

# SALT MARSH ECOSYSTEM SUPPORT OF MARINE TRANSIENT SPECIES

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## Abstract

One of the most important reasons stated in legislation for protecting salt marshes is their support of commercially and recreationally important nekton (fish and crustaceans). Yet, there is a surprising level of uncertainty among scientists regarding the role of salt marshes in supporting secondary production. The emphasis has been on “marine transient” species (in earlier literature often referred to as “estuarine dependent”) because they have life histories that seem designed to place young-of-the-year or juveniles in marsh habitats and because these species are often of commercial or recreational value. Salt marshes are believed to provide: 1) trophic support resulting in high growth rates, 2) increased survivorship due to lowered mortality, and 3) a suitable physico-chemical environment for development of young fishes. In this paper, we consider the evidence for each of these, with an emphasis on the trophic and survivorship aspects. The seasonally warmer temperatures of estuaries and salt marsh creeks apparently provide a metabolic advantage that supports high growth rates. The influence of marsh-derived organic matter in estuarine food webs is apparent, and its importance to marine transient fishes is supported by dietary, behavioral, and isotopic evidence. The major pathways by which marsh organic matter is transferred to fish are largely indirect, through microbial and invertebrate intermediaries. Invertebrates are the primary link to fish consumers of marsh-associated production, transforming microphytes, organic detritus, and microbial detrital heterotrophs into available biomass. Although most detrital organic carbon entering salt marsh systems, mainly from emergent grasses, is apparently respired by heterotrophs, the support of consumers by marsh plant detritus and microalgae can be equally important. The use of salt marsh detritus in food webs usually occurs in close proximity to the salt marsh indicating that outwelling of salt marsh organic matter offshore is not the dominant way that salt marshes support offshore fisheries. Salt marsh support of offshore fisheries is more probably by direct export of juvenile fish biomass and a trophic relay involving ontogenetic and cyclic migrations of nekton species, rather than export of organic detritus. Understanding the controls on marine transient fish mortality is

probably the most problematic and least studied aspect of their ecology. The few estimates of mortality rates of fishes in estuaries are as high as, or higher than, mortality rates of fishes in other marine and freshwater ecosystems. However, because of faster growth rates, fish spend less time in the small stages with the higher mortality rates. Within estuaries, mortality rates for some species, but not all, are lower in marsh creeks compared to more open areas. The value of marshes as refuge habitat is probably due to the interaction of temperature, turbidity, and vegetative structure in restricting the foraging of piscine predators.

## **1. Introduction**

The importance of estuaries and their constituent habitats in the support of coastal commercial and recreational fisheries has been recognized since the early 19<sup>th</sup> century (Baird 1873). In some parts of the country, coastal species are the major component of commercial and recreational fisheries. According to many accounts, estuaries provide an essential habitat for approximately two-thirds of the commercially and recreationally important species along the east coast of the United States (e.g., Boesch and Turner 1984, Houde and Rutherford 1993). Even where the direct harvesting of estuarine and coastal species is not numerically or economically significant, estuaries and coastal embayments may still be essential for fisheries because they serve as nurseries for the juvenile stages of species harvested offshore or for the prey of commercially important species.

The importance of salt marshes as an essential habitat has been inferred from the high abundance of fishes, particularly young-of-the-year and juveniles, found in these habitats (e.g., Cain and Dean 1976, Weinstein 1979, Weinstein et al. 1980, Haedrich 1983, Weinstein and Brooks 1983). Yet, there is a surprising level of uncertainty about the role of salt marshes in supporting secondary production.

### **1.1 WHAT SUPPORT DO SALT MARSHES OFFER THAT MAKES THEM ESSENTIAL FISH HABITAT?**

The once-stated and oft-repeated hypothesis proposed to explain the widespread use of estuaries by young-of-the-year and juvenile fishes and crustaceans is that these areas provide a refuge from predation in a location where food supplies are abundant and physical factors are suitable (e.g., Joseph 1973, Boesch and Turner 1984, Deegan and Day 1984, Day et al. 1989, Baltz et al. 1993, Miltner et al. 1995). These factors result in high growth rates, low mortality and high abundances of nekton. In this paper, we consider the evidence for each of these, with an emphasis on the trophic support and survivorship aspects. We will examine the growth and mortality of nekton in salt marsh ecosystems in comparison to other habitats and consider evidence for the role of salt marsh in food webs that support nektonic production.

## 1.2 WHAT ARE MARINE TRANSIENT SPECIES?

Our focus is on the importance of salt marshes to “marine transient” species. Fish that use estuaries can do so for all (resident) or only part (transient) of their lives. Transient species spend varying amounts of their lives in other habitats such as the open ocean or in lakes or streams (Fig. 1). Perhaps the most common nektonic life history among the transient species that use estuaries is that of species that spawn in salt water. These marine transient species usually spawn in nearshore coastal waters, then the eggs or larvae move into estuaries where the juveniles spend several weeks to several years before moving offshore to return to adult feeding and spawning grounds. Examples of typical marine transient species are menhaden (*Brevoortia* spp.), mullet (*Mugil* spp.), croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and flounder (*Paralichthys* spp. and *Pseudopleuronectes* spp.). Day et al. (1989) list over 55 species of marine transient fish found in estuaries along the Gulf and Atlantic coasts of North America. Although offshore spawning is most common, some species spawn inside estuaries (winter flounder, *Pseudopleuronectes americanus*) or in salt marshes (Atlantic silverside, *Menidia menidia*). Another variation in the marine transient life history is a group of species that are spawned offshore and enter estuaries as juveniles (e.g., bluefish, *Pomatomus saltatrix*). We admit to a “fish” bias in our review, although there are many examples of crustaceans (e.g., blue crab, *Callinectes sapidus*; penaeid shrimp, *Penaeus* spp.) that are also marine transients.

One problem with defining salt marsh support of transient species is that many of the behaviors of fishes seem very flexible. All of our observations on estuarine fishes, with few exceptions, point to flexibility in diet and habitat use. There are few species that exhibit behavioral or morphological adaptations designed solely for the use of marshes as a habitat. For example, most fish species use more than a single habitat during their stay in estuaries. They often occupy multiple areas, or use different parts of the estuary sequentially. It is difficult to determine if a salt marsh is “required” if the fish spends only a few weeks in that habitat or can apparently use another habitat. These weeks may correspond to a critical period in the life history of the species (e.g., Gulf menhaden, *Brevoortia patronus*, Deegan 1990) or they may occur at a time that does not seem important in determining year-class strength. In addition, the migration pattern of some species varies with latitude and with the size of the estuary. In more northern estuaries, all individuals of some species, such as Atlantic silverside, move offshore for the winter. In southern estuaries, a large portion of the population of the same species may stay in the estuary for most or all of the year. In large estuaries, some species may use the deeper, more saline portions of the estuary as if it were “offshore”. For example, bay anchovy (*Anchoa mitchilli*) spawns both outside and inside the mouth of Chesapeake Bay, (James Cowan, personal communication) while in smaller, shallower estuaries the entire population moves offshore to spawn. This flexibility in behavior often prompts the question of whether fish would use salt marshes if they had other habitat choices. Thus, answering the question of the importance of marshes to marine transient species becomes not a simple “Yes” or “No” issue, but requires resolution of the degree of marsh support.

