate reduction and methanogenesis have led to experimental studies to examine the competition for substrates (dihydrogen or acetate) between these two anaerobic groups (Mountfort and Asher, 1981). The addition of readily available dissolved organic carbon substrates to intertidal sediments (organic pollution) can deplete the interstitial sulfate levels, thereby favoring methanogenesis over sulfate reduction (Mountfort and Asher, 1981).

A model of sulfate reduction in marine sediments predicted that a high energy electron donor (carbohydrate) would result in a decrease of sulfate reduction and an increase in microbial biomass, while a low energy substrate (propionate) would lead to an increase in sulfate reduction and a decrease in microbial biomass (Reed, 1980). This represents a trade-off in the energy allocated to growth and respiration.

An area that has received only limited study is the transfer of volatile sulfides from the sediment to the atmosphere in a gaseous state. Potential candidates for transfer include hydrogen sulfide (H_2S), carbon disulphide (CS_2), methyl mercaptan (CH_3SH), dimethyl sulfide ($((CH_3)_2 S_2)$), carbonyl sulfide (COS), and sulfur dioxide (SO_2). A study of sulfur emission at the Flax Pond salt marsh on Long Island reported hydrogen sulfide, dimethyl sulfide, and methyl mercaptan as the predominant gaseous components (Hill et al., 1978). A study using similar techniques in North Carolina salt marshes found that dimethyl sulfide was the dominant gas emitted in the *Spartina* zone, while hydrogen sulfide and carbonyl sulfide dominated the emissions over a mud flat (Aneja et al., 1979 b.). Carbon disulfide emission in the *Spartina* zone in North Carolina occurred under aerobic conditions at the sediment-air interface (Aneja et al., 1979 a.).

Methanogenesis utilizes carbon dioxide or a methyl group as an electron acceptor to produce methane gas under anaerobic conditions. Potential electron donors include carbon dioxide, dihydrogen, formate, methanol, acetate, and methyl-amine (Wiebe et al., 1981). The organic carbon substrates can serve as both a carbon source for new cell protoplasm and as an energy source for anaerobic respiration (Fenchel and Jorgensen, 1977). It is not known whether methane producers have a cytochrome-based electron transport system (Wiebe et al., 1981). *In situ* methane production can be measured by covering a section of marsh soil with a bell jar and periodically determining the methane concentration in the gaseous head space with a flame-ionization gas chromatograph. Sediment cores can be collected and partitioned in order to conduct a sediment slurry analysis of methane release.

In situ methane release (g CH_4-C/m^2 yr) rates in a Georgia *Spartina alterniflora* marsh were 53 in the short zone, 14 in the mid-marsh zone, and 0.4 in the tall zone (King and Wiebe, 1978). The methane release rate, when compared to the net photosynthesis of the vascular plants, ranges from 9% in the short *Spartina* zone to 0.002% in the tall *Spartina* zone (Wiebe et al., 1981). The rate of methane production in soil cores from the tall *Spartina* zone was enchanced by restricting interstitial water flow and by incubating in an 80% H_2 - 20% CO_2 atmosphere. These manipulations may reduce substrate competition from sulfate reducing bacteria. The reduced interstitial water flow was accompanied by a dramatic decrease in the sulfate concentration (Wiebe et al., 1981). Counts of the methanogenic bacteria in the top 7 cm of the soil revealed an order of magnitude more bacteria in the short *Spartina* zone than in the tall *Spartina* zone. In both the tall and short *Spartina* zones the number of bacteria was similar in winter and summer (Jones and Paynter, 1980). Measured methane release rates *in situ* exhibited a summer peak and winter minimum (King and Wiebe, 1980). It is hypothesized that temperature controls the in situ methane production. Some of the methane released in methanogenesis can be oxidized in the surface layer of the marsh soil (King and Wiebe, 1978). Recent work supports the existence of anaerobic oxidation of methane in the sulfate reducing zone of marine sediments (Reeburgh, 1980). The reaction for anaerobic methane oxidation is:

$$CH_4 + SO_4{}^{-2} + 2H^+ \rightarrow H_2S + CO_2 + H_2O$$

C. Physical and Geological Factors Influencing the Transport of Organic Matter from Wetlands

1. Geomorphology of Wetlands and Morphometry of Embayments

In this section, geomorphology is used to describe the surface characteristics of wetlands (area, topography, slope, soil texture) and their associated drainage channels. Morphometry refers to the shape, area, volume, depth, and bottom gradient of the larger embayments into which the wetland drainage system empties. This division is arbitrary, especially with respect to many coastal drainage systems which lack a significant freshwater input and in which water moves in and out as a result of tidal action or meterological factors (wind and atmospheric pressure changes). These latter systems are technically extended embayments. It was not possible to locate literature which quantitatively related geomorphology or morphometry to the transport of organic matter from marsh-embayment systems to adjacent coastal waters. Thus this factor could only be incorporated in a model for estimating a transport coefficient in a qualitative manner, such as employing importance values. It is an area in which remote sensing could provide a valuable tool through computing the relative areas of wetlands and water, measuring the area occupied by different vascular plants in the marsh in relation to the areas of bare mud, inferring the topography of wetlands from the expanse of marsh covered by water at different tidal levels, and by the ability to estimate morphometric properties of embayments through a combination of remote sensing data and the information found on National Ocean Survey maps.

A circular wetland basin connected to a larger water body by a narrow channel with a sill at its mouth will act as a trap for particulate organic matter. If this basin is deep compared to its surface area, it is possible that dissolved organic carbon may be mineralized by respiratory activities in the bottom water and sediments. A large volume to surface area ratio would also tend to trap and eventually mineralize the particulate organic carbon. This represents the worst case scenario for the export of organic matter from the marsh-embayment system to adjacent waters. A favorable configuration for exporting dissolved and particulate organic carbon would be a V-shaped basin which deepens and widens at its mouth (Odum, W.E., et al., 1979). A small volume to surface area ratio would tend to keep the particulate organic matter in suspension and decrease the likelihood of mineralization in the sediments. The bathymetry of coastal lagoons can influence the water transport, especially in systems with salt wedge in which saline bottom water is entrained into the surface brackish layer, resulting in a large increase in the volume transported out of the lagoon. Even in the shallow, well mixed estuaries characteristic of the southeastern United States, a cross section of the channel reveals a deeper section in which the net current is ebb-directed (moves out of embayment), a point bar overlaid by shallow water, and a second, moderate depth section in which the net current is flood directed (moves into embayment). This lateral reversal of the net current is called pumping. The side of the waterbody on which the deeper ebb-directed section is located is controlled by the distribution of channel meanders (Kjerfve, 1978).

