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Examination of Tidal Flats:

A Review of Identified Values

Submitted to the

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by

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Preface

The work reported herein was performed under contract DOT-FH-11-9360 entitled "The Evaluation of Wetland Tidal Flat areas for Highway Planning and Design: A Literature Review." The research was sponsored by the Federal Highway Department under the supervision of Mr. Doug Smith and Mr. Fred Bank, and conducted at the Virginia Institute of Marine Science, College of William and Mary, Gloucester Pt., Va.

This report summarizes the available information from the literature concerning the physical, chemical and biological processes characteristic of the tidal flat habitat and suggests possible techniques for the evaluation of coastal wetlands types for management or scientific purposes. Companion to this volume is an evaluation methodology for assessing tidal flat ecological value.

Research was conducted under the supervision of Dr. Robert Orth and Dr. Richard Wetzel. Editorial assistance was provided by Dr. Robert Diaz and Dr. Morris Roberts. Library and field support was given by Lee Stone, Glenn Markwith, Bill Rizzo, Deborah Penry, and Kimberly Storey. Clerical support and limitless patience was provided by Mrs. Shirley Sterling throughout all phases and preparation of this report.

1.0 PHYSICAL PROCESSES

1.1 Definition of Tidal Flats

Although there are many schemes for classification of estuaries (Ketchum 1951, Emery and Stevenson 1957, Hedgpeth 1957, Caspers 1967, Pritchard 1967, Cowardin et al. 1979) and emergent vegetated wetlands (Martin et al. 1953, Shaw and Fredine 1956, Silberhorn et al. 1974, Cowardin et al. 1979), there has been no attempt to define systematically those habitats vaguely referred to as tidal flats. Cowardin et al. 1979) define tidal flats as those level land forms of unconsolidated sediments ranging from gravel to mud, which occur in sheltered areas which are not continuously submerged. Cowardin et al. (1979) technically exclude vegetated areas and shallow waters not exposed by the tide although the term "flat" is often commonly applied to both cases, as in "grass flat."

For this review and discussion of "tidal flat" values and function, we will use a broad definition to include those marine and estuarine habitats, exposed or nearly exposed by the tide, which have unconsolidated sediments and slight bottom declinity. Tidal flats may be intertidal or subtidal (to about 1 meter depth at mean low water), with or without submerged vegetation (vascular plants or macroalgae) but without emergent vegetation, and having sediments consisting of either mud, sand, shell or peat.

1.2 Geological Development

The geologic development of tidal flats has been, for the most part, inferred from study of the geological processes operating on existing tidal flats. Tidal flat areas can exist in both protected areas and areas exposed to strong tidal and wave action. There are two basic models postulated for tidal flat development that depend upon the nature of the tides and sediment sources.

The first model involves tidal flats which develop in the lee of barrier islands or protected bays (Klein 1971). Many such habitats exist along the east coast of the United States. These areas have restricted inlets between barrier islands which cause strong tidal currents and development of elaborate tidal channels which control sedimentation. These areas also contain large quantities of sand, subtidally derived from long-shore drift. The typical tidal flat sediment structure consists of subtidal cross-bedded and cross-laminated sand beneath interlaminated sand and mud in the intertidal zone, with organic-rich clay and peat in the supratidal zone.

The second model relates to tidal flats like those which developed along the Gulf coast (Thompson 1975). Here there is a large mud supply, low wave energy, and a different circulation system where tidal currents have little restriction and move over flats in a broad uniform flow with little channel development. Consequently, coastal mud flats develop by depositional regression (due to low wave energy) around the existing alluvial fans of river mouths. Occasional historical periods of drought result in low levels of mud input, thus allowing waves to re-work sediments, resulting in the concentration of coarse sediments. These processes typically cause silts and clays to accumulate in the subtidal, intertidal, and supratidal zones as a consequence of uniform flow, with uniform horizontal bedding on intertidal flats.

The primary factors involved in the formation of a tidal flat are 1) the physical environment (waves, wind, tidal currents) and 2) available sediment type. Some secondary factors include geographic location, which basically determines the physical environment, and living organisms.

On some tidal flats wave action often predominates over current action (Carling 1976, Hayes 1975, Postma 1967, Harrison 1975, Thompson 1975, Anderson 1972, Reineck 1967, Van Straaten 1954, Klein 1963, 1967, 1970). Wave activity is determined by the force of incoming waves plus wind waves generated on tidal flats themselves (Postma 1957, Anderson 1972, Miller 1975). Relatively small amplitude waves (less than 0.5 m) may be sufficient to suspend the unconsolidated fine silts and clays of many tidal flats, particularly in intertidal areas (Carling 1976, Anderson 1972, Miller 1975). Waves with a height of only 0.25 m and a period of 4 seconds will resuspend and transport fine materials in two meters of water. Also, as the depth of water decreases, the amount of sediment resuspended increases for waves of a given height and period (Carling 1976, Anderson 1972, Postma 1967, Van Straaten and Kuenen 1957).

Currents associated with ebbing and flooding tides also act to transport and resuspend sediment (Carling 1976, Boon 1975, Anderson 1972, Land and Hoyt 1966, Schubel 1971, Hayes 1975, Harrison 1975, Thompson 1975, Knight and Dalrymple 1975, Groen 1967, Postma 1967, Reineck 1967, Klein 1967, 1970). The net velocity and direction of sediment movement is determined by the physical structure and hydrodynamic processes on a tidal flat. In many cases, the amount of water entering and leaving a flat is not the same and the duration of maximum flood and ebb currents not necessarily equal. This results in a definite flood or ebb transport of sediment, and a definite orientation of sedimentary structures such as bars and flats with respect to the shoreline (Knight and Dalrymple 1975, Land and Hoyt 1966, Boon 1975, Carling 1976). However, even where net water transport is zero, and ebb and flood velocities are equal, build-up and maintenance of flat areas can occur despite strong tidal flushing (Groen 1967).

During a flood tide, the water mass spreads horizontally over tidal flats and looses velocity which allows settlement of suspended sediments (Van Straaten and Kuenen 1957, Postma 1967, Carling 1976, Schubel 1971). This sedimentation occurs until ebb currents resuspend particles. However, the water mass from which a sediment was deposited does not have sufficient velocity to resuspend it. Therefore a particle tends to be carried into a lower energy environment than the point at which it first began to settle (Postma 1967). Furthermore, maximum flood velocity and maximum ebb velocity are not reached at the same point during flood and ebb tides respectively. There is a longer time interval between maximum flood current and maximum ebb current than between maximum ebb current and maximum flood current (Postma 1961, 1967, Groen 1967, Klein 1970). This allows a longer settling time for particles at and sometimes after high slack water when ebb velocities are low (Postma 1954, Groen 1967). Consequently, ebb currents carry less sediment than flood currents, even though ebb currents resuspend more sediments (Postma 1954, Groen 1967, Carling 1976, Schubel 1971, Anderson 1972).

In environments in which there is a large amount of sediment input from rivers, flats may build rapidly outward predominantly through fluvial processes, with waves and currents simply reworking the sediments (Thompson 1975, Reineck 1967, Klein 1963).

In cold regions, blocks of ice, which incorporate sediments as they scrape over a tidal flat may become important in sediment movement (Dionne 1972, Knight and Dalrymple 1975, Klein 1970).

1.3 Physical Processes and Sedimentology

Waves, currents, tides and winds are the dominant physical parameters affecting tidal flats and grain size distribution on the flats. These factors act both separately and in concert to produce a variety of different sediment types in tidal flat areas. Despite the diversity of sediment types in tidal flats, there are some features common to most of them.

Although a wide variety of tidal flat grain-size deposits have been found ranging from coarse sand to clay, grain size often decreases in the landward direction leaving the finer sediments, usually silts, nearer to shore (Postma 1967, Dale 1974, Land and Hoyt 1966, Harrison 1975, Knight and Dalrymple 1975, Klein 1970, 1971, Dionne 1972, Reineck 1967, Van Straaten 1954). This trend holds true whether the sediment is primarily sand (Klein 1963, 1970, Van Straaten 1954, Reineck 1967) or silt (Thompson 1975, Knight and Dalrymple 1975, Dale 1974, Dionne 1972, Land and Hoyt 1966, Harrison 1975). This pattern of grain-size distribution from offshore coarser sediments to nearshore finer sediments is due to many factors: 1) landward decrease in tidal current velocities, 2) landward decrease in wave action, 3) supply of fine sediments from land, 4) asymmetry of maximum current velocities.

There are several other characteristics of mud flats which may be important in determination of sediment distribution:

1) Shellfish and other filter-feeding invertebrates may filter suspended sediments and deposit them on the bottom as difficult to erode feces or pseudo-feces (Postma 1967). Populations of some shellfish are sufficiently large to filter the entire water mass of the system in a short time (Verwey 1952).

2) Benthic diatoms, which form thick cohesive layers of organic matter, may prevent erosion of fine particles, particularly clays (Postma 1967, Holland *et al*. 1974).

3) Meandering channels crossing on tidal flats are particularly prevalent on mud flats (Reineck 1967, Klein 1963, 1967, 1970, Van Straaten 1954). Sand flats do not have well developed channels, since sand lacks cohesiveness, and tends to collapse into any channels which are cut into it (Van Straaten 1954). Deposition of mud is favored by the presence of shifting gullies and channels (Van Straaten 1954).

Exception to both are numerous. Terwindt (1975) reports that for subtidal flats 40% showed decreasing grain size with increasing elevation, 20% showed the reverse, 20% showed a decrease in grain size followed by an increase, and three other less common sequences were observed. Terwindt's study shows the variability of tidal flat structure and the variety of sedimentological processes which form the flats.

Despite sediment mobility on tidal flats, flats are generally persistent rather than ephemeral features. This is not surprising since flat development requires a long-term dynamic equilibrum of depositional and erosional forces. Tidal flats are often colonized by marsh grasses in intertidal situations or submerged aquatics in subtidal situations. Old flats frequently underly marshes and marshes are often found adjacent to existing flats (Redfield 1967, Armentano and Woodwell 1975, Harrison 1975, Knight and Dalrymple 1975, Land and Hoyt 1966, Carling 1976, Pomeroy 1959, Williams 1962, Gallagher and Daiber 1974, Wetzel 1977, Rizzo 1977).

In summary, factors governing the type of sediment which forms a tidal flat include tidal currents, wind waves especially in shallow systems, source of sediment, amount of protection afforded from strong tidal currents and large waves, and asymmetrical tidal current velocities. Grain-size distributions are highly variable, even in local situations. Sediments, especially fine sediments, are resuspended on each tidal cycle and deposited during slack water. Amount and direction of transport during a tidal cycle depends on tidal current and wave properties in the system. Flats may be built from sediments derived from land or sea or both. Once established, flats are generally stable and often furnish an environment in which intertidal marsh grasses or subtidal grasses may become established.

2.0 ECOLOGY

2.1 Primary Producers

2.1.1 Microalgae

Benthic microalgae are important constituents of intertidal and shallow water ecosystems due to their high year-long productivity, fast turnover, and utilization as food by primary consumers. However, knowledge of the community is sparse compared to many other communities of primary producers. Researchers have become interested in benthic microalgae only recently. This discussion will center on 1) the production and productivity of benthic microalgae, 2) the physical factors influencing benthic algal ecology, and 3) biotic interactions of this community with other populations and communities.

Productivity

Benthic microalgal communities are composed primarily of motile, pennate diatoms, though flagellates and blue-green algal mats do occur and are sometimes very abundant (Pomeroy 1959, Williams 1962, Leach 1970, Sullivan 1971, Riznyk and Phinney 1972a, 1972b, Gallagher and Daiber 1974, Rizzo 1977, Burkholder, Repak, and Sibert 1965, Drum and Webber 1965, Marshall *et al*. 1971, Admiraal 1977).

Benthic microalgal communities can be very productive and frequently exceed phytoplankton production in shallow and turbid, coastal waters (Pamatamat 1968, Riznyk and Phinney 1972b, Bunt *et al*. 1972, Pomeroy 1959, Ragotzkie 1959, Leach 1970, Burkholder *et al*. 1965, Marshall *et al*. 1971). Salt marsh systems are among the most productive ecosystems in the world, including cultivated crop systems

(Schelske and Odum 1961). Benthic microalgae can contribute a substantial amount of production in East coast salt marshes, 25-33% of the net annual angiosperm production (Pomeroy 1959, Schelske and Odum 1961, Gallagher and Daiber 1974, Van Raalte and Valiela 1976) and 80-140% in a California marsh (Zedler 1980).