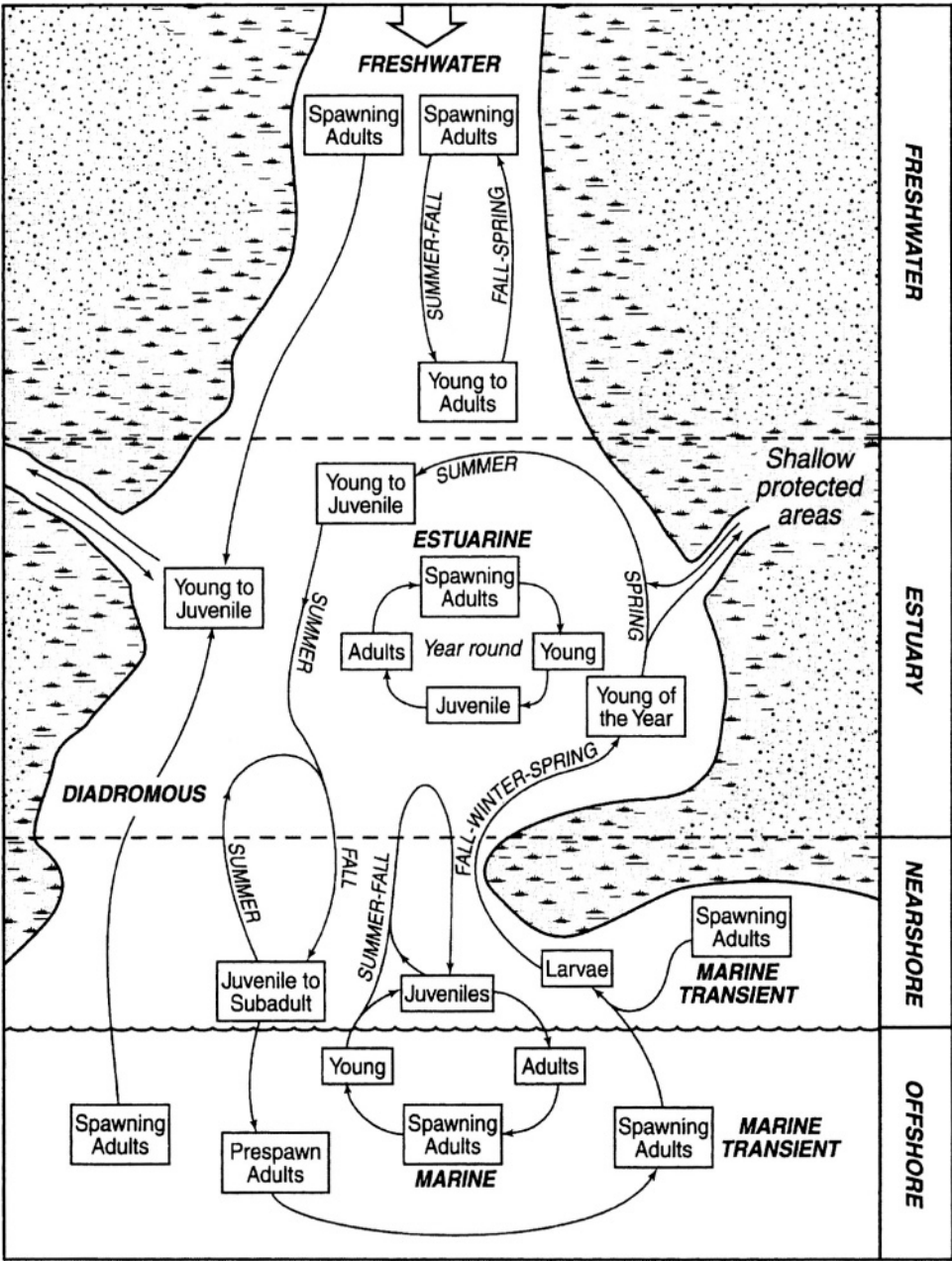


Figure 1. Diagram of temporal and spatial use of estuaries by freshwater, estuarine, marine and estuarine-dependent marine nekton. Adapted from Deegan and Thompson (1985).

### 1.3 WHAT DO WE MEAN BY SALT MARSH?

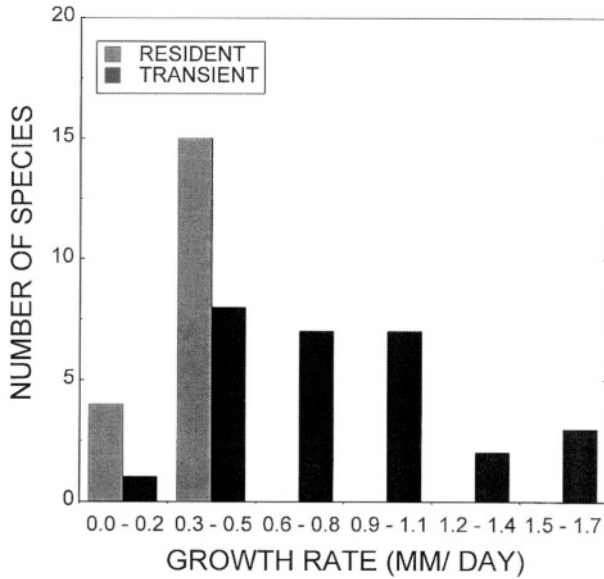
One difficulty with defining “salt marsh support” is knowing what different researchers mean by the salt marsh ecosystem. In this paper, we include several contiguous habitats in our definition of a salt marsh ecosystem: the irregularly flooded marsh surface (including vegetated areas and pools or pannes), the regularly flooded intertidal surface, intertidal marsh creeks and small subtidal marsh creeks. We include small subtidal creeks because from the perspective of a fish they are part of the intricate network of channels and pools surrounded by salt marsh vegetation. Our definition differs from Kneib (1997) because we include small subtidal creeks as part of the marsh system. We do not include large open bay areas. These areas are clearly connected to salt marshes by subtidal and intertidal channels and by the movements of marsh-derived materials and animals, but we consider them a different ecosystem because of their hydrology, geomorphology and patterns of productivity. We acknowledge that scale and perspective are somewhat subjective and that small subtidal creeks, large subtidal channels, and the adjacent bay fringed by salt marsh are all connected. When we discuss “estuarine” in general, this includes the larger open bay areas. If we were not certain that the data came from a “salt marsh ecosystem”, then we called it “estuarine.”

## 2. Growth and Trophic Support of Nekton

It is universally acknowledged that fish, particularly the young of marine transients, grow rapidly in estuarine environments (e.g., Boesch and Turner 1984, Deegan and Day 1984, Yanez-Arancibia 1985, Day et al. 1989). These high growth rates have been offered as one explanation for the evolution of the marine transient life history (Blaber and Blaber 1980). While growth of young fish in estuaries is indisputably fast, is it faster than we might expect in any other ecosystem?

### 2.1 COMPARISON OF GROWTH RATES BETWEEN ESTUARIES AND OTHER ECOSYSTEMS

In a recent compilation of growth rates for fish found in estuaries along the mid-Atlantic coast, Able and Fahey (1998) found that the growth rate of marine transient species was substantially higher than that of estuarine resident species in the same estuaries (Fig. 2). This comparison, however, is complicated because growth rates are known to be positively related to adult animal size (Valelia 1995) and the adult size of marine transients is larger than estuarine residents (Able and Fahey 1998). Therefore, based on adult size alone we would expect the growth rates of marine transients to be higher than resident species.



FROM ABLE AND FAHAY (IN PRESS)

Figure 2. Distribution of growth rates among resident and transient estuarine fishes. From Able and Fahay (1998).

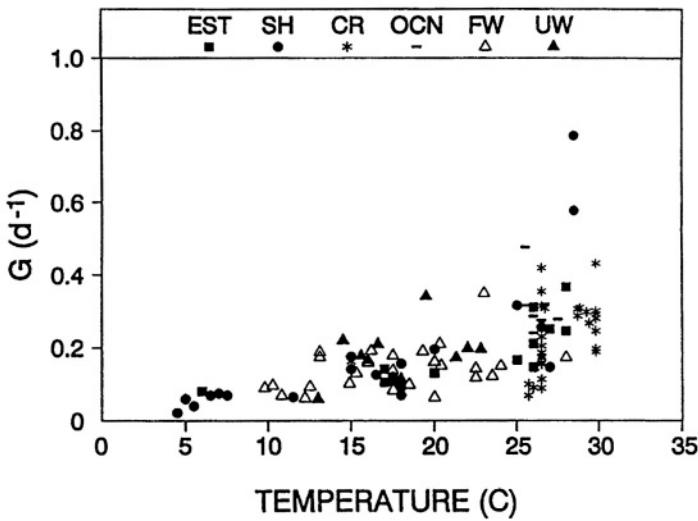


Figure 3. Ecosystem-specific, weight-specific growth coefficient  $G$  ( $d^{-1}$ ) of fish larvae versus water temperature. EST = estuarine, SH = shelf, CR = coral reef, OCN = oceanic, FW = freshwater, UW = upwelling system. From Houde and Zastrow (1993).

In a comparison across many taxa and ecosystems, Houde and Zastrow (1993) found instantaneous growth rates of larval fish were highly correlated with temperature (Fig. 3). The growth rates of larval fish in estuaries, while among the highest measured, were no higher than expected based on the relationship with temperature. In a comparison among habitats within an estuary, Deegan (1990) found higher growth rates of Gulf menhaden correlated with warmer temperatures in marsh creeks compared to open bay areas. This implies that there is a growth advantage to moving into estuarine waters in the spring as these waters are often warmer than the adjacent offshore areas.

## 2.2 POTENTIAL FOOD SOURCES AT THE BASE OF FOOD WEBS THAT SUPPORT NEKTON

Sustaining high somatic growth in addition to the elevated metabolic demands at high temperatures implies an adequate food supply to leave a sufficient “scope for growth” (Hoar et al. 1979, Valelia 1995, Evans 1998). The suggestion that the high primary productivity of salt marsh habitats, in particular intertidal *Spartina* vegetation, supports these high growth rates has been debated for more than three decades (e.g., Darnell 1961, Teal 1962, Nixon 1980, Peters and Schaaf 1981, Pomeroy and Wiegert 1981). We focus first on the processes by which salt marsh-associated organic matter is incorporated into food webs supporting marine transient fish production in estuaries and then discuss the potential for support of more distant areas and coastal fisheries.

The organic matter supporting nekton production in salt marsh estuaries has its origin in several potential sources: 1) marsh macrophytes (e.g., *Spartina* spp.), 2) marine and estuarine phytoplankton, 3) edaphic microphytes, and 4) terrestrial plants of the upland watershed. Although the relative importance of these source materials is only partially resolved, some patterns are clear.

The influence of marsh-derived organic matter in estuarine food webs is apparent, and its importance to marine transient fishes is supported by dietary, behavioral, and isotopic evidence. Stable isotopic analyses ( $^{13}\text{C}$ ,  $^{15}\text{N}$ ,  $^{34}\text{S}$ ) demonstrate that marsh-associated organic matter supports nekton in a variety of geographic settings. Research using the multiple stable isotopic content of organic source materials and salt marsh consumers (Peterson et al. 1985, Peterson and Fry 1987, Peterson and Howarth 1987, Currin et al. 1995), and studies of vascular plant diagenesis (Howarth and Teal 1980, Peterson et al. 1980, Benner et al. 1987, Ember et al. 1987, Fogel et al. 1989) have shown that *Spartina* detritus provides important trophic support in salt marsh estuaries. Stable isotopic analyses also indicate that, notwithstanding the immense productivity of salt marsh plants, phytoplankton and benthic algae are also essential in supporting secondary production in the marsh and adjacent estuary (Haines 1977, 1979a, Haines and Montague 1979, Kneib et al. 1980, Hughes and Sherr 1983). Although most detrital organic carbon from emergent grasses either forms peat or is apparently respired by heterotrophs, the support of consumers by marsh plant detritus and microalgae can be equally important (Peterson and Howarth 1987). However, because the relative contribution of micro- and macrophytes to salt marsh estuarine food webs shows considerable geographic variation (Sullivan and Moncreiff 1990), a generalization as to the predominance of either is not possible (Haines 1979a, Mallin et al. 1992 and reply by Schaff and Peters 1992).