Drainage density refers to the total length of all segments within a drainage network divided by the area of the drainage basin. An increase in drainage density is accompanied by a decrease in basin water storage and a greater proportion of the flow being confined to channels rather than occurring as overland flow across the wetlands (Gael and Hopkinson, 1979). A study in the Barataria Basin of Louisiana found that 60% of the variation in water quality (as measured by a trophic state index) could be explained by the cumulative drainage density at a particular location in the watershed (Gael and Hopkinson, 1979). The hypothesis advanced to explain the relationship between water quality and drainage density is that sheetflow across the wetlands allows for an increase interaction between the plants and sediment and the chemicals in the water. Flow that is transmitted primarily through natural channels and canals leaves the wetlands more rapidly, thus having less time for interaction between the water and the wetland plants and sediments.

An investigation of the hydrology in the Lac des Allemands portion of the Barataria Basin using the U.S. Environmental Protection Agency's Storm Water Management Model (SWMM) predicted that upland runoff could be discharged more efficiently (22% increase), primary productivity in the swamp increased (100%), and eutrophication in the lakes decreased (43%) if the spoil banks surrounding the canals were removed and if upland drainage was introduced directly into the backswamp areas (Hopkinson and Day, 1980 b). The upland runoff integrates the effects or rainfall, infiltration, evaporation, detention, overland flow, and canal flow. A sensitivity analysis of the model indicated that the critical parameters on land were the area, slope, percent imperviousness (land surface that limits water percolation in the soil) and minimum infiltration rate (Hopkinson and Day, 1980 c). Investigations in freshwater streams in various regions of the United States failed to find a relationship between the concentration of particulate organic matter (POM) and drainage density. The investigators hypothesized that channel geometry is more important in POM transport than basin morphology (Sedell et al., 1978).

The natural levees along the creek banks in salt marshes in the southeastern United States prevent tidal waters from overflowing the banks and moving into the inland marsh. At high spring tides, tidal creek bank overflow can occur. During regular tides the water reaches the inland marsh by flowing to the head of the channel and moving back inside the natural levees (Pomeroy and Imberger, 1981). This waterflow pattern results in an interstitial water exchange of two to three days in the tall Spartina alterniflora zone along the natural levee of Georgia marshes, compared to weeks to months in the short Spartina alterniflora zone (Wiebe et al., 1981). Much of the inland marsh zones have a perched water table (separated from the main ground water table by an unsaturated soil layer) which exhibits little lateral flow and the interstitial salinity of which is controlled by evaporation and transpiration. The interstitial salinity in the natural levee soil follows that in the water and at Sapelo Island varies from 15 to 28 parts per thousand (ppt). Inland marsh zones have higher, more constant interstitial salinity concentrations (short Spartina alterniflora at 35 to 40 ppt and Salicornia sp. in excess of 40 ppt). In regions in the inland marsh in which ground water intrudes to lessen the interstitial salinity, Juncus sp. dominate the vegetation (Pomeroy and Imberger, 1981). Mention has been made previously on the importance of water flow in the marsh soil on the primary production in the vascular plants and in the respiratory activities of the sedimentary microorganisms.

Topographic differences in the marsh also influence the length of time the vascular plants are inundated by the tide each day. A study of Nehalem Bay, Oregon, found that the lower marsh plant dominants, Carex lyngbei, Scirpus maritimus, and Troglochin maritimum, do not extend below an elevation of 1.0 to 1.2 meters above mean lower low water (MLLW). The maximum period of inundation at this elevation changes from 17.8 to 9.4 hours. A second discontinuity in the maximum period of inundation (roughly 3 to 0.5 hours) occurred at an elevation from 2.6 to 2.7 meters above MLLW (Eilers, 1979). In this system the low marsh extended from 1.0 to 2.3 meters above MLLW, the middle marsh occupied the elevation 2.3 to 2.7 meters above MLLW, and the high marsh occurred above 2.7 meters MLLW. The primary production (g dry wt./m^2 yr) at Nehalem Bay was 1,200 in the low marsh, 1,400 in the middle marsh, and 1,700 in the high marsh (Eilers, 1979). In Oregon, the length of inundation variable appears to be more important than the water drainage through the soil in its influence on the change in plant production along an elevation gradient. If one compares the tidal datum for the transition from marsh to uplands in a number of western estuaries, no consistent relationship is found (Frenkel et al., 1981).

Aerial photography (color infrared and natural color) was employed to investigate the influence of marsh vegetation on the stream channel morphology (Garofalo, 1980). Marshes supporting saline vegetation had lateral stream channel migration rates of 0.2 m/yr, while marshes dominated by freshwater vegetation had larger channel migration rates (0.3 m/yr). This difference was attributed to the facts that freshwater vascular marsh plants have less extensive subsurface roots and rhizomes and that the muddy soils in the freshwater zone are more susceptible to erosion. The rate of channel migration was not highly correlated to either water discharge or stream channel morphology (sinuosity, mean width, amplitude, and meander length). Remote sensing offers a powerful tool to relate wetland geomorphology and plant distribution to drainage patterns and tidal channel morphology.

2. Hydrology of Marsh-Embayment Systems

Hydrology influences the transport of organic matter from wetlands directly through the removal of detritus by tidally induced sheet flow across the marsh and indirectly by influencing the growth rates of marsh plants and the respiration rate of sedimentary microorganisms. The duration of tidal inundation of various elevation zones in the marsh and the strength of the current play an important role in organic matter transport (balance between import and export). A study of the Shark River Slough in the Everglades National Park in Florida utilized a density slicing technique of band 7 (0.8-1.1μm, near-infrared band) of the Landsat Multispectral Scanner data to differentiate inundated from non-inundated areas (Rose and Rosendahl, 1979). In this system surface water flows over the flat wetlands, but the surface area of wetlands inundated varies between the wet season in the fall and the dry season in the spring.