Gross productivity of microalgae in salt marshes has been reported to range between 100-680 mg C/m^2/day over the coarse of a year's study in Delaware (Gallagher and Daiber 1974). Daily rates were obtained by taking the author's hourly estimates and assuming production for 10 hours/day. In Georgia marshes rates of 200-1100 mg C/m^2/day were reported for microalgae by Pomeroy (1959), while Williams (1962) reported rates of 330-680 mg C/m^2/day in the same system, based on cell abundances and cell volumes. Productivity measurements, based on ^{14}C, in Massachusetts salt marshes ranged from 0-115 mg C/m^2/day (Van Raalte and Valiela 1976). In California algal mats in a salt marsh have ranged as high as 2000 mg C/m^2/day (converted from the author's oxygen values, using a Photosynthetic Quotient of 1.0) (Zedler 1980).

Similar high rates of microalgae productivity have been observed on intertidal sandflats. Pamatmat (1968) reports rates of 18-97 mg C/m^2/day at one site and 3-175 mg C/m^2/day at two others in Oregon based on oxygen determinations. A high energy sand beach containing both intertidal and submerged study sites yielded a range of values from 12-20 mg C/m^2/day (Steele and Baird 1968).

Mudflats have been more extensively studied. On Georgia mudflats associated with Spartina marshes observed productivity rates in air range 3-397 mg C/m^2/day and in water from 118-577 mg C/m^2/day. Daily rates for a similar Georgia mudflat were 660-1420 mg C/m^2/day (Williams 1962). On an unvegetated bank in a Delaware salt marsh, productivity rates of 160-210 mg C/m^2/day based on oxygen changes were observed (Gallagher and Daiber 1974). In Europe, studies of a number of locations over many years on the extensive mudflats of the Wadden Sea have shown productivities of 1-1200 mg C/m^2/day (Cadee and Hegeman 1974, 1977). In England, Joint (1978) found rates of 50-1150 mg C/m^2/day (measured by the ^{14}C method) where flats were exposed at low tide, but could detect no productivity of benthic microalgae at high tide. Leach (1970) found ^{14}C productivity rates of 10-240 mg C/m^2/day in water, and similar rates of 40-200 mg^{2}C/m^2/day in air on a Scottish mudflat.

Unvegetated permanently submerged areas may also have high productivities. Pomeroy (1960) found an unvegetated area near a turtle grass bed to have a productivity of 650-1900 mg C/m^2/day, about the same productivity measured in the sea grass bed itself. Estimates from four subtidal sites in Rhode Island and Connecticut show ranges of 74-431 mg C/m^2/day (Marshall *et al*. 1971). Bunt *et al*. (1972) reported rates of 40-140 mg C/m^2/day for Caribbean sediments in depths of water varying from 3-60 m. Gargas (1970), in a study of various submerged habitats in Denmark, measured productivity rates of 50-1100 mg C/m^2/day in a year of study at sites ranging from 0.12-8.0 m in depth. Depths greater than 10 m had negligible productivity.

Indirect estimates of standing stock such as cell counts and chlorophyll *a* are often made in lieu of productivity measurements because they can be done more quickly, cheaply, and with greater replicability. However, high standing stocks do not necessarily correlate with high productivities (Burkholder *et al*. 1965, Leach 1970, Rizzo 1977).

Reported chlorophyll *a* estimates are quite variable because of the study site chosen, patchiness of the algae, and especially the variety of chlorophyll measurement techniques employed. Many chlorophyll *a* values which have been reported to date include some contribution from degradation products of chlorophyll (phenophytin, chlorophyllide, phenophorbide). Even those techniques which correct for pheophytin may be inaccurate measurements of chlorophyll *a* (Whitney and Darley 1979, Jacobsen 1978). Nevertheless, the measure is useful as an indication of the dynamics of the community.

Chlorophyll *a* concentration in *Spartina* marsh sediments can range from less than 10 to nearly 200 mg/m^2 (Estrada *et al*. 1974, Sullivan and Daiber 1975, Rizzo 1977). Chlorophyll *a* concentrations for intertidal flats vary over a wider range but are usually higher with reported ranges of 4-150 mg/m^2 (Bunt *et al*. 1972, Riznyk and Phinney 1972a, Rizzo 1977). Subtidal systems range between 25 and 80 mg/m^2 having chlorophyll *a* concentrations similar to those of intertidal flats (Bunt *et al*. 1972, Rizzo 1977).

Cell counts are made less frequently than other measurements but show about the same similarity among studies as do productivity and chlorophyll data. Cell densities in marshes have ranged from 40-1000 $cells/mm^2$ (Williams 1962, Rizzo 1977), while intertidal flats have more variable cell densities equal to or higher than those in marshes with a range from 2-37000 $cells/mm^2$ (Leach 1970, Williams 1962, Riznyk and Phinney 1972b, Rizzo 1977).

Physical and Chemical Factors

Though benthic microalgae are adapted for photosynthesis at very low light intensities (Gargas 1971), light is still the factor which is most critical in limiting production of this community (Pamatmat 1968, Van Raalte *et al*. 1976, Sullivan and Daiber 1975, Estrada *et al*. 1974, Gargas 1970, Van Raalte and Valiela 1976, Cadee and Hegeman 1974, Leach 1970, Welch *et al*. 1972. High light levels inhibit photosynthesis in phytoplankton (Ryther 1956). Photo-inhibition has been suggested to occur in benthic microalgae by analogy to phytoplankton (Pomeroy 1959), but most investigators feel that benthic microalgae are not significantly inhibited even by the high light levels (ca. 50 klux) at low tide in summer (Gallagher and Daiber 1974, Burkholder *et al*. 1965, Taylor and Palmer 1963, Taylor 1964, Colijn and van Buurt 1975, Amspoker 1977, Gargas 1971).

The initial light reaction in photosynthesis is a physical reaction independent of temperature. Since light is limiting to benthic microalgae it is not surprising that temperature has been found to exert little influence on the productivity of benthic algae (Pamatmat 1968, Welch *et al*. 1972, Van Raalte and Valiela 1976). However, temperature may become important during those periods when light levels saturate the community. Leach (1970) found that temperature was much less important than light in affecting productivity under natural conditions, but also found that under constant high light levels productivity increased as temperature increase. In another study photosynthesis was found to increase 10% per 1°C temperature increase between 4 and 22°C, if light levels were saturating. Below light saturation temperature exerted no effect (Colijn and van Buurt 1975).

Nutrients added to the microalgal community, particularly nitrogen compounds, can increase productivity at least during some seasons (Van Raalte *et al*. 1976, Sullivan and Daiber 1975). These increases were slight when compared to the limitation of the community by light. Nutrient addition may increase productivity only when light levels are low (Van Raalte *et al*. 1976). A late summer experiment in Massachusetts showed algal production (as chlorophyll *a*) to decreased due to greater shading by marsh plants, but nutrient addition increased growth of the algae (Estrada *et al*. 1974).

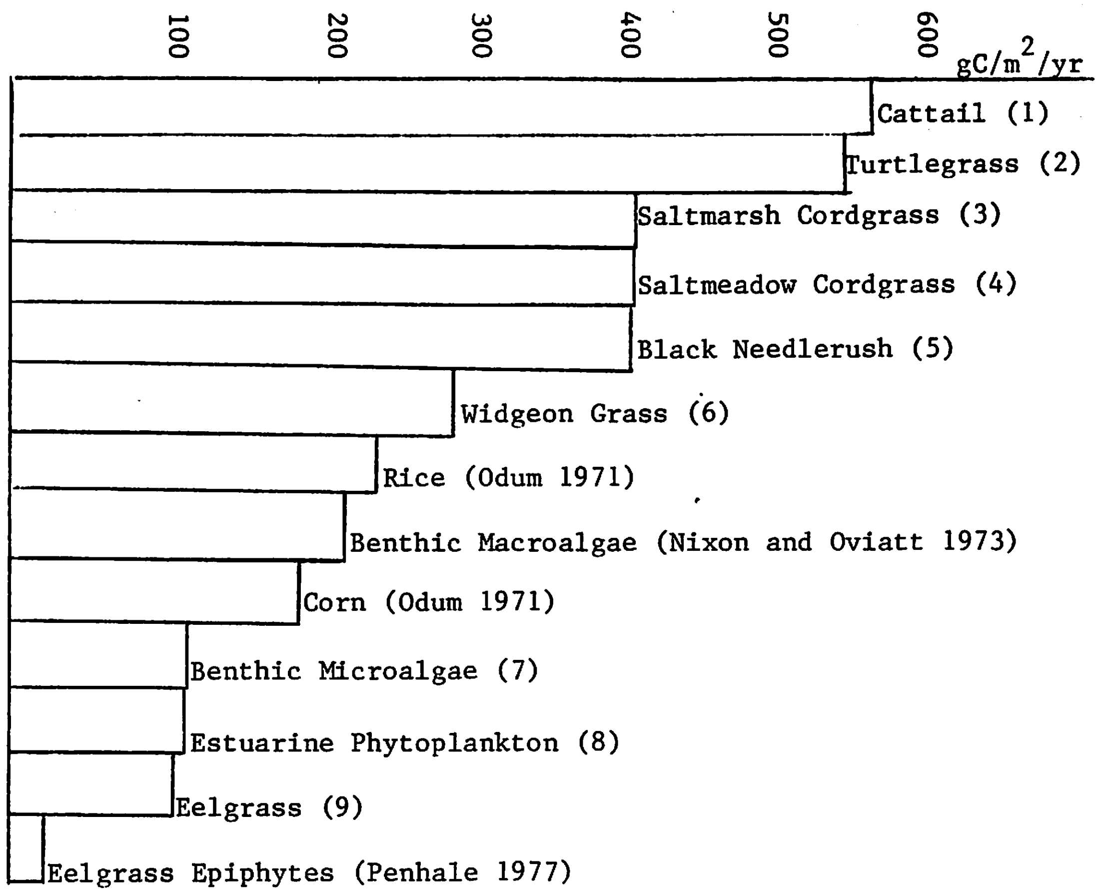
The action of waves, currents, and runoff may have important impacts on benthic algae, but have received virtually no quantitative study. Runoff from rainfall during low tides can have a severe scouring effect on benthic microalgal communities (Williams 1962, Gallagher and Daiber 1974). Currents can suspend and transport algae of the tidal flats (Pamatmat 1968, Holland *et al*. 1974). Tides affect algae by changing the ambient light, nutrient, and temperature regimes. Wave action can bury algae through mechanical mixing of the sediment (Steele and Baird 1968, Gargas 1970). Burial may even be more important than light in limiting production on sandy beaches (Steele and Baird 1968). Intertidal areas frequently experience rapid settling of suspended sediments which may bury algae (Bender *et al*. 1977, Rizzo 1977, Riznyk and Phinney 1972b). Algae may also stabilize sediments by secreting mucus which binds sediment particles and prevents them from being resuspended by incoming tides (Williams

1962, Holland et al. 1974, Postma 1967). Since many of the algae are motile they may also bury themselves in the sediments to escape scouring by tidal currents (Pamatmat 1968, Leach 1970).

Biological Interactions

Benthic algae are important not only because of their substantial productivity, but because they have a rapid turn-over, can be consumed directly by herbivorous animals, and are productive in winter months when other autotrophic production is low (Pomeroy 1959, Gallagher and Daiber 1974, Van Raalte et al. 1976). Benthic microalgae are used directly as food and are also consumed as part of the bacterial-algal-detrital pool so important in estuaries. A diverse assemblage of organisms depends to some extent on this community, including blue crabs, fiddler crabs, hermit crabs, benthic copepods, chironomid (midge) larvae, ostracods, cumaceans, mysids, amphipods, gastropods, many bivalves, and certain polychaetes and fishes (Darnell 1961, Darnell 1964, Odum 1968, Roberts 1968, McIntyre 1969, Nixon and Oviatt 1973, Odum 1971, Kraeuter and Wolf 1974, Wetzel 1977, Nichols and Robertson 1979). Grazing of intertidal flats can be so extensive at times that algal productivity and biomass are limited (Wetzel 1977, Williams 1962, Riznyk and Phinney 1972b, Pamatmat 1968, Pace 1977).

It is also of interest to compare production of tidal flat habitats with other communities of primary producers. Comparison of these communities appears in figure 1 . Values used are a mean of all the studies cited. It should also be borne in mind, that these values are per unit area. The relative importance of each community



(1) Harper 1918, Jervis 1964, Boyd 1970, Nixon and Oviatt 1973, Kowalski 1979
(2) Thayer *et al*. 1975
(3) Smalley 1959, Morgan 1961, Williams and Murdoch 1966, 1969, Stroud and Cooper 1969, Nixon and Oviatt 1973, Stevenson *et al*. 1977, Kowalski 1979
(4) Harper 1918, Waits 1967, Nixon and Oviatt 1973
(5) Williams and Murdoch 1966, Waits 1967, Foster 1968, Heald 1969, Stroud and Cooper 1969
(6) Anderson 1966, Nixon and Oviatt 1973
(7) Pomeroy 1959, Grontved 1960, Pamatmat 1968, Leach 1970, Marshall *et al*. 1971, Gallagher and Daiber 1974, Cadee and Hegeman 1977
(8) Ragotzkie 1959, Smayda 1962, Williams 1966, Marshall 1967, Flemer 1970, Nixon and Oviatt 1973
(9) Burkholder et al. 1968, Conover 1968, Dillon 1971, Nixon and Oviatt 1972, Thayer *et al*. 1975, Penhale 1977

Figure 1. Comparative primary production of various autotrophs.

is also dependent on the extent of area covered by each type. For example, benthic microalgae and phytoplankton are ubiquitous inhabitants of intertidal and shallow water areas, whereas mats of macroalgae are relatively rare, and consequently contribute a smaller proportion to total estuarine primary production despite high production within a mat.