A wide variety of nekton have stable isotope values that indicate that salt marsh production is important in the food web. Marsh resident nekton, such as killifish and palaemonetid shrimp generally have a  $^{13}\text{C}$ ,  $^{15}\text{N}$ , and  $^{34}\text{S}$  content that reflects feeding in food webs supported by benthic microalgae of the marsh surface (Sullivan and Moncreiff 1990), or *Spartina* detritus (Peterson and Howarth 1987), or both (Hughes and Sherr 1983, Currin et al. 1995, Deegan and Garritt 1997). Similarly, the following benthic- and pelagic- (water column) feeding marine transient nekton from a wide variety of estuaries show a strong connectedness to marsh-based organic matter: menhaden (pelagic), and striped mullet, American eel, blue crab, and penaeid shrimp (benthic) in Georgia salt marsh creeks and tidal rivers (Peterson and Howarth 1987); menhaden in a Louisiana salt marsh embayment (Deegan et al. 1990); menhaden and striped anchovy (pelagic), and spot, silver perch, white perch, and blue crab (benthic) in a Chesapeake Bay tidal marsh creek (Stribling and Comwell 1997); bluefish, rainbow smelt, and Atlantic silverside (pelagic), and winter flounder, black-spotted stickleback, and green crab (benthic) in a northern Massachusetts salt marsh estuary (Deegan and Garritt 1997).

Although both pelagic and benthic fishes in salt marsh estuaries show a dependence on salt marsh organic matter, in general, benthic-feeding fishes show a greater dependence on salt marsh production than do most fishes that feed in the water column. Analysis of  $^{13}\text{C}$  and  $^{15}\text{N}$  content of a variety of organisms, including several marine transient fishes, indicates that benthic-feeding organisms show the strongest connection to marsh-based production (Fig. 4) in a northern Massachusetts salt marsh creek (Deegan and Garritt 1997). Most benthic-feeding fishes had  $^{13}\text{C}$  values closer to *Spartina* and benthic algae, while pelagic feeders had  $^{13}\text{C}$  values closer to phytoplankton.

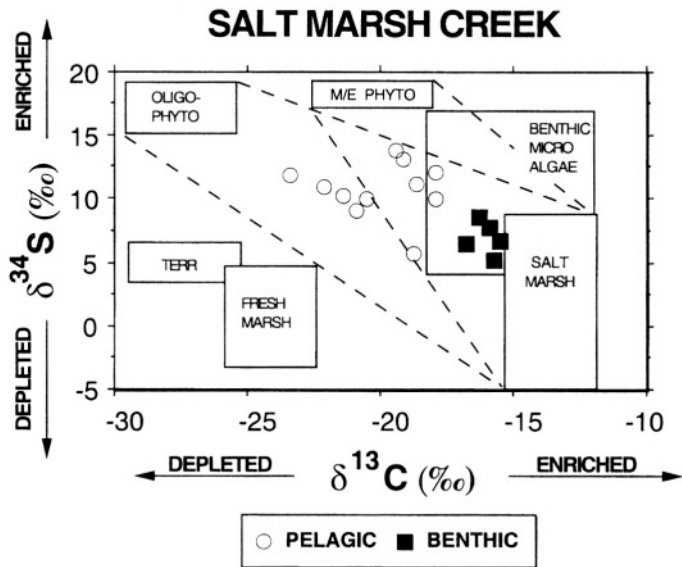


Figure 4. Cross plot of sulfur and carbon stable isotopic values for pelagic and benthic consumer organisms in the salt marsh creek habitat of a northern Massachusetts estuary. Boxes represent typical ranges for candidate organic matter source materials. Abbreviations: “Oligo phyto” is oligohaline phytoplankton, “Terr” is terrestrial plants, and “M/E Phyto” is marine and estuarine phytoplankton. From Deegan and Garritt (1997).



Phytoplankton can be differentiated from marsh primary production using  $^{13}\text{C}$  because of distinct sources of dissolved inorganic carbon (Sherr 1982). However, phytoplankton and marsh are potentially linked through the uptake by phytoplankton of remineralized nitrogen from marsh detritus (Thayer 1974, Heinle and Flemer 1976, Valiela et al. 1978, Haines 1979b, Holmes et al. 2000) and the deposition of phytoplankton onto the marsh surface. Because the salt marsh acts as a particle trap and removes phytoplankton and bacteria during marsh flooding (Haines 1979a, Chrzanowski and Spurrier 1987), deposited organic seston should be considered a potential food source for marsh consumers.

The overlap of isotopic values in primary producers sometimes confounds attempts to differentiate organic matter sources at the base of estuarine food webs. One approach to overcoming this limitation is to differentially label one of the primary producers. A recent study applied  $^{15}\text{N}$ -nitrate tracer to investigate nitrogen cycling in the food web of the oligohaline tidal reach of a northern Massachusetts estuary (Holmes et al. 2000, Hughes et al. 2000). The addition of  $^{15}\text{N}$ -nitrate differentially labeled the phytoplankton, making it isotopically very distinct from marsh production. Uptake of the  $^{15}\text{N}$ -nitrate tracer showed that most of the nitrogen assimilated by zooplankton and planktivorous juvenile alewife was based on an oligohaline phytoplankton bloom (Hughes et al. 2000). Many of the epibenthic crustacean consumers (amphipods, white-fingered mud crabs, and palaemonetid shrimp) and juvenile white perch, also depended on phytoplankton for 40 to 70% of their assimilated nitrogen, either through consumption of deposited phytoplanktonic detritus or planktonic copepods. The largely unlabeled detrital material derived from the tidal marsh most likely supported the remainder of their assimilated diets. This detrital trophic base was especially important to the production of benthivorous fishes, including mummichog and white sucker (the numerical and biomass dominants in the reach), and American eel. These results reinforce the idea that estuarine benthic food webs are more closely tied to marsh production than are pelagic food webs (see also Fig. 4).

The importance of terrestrial plant material to consumers in salt marsh food webs has been suggested by some stable isotopic studies (e.g., Hackney and Haines 1980, Stribling and Cornwell 1997). The influence of terrestrial material is expected to decrease with distance from the freshwater source (Cifuentes 1991), and is apparently minimal in salt marsh estuaries with low riverine input (Peterson et al. 1985, Peterson and Howarth 1987, Deegan and Garritt 1997).

### 2.3 USE OF MARSH FOOD RESOURCES BY NEKTON

Only a few fish species can directly utilize marsh-associated production. Some fishes consume and assimilate algae, including some cyprinodonts and mugilids (Kneib 1997). Vascular plant detritus can comprise a large part of the stomach contents of killifish (Allen et al. 1994), although the importance of this material to the assimilated diet has been questioned (Boesch and Turner 1984, D'Avanzo et al. 1991, Kneib 1997). Gulf menhaden, however, may derive a substantial portion of their assimilated diet from *Spartina* detritus, and contain cellulase-producing microorganisms in their gut (Fig. 5, Deegan et al. 1990). Juvenile menhaden captured in salt marsh creeks had  $^{13}\text{C}$  and  $^{34}\text{S}$  values closer to *Spartina* than did larvae that had fed offshore on zoo- and

phytoplankton. Recent research has suggested that amorphous detrital aggregates may be important in the diets of several nektonic species, including palaemonetid shrimp, sheepshead minnow (*Cyprinodon variegatus*), Atlantic menhaden (*B. tyrannus*), and two species of mullet (D'Avanzo et al. 1991, Lewis and Peters 1994, Larson and Shanks 1996). The labile dissolved organic matter (DOM) that is the basis for the aggregates is derived in large part from *Spartina* leachate and algae (Turner 1978, Ribelin and Collier 1979, Coffin et al. 1989, Fry et al. 1992, Alber and Valiela 1994, Peterson et al. 1994). The importance of DOM to food webs is potentially large because it is a major component of total organic matter in salt marsh estuaries (Mann 1988, Peterson et al. 1994). However, the degree to which DOM supports fish production, either by detrital aggregates or by way of transfer through microbial heterotrophs and zooplankton (Mann 1988), remains an intriguing but unresolved issue.

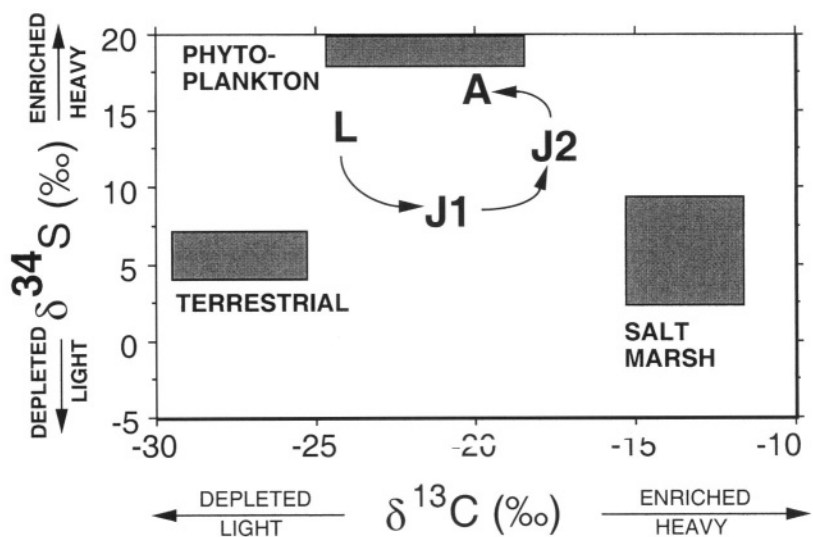


Figure 5. Cross plot of sulfur and carbon stable isotopic values for Gulf menhaden in different life history stages and possible organic matter sources. L = larvae, J1 = small juveniles in marsh creeks, J2 = larger juveniles of the open bay, A = adult. From Deegan et al. (1990).