The band 7 density slicing technique during the dry season had be be supplemented with a parallelepiped classification which extracted the information in all four Landsat bands. During the dry season the intermediate and tall sawgrass which was inundated by water produced a vegetative spectral signature if only band 7 was utilized. The parallelepiped classification, applied to training samples from vegetation which was inundated with water versus vegetation which was not, produced a 100% classification accuracy. In this study 30 hydrological monitoring stations were used for training and an additional 45 stations were used for verification (comparing predictions from classified Landsat data with field information from the hydrological monitoring stations). Landsat inundation masks of the surface area covered by water in Shark Slough varied from 245,427 acres in October to 90,402 acres in May (Rose and Rosendahl, 1979). Water storage in the Shark Slough was computed from a water depth contour program and varied from 208,247 acre feet in October to 26,016 acre feet in May. The digital format of Landsat data makes it easy to combine remotely-sensed and ground-based data to make a volume computation. The parallelepiped classification identified four land use categories with the following accuracies: water (100%), hammock (100%), intermediate sawgrass (93%), and tall sawgrass (96%). Sawgrass represents a variety of species of freshwater plants. Current Landsat coverage (every 18 days) is not frequent enough to accurately determine the extent of inundation for tidally-dominated wetlands, but it may prove to be a feasible technique in Gulf Coast wetlands where water levels in the marsh are dominated by meteorological forces.

A second approach to estimating inundation time is to relate tidal heights from a recorder in the water with topographic elevation within the marsh. A study in Denmark reported fairly large differences in inundation time between computations made from a tide curve recorder 400 meters from the study plot and that measured by an electronic sensor placed in the marsh soil at the study plot (Jensen, 1974). Measurements of basin hypsometry (change in basin surface area with tidal height) can be estimated from infrared aerial photography and changes in the area of submergence with time can be converted to a basin water storage curve (Miller and Gardner, 1981). The hypsometric (area-height) relationship for wetlands is given by (Boon and Byrne, 1981):

$$\frac{a}{A} = \frac{G}{(r + G\,(1-r))} \quad ; \quad G = \left(1 - \frac{h}{H}\right)^{\frac{1}{z}}$$

where: G: a factor derived for computational simplicity
a: basin area lying above elevation contour of height h
A: maximum basin area
r: ratio of minimum to maximum basin area
h: height above reference minimum basin elevation
H: height difference between maximum and minimum elevation
z: a positive exponent related to the area below the hypsometric curve.

In practice, h/H is plotted against a/A and the values for r and z are determined empirically. The water surface area corresponding to a given water height is simply A-a, while the wetland surface area equals a. A study of a marsh-embayment complex near Wachapreague, Virginia, reported that the exponent 1/z varied from 1.8 in a sediment-filled basin to 5.0 in an open basin with nearly vertical sides (Boon and Byrne, 1981). The plot of h/H versus a/A can be used to compute the tidal prism. The tidal prism is the difference in estuarine volume between mean high water and mean low water. The use of tidal prism volume in estimating the flushing time of water in an estuary will be discussed subsequently. The Inlet 2 numerical model was employed to examine the relative influence of channel configuration and basin hypsometry on the mean vertical tide in the basin and horizontal tide (velocity of inlet) in the channel (Boon and Byrne, 1981). If the duration of the flood and ebb tide within a basin are not the same, then a time-water discharge asymmetry develops which will favor either net ebb discharge or net flood discharge from the water in the basin. Phase displacement interactions between the principal lunar semidiurnal tidal constituent, M_2, and its first harmonic M_4 (lunar quarterdiurnal constituent) can cause the ebb and flood tide to have either equal rise and fall durations, but unequal maximum and minimum amplitudes, or *vice versa*.

A positive difference between the rise and fall duration of the basin tide favors net ebb transport, while a negative difference favors net flood transport. When the basin fills with sediments without excessive restriction of the inlet channel, net ebb transport occurs, which would tend to export organic matter from the system. When basin filling is not advanced and the inlet channel is unrestricted, net flood transport occurs, which would tend to counteract organic matter export. In a filled marsh basin the channel cross sectional area is the predominant influence on the time-discharge asymmetry, rather than the basin hyposometry factor (Boon and Byrne, 1981). It should be emphasized that the foregoing observations came from analyzing a numerical model and that the situation in nature is more complicated.

In an earlier section discussing input-output studies of organic matter from wetlands, the method of estimating net transport by measuring changes in the velocity and concentration over time, depth, and width in a channel cross section was presented. This approach suffers from two problems: the width is indeterminate when the tidal height exceeds the elevation of the creek banks and net transport is measured by difference between two larger quantities, flood and ebb transport. A comparison of basin water storage (near North Inlet, South Carolina) between the input-output technique of current measurements over time and a technique utilizing direct measurements of marsh topography and hypsometry showed that at high tide the topographic storage curve yielded 110 million liters, while the current measurement technique estimated 43 million liters in the channel (Miller and Gardner, 1981). The difference represents the sheet flow that moves over the marsh at high tide plus the error associated with the measurements. The authors (Miller and Gardner, 1981) present the analogy that in hypsometry the marsh resembles a saucer-shaped vessel which increases in water area as it is filled, while the direct current measurement technique is like a wine bottle in which storage volume rate of change levels off as the bottle is filled. The result of this is that the tidal prism is 2.5-fold greater for the topographic storage curve than that for the current measurement storage curve.

A parameter that can be used to estimate the mean time that a particle of tracer remains in an estuary is the flushing time or mean detention time. Flushing time is a measure of the time required to replace all of the freshwater that enters an estuary from river discharge. If the system is completely mixed, then the high water volume of an estuary divided by the tidal prism volume equals the flushing time. Sometimes the results are expressed in terms of the flushing rate which equals the reciprocal of the flushing time. An alternative method for computing flushing time is to divide the volume of freshwater in an estuary by the freshwater discharge rate from the rivers. The salinity difference between the coastal water and estuary is used to compute a freshness factor. The freshness factor multiplied by the volume of water in the estuary gives the volume of freshwater in the estuary (Fischer et al., 1979).

The discharge rate of the tributaries can be measured directly if the rivers are gaged by the U.S. Geological Survey or can be estimated from information on the size of the drainage basin and the annual precipitation in the drainage basin. Flushing time is a useful parameter to determine the fate of conservative tracers (those substances whose distribution are influenced by physical mixing, but not biological or chemical processes in the water column). Pomeroy and Imberger (1981) present evidence to support the concept that 80% of the dissolved organic carbon (refractory material) behaves as a conservative substance, while the labile dissolved organic carbon and particulate organic carbon behave non-conservatively.