2.1.2 Vascular Plants

Many sections of tidal flats and shallow coastal areas contain beds of submerged aquatic vascular plants. Because these plants require an adequate amount of light for photosynthesis, they are restricted to a relatively narrow fringe adjacent to the shoreline. Despite their limited distribution in the coastal zone, their relative contribution to the total productivity of this area is significantly greater than similar, unvegetated areas, and in many areas, may be the most productive community. These communities serve multiple functional roles in coastal ecosystems as a source of material for the detrital food chain and providing a substrate for numerous epiphytic organisms, whose biomass may equal that of the grass itself (Penhale 1977). The large densities of invertebrates supported by the grass in turn serve as a food source for higher consumers. Grass rhizomes tend to bind sediments. While the blades reduce currents and wave action affording some protection against the bottom and adjacent shoreline. The plants also act as nutrient "pumps", removing nutrients from the water column and transporting them to the sediments and vice versa (Wood *et al*. 1969, Thayer *et al*. 1975, McRoy and Helfferich 1977, Phillips and McRoy 1980).

Submerged vascular plants are flowering plants. They have root and rhizome structures and reproduce both vegetatively and sexually. However, their entire life is spent underwater or, with intertidal species, a significant portion of their life cycle. Pollination is subaqueous (some species do have airborn pollen, e.g. water milfoil) and currents or wave action are the principal means of pollen and seed dispersal. There are no known insect or other invertebrate pollinators as in land plants.

Submerged aquatic vegetation (SAV) is found in a broad range of shallow coastal habitats ranging from fresh to full strength seawater and from the arctic to the tropics. Different species occupy these different habitats but their basic functions and importance values remain similar.

There are approximately 50 species in 12 genera adapted to the marine environment (Hartog 1970), while there are many more species adapted to fresh and brackish water areas. One species, widgeon grass, *Ruppia maritima*, is found along the entire salinity range as well as being abundant in fresh water.

Primary productivity in beds of SAV can be very high and in some cases, rival that of phytoplankton production in upwelling areas. Two species of seagrass have been widely studied, turtlegrass, *Thalassia testudinum*, and eelgrass, *Zostera marina* for productivity measurements. Values for annual production of turtlegrass range from 200 grams Carbon (g C) per m^2 to 3000 g C/m^2 and annual values for eelgrass range from 5-600 g C/m^2 (Thayer *et al*. 1975). These productivity figures are higher than those values for many cultivated crops (corn 412 g C/m^2, rice 497 g C/m^2, hay fields 420 g C/m^2 (Odum 1971). In addition to the productivity of the plant, there are additional inputs from associated epiphytic algae and benthic macro- and microalgae. The production from these components may be equal to or greater than that from the production of the plant (Dillon 1971, Penhale 1977).

Nutrient cycles in grass beds are complex and the problems associated with nutrient limitation, sites and rates of uptake still need further work. Recent work on eelgrass indicates that leaves and roots can absorb phosphorus and nitrogen transporting it to other parts of the plant (McRoy and Barsdate 1970, McRoy et al. 1972, McRoy et al. 1972, Barsdate et al. 1974, Penhale 1976). Eelgrass also serves as a "nutrient pump", pumping phosphate from the sediments through the plant and releasing it into the ambient water. The flow of phosphorus can occur in the opposite direction, but the net effect is to transport phosphorus from the sediment to the water, effectively increasing the concentration of these nutrients in the water column. More recently, Cardgnar and Kalff (1980) showed experiments that fresh water SAV in nature overwhelmingly depend on the sediment for their phosphorus supply.

This transport of nutrients is very important to epiphytic algae because they apparently utilize carbon, nitrogen and phosphorus excreted by SAV (Harlin 1971, McRoy and Goering 1974, Penhale 1976). This would potentially allow greater growths of algae on grass blades in nutrient poor waters than would otherwise be possible. The response of SAV to nutrient enrichment of sediments has been little studied. The additions of two commercial fertilizers (5-10-10 and 10-10-10) did significantly increase the production of eelgrass in terms of biomass (standing crop), and length and number of vegetative turions of eelgrass in the Chesapeake Bay (Orth 1977).

Eelgrass was also found to be very effective in concentrating various major elements such as carbon, nitrogen, and phosphorus, minor elements such as manganese, aluminum and iron, and trace elements such as copper, cobalt and beryllium from the water column (McRoy 1970, Barsdate *et al*. 1974).

SAV can be found on all types of substrates ranging from pure sand to pure mud. Many species will grow in a range of sediment types with optimal growth being in a particular type sediment. The maximum density of milfoil, *Myriophyllum spicatum*, occurred on very fine sediments with sparse growth on sandy substrates (Patten 1956, Philipp and Brown 1965, Anderson 1972, Nichols 1975, Grace and Tilly 1976). Wild celery, *Vallisneria americana*, also thrives best in a silty-sand substrate (Schuette and Alder 1927, Hunt 1963, Lind and Cottam 1969).

The depth distribution of SAV depends upon a complex of interrelated variables (waves, currents, substrate, turbidity) which effect light penetration. Light penetration may be the most critical parameter as the plants require an adequate amounts for photosynthesis. SAV may grow to depths of 20-30 meters in relatively clear waters (Shelden and Boylen 1977). In estuarine tidal areas where currents and wave action continually stir up bottom sediments, SAV is restricted to much more shallow depths, usually 2 meters (mean low water) or less.

Several experiments have demonstrated the importance of light for growth of eelgrass. Burkholder and Doheny (1968) placed cages with nylon screen shades over eelgrass and found at light levels of 20%, 10% and 1.6% of incident daylight in Long Island, eelgrass became stunted and eventually died in cages, while it flourished in control areas.

They also examined photosynthetic rates and found that at levels of 10% and 1.6% of incident daylight in their experiments, the fixation of carbon was reduced to 1/3 and 1/7 the value obtained in full daylight. They suggested that 1% incident daylight may be the threshold for photosynthetic maintenance. Backman and Barilotti (1976) also found a direct relationship between irradiance received by the plants and plant density. Plant density decreased in plots of eelgrass that were artificially shaded and that flowering was inhibited by lowered light intensity.

Temperature is a critical factor especially for temperate species as their growth, reproduction, and senescense are all cued to changing temperature. Studies on the growth of eelgrass indicated that active vegetative growth occurred between 10-15°C, sexual reproduction between 15-20°C, above 20°C heat rigor or no growth, and below 10°C cold rigor (Setchell 1929). These temperatures do not adequately describe all eelgrass populations because of latitude effects (Dillon 1971, McRoy 1966, 1969). Optimal temperatures for growth of wild celery are 25-32°C with growth ceasing below 19°C and above 50°C (Hunt 1963, Lind and Cottam 1969, Boylen and Sheldon 1976). The optimal temperatures for milfoil are 23-25°C (Anderson 1964). Setchell (1924) concluded that a temperature of 15 to 20°C was needed for germination and seedling development of widgeon grass, and 20 to 25°C was needed for vegetative growth and reproduction.

Salinity is another major limiting factor of SAV especially in tidal estuarine areas. Distribution limits of many of the fresh water species (Vallisneria, Potamogeton, Zannichelia, Myriophyllum) are at salinities of 5-10 $^{o}/oo$ (Bourn 1934, Haller et al. 1974, Davis and Brinson 1976, Anderson 1964) while the lower limit of the estuarine eelgrass is approximately 10 $^{o}/oo$ (Phillips 1974). Wiegeon grass occurs from freshwater to full saline conditions, though flowering may be limited to waters whose salinity is less than 30 $^{o}/oo$.

SAV are prime food for ducks, coots, geese, grebes, swans, marsh and shore birds, and game birds of the Atlantic, Pacific and Gulf Coasts (Martin and Uhler 1939, Sculthorpe 1967). Dugongs, manatees and turtles are about the only other animals to consume SAV as a nutritional source (Campbell and Irvine 1977, Heinsohn 1977, Ogden 1980). Some fishes and sea urchins consume seagrasses (Ogden et al. 1973, Greenway 1976, Ogden 1976, 1980) but it is still questionable whether these animals are consuming the grass as a food source or for the epibiota attached to the leaves. There are no known invertebrate consumers of SAV despite the fact that there are dense concentrations of invertebrates associated with SAV.

2.2 Animal Communities

The distribution of the animal communities of tidal flat areas varies according to the prevailing physical and chemical conditions, as well as biological processes. Such parameters as duration of inundation or exposure, degree of wave and tidal action, nature of the substratum, topography of the shore, dissolved oxygen, temperature and salinity are important in determining zonation patterns. The situation is further complicated by biological interactions between the organisms themselves, such as inter- and intra-specific competition for food or space, or predation. These parameters vary spatially and temporally, making it difficult to attribute specific zonation patterns to one single factor.

There are several methods that can be employed in the categorization of animals associated with tidal flat habitats. One method is based on particle size of the sediments (pebble, sand, and mud fauna). There is a characteristic fauna associated with sand and mud habitats. Another method employed in the categorizing species is based on their life position relative to the sediment surface. Species that are found on the surface of the sediment or on a particulate substratum (shell or vegetation) are defined as epifauna, while burrowing forms in the sediment are termed infauna. Also, due to the extreme size ranges associated with species it becomes necessary to categorize them by size, macrofauna are generally larger than 500 μm, meiofauna 50-500 μm and microfauna smaller than 50 μm.

In addition to these basic size differences, the fauna may also be divided into groups according to various feeding modes (deposit feeders, suspension or filter feeders, and predatory organisms) (Newell 1970). Deposit feeders directly ingest sediments in which they live. Suspension feeders filter particles from the overlying waters for their main source of nutrition. Predators or carnivores feed by preying on other individuals. Some carnivores are able to switch feeding mode when their preferred prey items are scarce. These animals are referred to as omnivores.

It is important to know the type of feeding method employed by the various tidal flat animals in order to fully understand the ecology of these habitats. Filter feeders depend on water currents to bring food to them and in some cases, require large amounts of water to filter an adequate amount of food. Many of filter feeders are restricted by the particle size of their food items. When particle size of filterable material reaches a minimal size and there are large amounts present in the water column, the filtering mechanisms become clogged which prevents effective feeding. For this reason, filter feeders tend to be found in coarser grained (sandy) sediments (Eltringham 1971). Deposit feeders are more characteristic of finer grain (muddy) sediments. The finer grained deposits provide a large surface area which can support larger populations of micro-ogranisms. This would result in more food available to deposit feeders per unit volume of material (Newell 1965).

2.2.1 Macrofauna

Non-commercial molluscs

Pearse *et al*. (1942) described the distribution patterns of burrowing snails and clams which are characteristic of both sand and mud flats at Beaufort, NC. Among the snails, *Oliva* and *Sinum* were found in predominantly sandy areas, while *Polinices* was indicative of a mixture of sand and mud, and *Terebra* and *Nassarius* were more commonly associated with muddy areas. A similar distributional pattern was found for the clams, with *Cardium* and *Donax* being most characteristic of sandy tidal flat areas, *Mercenaria* and *Dosinia* predominating in a mixture of sand and mud, and *Macrocallista* and *Tagelus* being most common in muddy areas. In addition to the burrowing snails, others such as Hydrobia and Ilyanassa may be present in very high numbers either on or directly beneath the surface of the muddy areas. Indeed, during periods of low tide, very little may be seen on the mud surface except for Hydrobia or Ilyanassa. Another snail Littorina littorea has also been observed on muddy tidal flats (Moore 1940), but is most commonly associated with rocky shorelines or marshlands and is not usually included as a characteristic species of tidal flats.