The major pathways by which marsh organic matter is transferred to fish are largely indirect, through microbial and invertebrate intermediaries (Tenore et al. 1982, Newell and Langdon 1986). Invertebrates are the primary link to fish consumers of marsh-associated production, transforming microphytes, organic detritus, and microbial detrital heterotrophs into available biomass (Heinle et al. 1977, Tenore et al. 1982, Boesch and Turner 1984, Zagursky and Feller 1985, Kneib 1997). Zooplanktonic, small epibenthic, and shallow-burying invertebrates are abundant in the salt marsh estuary, on the marsh surface, and in adjacent subtidal sediments (Montague et al. 1981). Invertebrates that are important in the diets of juvenile and smaller-sized marsh fishes include polychaetes and oligochaetes, snails, insects and their larvae, and a host

of crustaceans - harpacticoid and calanoid copepods, ostracods, mysids, tanaids, amphipods, small crabs (e.g., *Uca* spp.), and palaemonetid shrimp (Feller et al. 1990, Rozas and La Salle 1990, Zimmerman et al. 1990, Cattrijse et al. 1994, Walters et al. 1996, Gregg and Fleeger 1997, Kneib 1997). These invertebrates can be considered the major primary consumers of marsh production, although "opportunistic omnivory" (Haines 1979) typifies many of their feeding habits (Kneib 1997). Studies of the natural abundance of stable isotopes have demonstrated the trophic linkage of many invertebrate primary consumers to salt marsh organic matter (Haines and Montague 1981, Peterson et al. 1986, Couch 1989, Currin et al. 1995).

It is readily apparent from studies of gut contents that both marsh resident and marine transient nekton feed actively on invertebrate primary consumers during tidal foraging on the marsh surface (reviewed by Kneib 1997). The distribution, abundance, and size composition of invertebrates in the marsh can be correlated with the foraging behavior and abundances of nektonic predators, providing indirect evidence of consumption of marsh prey such as harpacticoid copepods, amphipods, tanaids, and snails (Kneib 1997). Access to the intertidal marsh surface offers increased feeding opportunities for nekton, and promotes growth (Weisberg and Lotrich 1982, Javonillo et al. 1997), although it should be noted that all manipulative field experiments on nekton growth and consumption of marsh prey have been conducted with marsh residents, particularly fundulid fish and palaemonetid shrimp. Caging studies of foraging by nekton have shown significant impacts on marsh invertebrate densities and species composition (Virmstein 1977, Wiltse et al. 1984, Hines et al. 1990). However, fish predator inclusion/exclusion effects on benthos have been equivocal (Kneib 1986, 1988). Nekton behavior interacts with geomorphology and hydrology of estuarine salt marshes to strongly influence the trophic transfer of marsh resources. In a Georgia (USA) salt marsh larger resident nekton range farthest onto the shallow-water vegetated marsh surface during tidal inundation, while smaller nekton remain in deeper water near intertidal creeks (Kneib and Wagner 1994). Accordingly, the effects of nektonic predators on marsh invertebrates should show a spatial dependence based on predator size and species (Kneib and Wagner 1994). In a Louisiana study (Peterson and Turner 1994), the edge of the marsh within a few meters of creek banks was frequented by both marsh resident nekton (e.g., fundulid and gobiid fishes, palaemonetid shrimp) and transient marine nekton (e.g., engraulid fish, penaeid shrimp, portunid crabs). The inner portion of the flooded marsh surface was only of importance to resident species. Marsh edge habitats may be particularly supportive of nekton by providing increased feeding area, elevated prey densities, and protection (Baltz et al. 1993, Rozas and Reed 1993, Miltner et al. 1995).

## 2.4 THE SPATIAL EXTENT OF MARSH INFLUENCE ON ESTUARINE FOOD WEBS

The influence of salt marsh production at the base of the food web is confined for the most part to the marsh surface and subtidal creeks and embayments immediately adjacent to the marsh. Evidence for a limited spatial scope of "direct" marsh influence in estuarine food webs stems from studies of the composition of estuarine seston and sediments, and from stable isotopic analyses along estuarine gradients. Sherr (1982) found that *Spartina* carbon was an important component of organic matter in intertidal sediments of a Georgia salt

marsh, but its contribution was lower in adjacent subtidal sediments, and was scarcely present in seston. An abrupt decline of sedimentary *Spartina* detritus with increasing distance offshore from a salt marsh was reported by Wilson et al. (1985) in a study of subtidal sediments of a Massachusetts coastal embayment. In a Louisiana salt marsh system, the contribution of *Spartina* detritus to subtidal sedimentary organic matter was inversely correlated with the size of the receiving water body (DeLaune and Lindau 1987). Sedimentary  $^{13}\text{C}$  content was more similar to *Spartina* in smaller embayments, and more similar to phytoplankton in larger embayments. Cifuentes (1991) concluded that salt marshes exported little organic matter to the Delaware estuary based on the analysis of diagenetic sedimentary components. Similarly localized effects of *Spartina* were observed in sediments of a North Carolina estuarine salt marsh system (Ember et al. 1987) and in western European salt marshes (Hemminga et al. 1996). Bivalve filter-feeders in a Cape Cod salt marsh (Fig. 6, Peterson et al. 1985) and the fauna of a tidal creek in a Georgia estuary (Hughes and Sherr 1983) have  $^{13}\text{C}$  contents that suggest highly localized effects of *Spartina* in food webs. In their multiple isotopic study of the biota of a northern Massachusetts salt marsh estuary, Deegan and Garritt (1997) showed that local sources of production were most important to consumers. Fish and invertebrates showed distinct isotopic shifts among habitats that correlated with changes in the isotopic values of marsh plants at the base of the food web. These results echo those of Hughes and Sherr (1983), in which resident and transient nekton in Georgia tidal creeks fed on prey closely related isotopically to local detrital foods.

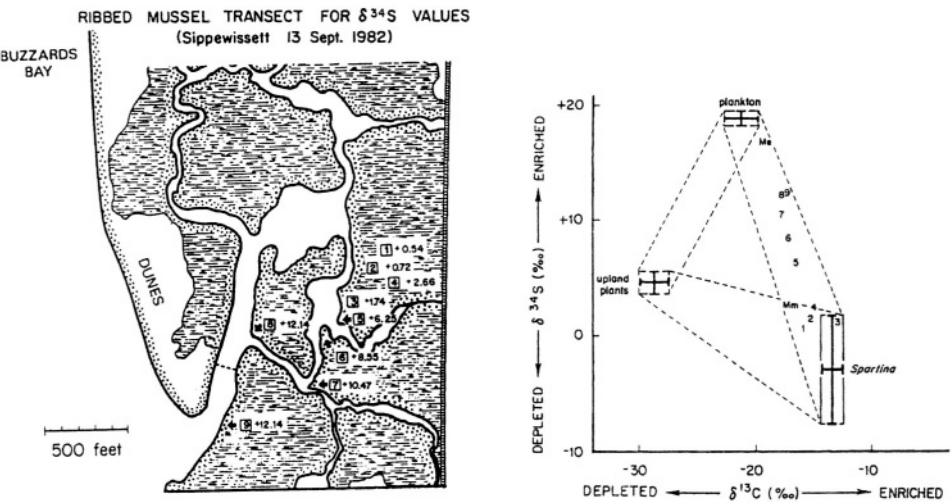


Figure 6. (Left panel) Map of sampling sites and  $^{34}\text{S}$  content (per mil) of ribbed mussels (*Geukensia demissa*) in Great Sippewissett Salt Marsh, Massachusetts. (Right panel) Cross plot of sulfur and carbon stable isotopic values for filter-feeding bivalves obtained at corresponding sites in the mapped area. Numbers 1-9 refer to ribbed mussels taken along the transect from the marsh interior (#1) to the adjacent coastal bay (#9). "Mm" is the hard clam *Mercenaria mercenaria* from marsh creek sediments. "Me" is the blue mussel *Mytilus edulis* from a coastal bay. Boxes in cross plot enclose mean  $\pm 1$  SD of isotopic values for candidate organic matter source materials. From Peterson et al. (1985).

The trophic “sphere of influence” of marsh-derived organic matter at the base of estuarine food webs may vary among estuaries, depending in part on the geomorphology of the estuarine basin, the relative magnitude of tidal range and freshwater input (Odum et al. 1979), and the behavior of nekton. The importance of marsh production to nekton production in estuaries depends on the relative area and productivity of marshes compared to other adjacent habitats, which is in part determined by the geological setting (Deegan et al. 1983). In a study of eight Gulf of Mexico estuaries (Deegan et al. 1983), the contribution to total estuarine primary production varied from 16 to 53% for phytoplankton and 0 to 72% for marshes. Undoubtedly the relative importance of phytoplankton and marsh production in the food web also varied.

### **3. The Marsh as a Refuge From Predation**

Reduced risk of mortality is often suggested as a reason for the use of estuaries by young-of-the-year and juvenile fishes (e.g., Joseph 1973, Blaber and Blaber 1980, Boesch and Turner 1984, Deegan & Day 1984). It has been suggested that lower mortality of young nekton in estuarine areas compared to offshore marine areas could be an evolutionary driving force behind the development of complex oceanic-estuarine migration patterns (e.g., Joseph 1973, Blaber and Blaber 1980). We will first examine the evidence for lower mortality rates in estuaries versus offshore areas, and then in salt marshes versus other estuarine habitats. We conclude by discussing the mechanisms governing mortality rates in salt marsh ecosystems.

#### **3.1 COMPARISON OF MORTALITY RATES BETWEEN ESTUARIES AND OTHER ECOSYSTEMS**

Comparison of larval mortality rates across a wide variety of marine and freshwater ecosystems does not indicate lower mortality rates in estuarine systems (Fig. 7). In the most comprehensive assessment to date, Houde and Zastrow (1993) found that instantaneous mortality rates of larval fish were correlated with temperature across a wide variety of taxa and ecosystems. Absolute and temperature-adjusted mortality rates for larvae from estuarine systems were high compared to other ecosystems, including the offshore shelf environment. Even though this study includes only a few mortality measurements from estuarine systems ( $n = 6$ ), the estuarine data are consistent with the general temperature-dependent trend seen across many ecosystems and taxa.