The flusing time has be be adjusted for the tidal exchange ratio, R (sometimes called remixing coefficient), which accounts for the fraction of the ebb tide volume that reenters the estuary on the next flood tide. This needs to be done since the flushing time concept assumes that all the water entering on the flood tide is new water, whereas in the real world the same water in a diluted form moves in on the flood tide (Summers and McKellar, 1979). The simplest way to compute the tidal exchange ratio (Fisher et al., 1979) is:

$$R = \frac{(S_f - S_e)}{(S_o - S_e)}$$

where: S_f: average salinity of water entering on flood tide
S_e: average salinity of water leaving on ebb tide
S_o: salinity of coastal water adjacent to estuary

An accurate estimate of S_f and S_e requires a measurement of both salinity and velocity in a channel cross section for a complete tidal cycle. Summers and McKellar (1979) present an example of how the net exchange between the North Inlet embayment and the coastal water is adjusted for flushing time (using tidal prism method) and the tidal exchange ratio. In the North Inlet system the tidal exchange ratio varied from 0.10 in the winter, when strong longshore currents occurred, to 0.90 in the summer, when longshore currents are weaker (Summers and McKellar, 1979).

The export of total organic carbon (TOC) for the Barataria Bay in Louisiana was estimated from the flushing time (corrected for tidal exchange ratio) and the inshore-offshore gradient in the concentration of TOC (Happ et al., 1977). In this case the TOC concentration inshore and offshore is assumed to be unaffected by biological and chemical processes in the water column (behaves conservatively). The equations used by Happ et al. (1977) are based on the water replacement rate, which equals the average depth of the water times the flushing rate. The net TOC transport equals the inshore-offshore TOC concentration gradient times the water replacement rate times 365. The flushing times utilized varied from 18 days to 137 days (depending on degree of wind-induced net transport), which resulted in net total organic carbon export ranging from 156 to 118 gC/m^2 yr. These values agree well with Day et al.'s (1973) estimate of 250 gC/m^2 yr, which was estimated from metabolic energy balance considerations. The estimates of Day et al. (1973) include a loss of TOC from the water column to the sediments.

The transport of particulate and dissolved organic carbon by the methods discussed so far assume that these substances move passively with the water. An alternative method to compute the flux of organic carbon between wetlands and estuaries utilizes the Lagrangian transport model, in which the change in a conservative (salinity or chloride) chemical parameter is followed in a parcel of water as it moves down the estuary (Fischer et al., 1979). The time-concentration history of a pulse of freshwater introduced into the headwaters of the Duplin River in Georgia has been used by Pomeroy and Imberger (1981) to compute the longitudinal mixing flux of total salts. A model was then developed to compare the distribution of selected nonconservative chemical substances (particulate or dissolved) with that of salinity.

The time-averaged and space-averaged concentration of the nonconservative substance could be altered by air-water exchanges, benthic sediment-bottom water interactions, and the chemical conversion from one form to another within the water column (uptake of chemical by plankton).

Tidal excursion is a measure of how far a parcel of water travels during one-half of a tidal cycle (ignoring mixing and differential current velocities across a channel cross section). The Duplin River has a tidal excursion of 4.8 km, which implies that the river is divided roughly into three distinct tidal segments (Ragotzkie and Bryson, 1955). The Lagrangian transport model predicted that a dissolved substance that behaves like salinity would pass through the uppermost tidal segment in 36 hours, which is three times the length of the tidal cycle (12 hours). The Lagrangian transport model estimates net downstream movement. This calculation suggests that the uppermost tidal segment is only weakly coupled temporally and spatially to the lower part of the estuary. An analysis of the relative importance of longitudinal mixing versus the chemical and biological processes available that alter the concentration of nonconservative substances, suggests that (Pomeroy and Imberger, 1981):

1) labile dissolved organic carbon (DOC) concentration is controlled by water column recycling, sediment-water flux, or biological flux.

2) refractory DOC concentration is controlled by longitudinal mixing.

3) labile particulate organic carbon (POC) concentration is influenced by the balance between photosynthesis and respiration in the water column.

4) refractory POC concentration is altered by resuspension of material off the bottom during ebb and flood tides.

5) storm events probably influence the distribution of POC more than day-to-day biological processes and physical transport.

It is important to bear in mind both DOC and POC represent a heterogeneous assemblage of chemical compounds that have much different fates resulting from biological, chemical, or physical processes. Some workers (Pomeroy and Imberger, 1981) feel that the bulk of the DOC in the water is not available to the estuarine food web. The POC is thought to be dominated by bacteria, unicellular algae, and fecal products from invertebrates (Pomeroy and Imberger, 1981). Variations in the shape and density of particulate organic carbon particles coupled with the turbulence coefficient in the moving water determine whether the POC is transported as floating material, suspended matter, or bedload which rolls along the bottom (Odum et al., 1979). The high density of water-saturated organic matter particles coupled with the lower water velocities near the stream bed favor bedload transport and increasing concentrations of organic detritus particles (greater than 0.2mm) with depth (Odum et al., 1979).

Very few studies have been made of bedload transport. A study of the benthic detritus transport in a salt marsh tidal creek in Virginia found that organic detritus is deposited on the inside of a meander and that organic detritus is transported as bedload on the outside of a meander where the current velocity is greatest. Lightweight, slowly settling organic detritus particles (leaf, root, and fine material) are eroded from the inside of an upstream meander and appear as suspended load or bedload on the outside of the next meander downstream (Pickral and Odum, 1976). The "meander pattern" of benthic detritus distribution was found even in a relatively straight section of this tidal stream. Freshwater stream ecologists have utilized the concept of stream power to measure the potential of organic detritus particles of different sizes to be transported as part of the suspended load. Stream power is equal to the discharge rate (m^3/sec) times the gradient (percent slope) times the water density (kg/m^3). The distribution of organic detritus particles between the suspended load and benthic detritus reflects the interaction of stream power with retention structures in the stream which trap organic matter (Sedell et al., 1978). This might be a useful perspective from which to view POC transport in tidal streams.

Detailed studies of the variation with time of current velocity and the concentration of ecologically important chemicals in a channel cross section has provided a basis for evaluating the potential errors accompanying input-output studies of total organic carbon transport from wetlands. Generally these studies are conducted over two to three consecutive tidal cycles. Only some highlights of this work done by investigators at the University of South Carolina will be discussed, since it lacks a suitable spatial and temporal perspective for supporting the remote sensing-based productive capacity model. The temporal coupling between tide level (water height) and current velocity (cm/sec) has an important influence on the direction of net transport of suspended matter in the water column. In the Dutch Wadden Sea, maximum ebb and flood current velocity occurs near low tide, which results in a net landward transport of suspended matter. Tidal channels in wetlands in South Carolina have maximum ebb and flood current velocity occurring near high tide, which results in a net seaward transport.