By far, the most numerous shellfish populations are found beneath the surface of the substrata due to the widespread burrowing habit of most clams. One of the principal differences between sand and mud as far as burrowers are concerned is that in sand permanent burrows are rarely possible since the relatively large particle size and the characteristically strong wave action in these areas soon cause the collapse of any that are formed (Eltringham 1971). Wade (1964) showed that Donax denticulatus, a small bivalve characteristic of sandy foreshores, is especially adapted to life on a high energy wave-swept beach. As the tidal level rises and falls D. denticulatus migrates up and down the beach front in order to maintain its level in the splash zone. It is therefore necessary that this species be an exceptionally fast burrower, to avoid being swept away by wave action. Other slim shelled species such as Tellina are also rapid burrowers and may be characteristic of relatively high energy beaches and sandy foreshores (Stephen 1928). Other clams characteristic of the tidal flat environment include Gemma gemma, which may reach densities of up to $10^5/m^2$ in shallow sandy sediments along the Atlantic coast of North America (Green et al. 1970). The structure and distribution of the G.

gemma community is a function of spatial and temporal variations in temperature, inter- and intraspecific competition, and amount of feeding time available to the organism. Consequently, this species is found in the lower intertidal and subtidal zones where the water cover is longer allowing more time to feed, and the physical environment is less variable (Green *et al*. 1970).

The characteristic molluscan fauna of muddy flats show distinct zonation patterns with depth. The rate of change across a flat is a function of its size, larger expansive flats show a very gradual change in fauna along the depth gradient assuming sediments do not change. Changes in sediment type will cause an even greater rate of change in the fauna than depth. On most tidal flats both depth and sediment type interact to produce a complex mosaic of species distributions governed by very localized changes in both depth and sediments.

Epifaunal Species

The organisms living in tidal flat areas are primarily burrowing forms. Epifauna is comparatively scarce unless a shell or aquatic vegetation substrate is present. When clams die their shells may become exposed on the surface and provide a stable substratum for the attachment of epifauna. In some areas suitable substrates for attachment are extremely scarce, competition for space by the larvae of epifaunal species is intense, and soon the shells become encrusted with barnacles, algae, oysters, and mussels. Localized mussel or oyster beds may develop. As the numbers of epifaunal shellfish gradually increase, they deposit large quantities of consolidated sediments (pseudofeces) and further stabilize the surrounding sediments. These beds may be torn up and swept away during severe storm conditions, but in most cases mussels are attached to one another (as well as the shells below) via byssus threads or in the case of oysters each cement itself to another oyster forming a stable compact mound which is relatively resistant to natural destructive forces. The shellfish beds eventually provide the substrata for attachment of other epifaunal species and thereby facilitate their invasion into the tidal flat area.

Annelids and Crustaceans

Other components of the macrofauna such as insect larvae, crustaceans, oligochaetes, and polychaetes may also exhibit distinct zonation patterns on tidal flats. Deposit feeders such as the lugworm *Arenicola marina*, the sand mason *Lanice conchlega*, the sedentary polychaete *Scolopos* spp. and *Phyllodoce maculata* (a surface-dwelling polychaete), become abundant in sands containing appreciable quantities of fine material and organic debris. Other species such as the amphipod *Corophium volutator*, the terebellid worm *Amphitrite johnstoni*, the nereid *Nereis virens*, and the spionid worm *Pygospio elegans* are more characteristic of muddy tidal flat deposits (Newell 1970). It must be emphasized, however, that faunal distributional patterns are not determined by particle size alone. Other parameters such as water content of the substrata, pore size, wave, tidal and current action, salinity, temperature, oxygen content of the interstitial water, and quantity of organic matter present are also of importance (as reviewed by Yonge 1952 for muddy shores and Stephen 1952 for sandy shores).

Although permanent burrows are rarely possible in high energy sandy shores due to the relatively large particle size and characteristically strong wave action, many of the sedentary polychaete worms have succeeded in quieter areas and produce permanent burrows by secreting a mucous lining or cementing sand grains together.

These worms are tightly enclosed in a tube which may be sandy (Sabellariidae), membranous though often encrusted with sand grains (Terebellidae), or mucus as in the case of many Sabellidae (Eltringham 1971). Cistena commonly called the ice cream cone worm, also constructs a sand-grain tube similar to the Sabellariidae (Barnes 1974), but differs from other sedentary polychaetes by possessing the ability to move within the sediments. The activity of these tube-dwelling annelids, ingesting and transporting sediment, is very important in the reworking of the sediments to cycle nutrients and the establishment of biogenically graded deposits (Rhoads 1963, Gordon 1966).

In addition to these characteristic species of polychaetes, the burrowing shrimp Upogebia is also common in sandy or shelly intertidal areas (Barnes 1974). Other burrowing shrimp include Callianassa which is commonly found in muddy deposits and turtlegrass associated with mangroves. In general, the number of crustacean species characteristic of tidal flat habitats usually increases with a corresponding increase in particle size (Howard & Doerjes 1972). Other burrowing crustaceans which may frequent sandy inshore deposits include Lysiosquilla, Arenaeus, Ovalipes, Calappa, Lepidopa, and

Callinectes (Stephenson *et al*. 1952). One of the most common group of crustaceans associated with muddy deposits are the surface tube building corophiid amphipods (Eltringham 1971).

It must be recognized that even though certain species may be most characteristic of either sandy or muddy habitats they are not necessarily restricted to one type of habitat and may reach appreciable densities in subtidal bottoms and in other types of substrata. Sanders *et al*. (1962) recorded large densities of deposit feeders in an intertidal sand flat that was low in organic matter. The presence of large populations of deposit-feeders was found to be positively correlated to the stability of the sediment surface. In such areas, ripple marks were absent and the stabilized sediments supported dense populations of diatoms and dinoflagellates which in turn provided the major food source for the large biomass of deposit feeders. As a result, those organisms which were normally associated with muddy deposits could now exist on sandy substrata by utilizing local dense populations of diatoms and dinoflagellates.

2.2.2 Meiofauna

Tidal flat sediments also support large populations of meiofauna. Various aspects of the ecology of meiofauna have been studied in Europe (Boaden 1960, 1961a, b, 1962, 1963a-d, Govindankutty *et al*. 1965, Barnett 1968, 1970, Gray *et al*. 1971, Swedmark 1964, Fenchel *et al*. 1967, Harris 1972, Jansson 1968, McIntyre 1964, Perkins 1958, Straarup 1970, Warwick *et al*. 1971) as well as in the United States (Pollock 1970, Croker 1968, Sameoto 1969, Pennak 1940, 1950, Wieser 1956, 1957a, 1957b, 1959). The meiofauna inhabiting the interstices of marine and estuarine sediments is highly specialized and adapted for such a life (Swedmark 1964). Nematodes turbellarians, gastrotrichs, and copepods are the numerically dominant groups.

The structure and distribution of meiofaunal populations varies with the size and mineral composition of the sediments. Thus a predominantly sandy substrata will support a different faunal population than that of shell or mud. In general, the meiofauna of sandy tidal flat sediments will be larger than the animals found in finer grained substrata. Examples of some small metazoans found typically in sandy areas are the hydroid Psammohydra nana (1 mm), the archiannalid Diurodrilus minimus (350 μm), the prosobranch mollusc Caecum glabrum (2 mm), and the sea cucumber Leptosynapta minuta (2 mm) (Eltringham 1971). The meiofaunal populations of muddy sediments, however, are usually much smaller, and include such organisms as harpacticoid copepods which rarely reach one millimeter in length.

These observed variations in the distribution and abundance of meiofauna in different sediments is related to grain size and pore water content (Jansson 1967a, Wieser 1959, Ott 1972). Other physical parameters important in the establishment of faunal boundaries include temperature, salinity, and dissolved oxygen (Jansson 1967b, Fenchel et al. 1967, Barnett 1968) as well as water movement (Boaden 1968) and degree of exposure (Gray et al. 1971). Harris (1972a, b) has shown distinct seasonal variations in the interstitial fauna of the sands of Whitsand Bay, East Cornwall, England, illustrating a characteristic vertical zonation pattern with the majority of the population being concentrated in the surface layers in the summer and migrating to as deep as 50 cm in the winter.

2.2.3 Commercially Important Species

Tidal flats, in addition to supporting large number of small invertebrate animals, can support large commercial shellfish populations. One of the dominant shellfish along the Atlantic, Gulf and Pacific coasts is the oyster (Chestnut 1974). The species that is dominant along the Atlantic and Gulf Coast is *Crassostrea virginica*. Along the Pacific Coast *Ostrea lurida* is dominant along with the imported Japanese oyster *Crassostrea gigas*.

Because of the nature of oyster growth, requiring a hard substrate to which planktonic larvae attach, sometimes massive reefs are formed which may rise several feet above the bottom (Galstoff 1964). This reef development will alter current patterns changing the structure of the bottom. An oyster reef can develop on both mud or sand bottoms and may cause a firm sand bottom to become muddy from the deposition of pseudofeces and feces adjacent to and in the reef (Grave 1901). In addition to providing a substrate for other oysters to set and survive, the oyster reef enhances the development of an associated complex community. The oyster reef contains a myriad of attached and free living micro-, meio-, and macrofauna (Wells 1961, Larsen 1974).

Oysters are euryhaline (can survive a wide range of salinity fluctuation) and are widely distributed along the estuarine gradient. Growth is substantially reduced at salinities less than 5 $^{o}/oo$ and they are not found in freshwater areas. Because oysters have the ability to close their shells for extended periods they can survive periods of fresh water intrusion which kills many of its predators. Thus periods of low salinity may even be beneficial to the oyster by eliminating many of its natural predators (Galstoff 1964). It is very important to note that in high salinity areas, oyster growth is mainly intertidal because of intense predation pressure in the subtidal habitats.

Several other important shellfish species found in saline tidal flat areas are the soft clam Mya arenaria, the quahog or hard clam Mercenaria mercenaria, and the bay scallop Aequipecten irradians.

Mya is a boreal species (Ekman 1953, Turgeon 1968) ranging along the North American east coast from Labrador to North Carolina and the west coast from Alaska to California (Abbott 1974). Prior to 1950, Maine and Massachusetts had been the major harvesting states (Shaw and Hamons 1974) with most of the fishery concentrated in the intertidal zone. After 1950, because of a decline in the New England fishery, Maryland developed a soft clam fishery primarily utilizing subtidal populations. The East Coast soft clam industry is the third largest commercial clam industry in the United States (Ritchie 1977).

The hard clam has an extensive range and inhabits most bays, coves and inlets from the Gulf of St. Lawrence to the Gulf of Mexico (Merrill and Tubiash 1970). It can be found in sediments ranging from sand to mud. The hard clam industry is the largest commercial clam industry in the United States (Ritchie 1977). It occurs intertidally to depths up to 25 feet.

The bay scallop is found predominantly in seagrass beds, primarily eelgrass, along the east coast of the United States from

Cape Cod to the Gulf of Mexico. The life cycle of the scallop is dependent upon the presence of eelgrass as a setting substrate for larvae (Gutsell 1931). Marshall (1947, 1960) suggests that in some areas the hydrodynamics are more important than the substrate for scallop setting. Because the life cycle of the bay scallop is short (2 years maximum), their occurrence tends to be erratic. They may be abundant one year and completely absent the next. Fluctuations in abundance of grassy bottoms is usually paralleled by similar fluctuations in scallops (Merrill and Tubiash 1970, Orth 1977c). The commercial fishery for this species is not large and is limited to only a few states, primarily North Carolina.

Other less commercially important shellfish found in tidal flat along the East Coast are: the razor clam, Ensis directus, which inhabits sandy beaches and bars close to the low watermark from Labrador southward (Abbott 1954); the sunray venus clam, Macrocallista mimbosa, found in sand just below the low watermark from Cape Hatteras to the Gulf of Mexico; and whelks, Busycon caricea and B. canaliculatum, found in shallow waters with sandy bottoms from Cape Cod to Florida.

Along the west coast of the United States, California and Oregon lack any extensive tidal flat areas for supporting large clam populations (protected bays and estuarine areas), though there are species which are of recreational importance. The pismo clam, Tivila stultorum, is locally abundant and dug commercially. Species of commercial importance in Washington and Alaska are the littleneck clam, Protohaca staminea, butter clam, Saxidomus giganteus, Japanese littleneck clam or Manila clam, Venerupis japonica, the horse clam or gaper, Tresus copax, the geoduck, Penope generosa, soft clam, Mya *arenaria*, razor clam, *Siliqua patula*, and the cockle, *Clinocardium nuttolli*.

A comprehensive review of the commercial clam industries in the United States can be found in Ritchie (1977) and Merrill and Tubiash (1970).

Bait worms (*Glycera* spp. and *Nereis* spp.) are a very important commercial species on the tidal flats of the Northeast United States. They are hand dug at low tide from mud and sand flats.

2.2.4 Submerged Vascular Vegetation

The benthic communities associated with submerged vascular vegetation is quite distinct from communities in adjacent unvegetated areas. The ecological significance of grass beds as a structural habitat for shelter and food source allows the development of a much more diverse and dense assemblage of animals. The animal community associated with a grass bed can be subdivided by microhabitat structure and mode of life as follows (Kikuchi and Peres 1977):

- Biota on the green leaves. There are several subgroups: a) epiphytes and the associated micro- and meiofaunal elements (nematodes, copepods, ostracods); b) sessile fauna (anthozoans, ascidians, barnacles, tube-building insects); and c) motile epifauna (gastropods, polychaetes, turbellarians, isopods, amphipods).
- Tube-building sessile forms that utilize the stems and rhizomes as attachment sites (tube-building polychaetes and amphipods).
- Mobile species living in or around the leaf canopy (decapod crustaceans, cephalopods, fishes).