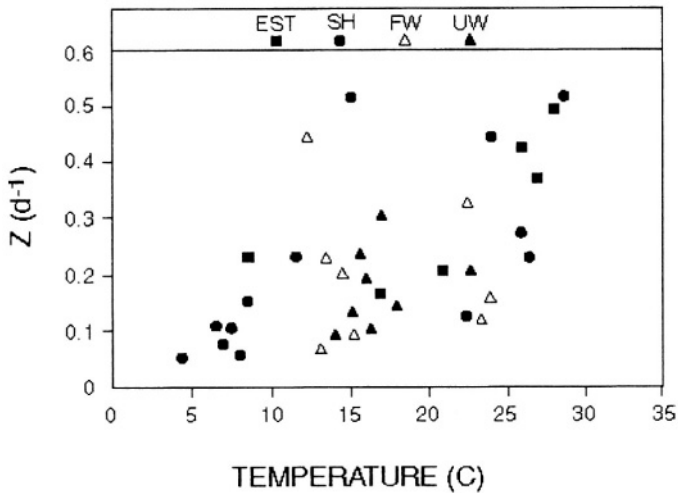
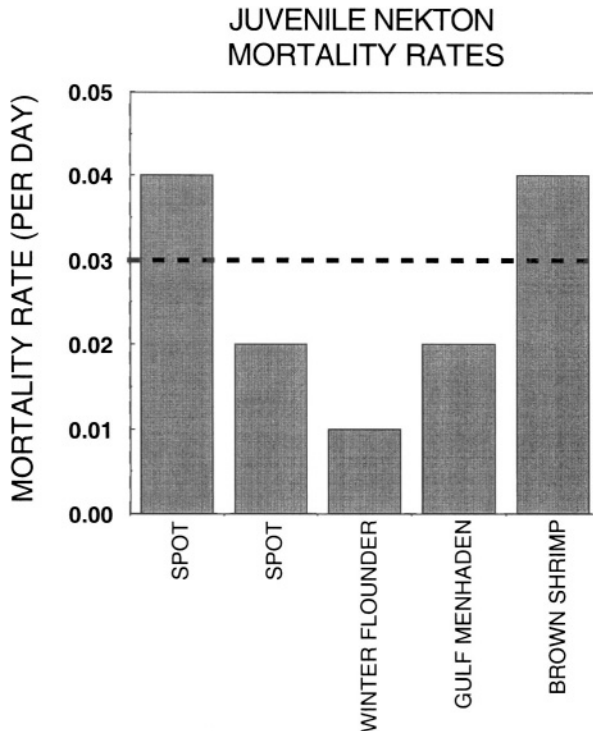


Figure 7. Ecosystem-specific instantaneous mortality coefficient  $Z$  ( $d^{-1}$ ) of fish larvae versus water temperature. EST = estuarine, SH = shelf, FW = freshwater, UW = upwelling system. From Houde and Zastrow (1993).

Estuarine versus offshore comparisons for juvenile nekton are difficult to make because of lack of information on mortality rates in estuaries. Mortality rates for spot ( $0.02$  to  $0.05 d^{-1}$ , Weinstein and Walters 1981, Weinstein 1983), and brown shrimp (*Penaeus aztecus*) ( $0.04 d^{-1}$ , Minello et al. 1989) were above the average for marine fishes ( $0.03 d^{-1}$ , Gulland 1964), while the mortality rates for Gulf menhaden ( $0.02 d^{-1}$ , Deegan 1990) and winter flounder ( $0.01 d^{-1}$ , Pearcy 1962) were below (Fig. 8). Mortality estimates for a single species, spot, are both above and below the marine average and show wide year-to-year and geographic differences (Weinstein and Walters 1981, Weinstein 1983). From the limited data available, it is unclear whether mortality rates of juvenile fishes in estuarine systems are in general lower than in offshore ecosystems.



*Figure 8.* Instantaneous mortality rates of juvenile salt marsh estuarine nekton compared to the average value for juvenile marine fish (dashed line, from Gulland 1964). Spot data at left from Weinstein (1983); other spot data from Weinstein and Walters (1981); winter flounder (Percy 1962); Gulf menhaden (Deegan 1990); brown shrimp (Minello et al. 1989).

The scarcity of data indicates the need for more work on the mortality rates of young-of-the-year and juvenile fishes in estuarine environments. The few data available do not indicate that size-specific mortality rates are lower in estuarine environments compared to offshore environments. However, the higher growth rates of young fish in estuaries may “overcompensate” for mortality resulting in net advantage to the fish. Because of the faster growth rates in warmer waters, estuarine fish spend less time in the vulnerable larval stage compared to those in offshore marine areas (Houde and Zastrow 1993). Thus the main advantage of moving into warmer estuarine areas maybe to accelerate growth and decrease the amount of time that fish experience high mortality due to their small size. This may result in a higher net production than if the fish had remained offshore.

### 3.2 COMPARISON OF MORTALITY RATES AMONG ESTUARINE HABITATS

Within estuaries, salt marshes are suggested to provide protection from predators, resulting in lower mortality rates. For some species there is evidence that mortality rates in marshes may be lower than in open bay areas. Estimates of mortality for Gulf

menhaden suggest that, when adjusted for size, fish in marsh creeks may have lower mortality rates than fish in open bay areas. The estimates for mortality ( $0.0070$  to  $0.0208\text{ d}^{-1}$ ) were the same in the open bay and in marsh creeks (Fig. 9, Deegan 1990), even though fish in the marsh creek were much smaller (20 to 50 mm) than fish in the open bay areas (50 to 100 mm). Because mortality is expected to decrease as fish get larger, we anticipated that mortality rate in the open bay areas should have been much lower than in marsh creeks. Mortality rates in the two habitats were similar despite the difference in fish size, implying that the marsh creek habitat provided some protection from mortality to the smaller fish. Unfortunately, direct comparison of the mortality rates of similar sized menhaden in the two habitats is not possible because use of these habitats by menhaden is size-related (Deegan 1990). However, lower mortality rates of nekton in salt marsh creeks compared to other estuarine habitats are not universal. Wilson et al. (1990) found no evidence for lower mortality of tethered juvenile blue crab (Fig. 10) in marsh creeks compared to seagrass or algal habitats.

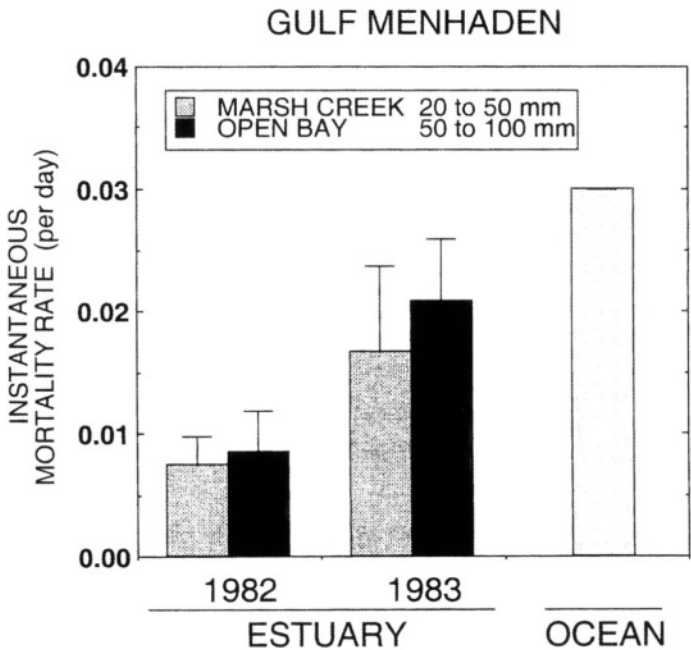


Figure 9. Size-dependent instantaneous mortality rates in two size classes of Gulf menhaden (+ SE) in a Louisiana salt marsh estuary, and the average value for juvenile marine fish ("OCEAN", from Gulland 1964). From Deegan (1990).



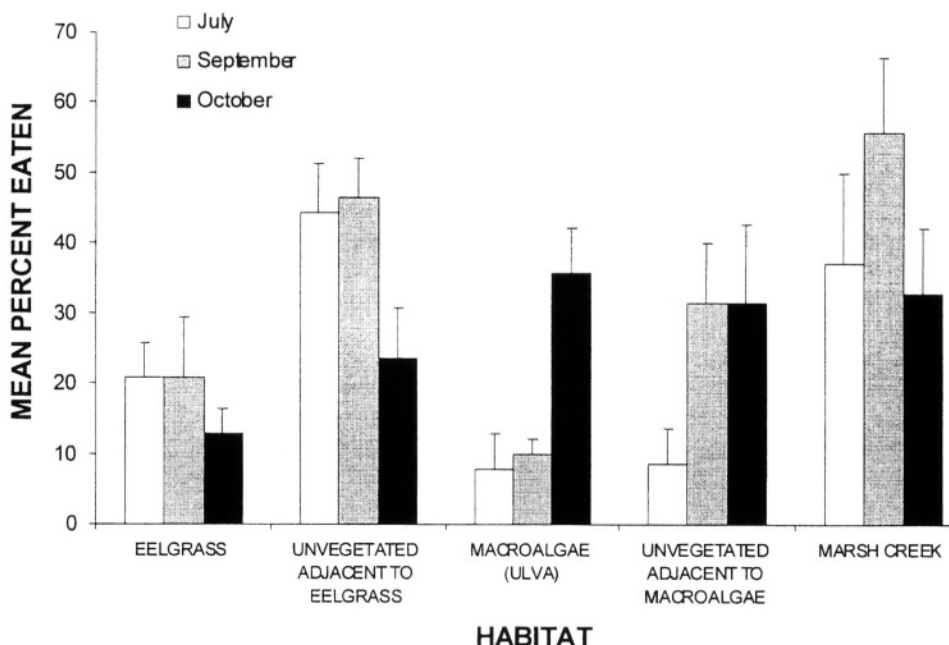


Figure 10. Mean percent (+1 SE) of tethered juvenile blue crabs eaten in eelgrass, adjacent unvegetated substrate, macroalgae (*Ulva lactuca*), and in a marsh creek. From Wilson et al. (1990).