Since the largest suspended matter concentrations occur at or slightly after peak current velocity, it is of significance that South Carolina tidal channels have a 60% greater peak ebb current than the average peak flood current. This results in maximum flood transport of suspended matter lasting for 1.5 hours in South Carolina, while maximum ebb transport lasts for 3 hours (Ward, 1981). A study at North Inlet, South Carolina, found a time lag between the tidal height curve and the water discharge curve of 3 hours at high tide and 4.5 hours at low tide. In this study, differences in mean tidal range between low and high tide on consecutive tidal cycles can be used to predict the direction of net discharge (Kjerfve and Proehl, 1979).

Variations in the direction and quantitative value of the net discharge rate implies that a portion of the tidal prism is either flushed from or stored in the marsh-embayment system from one tidal cycle to the next. Three consecutive tidal cycles at North Inlet, South Carolina, showed that the net discharge rate varied from -118 to 340 m^3/sec (Kjerfve and Proehl, 1979). It is common practice in stream and river studies to estimate the water discharge rate from the height of the water in the channel. A multiple regression technique has been developed by Kjerfve and McKellar (1980) to extend this approach to tidal channels. The instantaneous phase parameter and the coefficients associated with the other parameters in the model were estimated from a three tidal cycle data set that related discharge rate to water elevation (Kjerfve and McKellar, 1980).

Different particulate and dissolved chemical substances in the water are transported in characteristic ways in relation to the net water discharge rate. For example, over two consecutive tidal cycles at the North Inlet in South Carolina, the net water flow was ebb-directed, dissolved ammonium ions were exported, and adenosine triphoshate (ATP) was imported (Kjerfve et al., 1981). ATP is a chemical measurement of the living particulate organic carbon biomass in the water column and its concentration is usually a measure of the bacterial and phytoplankton standing crops in the water. The estimation of the long-term transport of ecologically significant chemicals using this methodology may require the measurement of 30 or more consecutive tidal cycles (Kjerfve et al., 1981).

Even though the turbulent flow and current velocities characteristic of tidal channels in the North Inlet region of South Carolina ensure a homogeneous distribution of salinity over a channel cross section, both the current velocity and the ATP concentration are heterogeneously distributed over the channel cross section (Chrzanowski et al., 1981). A study which investigated ATP transport through cross sections located at different ends of the same creek reported ATP import at the estuarine interface (40 mg/s) and ATP export (3.6 mg/s) at the cross section within the wetlands (Chrzanowski et al., 1981). Even though this study was of short duration (25 hr), it points out the longitudinal variability that exists in net ATP transport and the difficulties inherent in the utilization of input-output studies to estimate the transport of organic carbon from wetlands.

IV. USE OF INPUT-OUTPUT FLOW MODELS TO RELATE PRODUCTIVE CAPACITY TO FISHERIES

A joint project is being initiated in FY1982 between the Earth Resources Laboratory, an element of the NASA National Space Technology Laboratories, and the National Marine Fishery Service's Southeastern Fishery Center. This project plans to utilize the output of the Productive Capacity Model developed by M.K. Butera as an input to a fisheries-based Aquatic Energy Flow Model being developed by Dr. J.A. Browder. The Productive Capacity Model was initially developed as a potential tool to aid coastal zone planners in attaching a qualitative value to different zones within a wetland. The Transport Coefficient Model discussed in this report was developed to provide a conceptual methodology for estimating the transport of particulate and dissolved organic carbon from the marsh-embayment system to the adjacent estuary which supports the aquatic fisheries. A methodology which may prove useful in coupling the Productive Capacity Model with the Aquatic Energy Flow Model is the use of input-output flow analysis. The utilization of input-output flow analysis in ecology has been reviewed by Barber et al. (1979).

Due to space limitations the discussion of flow analysis will ignore the mathematics and discuss the basic concepts qualitatively, emphasizing how the system structure controls flow within the system and storage within system compartments. Flow analysis represents an ecological system as a series of interconnected compartments which exchange energy or nutrients with the universe external to the system. Each compartment can receive flow from other compartments, can receive flow from itself (intercompartmental flow), or receive inflow from outside the system. Besides being a recipient of flow, a compartment can act as a donor, sending flows to other compartments or transporting outflow to the external universe. Mass-balance relationships between compartments require that compartmental throughflow be equivalent to the total flow leaving the compartment plus storage within the compartment (compartmental accumulation) or the total flow entering the compartment plus compartmental reduction of storage. The flow from one compartment to another is proportional to the throughflow of both the donor and the recipient compartment (the proportionality constant is different for the donor and recipient compartments).

As a consequence of this two-way proportionality, flow analysis can be performed in a forward-looking manner (the flow in the recipient compartment due to direct, indirect, and cycled flows from the donor compartment) or a backward-looking manner (portion of a unit flow in the recipient compartment that passed through the donor compartment, when all direct, indirect, and cycled flows are examined). Flow analysis partitions each flow in the system into portions attributable to each inflow or outflow (Finn and Leschine, 1980; Dame and Patten, 1981). Direct flows refer to those that actually pass through a compartment, while indirect flow represents support flows required to allow direct flows to occur. Cycled flow represents the portion of the through-flow from a compartment that returns to that compartment. Input-output flow analysis can utilize deterministic (static and dynamic) or stochastic methodologies. The relative advantages of deterministic and stochastic models have been reviewed by Barber et al. (1979).

In practice, normalized flow diagrams are used which, in backward-looking analysis, follow the path taken through the system by a unit of inflow to a given compartment; the throughflows in each compartment are those required to generate a given unit of outflow at a selected compartment. The procedure is referred to as input environments analysis. A flow analysis of an intertidal oyster reef in a South Carolina marsh introduced one unit of input into the filter feeders (oysters and mussels) and found that 0.753 unit flowing from filter feeders plus 0.252 unit from deposit feeders (invertebrates in sediments) supported one unit of output from the predators (crabs). Forward-looking analysis of the same intertidal oyster reef found that a unit input to the filter feeders resulted in the following unit outputs: 0.607 for filter feeders, 0.149 for deposited detritus, 0.139 for microorganisms, 0.086 for meiofauna, 0.010 for deposit feeders, and 0.009 for predators (Dame and Patten, 1981). These fractions are simply the outflow from each compartment in Kcal/m^{2}d divided by 41.5 Kcal/m^{2}d (input into filter feeders). Figure 4 presents the energy flow model through the intertidal oyster reef that formed the basis for the input-output flow analysis. Energy cycling in the intertidal oyster reef model represents potential energy which is not used on its first passage through the system. For the intertidal oyster reef model, total system throughflow is 83.6 Kcal/m^{2}d, of which 74.3 Kcal/m^{2}d represents straight throughflow and 9.2 Kcal/m^{2}d represents cycled throughflow (Dame and Patten, 1981). The cycling index (cycled throughflow/total throughflow) for the oyster reef is 0.11.