◦ Species living on or in the sediment (bivalves, polychaetes, isopods, amphipods, gastropods, and insects).

Infauna of a eelgrass bed increases in density and diversity along a gradient from the edge of a bed to the center and also with increasing size of a bed (Orth 1975b, 1977b). Orth related this increase to sediment stabilization by eelgrass and showed that decreasing the stability of sediments experimentally and naturally, decreased the density and diversity of the infauna. Microhabitat complexity, food supply, and protection from predators are also important factors in maintaining the community structure of grass beds (Kikuchi 1966, Williams and Thomas 1967, Nelsson 1969, Adams and Angelovic 1970, Tenore 1975, Thayer et al. 1975).

There are distinct differences in animal communities associated with grass beds in different ecological and geographical situations. This is a result of 1) different species of grass (Kikuchi and Peres 1977), 2) difference in growth form of the same grass species, some species have forms that exhibit narrow leaves under one set of environmental conditions and wide leaves under another set (Orth 1977a), and 3) direct influence of environmental conditions such as salinity, turbidity, tidal range, and water movement, for example, suspension feeders with grasping appendages predominated in high energy environment grass beds while tube-building detritus feeders were found in low energy environments (Nagle 1968).

2.3 Tidal Flat Habitat Utilization

Tidal flat communities must be able to withstand fluctuating physical parameters such as temperature, salinity, duration of exposure/inundation, and degree of wave and tidal action. Such communities are also subject to predation by fishes and various crustacea when the tide is high, and by shorebirds and other wildlife when the tide is low (Dexter 1947, Odum 1971, McIntyre 1977). It is remarkable that these communities can withstand the physical environment and biological stresses, both from aquatic and terrestrial sources, characteristic of the intertidal environments. Their survival and reproductions is evidence in support of the relatively high productivity of such areas (Beukema 1974, 1976, Abele 1974, Verwey 1965).

2.3.1 Temporary Residents

The temporary members include fish, plankton, and swimming invertebrates. It is necessary to note at this point, however, that plankton are essentially carried into the area by tidal action. Fish and swimming invertebrates actively move into tidal flat habitats for breeding, protection, or in search of food and are not dependent on tidal action to move them.

Fishes

Of the fish populations classified as temporary members of the tidal flat community, very few are considered to be truly intertidal species. Fish which are genuinely adapted to the rigors of intertidal life are more commonly found associated with rocky coasts than depositional shores, due to the presence of various rock pools associated with the former (Gibson 1969, Eltringham 1971). These pools provide a protective aquatic media when the tide goes out guarding against dessication and the extremes in temperature associated with depositional shores.

Although most of the inshore fish are found in the intertidal zone at some time or another bottom-dwellers such as flat fish are relatively common species. These fish are active carnivores and feed mainly upon the polychaetes and bivalves (Steven 1930). Due to the relatively high productivity of such areas, the intertidal flats are therefore important feeding grounds for young flat fish. In addition Virnstein (1977) demonstrated experimentally that other fish such as spot, Leiostomus xanthurus, can have a significant impact on the macrobenthos in shallow water areas.

As further evidence of the importance of tidal flat habitat for the development of young flat fish, Kuipers (1973) observed entire populations moving with the incoming tide onto the flats and then back to the surrounding channels on falling tides. These movements were related to their feeding cycle as stomach analysis showed them to gradually fill during their stay in the intertidal zone. This postulation is further supported by Zilstra (1972) and McIntyre (1977), who found indications that the intertidal flats of the Dutch Wadden Sea are important nursery grounds for young flat fish.

Smaller species of fishes such as Fundulus spp. and Menidia spp. exhibit localized movement in response to tidal fluctuations (Butner et al. 1960). Menidia spp. were observed to follow the incoming tide into small channels to avoid predation, to feed, and to breed. Fundulus spp. were found to ascend high into the intertidal areas to forage for food and to lay eggs. Cain et al. (1976) observed large numbers of Fundulus spp. and Menidia spp. to be associated with intertidal creeks and nearshore waters in South Carolina and concluded that these species provide a vital link in the food chain of such areas during all seasons.

Commercially Important Invertebrate Species

Numerous invertebrate species such as shrimps and crabs also temporarily utilize these tidal flat habitats and adjacent creeks and marshes as food sources, protection from predation, and for reproduction. Young blue crabs utilize shallow water areas such as tidal flats, submerged grass beds and marshes as a nursery ground where they can take advantage of protection and abundance of food. Blue crabs are omnivorous and thrive in such areas and have a significant impact on communities through their foraging activity (Virnstein 1977, Orth 1975).

Other commercially important species such as penaeid shrimp are extremely dependent on shallow water estuarine habitats such as tidal creeks and flats during juvenile stages (Odum 1971). The adult shrimp spawn at some distance offshore. The larval stages then enter estuaries, especially the shallow bays and marshes. Here the abundance of food and protection from predators afforded by such habitats are ideal for rapid growth and development. The maturing shrimp then complete their life cycle by moving out of the shallow bays and marshes and back into the open ocean.

2.3.2 Waterfowl

Avian uses of tidal flat habitats are primarily for feeding, and for resting and refueling stops during migration. Through the course of the year, the habitat needs of various avian species may change. Diverse but closely associated wetland types may be utilized or even required by waterfowl (Flake 1979). Only the oyster-catcher (Haematopus ostralagus) and the ringed plover (Charadrius hiaticula) are considered truly obligate species of tidal flats. Other waterfowl require tidal flat habitats to some degree, mainly as a preferred food source. Flats with associated wetlands are the most highly favored regions by the majority of waterfowl.

The food habits vary from species to species and habitat to habitat. Some are herbivorous, while others prefer diets of mollusks, crustaceans, or other invertebrates. Examination of the general diet of waterfowl and shorebirds indicates that crustaceans tend to be overrepresented, while worms are underrepresented (Beukema 1976). Reasons for crustacean preference may be attributed to availability (less deeply burrowed) and greater palatability.

Many bird species are end-points in the consumer food chains. As adults, few natural enemies exist. The shorebirds are vitally dependent upon the resources provided by tidal flats and as top predators are an important link in the food web (Peterson and Peterson 1979).

Studies in shorebird ecology by Recher (1966) suggest that available space versus available food is the most important limiting factor to bird population size and density. Space restrictions occur during: 1) all high tides, 2) the first stages of falling tides, and 3) tidal sequences having limited exposure during low water. The third reason is probably the most significant factor. Daily tidal fluctuations determine the amount of feeding space available to shorebirds, particularly wading species. The amount of exposed area also differs seasonally. On the west coast of the United States tidal flats exposed at low tide in the spring are greater than the area uncovered in fall. The highest concentrations of bird species occur on the flats shortly follows low tide (Burger et al. 1977).

Migration and wintering usage of wetlands is also important. Migration is not a gradual increase and decrease in numbers of birds, but rather a sequence of successive groups entering and leaving an area. A wave-like pattern is exhibited which is often obscured when total numbers of all bird species are considered. On both coasts of North America, the rate of spring migration is greater than that in the fall (Recher 1966). This difference is due to the main migration period being compressed and the individuals moving more rapidly. Therefore, greater population densities are observed in the spring rather than the fall.

The birds which utilize the intertidal flats may be grouped into different ecological categories or guilds. At least one representative from each guild may be found on tidal flats worldwide. Some categories are more diverse, and the importance of each is variable. Following a scheme by Peterson and Peterson (1979) the guilds are: 1) waders, 2) shallow-water shorebirds, 3) deep-probing, 4) aerial-searching birds, 5) floating and diving waterfowl, and 6) birds of prey.

Waders

The waders include herons, egrets, ibisies, and yellowlegs. These species are characteristic of all tidal flat habitats, emphasizing the importance of this environment to waders. These birds search the shallow water for various small fishes (killifishes, silversides, anchovies) and/or crustaceans (primarily fiddler crabs, *Uca* spp.). To locate their prey, these birds may plunge their heads under water to spear fish, use their long bills to strain plankton, or probe the substrate for burrowing organisms. It has been estimated that 75 percent of their diet consists of non-commercial fish and crustaceans with insects and amphibians also present.

Shallow-water Shorebirds

Sandpipers, plovers, knots, and oyster-catchers are members of this group. It is probably the most diverse and most abundant guild of any in the tidal flats. Some members obtain only a small portion of their diet from the flats, often supplementing it with insects from inshore regions. However, most species depend upon the tidal flat habitat for most of their food requirements (Palmer 1962).

Searching the shallow water, these birds are opportunistic feeders. They consume whatever is the most abundant of several prey species. Polychaetes, amphipods, small crustaceans, and insects make up much of their diet. The many members of this guild seem to have behavioral and ecological differences, permitting greater exploitation of habitat and accounting for their great abundances. Rails, for example, will forage the muddy flats at low tide, pursuing decapod crustaceans. Oyster-catchers have the ability to harvest the bivalve molluscs of the intertidal zone. Their diet is relatively limited, consisting of small cockles and a few types of polychaete worms. As their food source is restricted to this region, the oyster-catcher is often considered the only true obligate resident of the tidal flats.

Deep-probing Birds

These shorebirds are ecologically different from the shallow-water guild. Because they can probe deeper, a large group of burrowing invertebrates is available for consumption. Wet areas on tidal flats (those areas with standing water) tend to be utilized more frequently by this group. It is assumed they are more efficient at feeding when the substrate is water covered. While the substrate is covered with water, burrowing invertebrates are most likely to be near the surface where they would be more easily detected. Birds in this guild are also efficient waders, which permits them to search the lower reaches of the shoreline. The shallow-water guild species are largely restricted to exposed areas.

This guild appears more abundant on the west coast than in the east. Differences in the invertebrate communities of the two coasts may be responsible for this observation (Peterson and Peterson 1979). West coast infaunal invertebrates (especially ghost shrimp and mud shrimp) exhibit greater abundances, supporting larger bird densities. Therefore, tidal flats with an abundant population of the larger infaunal crustaceans are especially important.

During warm months, willets may pursue the mole crab (Emerita) on sandy beaches. But, as Emerita moves to deeper water for the winter, the willets are found once again on the intertidal flats.

Aerial-searching Birds

This group includes terns, gulls, skimmers, pelicans, and kingfishers. Feeding predominantly on fishes like silversides, mullets, and anchovies, the importance of tidal flats to this guild is restricted. While prey is often found far removed from tidal flats, some species consume a significant portion of their diet in the shallow waters over the intertidal zone.

Gulls and terns hunt from the air,' spotting their prey, then diving to capture it. Sometimes gulls will forage from a floating position. Terns prefer live prey, while gulls are known to scavenge dead fish. These birds feed most heavily along shorelines in shallow waters. Kingfishers are also limited to shallow water fishing, in the subtidal areas at low water, or in the intertidal zone at high tide. This bird typically perches from a vantage point, spots its prey, and then dives to attach. Skimmers and pelicans glide over the open water, trailing their lower mandible in the water. The black skimmer generally feeds in shallow water. Pelicans are not restricted by water depth, preferring to hunt around tidal inlets.

Floating and Diving Waterfowl

This guild includes swans, geese, cormorants, loons, grebes, and ducks. This heterogeneous mix of waterfowl exhibits a varied dependence on intertidal flats. Cormorants, loons, and grebes are often deep-water habitat members, but they will occasionally forage over intertidal flats. Their utilization of this habitat is limited. The other members of this group, however, are closely linked to the shallow water environment and its associated food supplies.

Three different trophic levels are represented in this guild fish eaters, benthic invertebrate feeders, and herbivores. Loons, grebes, and cormorants feed upon fish. Swans and geese are largely herbivorous. Most species of the guild feed in the shallow waters of the subtidal, but some foraging occurs in the flats. Brants and geese are particularly dependent upon eelgrass as a primary food source. In the past, declines in eelgrass beds resulted in population reductions of Brant.

Three general classes of ducks are recognized: divers, dabblers, and mergansers. Behavioral differences are the key to differentiating these groups. Divers feed by plunging to the bottom and can travel considerable distances under water. Some species may dive to depths of forty feet in search of food (Wass 1974). Most prefer benthic invertebrates, especially clams. The dabblers prefer shallow water, small ponds, marshes, and grain fields. They feed predominantly on submerged aquatic vegetation, dipping just below the water surface in a behavior called dabbling. Mergansers are the fish-eating ducks, often recognized by their slender bills with toothed edges. There is only one saltwater species, the Red-breasted (*Mergus serrator*).