Mortality rates are notoriously difficult to measure and there are very few estimates for estuarine fishes. Because of the paucity of data, it is difficult to make any broad conclusions about mortality rates in salt marsh creeks versus other habitats. The development of new mathematical models to estimate mortality based on mark-and-recapture studies (USFWS, May 1998; <http://www.mbr.nbs.gov/software.html>) as well as advances in tagging technology should allow progress in estimating population level mortality rates in the near future. Estimating the mortality rates of nekton is clearly an area of research that needs more work.

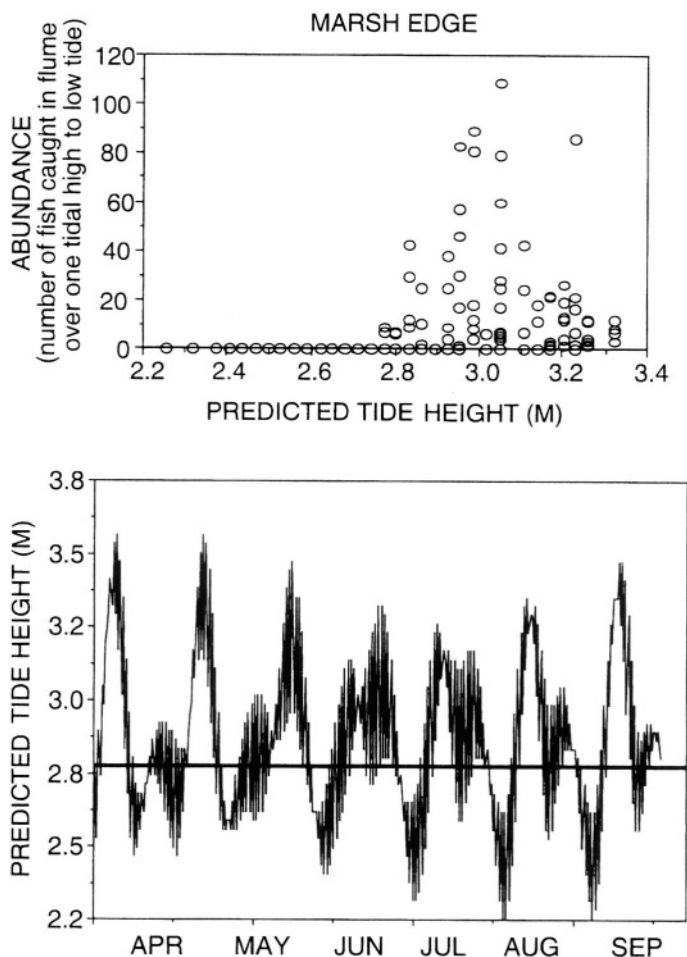
### 3.3 MECHANISMS GOVERNING MORTALITY RATES

Predation is an important source of mortality for small nekton. Mortality rates of brown shrimp in marshes declined from ~40% to 3% when predators were excluded, indicating that predators are a major source of mortality for brown shrimp (Minello et al. 1989). Weinstein and Walters (1981) found that mortality of spot was significantly higher in polyhaline creeks than in lower salinity creeks. The difference was attributed to the greater numbers of stenohaline marine predators seasonally occupying higher salinity marshes. Thus, we might expect mortality rates to vary with the attributes of salt marsh creeks. In other habitats, such as submerged aquatic vegetation, complex physical structure affords small fish some measure of protection from larger predators (e.g., Heck and Crowder 1991). It is uncertain if this hypothesis holds for salt marshes because nekton do not live continuously among marsh grass stems, but frequent the

marsh and its creeks only during tidal inundation. Marine transient nekton often remain near the edges of salt marshes, even during spring tides, in contrast to marsh resident species such as killifish and palaemonetid shrimp (Murphy 1991, Kneib and Wagner 1994, Peterson and Turner 1994). The vegetative structure available at the marsh edge, the shallow depth, physico-chemical environment and high turbidity of marsh creeks have all been suggested as conveying to nekton protection from predation.

Marsh vegetation near the edges of creeks may provide some protection to transient nekton from predation by large piscine predators. The high densities of fish, penaeid shrimp and portunid crabs along the edges of flooded marsh creeks may be the result of predator avoidance (Weisberg et al. 1981, Murphy 1991, Rountree and Able 1993, Kneib 1997). Most manipulative studies of the effects of marsh vegetation in deterring predation have focused on predatory fish - invertebrate prey interactions (e.g., Vince et al. 1976, Minello and Zimmerman 1983, Minello et al. 1989), and have demonstrated the protective function of vegetated surfaces. In laboratory experiments, simulated *Spartina* vegetative structure reduced predation on brown shrimp by pinfish and Atlantic croaker from 2.5 to 1.5 shrimp  $d^{-1}$  (Minello and Zimmerman 1983). Vegetative structure did not, however, affect predation on brown shrimp by red drum or speckled trout (Minello and Zimmerman 1983). After many trials with several predatory species, Minello and Zimmerman found that overall mortality of brown shrimp was reduced by about 40% in marsh edge habitats compared to unvegetated habitat.

The relative importance of the marsh edge as a refuge from predation will vary with the physiography of the marsh (amount of edge), whether the marsh is subsiding or aggrading, and the tidal amplitude. For example, in a northern New England salt marsh that is subsiding relative to sea level rise, the marsh was flooded to a depth used by fishes substantially more often than the typical 25% estimate for New England marshes (Fig. 11; Murphy 1991). Subsiding marshes may provide a better habitat for marine transients than a typical New England salt marsh because fish have more frequent access to the marsh surface. Abundance of penaeid shrimp in some Gulf Coast marshes is greatest in fragmented *Spartina* marshes undergoing submergence, possibly as a result of greater marsh edge habitat (Zimmerman et al. 1984), or because of increased time to forage (Rozas and Reed 1993, Rozas 1995).



*Figure 11.* (Top panel) Total abundance of fishes captured in marsh edge flume nets during different tidal heights (m) in two Maine salt marsh estuaries, May-September, 1989. (Bottom panel) Predicted tidal heights (m) in these estuaries, 1989. Horizontal line indicates the minimum height required to capture fish on the marsh surface. From Murphy (1991).

Occupying a habitat that provides protection from predation, even if for only short periods of time, can substantially increase the number of individuals surviving. For example, consider a nekton cohort with a population size of 10,000 when they enter the salt marsh ecosystem. This species uses the marsh ecosystem for 100 days (e.g., June, July and August) before moving to other habitats. Assume the fish experience a mortality rate of  $0.04 \text{ d}^{-1}$  in the creek and that by moving up into the vegetated marsh creek edge on high tides their mortality rate decreases by 40% to  $0.025 \text{ d}^{-1}$ . If the marsh edge is flooded enough to allow the fish access to the vegetated edge 25% of the 100 day period, 1.5 times more individuals will survive by moving into the marsh than by staying in the creek (260 survive with marsh access compared to 180 without marsh

access). Obviously, the more time the species can spend in the flooded edge habitat, the greater the number of individuals that will survive.

The distribution of larval and juvenile nekton on the marsh surface and in shallow tidal creeks indicates that shallow-water habitat may also minimize predation. Lower predation pressure was offered as the explanation for the prevalence of molting blue crabs in tidal creeks versus deeper water (Hines et al. 1987). Ruiz et al. (1993) suggest greater predation risk in deep water as a factor causing the concentration of small nekton in shallow bay habitats. Shallow intertidal marsh puddles and small rivulets have been shown to offer a partial refuge from predation and cannibalism for young nekton (Kneib 1987, 1993, 1997). Small fish have often been observed to remain near the water's shallow edge, often in less than 1 cm of water, as the tide creek drained (Deegan, personal observation). McIvor and Odum (1988) found higher abundances of small fish associated with shallow-sloped, depositional creek banks rather than steep-sided, erosional banks. They attributed this distribution to the continuous availability of very shallow areas as the water ebbed in the depositional sites compared to the erosional edge. McIvor and Odum (1988) also found predation on tethered mummichogs was much less off shallow, depositional banks compared to steep-sided, erosional banks.

There are very few studies that examine the depth preferences of fishes, but in one study of hake preying on spot, hake avoided the shallow end of the experimental tank (Miltner et al. 1995). The physical constraints imposed by shallower waters, and the generally more stressful physico-chemical environment of intertidal creeks, where high temperatures and low dissolved oxygen during summer are common, may exclude piscivorous predators (Rozas and Odum 1987). The large environmental variations in shallow marsh creeks may exceed the tolerance of adult predators, but not juvenile fish (Cushing 1975, Hyatt 1979, Heck and Orth 1980). Some studies indicate few large (> 40 cm) piscine predators in these areas (less than 1 to 2% of the total catch; Bozeman and Dean 1980, Weinstein and Walters 1981, Miltner et al. 1995). On the other hand, marsh resident nekton that abound in shallow marsh habitats are tolerant of a wide range of physico-chemical conditions (Kneib 1987). However, fish are more susceptible to predation by wading birds in shallow marsh habitats compared to deeper areas (Kneib 1982, 1987). Thus, shallow water does not provide a perfect refuge from all predators.