For any given compartment a recycling efficiency can be computed. For example, when the input environment for the oyster reef model has an outflow of 1.0 from the deposited detritus compartment and a throughflow in the compartment of 1.39, the recycling efficiency for this compartment is equal to (1.39-1.00)/1.39 or 0.29. Thus 29% of the energy entering the deposited detritus compartment is eventually cycled back from other compartments (Dame and Patten, 1981). The relative magnitude of the throughflows from a given compartment in the input and output environments can be used to infer which compartments exert controls over other compartments in the system. Since the filter feeders received the only input from outside the system in this model, it is not surprising that filter feeders exert control over all other compartments. The predator compartment controls deposited detritus, microbiota, and meiofauna. This control would not be apparent in an inspection of the model presented in Figure 4.

Input-output flow anlaysis was utilized to describe the impact on the shellfish resources of fertilizing a Spartina alterniflora marsh with inorganic nitrogen. Models of two different wetlands were examined: the 48-ha Great Sippewisset Marsh in Massachusetts and the 370,000-ha wetland complex in the Barataria Bay of Louisiana (Finn and Leschine, 1980). The models of these two wetlands are different, which will result in somewhat different conclusions resulting from the flow anlaysis. Of the nitrogen fertilizer added to the marsh only 3% reached the shellfish in the Great Sippewisset Marsh and approximately 8% reached the mussels (intertidal) and oysters (subtidal) in Barataria Bay. A unit of nitrogen entering the sediments of the Great Sippewisset Marsh has 43% of the nitrogen leave the system through denitrification and tidal export, while 41% is taken up by the below ground parts of Spartina. The recycling efficiency for the sediment pore water compartment is 54%. A unit of nitrogen entering the marsh soil in Barataria Bay results in 5% leaving the system through denitrification, 55% accumulating as marsh detritus, 29% being exported by the tides as detritus and water flora (phytoplankton), and 9% being harvested as fish and shellfish (Finn and Leschine, 1980).

The recycling efficiency in the Barataria Bay marsh soil compartment is 147%. The recycling efficiency is higher in the Barataria Bay Model because it contains both the grazing food chain and the detritus food web. This

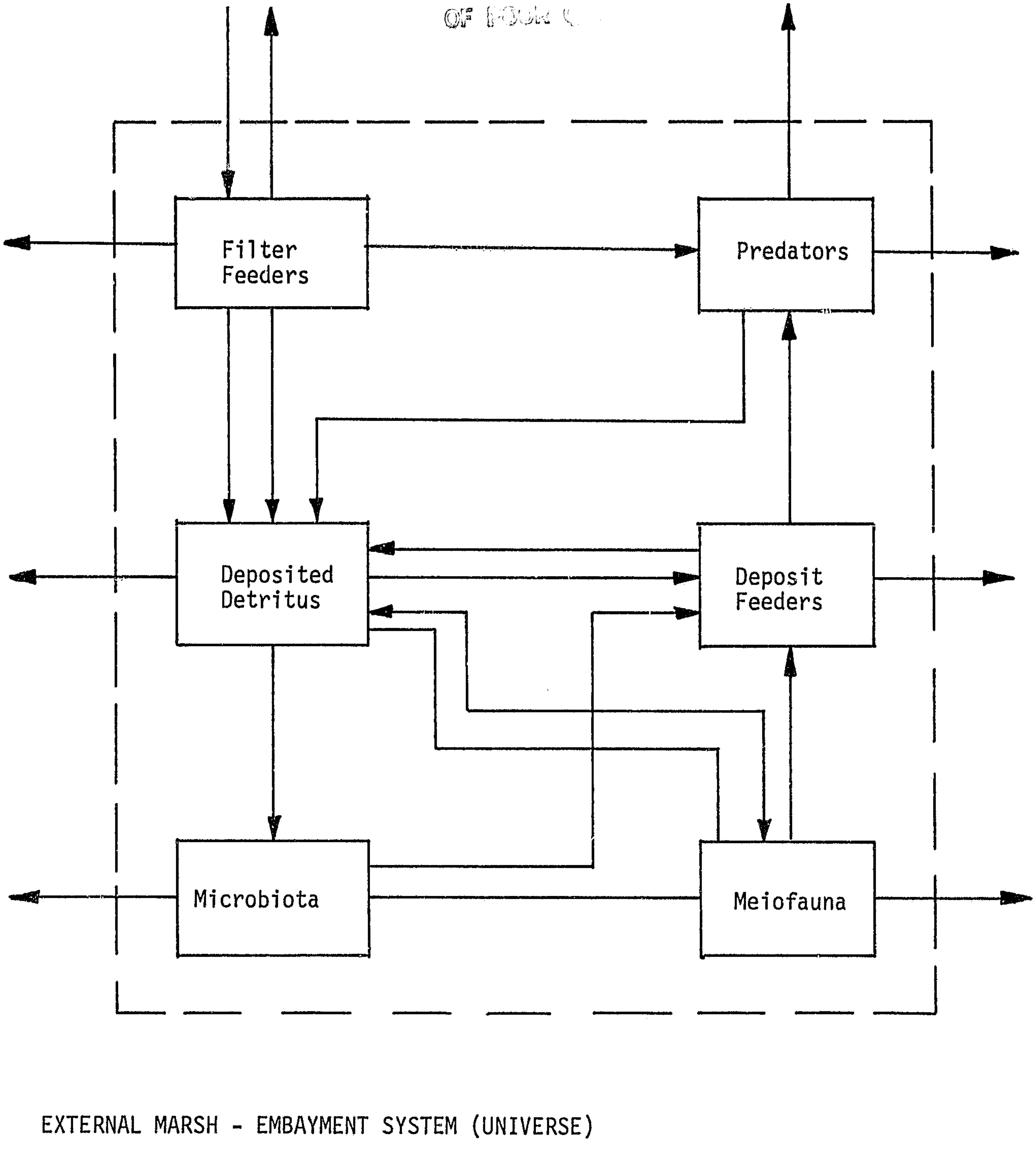


Figure 4. Intertidal Oyster Reef Energy Flow Model Used as the Basis for the Input-Output Flow Analysis (After Dame and Patten, 1981)

application of input-output flow analysis presumes that an energy flow or nutrient cycling model already exists for the important biotic and abiotic compartments in the marsh-embayment system. The potential applicability of flow analysis using a static, deterministic model to couple the productive capacity output with the aquatic energy flow model input for marsh production is fairly obvious. The nature of the temporal availability of Landsat Multispectral Scanner data, coupled with the uncertainties regarding the flow of energy through estuarine pelagic and benthic food chains, probably makes it more likely that a static, deterministic model could be successfully developed. A dynamic, deterministic model would be of greater use in predicting fisheries yields. The static, deterministic model should be useful for relating changes in wetland habitats to changes in the coastal fisheries on an annual basis.