Birds of Prey

Ospreys, hawks, eagles, and owls are the common members of this group. These birds have diets consisting mostly of fish. On occasion, hawks are known to feed on the smaller shorebirds. Most hunting is conducted in shallow coastal waters, but they may also forage over the intertidal flat regions when fish are abundant. The dependence and utilization of the tidal flats by birds of prey is limited.

Waterfowl Regions

Following the major migratory flyways across the United States is an effective means of regionalizing tidal flat usage by waterfowl. Four main routes are recognized: 1) the Atlantic Flyway, 2) the Mississippi Flyway, 3) the Central Flyway, and 4) the Pacific Flyway. The common waterfowl found along each flyway are listed in Table 3.

The Atlantic Flyway lies mainly along the eastern seaboard of the United States. It covers a total of 446 thousand square miles, with a coastline of 7 thousand miles. The irregular coastline has an abundance of bays, estuaries, islands, swamps, and wetlands. The majority of migrating and wintering waterfowl are attracted to the coastal habitats of the middle and southern portions of the flyway.

There are more than 32 million acres of wetland habitat in this region, most of it lying to the south of Maryland. But, only 4 million acres have moderate to high value to waterfowl (Addy 1964). Areas of greatest use are wetlands adjacent to upland and open-water feeding spots.

The Mississippi and Central Flyways have limited regions of tidal flat habitat, confined to the coastal areas of the Gulf of Mexico. Up to 90 percent of the migrating species of these flyways may be supported in extensive coastal lagoons and marshes.

The Pacific Flyway covers an area of some 825 thousand square miles, but less than 1 percent of this land is usable waterfowl habitat. Food, water, and shelter are limited to about 6200 square miles. The

Table 1. Common Waterfowl of American Flyways

	Atlantic	Mississippi	Central	Pacific
DABBLERS -				
Mallard	X	X	X	X
Pintail		X	X	X
Green-Winged Teal	X	X	X	X
Blue-Winged Teal		X	X	X
Cinnamon Teal			X	X
Shoveler		X	X	X
American Widgeon	X	X	X	X
Gadwall		X	X	X
Mottled Duck			X	
Wood Duck		X	X	X
Black Duck	X	X		
DIVERS -				
Redheads		X	X	X
Canvassback	X	X	X	
Lesser Scaup	X	X	X	X
Greater Scaup	X			X
Ring-necked Duck	X	X	X	X
Bufflehead			X	X
Harlequin			X	
Common Goldeneye				X
Ruddy Duck				X
MERGANSERS -				
Canada Goose	X	X	X	X
White-Fronted Goose		X	X	X
Ross' Goose			X	X
Lesser Snow Goose		X	X	X
Greater Snow Goose	X		X	X
Trumpeter Swan			X	X
Whistling Swan			X	
American Coot	X	X	X	X
Brant	X			

Sacramento-San Joaquin River system is a center for wintering waterbirds. Coastal bays and river valleys occur intermittently from the Canadian border to Mexico. However, many rivers are unsuitable because they are fast-moving. Tidal flat habitats around bays supply food to diving ducks and brant.

2.3.3 Endangered Species

Water-oriented species comprise most of the recognized endangered birds. It is believed that a lack of adaptability, as compared with perching birds, has contributed to this status. Additionally, waterbirds have been highly utilized by man for food and for their feathers. Dependence on the tidal flats directly is limited. Table 2 lists endangered species which are associated with this habitat.

Table 2. Endangered Birds Associated With Tidal Flats

Southern Bald Eagle	(Haliaetus leucocephalus)
Osprey	(Pandion haliaetus)
Peregrine Falcon	(Falco peregrinus)
Ipswich Sparrow	(Passerculus princeps)
Eastern Brown Pelican	(Pelecanus occidentalis)
Aleutian Canada Goose	(Branta canadensis leucopareia)
Light footed Clapper Rail	(Rallus longirostris levipes)
Yuma Clapper Rail	(Rallus longirostris yumanensis)
Whooping Crane	(Grus americana)
Mississippi Sandhill Crane	(Grus canadensis pulla)

2.3.4 Wildlife

Mammalian utilization of tidal flats is limited. Consistent and dependent association of specific species with flats is unsubstantiated (Dueser *et al*. 1976). Swamp and wetland areas with adjacent flats are favored habitats. While primarily feeding on available plants, some species of mammals will supplement their diet with invertebrates by hunting on tidal flats. With the incoming tide, they return to higher ground.

Muskrats, beavers, otters, and raccoons are the larger carnivores which will forage on the flats. Fish, soft-shelled crabs, and some shellfish are favored foods (Wass, personal communication). The brown rat will take much of its food in this habitat, feeding mainly upon organic rubbish washed along the shoreline. Shorebird eggs may also be taken by rats, but this has not been supported directly (Eltringham 1971). Voles and field mice are herbivorous and are found along flats boardering marshes. It is important to stress that these organisms can easily change to a different environment for food sources and are not dependent on tidal flats.

2.4 Submerged Aquatic Vegetation

Beds of submerged aquatic vegetation (SAV) represent a unique habitat for fish, crustaceans, and waterfowl. In many cases, communities associated with SAV represent a distinct assemblage from that of the surrounding unvegetated areas. Since SAV occurs in a variety of different areas the world over, the various animal species associated with each grass bed will differ according to the predominating physical, chemical and biological characteristics. However, regardless of its location, SAV provides shelter, feeding grounds, and a substrate for attachment for a wide variety of plants and animals (Thayer et al. 1975, Adams 1976a).

There have been relatively few detailed studies describing the community structure and function of species associated with SAV (Adams 1976a,b,c, Hellier 1958, 1962, Hoese and Jones 1963, Kikuchi 1961, 1962, 1966, Thayer et al. 1975, Briggs and O'Connor 1971, Heck 1976). Briggs and O'Connor (1971) in a study of naturally vegetated and sand bottoms in Great South Bay, New York, found that most species of fish clearly prefer vegetated areas. Important food and game fish such as the Atlantic herring, American eel, Atlantic tomcod, pollock, tautog, and winter flounder all showed a preference for grassbed areas, while only 3 species (striped killifish, mullet and northern kingfish) preferred sand bottoms. Near Beaufort, North Carolina, Adams (1976a,b, c) studied the structural and functional ecology of fish communities in eelgrass beds, with special emphasis on feeding habits of major species. The pinfish (*Lagodon rhomboides*) dominated the grass beds in this region, comprising between 45-67% of all fish biomass. Similar results have been observed in grass beds in the Chesapeake Bay region with spot (*Leiostomus xanthurus*), which is by far the most dominant fish species present (Orth and Heck, unpublished). Carr and Adams (1973) and Thorhaug and Roelssler (1979) have also documented the importance of SAV as a source of nutrition and protection for a variety of juvenile fishes in the estuarine zone of the Crystal River and Card Sound, Florida respectively. The west coast herring, *Clupea harengus pallsi* utilizes eelgrass blades as a substrate for the attachment of egg masses during its breeding season (Hardwick 1973).

Similar trends have also been recorded for the mobile macroinvertebrate communities associated with SAV. The commercially important blue crab and edible shrimp (*Peneaus* spp.), as well as grass shrimp (*Palaemonetes* spp.) and sand shrimp (*Crangon* spp.) occur in areas of SAV in relatively large numbers (Orth and Heck, unpublished). Extensive use of SAV beds by invertebrate species has been found by Allee (1923a,b), Burkholder and Doheny (1968) and Thorhaug and Roessler (1972). These studies revealed large numbers of invertebrates in areas of SAV than in nonvegetated areas. Lippson (1970) and Sulkin (1973, 1977) have all observed much greater abundances of adult and juvenile blue crabs in eelgrass beds than within nonvegetated areas.

The importance of the vegetated habitat becomes much more evident after its decline from an area. Declines in catches of commercial shrimp, crabs and squids in Japan have been attributed to decline in SAV in many of the bays and seas (Kikuchi and Peres 1977). There were major declines of some waterfowl species which utilize eelgrass as a food source after the massive decline of eelgrass in the 1930's along the east coast of the United States and west coast of Europe (Cottam and Munro 1954, Addy and Aylward 1944, Phillips 1974). Some of the recent declines of waterfowl, notably redhead ducks and whistling swans, in the Chesapeake Bay have been attributed to the recent decline of SAV in the Bay (Stephenson 1977).

Data strongly suggest that submerged aquatic vegetation is vital to many species either as a direct food source, indirectly by serving as a substrate for other forms which are preyed upon, by providing protection from predation, or serving as nursery area.

2.5 Decomposers

Decomposition of organic matter in the marine environment is achieved by a variety of microbes and heterotrophic plants. The role of these decomposing organisms is an important ecological factor in the tidal flat habitats and should not be underestimated. They exert a profound influence upon certain properties of the sediments and overlying waters. Despite the small size of decomposing organisms they may comprise a relatively high percentage of the overall biomass of tidal flat sediments because of their large numbers (Zobell *et al*. 1942).

The decomposition of organic matter in submerged sediments is slower, and the end products are different from that in well-drained soils. In a well-drained soil, decomposition of organic matter is accomplished by a large group of aerobic microorganisms. The organic matter disappears largely as carbon dioxide (Delaune *et al*. 1976). In submerged soils such as tidal flats and shallow bays, decomposition of organic matter is almost entirely the work of anaerobes. Anaerobic bacteria operate at a much lower energy level. As a result, organic matter can accumulate in such areas because the rate of decomposition is usually slower than the overall input of detrital material. This observed accumulation of organic matter has important implications in the distribution of tidal flat species, and influences the physical and chemical characteristics of the environment.

The tidal flat environment provides a region of relatively stabilized sediments and allows for the formation of a strong reducing layer (redox-potential discontinuity) below the surface (Odum 1970), a condition which is ideal for the growth of anaerobic micro-organisms.

The depth of the reducing layer below the surface is a factor of wave action and sediment porosity (Fenchel *et al*. 1970).

The establishment of such reducing conditions, along with the characteristic population of decomposing microorganisms is important for the recycling of elements such as carbon, nitrogen and phosphorous (Wood 1965). Without the action of decomposing organisms recycling processes would be disrupted and elements essential to the growth of all plants and animals would eventually become unavailable, creating major imbalances in food chain dynamics (Zhukova and Fedosov 1963).

As well as providing pathways for recycling of many vital elements, decomposers may also provide an essential food source for many tidal flat species. Newell (1965) has shown *Hydrobia* sp. and *Macoma balthica* to display distribution patterns over tidal flat sediments correlated with particle size. The greater surface area presented by fine grained deposits (rich in organic matter) provided more space for microorganisms on which *Hydrobia* and *M. balthica* feed.

Since tidal flat areas are relatively shallow the decomposition activities in the bottom sediments may have a profound effect on the overlying water (Baas, Becking, and Wood 1955). Reduced byproducts of bacterial respiration are largely responsible for the decreased oxygen tension in the water over mud flats (Zobell *et al*. 1942). As a result, tidal flat habitats may have slightly lower dissolved oxygen concentrations during periods of high bacterial metabolism, than open waters where bacterial respiration and decomposition of organic materials exert a negligible strain on the total dissolved oxygen pool. The system shows further variation on a diurnal basis, with a nocturanal decrease in the dissolved oxygen concentration due to community respiration after cessation of photosynthesis. Bella et al. (1972) observed that diel dissolved oxygen variations between 14 mg/l and 6 mg/l were not uncommon.

2.6 Elemental Cycling

Tidal flat sediments are important sites for converting complex organic detrital material into a simpler, more utilizable forms (Gosselink et al. 1974). Large detrital particles are mechanically broken down by a number of infaunal and epifaunal organisms (Hargrave 1970a, Hargrave 1970b, Fenchel 1970, Frankenberg and Smith 1967, Tenore and Rice 1980, Nixon and Oviatt 1973). These smaller particles are more easily colonized by microorganisms (Odum 1968, Christian and Wetzel 1978, Pomeroy et al. 1977). In addition, these smaller particles with their associated microbial flora are both more easily ingestable and more nutritious for detritovores than the original detrital particles (Squiers and Good 1974, Odum 1968, Pomeroy et al. 1977, Wetzel 1977, Gosselink and Kirby 1974, Darnell 1961, de la Cruz 1974, de la Cruz and Gabriel 1974, Schultz and Quinn 1973, Teal 1962, Burkholder and Bornside 1957). These steps are the basis for the estuarine detrital food web by which the enormous primary productivity of the coastal salt marshes and submerged macrophytes is made available to higher level consumers important to man.

Both aerobic and anaerobic processes take place in tidal flat sediments. However, the metabolic activity of benthic fauna coupled with the slow diffusion of oxygen through sediments, restricts aerobic processes to the top few centimeters of sediment (Darnell *et al*. 1976, Pamatmat 1968). The sediment depth at which aerobic processes are replaced by anaerobic processes is called the redox-potential discontinuity (RPD) layer. The depth of the RPD layer varies slightly depending on the sediment composition and the vertical mixing of the overlying waters (Fenchel *et al*. 1970).