Tidal creeks also have high turbidity that may provide protection to small nekton from predators by restricting the vision of predators. Although many senses are involved in feeding, sight is important in successful prey capture for most piscine predators (Nikolsky 1963, Hyatt 1979). The effects of turbidity on predator-prey interactions and feeding success have been researched in freshwater systems (e.g., Abrahams and Kattenfeld 1997), but relatively little work has been done in estuaries (Blaber and Blaber 1980). The effect of turbidity on predation rate depends on the specific predator, prey and even substratum of the habitat (Minello et al. 1987). The turbidity of tidal creeks may confer a survival advantage to juvenile nekton by reducing risk of predation by visual predators (Moore and Moore 1976, Cyrus and Blaber 1987, Hecht and van der Lingen 1992). Turbidity apparently reduced the perceived risk of predation in juvenile chinook salmon (Abrahams and Kattenfeld 1997). However, turbidity did not seem to affect the foraging efficiency of juvenile white perch (Monteleone and Houde 1992) or weakfish (Grecay and Targett 1996), and juvenile

weakfish occur abundantly in turbid regions. The role of turbidity in regulating predator/prey interactions is an area of research that needs much more attention.

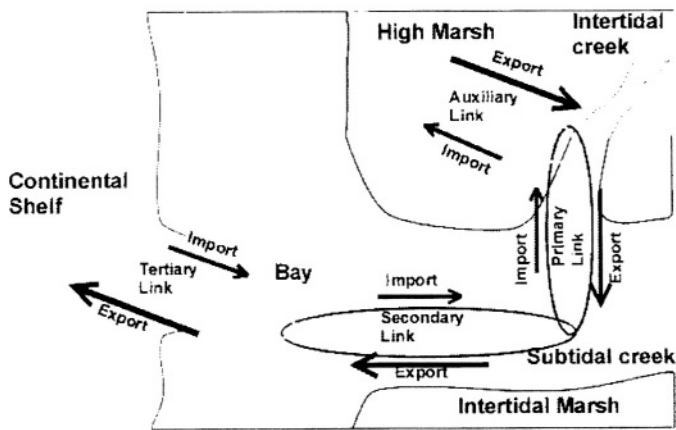
The protection from predation for small nekton attributed to salt marshes may derive from a combination of the effects of these four factors (vegetative structure, shallow depth, physico-chemical environment, and turbidity). For example, at high tide the marsh structure may physically interfere with piscivorous fish attacks and at low tide the shallow depth of the water may exclude predators. However, it is important to remember that juvenile stages of some nekton species prey on other juvenile nekton in marsh creeks (Juanes et al. 1993, Miltner et al. 1995) and that large fish have been shown to move into some creeks at night (Rountree 1992). Given that the optimum length of a piscine predator is often about 4 times the length of its prey, most small fish (usually 1 to 10 cm in length) in tidal creeks would be vulnerable to a predator that was only 20 to 40 cm in length.

#### **4. Migration as an Important Linkage among Habitats**

One of the original hypotheses of estuarine function was that estuaries produce annual excesses of plant organic matter, some of which is exported seaward as detritus (dissolved or particulate) and supports coastal fisheries (Odum 1968). Current understanding is that detrital outwelling is not a universal phenomenon and that when it occurs the amount transported is often small and relatively refractory (Nixon 1980, Dame 1989). An alternative mechanism for the support of coastal fisheries by salt marshes is by the migration of nekton. Estuarine fish faunas around the world are dominated in numbers and biomass by species that move into the estuary as larvae, accumulate biomass, and then move offshore after attaining a large proportion of their adult size (e.g., Yáñez-Arancibia 1985). Other species make seasonal forays into estuarine systems to feed on the high production of estuarine fishes (e.g., Yáñez-Arancibia 1985). Although many authors have suggested that emigration of fish may export energy from estuaries (Bozeman and Dean 1980, Odum 1980, Weinstein et al. 1980, Wiegert and Pomeroy 1981, Currin et al. 1984, Deegan and Thompson 1985, Zijlstra 1988), the mechanisms of energy transfer and the quantitative estimate of its importance have not been well studied.

The horizontal movement of energy and nutrients from the salt marsh to adjacent habitats and ecosystems via sequential consumption and migration of nekton has been described as a “trophic relay” (Kneib 1997) or the “chain of migration” (Rountree 1992). This concept is similar to Vinogradov’s “ladder of migration” hypothesis describing vertical transfer of energy from the photic to abyssal zones of the deep sea (Vinogradov 1953, 1955, Longhurst 1976, Rountree 1992). In much the same way as Vinogradov’s ladder rungs link adjacent depth strata, the trophic relay results from a chain of migration that links adjacent habitats (Fig. 12). The first and most important coupling is that between the intertidal marsh and adjacent subtidal habitats. This primary coupling is established by the foraging activities of both permanent and seasonally resident marsh fauna. A secondary coupling is established by the activities of faunal assemblages using subtidal marsh creeks and the marsh fringe and the

adjacent estuarine bays. A tertiary link couples estuarine bays with the continental shelf. In some areas auxiliary links might exist between the high marsh and the low intertidal marsh, and also between fully terrestrial habitats and the high marsh. Migration can also link habitats on other spatial scales, such as among freshwater, and upper and lower estuarine habitats.



*Figure 12.* Nekton migration patterns that can result in energy or nutrient exchange among habitats. Trophic coupling between adjacent habitats results from seasonal and ontogenetic migrations, or tidal and diel foraging movements. Three primary couplings are hypothesized: a) a primary link between the intertidal marsh (both marsh surface and intertidal creek habitats) and adjacent subtidal marsh (subtidal creek and shallow subtidal bay habitats along the marsh fringe); b) a coupling between the subtidal marsh and adjacent estuarine bay; and c) a third link between the estuarine bay and continental shelf.

The trophic relay can operate on several different temporal scales (tidal, diel, and seasonal), and through two basic mechanisms: 1) passive diffusion, or 2) migration, either ontogenetic or cyclic foraging migration (Fig. 13). The first and simplest mechanism involves a “diffusion” of energy between overlapping communities through spatially overlapping trophic webs. In natural estuarine systems faunal assemblages are rarely sharply divided, but rather, they tend to grade into each other across habitat clines. It is reasonable to assume then, that these overlapping communities would share overlapping trophic webs. It is difficult, however, to envision how a net one-way export from the marsh could occur by this mechanism. Alternatively, active ontogenetic and cyclic migration patterns result in the direct transfer of energy between habitats through animal movements.

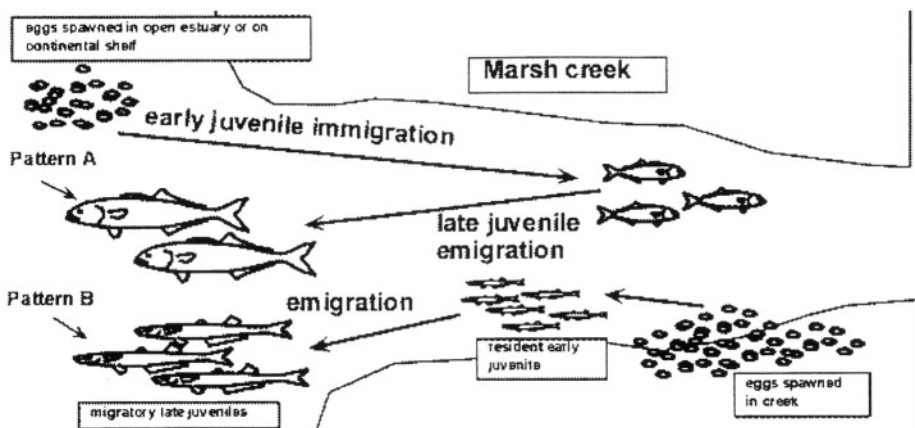


Figure 13. Patterns of trophic transfer of energy, derived from primary production on the marsh surface, through fish and invertebrate communities along an estuarine habitat cline. The simplest mechanism is through a diffusion of energy through the interconnecting food webs of spatially overlapping communities (e.g., estuarine bay, subtidal creek and marsh surface communities). Ontogenetic migration of species between adjacent habitats results in the direct export of energy assimilated in somatic growth. Cyclic foraging migrations of species between habitats also results in direct transfer of energy among the habitats through local consumption, fecal deposition, and mortality.

#### 4.1 ONTOGENETIC MIGRATION

Ontogenetic migration involves successive shifts in the use of adjacent habitats/ ecosystems by different life stages of a given species (Fig. 13), and can occur on several scales: between habitats within the salt marsh, between the salt marsh and estuary and between the estuary and coastal waters.

Numerous species of nekton generally considered true marsh residents, actually are only resident during early larval and juvenile stages, or seasonally during the summer and subsequently move into adjacent subtidal areas with growth or colder temperatures (e.g., mummichog and shore shrimp, *Palaemonetes vulgaris*; Murphy 1991, Rountree 1992, Kneib 1997). Subtidal habitats serve as a low tide refuge for the older juveniles and adults from which they migrate tidally into the intertidal marsh to feed. The primary coupling between the subtidal creek and intertidal marsh is best exemplified by mummichog (Fig. 13). This species is well known to forage on the intertidal marsh during tidal inundation and retreat to subtidal areas with the tide (Baker-Dittus 1978, Weisberg et al 1981, Kneib 1984, 1987, Rountree and Able 1992a, 1993).