V. RECOMMENDED FIELD STUDIES FOR ESTIMATING A TRANSPORT COEFFICIENT FROM MARSH-EMBAYMENT SYSTEMS TO ESTUARIES

A knowledge of the biomass and production of wetlands vascular plants along a transect from the marsh levee to the upland-wetland boundary is a prime prerequisite. A radiant power measurement instrument (RPMI) was utilized to measure the spectral reflectance of Spartina alterniflora plants in a Delaware salt marsh. The RPMI was used to simulate band 5 (0.6 to 0.7μm) and band 7 (0.8 to 1.1μm) of the Landsat Multispectral Scanner (MSS). The ratio of band 7 to band 5 correlated well ($r^2 = 0.81$) with the green standing crop biomass of Spartina (Bartlett and Klemas, 1980). The band 7/ band 5 reflectance ratio is also highly correlated ($r^2 = 0.72$) with the percentage of green biomass in the vegetation canopy, thus providing a means for estimating total Spartina biomass. The radiance values of Landsat MSS data were corrected for atmospheric effects and converted to reflectance values for each band utilizing the data provided by the RPMI measurements.

The minimum spot size (picture element or pixel) for Landsat MSS data is 1.1 acre. Based on the error in the regression equation and the minimum spatial resolution of Landsat MSS data, an area equivalent to 12 pixels in size would need to be integrated from the Landsat data to give a 90% confidence interval for the estimation of green biomass of Spartina (Bartlett and Klemas, 1980). In three Delaware Spartina alterniflora salt marshes the standing crop biomass estimated from the harvest technique was 1147 g dry wt/m^2, while that estimated from Landsat MSS data was 1113 g dry wt/m^2 (Bartlett and Klemas, 1980). The biomass estimates of the vascular plant standing crop can be converted to approximate estimates of plant production using the technique of Williams and Murdoch (1969). The rate of growth and longevity of stems in the field can be estimated by following the life history of tagged plants (Hopkinson et al., 1980 a). If the financial resources are not available to conduct a tagged plant study, turnover rates from the literature can be employed. It might appear that this is a crude technique, but the information in Table 7 showed that different harvesting procedures lead to a wide range of production estimates, so that a remote sensing-based production estimate should be reasonable.

The plant production estimated from Landsat MSS data represents above-ground plant parts. To estimate the loss of above-ground plant production by decomposition on the marsh surface and through tidal export, it would be possible to distribute litter bags at varying locations along a transect from the streamside to high marsh. Placing green leaves in the litter bags and measuring the weight loss over time could be used as an index of the mortality loss of green culms to dead plants and eventually to particulate and dissolved organic carbon. The surface decomposition of vascular plant detritus and tidal export are a function of the length of inundation of various zones in the marsh by water. As mentioned previously, the hypsometric curve could be used to estimate the area of wetland inundated at various tidal stages.

Aerial photography or imagery from airplane-borne scanners, like the Thematic Mapper Simulator (TMS) or Thermal Infrared Multispectral Scanner (TIMS), can be utilized to measure the area of marsh inundated at various water heights (measured by a continuously recording water height system). Since the Louisiana test site selected for the joint NASA-NMFS project is likely to have inundation time influenced by meteorological forces as well as tidal action, it would be wise to construct a winter hypsometric curve in January (when the water level in the marsh is low) and a fall hypsometric curve in October (when the water level is high). The airborne scanner system could also be used to measure the impact of a catastrophic hydrologic event (hurricane or prolonged rain event from a stalled frontal system) on marsh organic matter transport. The distance measurement in the current Productive Capacity Model should be made a function of the length of tidal inundation, rather than simple linear or exponential distance (Butera and Seyfarth, 1981). The litter bag decomposition rates could also be expressed as a distance function of tidal inundation.

If it is desired to incorporate below-ground production in the Productive Capacity Model, a measurement of the sediment respiration using the Electron Transport System (ETS) assay on various sections of cores gathered on a monthly or bimonthly sampling schedule should be used as an index. Since it appears that the below-ground plant biomass is in a steady state on an annual basis (Gallagher and Plumley, 1979; Valiella et al., 1976), it follows that aerobic and anaerobic sediment respiration must roughly balance the annual below-ground plant production rate. To estimate the chemical oxygen demand in the sediments using the ETS technique, it would be necessary to run the analysis on a section of the core which had not been sonicated to disrupt the cells. In this case the humic acids would couple reduced inorganic chemical forms to INT. Some microorganisms can absorb INT through their cell walls and reduce it intracellularly (Pamatmat, 1975), which would cause some interference. The INT reduced when the cells were disrupted would then measure potential biological respiration and chemical oxygen demand. The biological respiration alone could be estimated by difference. The sediment respiration would also have a component attributable to the above-ground plant production. The organic carbon produced by vascular plants on the marsh that is not respired in or on the sediments is the organic matter potentially available for hydrologic export. The ETS estimate of potential aerobic and anaerobic sediment respiration should be calibrated against the direct measurements of these processes using the methods discussed in Section III-B.

In order to get an independent measure of the dissolved and particulate organic carbon transported from the wetlands to the drainage creeks, a water sampler that collects a sample volume in proportion to the flow velocity should be placed in the water in the drainage channel. Boon (1978) has a good design for a water sampler that collects a velocity-weighted average of the time-varying DOC and POC concentration in the water. The size and shape of the drainage channel would determine how many water samplers would be needed to obtain a reasonable estimate of the net POC and DOC transport over a period of 3 to 7 days. The water samplers could be set up to measure ebb and flood directed currents separately. A biocide, such as mercury ions or cyanide, would have to be added to the water sample collection chamber to inhibit decomposition of the DOC and POC. The integrated water samples could also be analyzed for salinity in order to estimate the tidal exchange ratio and the flushing time using the freshness factor method (the volume of water in the creek or embayment can be estimated from the hypsometric curve). The integrated water samplers provide an approach for measuring the changes in water chemistry (DOC, POC, salinity) associated with catastrophic hydrologic events.