The anaerobic environment occurring below the RPD is known as the sulfide system. Though sulfur is an essential element, it is present in such abundance that the sulfur cycle is not critical for supplying the element to organisms. However, the normal functioning of the sulfur cycle is important in regulating the accumulation of hydrogen sulfide (DeLaume *et al*. 1976). Hydrogen sulfide is toxic to many organisms and its build-up may cause precipitation of iron, essential to plants, as an insoluble iron sulfide (Bella *et al*. 1972). The sulfur required by living organisms is supplied through plants which incorporate sulfate into organic molecules from the aerobic sediment zone. The metabolic processes occurring in the sulfide system also affect the cycling of phosphorus between sediment and water. Reduction of ferric iron to ferrous iron releases phosphates occluded or coprecipitated by iron oxides making phosphates more available to plants (De Laume *et al*. 1976).

Sediments of tidal flats continuously replenish the phosphate concentration of overlying waters (Pomeroy *et al*. 1965, Oppenheimer and Ward 1963, Pomeroy 1961). Sediments in Doboy Sound, Georgia, contain enough exchangeable phosphate to replace water concentrations 25 times (Pomeroy *et al*. 1965). The rate of exchange is governed both by physical factors such as adsorption to sediments and tidal flushing and by biological factors such as bioturbation, biodeposition, and translocation by macrophytic plants (Gessner 1960, Pomeroy 1961, Kuenzler 1961, Reimold 1972, Day et al. 1973). The abundance of phosphate in tidal flat sediments and its rapid exchange is the main reason that phosphate is seldom limiting to macrophytes or benthic autotrophic communities.

In contrast to the elements sulfur and phosphorus, nitrogen is frequently described as a limiting nutrient for primary producers, such as benthic micro-algae, marsh grasses, and submerged macrophytes (Estrada et al. 1974, Day et al. 1973, Nixon and Oviatt 1973b, Williams 1972). In tidal flat areas nitrogen may be supplied by nitrogen-fixation, runoff, rain, and re-mineralization of organic matter (Whitney et al. 1975, Haines et al. 1977, Valiela et al. 1978, Carpenter et al. 1978, Martens et al. 1978, Harrison 1978). Recent work indicates that re-mineralization is the most important source of supply for tidal marshes (Haines et al. 1977). Remineralization rates have been found to be greatest at the interface of marsh and mudflat (Haines et al. 1977).

In general, elemental cycling processes involve uptake of essential elements in an inorganic form (SO_4, PO_4, NO_3, etc.) by plants, which then make these elements available to higher consumers, through the food web. Plants may be consumed directly or the material transfer may require intermediate chemical transformations brought about by bacteria (decomposition). Those portions of plants not consumed are then remineralized into the original inorganic constituents, completing the cycle.

2.7 Importance of Tidal Flat Habitats in Wetland Ecocystems

It is necessary to formulate a working definition of the wetland ecosystem in order to conceptualize the importance of contributions from tidal flat habitats in relation to the production of the entire unit. Because of the high degree of interdependency and exchange between tidal flat habitats and adjacent habitats it is impossible to consider the functioning of any one habitat without considering others. As a result, the entire wetland system including marshes, flats, creeks, bays, and tidal channels must be considered as one productive unit (Odum 1961). The wetland ecosystem includes not only the biotic assemblages of organisms but their interaction with the abiotic physical environment as well. This interaction of the living and non-living components defines specific energy flow patterns (i.e., a characteristic trophic structure), biotic diversity, and material cycles which make up an ecosystem (Odum 1971).

The trophic structure of any ecosystem has two characteristic components the autotrophs or primary producers (which utilize light or chemical energy to manufacture organic carbon compounds from inorganic nutrients) and heterotrophs (which must obtain organic compounds from the environment by decomposition of more complex materials). The flow of energy from primary producers to consumers and decomposers is very complicated. Interruption of energy flow at any point can alter the character of the ecosystem. In the wetland ecosystem, the main sources of primary production are vascular plants such as marsh grasses, sea grasses, and mangroves (Odum 1970). However, the wetland ecosystem is not entirely dependent on vascular plants as a sole source of primary production. Benthic diatoms or microalgae which are abundant in tidal flat sediments and on creek banks constitute an important production unit. The relative importance of benthic algae seems to vary as a function of water depth and turbidity. Pomeroy (1959) found that primary production by benthic algae and turtlegrass were equally important in Boca Ciega Bay sediments in less than two meters of water (which constituted 75% of the bay).

It is also significant to note that the contribution of the benthic diatoms from intertidal flats to the overall primary production of the wetland ecosystem is not a seasonal occurrence. The microalgae constitute a beautifully adapted community which functions at approximately the same rate throughout the entire year. In summer photosynthesis occurs mainly when the tide is in, in winter the opposite situation holds as most photosynthesis occurs when the tide is out and the sun warms the sediments (Pomeroy 1959).

Another source of productivity is the chemosynthetic sulphur bacteria found in the reducing layer of intertidal flat sediments (Eltringham 1971). These bacteria utilize the chemical energy released in the reduction of ferric oxide to synthesize complex organic material from simple inorganic compounds. The contribution of epiphytic algae production may be very important. Epiphytic algae living on stems of marsh plants or SAV have been little studied. A recent study by Penhale (1977) found that the annual daily average productivity of epiphytes was 22% of the productivity of its eelgrass host.

In addition to benthic diatoms, phytoplankton, sulfur bacteria, and epiphytic algae, submerged aquatic vegetation may have significant local contirbutions to the overall primary productivity. The situation may be even further complicated by the periodic occurrence on the flats of primary producers imported from other habitats. Seaweed and macroalgae are occasionally stranded on tidal flat habitats and may continue to be productive for extended periods of time (Fahy *et al*. 1975).

Tidal flat habitats contribute to the wetland ecosystem by providing a supply of organic detritus and algae which is the basic food source for a large group of consumers. These areas are also the sites of decomposition of organic material imported from other systems such as salt marshes, rivers, and land. Bacterial populations of tidal flat sediments are not only important as a source of food for deposit feeders, but also for their role in decomposing organic matter and recycling vital nutrients.

In addition to providing this important detrital-algal food source, tidal flats also contribute to wetland ecosystems by providing favorable habitats to various levels of consumers. Sand flat areas support relatively large numbers of meiofauna and various types of crustaceans. Mud flats with a higher concentration of organic matter support large populations of bivalves and polychaetes. Tidal flat and shallow habitats are nursery grounds for many fish and crustaceans, such as *Menidia*, *Fundulus*, penaeid shrimp, and blue crabs (Day *et al*. 1973). On the other hand, numerous terrestrial species, especially birds, use tidal flat habitats as a feeding ground. These species all represent vital links in the food chains of wetland ecosystems.

Tidal flats and adjacent marshlands also perform important functions as buffer areas against storm erosion. These shallow water areas absorb the enormous energy of storm waves greatly reduce damage further inland (Gosselink et al. 1974, Wass and Wright 1969).

3.0 IMPACTS OF HUMAN ACTIVITIES

3.1 Dredging and Dredged Material Disposal

Dredging results in the need for disposal of the dredged material in some fashion. Some dredged material may be used as fill though filling may be accomplished by using soils or sediments from non-dredging sources. Filling is an operation whereby intertidal or shallow habitats (mud flats, marshes, grass flats) are "reclaimed" and made into fast land. Many problems related to dredging are the result of the displaced sediments involved.

Dredging and filling began with the country's initial settlement and remained essentially an unregulated activity in wetlands until very recently, when the value of wetland and estuarine ecosystems began to be appreciated. An estimated 291 million cubic yards of material are dredged every year (Kirby et al. 1975). Though this figure gives a gross estimate of the extent of dredging, it is most significant that many dredging operations are small. The total effect of these many smaller disturbances is hard to access. For instance, in 1972 in Virginia when records began to be kept after passage of a wetlands protection act, 130 of 160 applications for dredging involved volumes less than 10,000 cubic yards (Wetzel et al. 1976). Despite the recent and growing interest on the impacts of dredging, dredged material disposal, and filling in coastal areas, there are broad gaps in our knowledge of the effects of such impacts on the total estuarine system.

The most obvious effect of dredge and fill operations are removal of habitat, destruction or severe modification of the area upon which the dredged material is deposited, and turbidity. Turbidity increases are associated with suspension of sediments during dredging or from leaking disposal sites (Gunter et al. 1964, Cronin et al. 1967, Chapman 1968, Marshall 1968, Sherk 1971, Leathem et al. 1973, Bassi and Basco 1974). Increased turbidity may have effects on a variety of biota. Submerged aquatic vegetation, an extremely valuable habitat, may be eliminated through burial or increased turbidity (Odum 1963, Marshall 1968, Taylor and Salomán 1968, Sherk 1971).

Turbidity and sedimentation may also have effects on benthic communities. Since benthic organisms have little or no mobility they may often be completely destroyed by burial (Lunz 1942, Brehmer 1965, Cronin et al. 1967, Cairns 1968, Sherk 1971, May 1973a, Maurer et al. 1974). Mobile forms may escape if not buried too deep (Saila et al. 1972). Recovery of affected bottoms may be rapid (Pfitzenmeyer 1970) or require extended periods of time (Taylor and Saloman 1968). Elevated levels of suspended sediments also affect benthic organisms in other ways depending upon duration of exposure. Sediments may clog filtering apparati or cause juvenile mortality (Lunz 1942, Loosanoff and Tommers 1948, Davis and Hidu 1969, Price 1947). Fish populations being mobile fare better than benthos, though less mobile egg, larval, and juvenile stages have been affected by high turbidity (Bartsch 1960, Brehmer 1965, Huet 1965, Cairns 1968, Servizi et al. 1969, Sherk et al. 1975).

Another acute problem which may affect organisms as a result of dredging activities is lowered dissolved oxygen. Oxygen depletion can occur in a number of ways: 1) increased oxygen demand by reduced sediments during dredging, or by runoff from fill sites (Cronin *et al*. 1967, Brown and Clark 1968, Leathem *et al*. 1973, Kaplan *et al*. 1974, Maurer *et al*. 1974), 2) decreased dissolved oxygen production by phytoplankton due to inhibition from high turbidity (Brown and Clark 1968), and 3) from oxygen demand of reduced estuarine sediments in an area in which circulation has become restricted due to disposal of dredged material (May 1973a, Nelson 1960). Decreases in dissolved oxygen are usually only temporary, lasting only until sediments have dispersed or settled (Cronin *et al*. 1967, Leathem *et al*. 1973, May 1974). Acute dissolved oxygen depletion may suffocate sedentary organisms and drive away mobile organisms such as fishes but of more important consequences are long term effects arising from general habitat alterations. These changes have eliminated oyster beds (Galtsoff 1959, Nelson 1960), fishes, shrimp and blue crabs (May 1973a), and oyster spat (Nelson 1960).

Changes in sediment composition may result from disposal of dredged materials or filling operations. Changes in sediment composition are usually due to deposition of finer sediments (silt) which are the most commonly dredged materials (Marshall 1968, Leathem *et al*. 1973, Bassi and Basco 1974, Kaplan *et al*. 1974). Such changes alter the benthic assemblage present possibly changing the resource value of the bottom (Taylor and Saloman 1968, Kaplan *et al*. 1974) and have altered the species composition, biomass, and distribution of demersal fishes (Taylor and Saloman 1968).

The effect of a given dredging operation depends on many factors such as: 1) its extent, 2) the method of dredging, 3) the sediment composition, 4) the hydrologic conditions at the site, 5) the time of year, 6) the type of habitat involved, 7) the organisms present and 8) the presence of toxicants. Though the short term effects of altered dissolved oxygen and increased suspended sediments may be severe, they appear to have little long term effect. Alterations of circulation, salinity, sediment composition, which are long term problems, should be of major concern. Recovery from dredging and disposal operations may be slow or even result in permanent loss of habitats such as grass flats or oyster reefs. Though mobile organisms such as fishes and waterfowl can avoid these direct effects, they too will suffer from the loss of habitat, spawning areas, or food sources. The long term implications to the interactive food web of these changes are largely unknown.

3.2 Erosion

The basic erosional forms present in tidal flat habitats are tidal creeks and channels, exposed mainly at low tides. When ebb tide begins in such areas, water movement gradually increases and becomes erosive. These channels are also subjected to erosion by the inflowing water until the level is high enough to allow the water to spread over their banks (Schov 1967).

Changes in virtually any process that influences tidal flat sedimentation such as tidal currents, wave action, and lateral and down current shifting of water-courses may also have a profound influence or erosion rates in the tidal flat system. Sandy tidal flats predominate in areas of increased current flow, and are well represented along various coastlines, near inlets, and river mouths.