Numerous researchers have suggested that substantial biomass may be exported from estuaries as nekton undergo seasonal migrations into coastal waters (e.g., Smith 1966, Welsh 1975, Meredith and Lotrich 1979, Bozeman and Dean 1980, Weinstein and Walters 1981, Conover and Ross 1982, Deegan and Thompson 1985, Voughlitois et al. 1987, Zijlstra 1988, Rountree 1992, Kneib 1997). Two basic patterns of energy exportation through ontogenetic migrations of transient species have been suggested. In one pattern, fishes are spawned either in the open estuary (e.g., winter flounder) or on the continental shelf (e.g., Atlantic menhaden, summer flounder, bluefish, mullet) and recruit

to salt marshes during larval or early juvenile stages. In a second pattern, fishes spawn within the intertidal marsh and emigrate offshore after a period of growth (e.g., Atlantic silverside; goby, *Gobiosoma bosc*; striped killifish, *Fundulus majalis*). Net export is the difference between immigrating and emigrating biomass, taking into account local mortality (Deegan 1993).

Deegan (1993) demonstrated that biotic transport by one marine transient, Gulf menhaden, is important in the movement of energy and nutrients across coastal ecosystem boundaries. Gulf menhaden is considered a classic example of the marine transient fishes that are spawned offshore, use marsh ecosystems as young-of-the-year, and depend on marsh production (Deegan and Thompson 1985, Deegan et al. 1990). Estimates of offshore transport by Gulf menhaden varied with year class strength, but always indicated a net transport offshore. The offshore transport by Gulf menhaden of  $22 \text{ g C m}^{-2} \text{ yr}^{-1}$ ,  $3.1 \text{ g N m}^{-2} \text{ yr}^{-1}$ , and  $0.9 \text{ g P m}^{-2} \text{ yr}^{-1}$  represented approximately 5-10% of the primary production of inshore coastal Louisiana. The amount of N and P transported by this single species was of the same magnitude as estimates for passive outwelling.

Many other marine transient species also have the potential to transport nutrients and energy. The Atlantic menhaden is the ecological equivalent of Gulf menhaden along the Atlantic coast, with very similar production characteristics. Penaeid shrimp, blue crab, Atlantic croaker, spot and other species have a migration pattern similar to that of Gulf menhaden, suggesting that a net export of energy is likely (Rountree 1992, Deegan 1993). Conover and Ross (1982) estimated that less than 1% of the young-of-the-year population of Atlantic silverside survived the winter to spawn the following spring, suggesting a large one-way export of biomass to the continental shelf. Current work at the Plum Island Sound LTER site in northern Massachusetts is examining the potential of energy and nutrient export by Atlantic silverside (Deegan, Wright and Hughes, in progress). The cumulative transport of 6 to 10 additional species may represent a significant energy source to the offshore ecosystem. Understanding the importance of the translocation of energy and nutrients by the full array of species that use estuaries as juveniles is critical to understanding the role of estuaries in supporting offshore fisheries.

## 4.2 CYCLIC FORAGING MIGRATIONS

Both tidal and diel cyclic foraging migrations (Miller and Dunn 1980, Rountree 1992, Rountree and Able 1993, 1996, 1997) may be important pathways of energy exchange between the intertidal marsh, subtidal creeks and the adjacent estuary (Fig. 14). The key to this energy transfer is the spatial separation of foraging and refuge habitats due to tides, or diel changes in physical conditions. Energy obtained in the foraging habitat would potentially be transferred to the refuge habitat by two primary mechanisms: 1) through mortality or consumption of the migrant by species resident within the refuge habitat, and 2) through fecal deposition while in the refuge habitat. Energy would be exported from the local linked system through subsequent ontogenetic migration and by predation during migration of other species (i.e., passed along to the next link in the trophic chain).



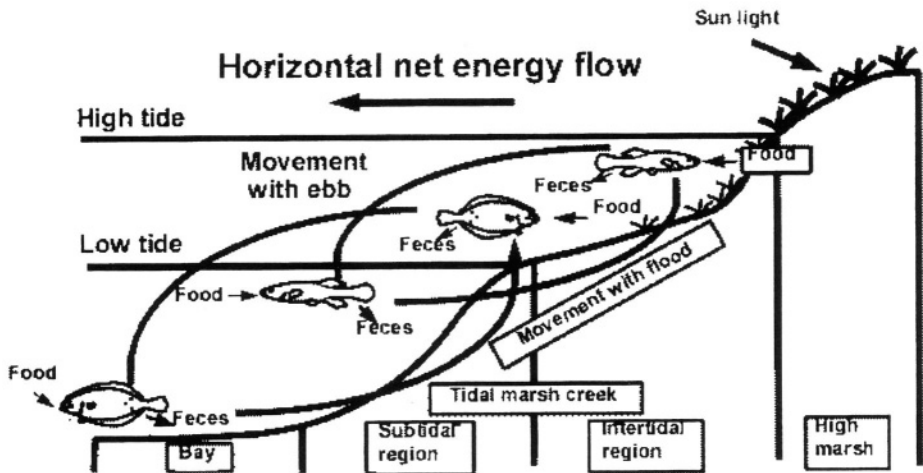


Figure 14. Hypothetical horizontal energy flow among intertidal marsh, subtidal marsh, and estuarine bay habitats through the trophic relay process. Foraging by *Fundulus heteroclitus* in the intertidal marsh results in a transfer of energy (fecal materials and mortality) to the subtidal marsh where the species retreats at low tide, thus establishing a primary coupling between subtidal and intertidal marsh habitats (see text). Predation on *F. heteroclitus* during the tidal foraging activity of *Paralichthys dentatus* results in an export of energy from the subtidal marsh to the adjacent bay establishing a secondary coupling between the bay and intertidal marsh.

Cyclic foraging linkages between the subtidal marsh creeks and adjacent bay habitat are illustrated by summer flounder. Late juveniles of summer flounder undergo regular tidal movements into New Jersey marsh creeks to feed (Rountree and Able 1992b). Individuals captured in gill nets on ebb tide (assumed to be leaving the creeks) had significantly higher gut fullness values than those captured on flood tide. Four marsh species, Atlantic silverside, shore shrimp, sand shrimp (*Crangon septemspinosa*) and mummichogs were the primary food items in summer flounder guts suggesting a close trophic link to the salt marsh. Fecal deposition and mortality while in the bay habitat result in an export of carbon from the subtidal creek to bay. Ultimately, energy derived from subtidal marsh foraging and incorporated into summer flounder biomass, would be exported from the system with seasonal migration of flounder onto the shelf. Hence, this one species is involved in both cyclic (feeding in marsh habitats) and ontogenetic (estuary to offshore) migration pathways of trophic relay, and serves as a vector linking habitats on two different spatial and temporal scales.

The transfer of energy from an area of foraging activity to another area through deposition of fecal material has not been examined in estuaries, although it has been recognized as important for nutrient-poor marine systems such as coral and artificial reefs (e.g., Bray et al. 1981, Meyer et al. 1983, Bray and Miller 1985, Meyer and Schultz 1985a, 1985b, Rountree 1990). It is not clear if this mechanism would be as significant in salt marshes where nutrients are usually high.

It is important to note that the couplings described above assume a two-way transfer rather than a one-way horizontal transfer of energy. We suggest, based on considerations

of the balance of growth and mortality that the net transport via trophic coupling and migration is out of the marsh, but mechanisms of import into the marsh must be more fully understood before net export via trophic relay can be confirmed for all migrating species.

## 5. Conclusions

Although there are many aspects of the relationship we do not yet understand, salt marsh ecosystems apparently do provide support to marine transient fishes. The warmer temperatures of estuaries and salt marsh creeks apparently provide a metabolic advantage that supports high growth rates. Current evidence indicates that estuarine food webs are a mixture of detrital-and algal-based pathways. The importance of salt marsh production to marine transient fishes is supported by dietary, behavioral, and isotopic evidence. Salt marshes support fisheries directly in the case of species that use the habitat as a nursery (e.g., Atlantic and Gulf menhaden, mullet), and in the case of estuarine transients that use many estuarine habitats but derive energy from the salt marsh through trophic relay (e.g., summer flounder, bluefish, striped bass). The salt marsh also indirectly supports fisheries by exporting abundant potential prey species for coastal carnivores (e.g., Atlantic silverside, blue crab and sand shrimp). Unlike nekton, exported detritus is often of low nutritive value and may be rapidly deposited or respired by bacteria without entering the food web. Current evidence suggests that estuarine support for marine fisheries resulting from the direct export of fish biomass and a trophic relay involving ontogenetic and cyclic migrations of nekton species is greater than support via the export of organic detritus. Understanding the controls on marine transient fish mortality is probably the most problematic and least studied aspect of their ecology. The few estimates of mortality rates of fishes in estuaries indicate they are as high or higher than mortality rates of fishes in other marine and freshwater ecosystems. However, the higher growth rates of young fish in estuaries may “overcompensate” for mortality resulting in fish spending less time in vulnerable larval stages. This may result in a higher net production than if the fish had remained offshore.

The value of the marsh as a refuge is probably due to the interaction of temperature, turbidity, and vegetative structure in restricting the foraging of predators. We also know that not all marshes provide the same degree of support to marine transients. We expect the importance of marshes to nekton populations to vary with the availability of different organic matter sources, the geomorphology of the estuarine basin, the areal extent and configuration of the marsh, hydrographic features such as frequency and duration of flooding, relative magnitude of tidal range and freshwater input, and behavior of nekton.

At this point in our understanding of the requirements of marine transient fishes, there are several questions we cannot answer. Estuarine areas used by young-of-the-year and juvenile fishes tend to be shallow areas with or adjacent to structure, that have high levels of nutrients, primary production, and invertebrate food. Would the production of these fish be just as high in another habitat that had the same essential features? Could salt marshes, for instance, be replaced by artificial reefs and provide the same benefits to

marine transient species? Do habitats with lower secondary production per unit area make an equal or greater contribution to total stock production because of greater areal extent? There are few comparisons of the production of the same species in different habitats within estuaries (e.g., Weinstein and Walters 1981, Weinstein and Brooks 1983) or in other coastal systems (Lenanton 1982) making these questions difficult to answer.

## 6. Acknowledgments

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