Once the DOC and POC reach the embayments, their fate is influenced by respiration in the water and sediments and hydrologic transport. The respiratory loss could be measured by the ETS method or the diurnal oxygen curve method (Hall and Moll, 1975). The area of wetlands in relation to the area of water in the embayments could be used in conjunction with values from the literature to estimate the magnitude of respiratory carbon losses from the water column and to determine whether such losses were of minor importance compared to the respiratory losses in the wetlands. Landsat MSS data provide a convenient method for determining the relative area of water and land in the marsh-embayment system.

The hydrologic transport of POC and DOC could be related to the tidal prism, flushing time corrected by the tidal exchange ratio, and the mean tidal excursion distance. This approach will be satisfactory as long as the DOC and POC concentrations act conservatively. The study of Happ et al. (1977) illustrates how data on the water replacement rate and TOC concentration along an inshore-offshore gradient can be used to estimate TOC export. This information on hydrologic export potential could be incorporated in the Productive Capacity Model through the importance values assigned to different water bodies (Butera and Seyfarth, 1981). If a quantitative value of the organic carbon export potential is desired, then the Lagrangian transport model appears to be the most feasible approach. The Lagrangian transport model can incorporate aspects of the non-conservative behavior of DOC and POC in the water column.

The transport coefficient postulated here would adjust the wetland vascular plant production for respiratory and hydrologic transport losses. The tidal inundation-distance to the wetland-water interface relationship would be formulated in such a way as to provide a common baseline for interpreting litter bag decomposition, hydraulic transport (a function of inundation time, current velocity, and size and density of organic matter to be exported), and sediment respiration. Characteristics of the tidal prism, such as volume, flushing time, and excursion distance, would be used as the basis for establishing different importance values to be assigned to each of the distinct classes of water bodies identified. The spatial resolution of Landsat data makes it difficult to detect channels less than one pixel in width. One can enter such channels into a geographic information system from a map base, but such channels will be one pixel wide in the data base, regardless of their true size. One way around this problem is to resample the Landsat data to a smaller spot size. The next generation of operational Landsat D satellites will have a spot size of roughly 30 meters, rather than the current spot size of 56 by 79 meters. Airborne scanners which have spot sizes down to 10 meters can be utilized. One faces a trade-off between decreased spot size and a greater number of pixels in the same area (which produces potential problems in data storage and manipulation).

The transport coefficient expressed as a conceptual functional relationship would be:

$$\text{T.C.} \infty \frac{B(x,t) - [R_S(x,t) + M(x,t) - R_S M(x,t)] + [H_I(x,t) - H_E(x,t)] - \Delta T(y,t) - R_W(y,t)}{B(x,t)}$$

where: B: standing crop of vascular plants in marsh
R_S: marsh soil respiration
M: conversion of living plant organic carbon to non-living DOC and POC (litter bag results)
$R_S M$: interaction term to correct for double counting
H_I: mean DOC and POC import from water to marsh
H_E: mean DOC and POC export from marsh to water
ΔT; net exchange of DOC and POC between embayment and estuary
R_W: water column and sediment respiration minus primary production in the water (diurnal oxygen curve method)
x: functional distance from marsh pixel to water based on hypsometric curve
t: month of year
y: functional distance in water based on mean tidal excursion

Note: each term in the above expression needs to be multiplied by a scaling factor to correct for the ratio of wetland area to water area and for time lags between events in the wetlands and in the water.

The embayment-to-estuary net exchange is given by:

$$\Delta T = (Z)\ (\Delta C)\ (K_{ex})(1-R)$$

where: Z: mean depth of embayment
ΔC: mean concentration gradient of DOC and POC between the embayment and estuary
K_{ex}: coefficient relating the influence of tidal exchange on the mean DOC and POC concentration in the embayment
R: fraction of ebb tide volume that reenters on next flood tide (tidal exchange ratio).

The exchange coefficient in a well-mixed embayment is computed as follows:

$$K_{ex} = C_{em} - \frac{[(V_l C_{em}) + (V_T\ C_{es})]}{V_H}$$

where: C_{em}: mean DOC and POC concentration in embayment
C_{es}: mean DOC and POC concentration in estuary
V_l : volume of water in embayment at low tide
V_H : volume of water in embayment at high tide
V_T : volume of water in tidal prism

VI. SUMMARY:

The outwelling hypothesis postulated wetlands as supporting coastal fisheries either by exporting nutrients, such as inorganic nitrogen, which stimulated the plankton-based grazing food chain in the water column, or through the export of dissolved and particulate organic carbon which provided a driving force for a benthic, detritus-based food web which provides the food source for the grazing food chain in a more indirect fashion. Recent research has emphasized the fact that coastal nekton may move up into the wetlands during high tide to feed and that wetlands may provide an important habitat to support critical life history stages of coastal fisheries. The bulk of the detritus exported from wetlands to adjacent estuaries may occur during infrequent storm events which are accompanied by flood tides and extensive rainfall. Much of this storm-exported detritus may not be readily available to aquatic food chains (refractory dissolved or particulate organic carbon) and thus will only become available following its conversion into microbial biomass. The most important organic carbon emanating from wetlands may be living organisms (from plankton to fish) and labile particulate detritus.

The role of the anaerobic degradation of the roots and rhizomes of vascular marsh plants has become the focus of much current research. The underground vascular plant production in wetland is poorly understood and its role in supporting aquatic food chains remains to be elucidated. Recent research indicates that the role of water movement through marsh soils plays an important role in the production of wetland vascular plants, controls the rate of aerobic and anaerobic metabolism in the sediments, and can transport reduced sulfur compounds to tidal creeks, where these energy-rich chemicals are converted into microbial biomass. The role of geomorphology and hydrology in controlling the transport of detritus from wetlands is discussed. The length of inundation of various zones in the marsh and the frequency of immersion are important variables which can be studied with the hypsometric curve technique. The hypsometric curve represents a good opportunity to combine remote information with ground-based data from a tide guage.

A conceptual model is presented to estimate a transport coefficient for the movement of nonliving organic matter from wetlands to the adjacent embayments. The transport coefficient is developed in a manner that makes it compatible with the Earth Resources Laboratory's Productive Capacity Model. The Transport Coefficient Model in its present form envisages detritus movement from wetland pixels to the nearest land-water boundary followed by movement within the water column from tidal creeks to the adjacent embayment. This conceptual model can be transposed to deal with only the interaction between tidal water and the marsh or to estimate the transport from embayments to the adjacent coastal waters. In a global perspective, each wetland system is assumed to have similarities in its ecological interactions, but to possess unique hydrological and geomorphological characters which would determine which version of the Transport Coefficient Model would be most applicable and how the model would be parameterized. Input-output flow models are discussed as an approach for linking the Productive Capacity Model to its impact on estuarine fish and shellfish populations.

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