In their natural condition, sandy foreshores are not stable, but exist in a state of dynamic equilibrium, and are therefore especially vulnerable to perturbations by man, via construction of groins, breakwaters, and sea walls (Ketchum 1972).

Beds of submerged aquatic vegetation are capable of modifying the depositional environment of a shallow bottom area through their ability to baffle currents and reduce wave energy. By modifying water circulation, areas with grass beds have recognizably different sediments than those areas without vegetation. Scoffin (1970) showed experimentally that vegetated areas are doubly resistent to erosional forces. The leaf portion of the plant reduces current velocity while the roots and rhizomes binds the sediment grains.

The density of the grass can also have a profound effect on water velocity. Scoffin (1970) found that sediments began to erode in a sparse turtlegrass bed around 50 cm/sec., whereas a current of 150 cm/sec. was required to move sediments in a dense bed. Epiphytic growth on the leaf blades can also increase this binding effect (Ginsburg and Lowenstam 1958, Phillips 1960, Scoffin 1970). Patriquin (1975) showed that erosion within a turtlegrass bed is less likely where a well developed epifauna and flora is present. Frequently, this modification of currents by grasses and their sediment binding abilities results in an elevation of the grass bed above the unvegetated bottom (Wood et al. 1969).

The importance of a grass bed as a preventive mechanism for beach erosion has best been shown in areas where the grass bed was removed. Wilson (1949) and Rasmussen (1973) describe the shoreline conditions before and after the demise of eelgrass in the 1930's. Wilson found that up to 2 feet of sediment was lost in areas where eelgrass had been found along the English coast and that a rubble layer of loose rock and stone had become exposed. Rasmussen described similar circumstances in Denmark when eelgrass declined.

The ability of submerged aquatic vegetation to prevent bottom scouring spurred the development of artificial substrates that had the properties of the grasses (Brashears and Dartnell 1967). Biotic techniques for shore stabilization has proved very successful using marsh species (Garbisch et al. 1975, Seneca et al. 1975) but the feasibility of using beds of aquatic vegetation for bottom stabilization has yet to be demonstrated even though transplanting methods for submerged grasses have proved successful.

3.3 Recreational Importance

As previously mentioned, tidal flats are capable of supporting large populations of edible shellfish, and many people may exploit this source by collecting cockles, clams, oysters, etc. as a weekend pastime. Also, since these areas are feeding and breeding grounds for many types of birds (both year round and migratory species), they are of special interest to hunters, as well as birdwatchers. Besides giving pleasure to a large and rapidly increasing number of people, birdwatching also supplies scientific feedback in that it provides much of the basic data about birds which depend on these habitats (Tubbs 1977). As well as providing for a wealth of waterfowl some tidal flat areas (mainly those backed by marshland) may be just as important to trappers.

Various fur bearing animals such as muskrats and racoons may frequent the area in search of food.

Tidal flats are important fishing areas for local anglers, since they are known to be feeding and nursery grounds for many fish species. Also, tidal flats may provide relatively safe moorings for small craft and "... contribute to the overall capacity of a given inlet to support sailing and other forms of marine recreation" (Tubbs 1977).

In sandy tidal flat areas, wading, sunbathing, picnicking, canoeing, etc., may also be of prime recreational importance. Virtually any type of recreation which requires sunshine and a peaceful atmosphere can be enjoyed in such areas. However, it is important to note that the greatest environmental impact from these activities upon the tidal flat ecosystem may not come directly from their utilization for recreational purposes. The major pressures are in fact located above the high water mark and are concerned with providing for the needs of a large influx of people and providing access to the beach and tidal flat areas (McIntyre 1977). In order for the public to enjoy these natural areas, roads and various conveniences must first be provided.

3.4 Commercial Importance

The utilization of tidal flats from a commercial standpoint is also most easily understood when one considers both the physical setting of the habitats and the ecological support provided to the associated animal species. In areas where populations of shellfish are commercially exploitable, shellfish industries have developed. Many tidal flats may also support extensive populations of worms such as Nereis spp. and Glycera dibranchiata, both of which are commercially valuable species marketed as fish bait.

The fish populations of tidal flats may reach significant proportions and can be commercially valuable sources of fish. For this reason, the tidal channels and creeks that drain the flats may support substantial local seine and stake-netting industries. Other commercially desirable species such as the blue crabs and penaeid shrimp may reach significant population levels and can also maintain important local fisheries. Tidal flats may have economic potential for the development of aquaculture of commercially valuable species such as oysters and shrimp (Tampi 1960, Gosselink et al. 1973).

Since much of our population is concentrated along rivers and coastal areas, there has been increased pressure for reclamantion of land for development of industries and water storage programs. Commercial exploitation of tidal flats may also take place by actually removing the sediments from the area. In sandy areas, industries may develop for the sole purpose of extracting silica sand or shell for a variety of commercial usages.

3.5 Highway Construction

Decisions involving the construction of highways through wetland areas such as tidal flats and marshland are usually a product of both economical and environmental considerations. It is indeed unfortunate, however, that the most economical type of construction may not necessarily coincide with preservation of the ecological stability of the region in question. For this reason, cost considerations have often been given higher priority than environmental protection. For example, in crossing wetland areas, roadway designers have often been persuaded to economize and choose solid-fill causeways in preference to ecologically protective elevated structures (Clark 1977). Due to the increased values placed on wetland habitats such as tidal flats and marshes, as well as the high cost of fill materials and disposal problems the solid-fill approach is rapidly declining and the use of open pile structures is now being increasingly used in highway construction.

The stresses placed on the wetland environment by the transportation system fall into several general categories: 1) location of the system, 2) type of system, 3) type of construction employed, 4) impact of the system upon future development, and 5) the actual function of the system itself (Gagliano 1973).

The overall impact of construction of highways depends largely upon the chosen location. It may be localized in an urban area or in an environment that has previously been undisturbed. Clearly, the location of transportation facilities in urban areas already developed to some degree will have less of an overall ecological impact than construction within the framework of delicate natural wetland systems. If the roadway cuts directly through large areas of marsh and tidal flats vast amounts of vegetation may be destroyed, normal water circulation patterns may be altered, and mud waves may be created (Clark 1977). The peculiar phenomenon of mud waves is an indirect consequence of the pressure of the roadbed upon the organic soils of tidal wetlands, creating buckling and disruption of the sediments as much as one hundred yards away from the site of the construction (Munday et al. 1977, Dawes et al. 1978). Because of these attendent problems roadbed construction has been recommended to conform to existing topographical features and require a minimum of alteration of vegetation and water circulation (Marine Resources Division 1974). Interruption of tidal flow by roadbeds can successfully eliminate characteristic marine species such as mussels and other invertebrates, and may eventually lead to the establishment of fresh water biota. It is therefore an absolute necessity to locate road systems as to avoid impingement on vital habitat areas or interference with surface- or ground water flow (Ketchum 1972, Clark 1977). Since the general flow of water that drains the land is normally perpendicular to the coastline and river banks, new roads should be constructed parallel to this dominant course of ground water and runoff or perpendicular to the coast (Clark 1977). This type of construction leads to various spurs or feeder roads that provide access to coastal areas from major highways further inland and minimizes interference with natural water circulation patterns.

Transportation systems are of two major types: rapid transit systems with minimal roadside development or secondary routes designed to generate land usage along the roadside (Gagliano 1973). The construction of the latter type of highway system through wetland areas would lead to further destruction and loss of natural habitat as it encourages land reclamation, construction of secondary roadways, increased storm water runoff, and other potentially detrimental activities. Even if the highway itself were designed for minimal environmental impact the potential roadside development may be the factor that ultimately degrades the tidal flat habitat (Clark 1977). When possible construction through tidal flat and marsh areas should be designed as to discourage further secondary development and destruction of habitat.

The elevating of highways upon piers or piling supports facilitates normal circulation of waters, exhcange of nutrients and organisms, and therefore contributes to the maintenance of the characteristic productivity of the wetland écosystem (Clark 1977). Solid fill roadbed systems can seriously alter tidal and ground water circulation, even when culverts are incorporated into construction techniques. Besides obstructing normal tidal flow, solid-fill systems can also act as water barriers during severe storms and thereby result in habitat loss of many ground nesting species by restricting normal runoff and creating flood conditions.

A further advantage to utilizing bridging techniques over tidal habitats is that less dredging is required and therefore loss of habitat and environmental impacts are considerably decreased. "When building a causeway over wetlands, construction activity should take place on the causeway structure and off the wetlands to the maximum extent possible; that is heavy equipment needed to place the roadway pillings - cranes, dredges - should be operated from the roadbed. This topside construction approach is recommended to avoid the need for barge canals" (Clark 1977). However, regardless of the construction technique employed, it is equally important that the area be restored to its original state when possible by the removal of construction debris that may have adverse environmental effects.

After solving the immediate questions of where to locate the highway and the type of construction to be employed, many long term problems may arise due to indirect effects of highway construction. One of the most difficult problems associated with roadways is that of storm drainage runoff. Traffic generates a continual supply of pollutants ranging from rubber particles to fuel, oil, deicing chemicals, lead, and other chemical agents. This "road dirt" becomes concentrated in water running from the road surface into the waters of the wetland (Gagliano 1973) and may contribute to detrimental environmental conditions. Other indirect effects associated with construction of highways may be increased turbidity resulting from actual construction procedures as well as runoff drainage from roadside slopes. Such areas are not easily revegetated and may require continued maintenance and expenditure of effort for some years to be successful (Gosselink et al. 1973). Myren and Pella (1977) observed changes in densities of juvenile Macoma balthica on a tidal mudflat adjacent to a highway. They attributed this decrease in juvenile bivalve density to the highway construction which concentrated and diverted surface runoff which formed erosion channels across the mudflat. Adults of this species occurred deeper in the sediment and were not affected by the erosion.

As a final consideration in the construction of highways through tidal lands, building and developmental phases should be scheduled so as to avoid critical periods of breeding, feeding, and migration of coastal species (Clark 1977). For example, excessive turbidity and silt from erosion and construction activities may interfere with oyster breeding. Construction should then be timed to miss late spring and summer spawning periods. It is important that engineers confer with biologists concerning seasonal cycles of aquatic life associated with tidal wetlands to ascertain the best time period for construction activities.

4.0 EVALUATION OF COASTAL WETLANDS

Evaluation of any particular habitat for management or scientific purposes is a very difficult task. There are a large number of variables involved in evaluating a habitat and knowledge of any one particular characteristic or combination of characteristics may not be sufficient for a complete evaluation. In many cases, any number of variables may act synergistically to create a significantly greater effect than if that variable was considered alone. While methodologies to evaluate habitats have proliferated in the past several years, most have gone unrecognized or underutilized. A problem common to all the approaches has been lack of adequate data on many of the important parameters that were critical to understanding, and consequently evaluation of, the habitat in question.

There are no less than 18 evaluation schemes that have been developed for evaluation of a variety of habitats (aquatic and terrestrial) for a variety of purposes (economic, development, planning, ecological, mitigation). Of the existing evaluation schemes there are at least 8 (USFWS 1980, Larson 1976, Galloway 1978, Battelle Columbus Lab. 1974, Shuldiner *et al*. 1979, Reppert *et al*. 1979, Silberhorn *et al*. 1974, Gosselink *et al*. 1974) that apply or were specifically developed for evaluation of wetlands. A good general summary of approximately 100 evaluation methods for all types of purposes is given by Salomon *et al*. (1977).

There are no evaluation schemes for non-marsh wetlands. Like marshes in the past, accurate data on and appreciation for the functions and values of tidal flat habitats are lacking or incomplete. Indeed, it may be true that many people consider tidal flat habitats unproductive. However, tidal flats, like tidal marshes, represent a diversity of habitat types important to the functioning of wetlands ecosystems.

Each evaluation approach has its strong and weak points. We have examined many approaches and developed a composite methodology that will best fit the needs of the Highway Departments for evaluation of projects that will effect tidal flat wetlands. The main criteria in developing our methodology were:

- Based on quantitative data.
- Accuracy in portraying the value of all tidal flat habitats.
- Replicability such that different users get equivalent results when evaluating the same area.
- Flexible in terms of time needed for application.
- Understandable and applicable by environmental scientists of different backgrounds.
- Need for site specific applicability.

The evaluation methodology for tidal flat wetlands should rank the salient features of each habitat on a scale of importance values. Features important for ranking are: primary and benthic secondary production, habitat utilization, feeding ground, protective nursery or refuge, shellfish, role in material flow (oxygen, nutrients, pollutants) and waterfowl utilization. There may be other important parameters to consider, but in the final evaluation, tidal flat wetlands will have to be evaluated over a broad range of values.

Further details of the evaluation of tidal flats can be found in the methodology manual that is a companion volume to this literature review.

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