

## Coastal Education & Research Foundation, Inc.

---

Considerations of Habitat Linkages, Estuarine Landscapes, and the Trophic Spectrum in Wetland Restoration Design

Author(s): Michael P. Weinstein, Steven Y. Litvin and Vincent G. Guida

Reviewed work(s):

Source: *Journal of Coastal Research*, , SPECIAL ISSUE NO. 40. Coastal Restoration: Where Have We Been, Where Are We Now, and Where Should We Be Going? (WINTER 2005), pp. 51-63

Published by: [Coastal Education & Research Foundation, Inc.](#)

Stable URL: <http://www.jstor.org/stable/25736615>

Accessed: 12/07/2012 16:29

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Coastal Education & Research Foundation, Inc. is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Coastal Research*.

<http://www.jstor.org>

# Considerations of Habitat Linkages, Estuarine Landscapes, and the Trophic Spectrum in Wetland Restoration Design

Michael P. Weinstein<sup>†</sup>, Steven Y. Litvin<sup>‡</sup>, and Vincent G. Guida<sup>‡</sup>

<sup>†</sup>New Jersey Marine Sciences Consortium  
Sandy Hook, NJ 07732,  
U.S.A.  
mweinstein@njmsc.org  
and  
Institute of Marine and Coastal Sciences  
Rutgers University  
New Brunswick, NJ 07732,  
U.S.A.

<sup>‡</sup>National Marine Fisheries Service  
James J. Howard Marine Science Laboratory  
Sandy Hook, NJ 07732,  
U.S.A.



## ABSTRACT

WEINSTEIN, M.P.; LITVIN, S.Y. and GUIDA, V.G., 2005. Considerations of habitat linkages, estuarine landscapes, and the trophic spectrum in wetland restoration design. *Journal of Coastal Research*, SI(40), 51-63. West Palm Beach (Florida), ISSN 0749-0208.

Wetland restoration designs do not frequently consider functional linkages among habitats in the estuarine landscape, nor do they focus sufficient attention on the role of marsh morphology in promoting the efficient exchange of materials and organisms between the intertidal and subtidal water column. These features should be considered, because many marine organisms may benefit from trophic subsidies from adjacent habitats without ever entering them. Stable isotopes were used to examine trophic linkages between primary producers and marine finfishes to highlight the importance of individual life history traits and to punctuate the argument for promoting habitat connectivity (exchange of materials and organisms) in restoration planning. We demonstrate that the trophic spectrum of an estuarine resident, the Morone americana (white perch), and two marine transients, *Anchoa mitchilli* (bay anchovy) and *Cynoscion regalis* (weakfish), are largely functions of locally available organic matter distributed along a gradient of estuarine resources. In both salt marshes and open waters, there was a transition in whole-body isotopic composition in all three species associated with the estuary-wide gradient in nutrient availability ranging from macrophytes and benthic microalgae in marshes, to phytoplankton (as suspended particulate matter) in the open estuary. As anticipated, phytoplankton contributed more to bay anchovy and weakfish biomass, especially in open waters, than to white perch. Our results also suggest that marine transients benefit from the presence of salt marshes without necessarily occupying them. Thus the estuarine "commissary" serves up different recipes in different regions, and the many estuarine-dependent species apparently take full advantage of these varied sources of primary production at the base of the food web when seeking energy for rapid growth and survival.

**ADDITIONAL INDEX WORDS:** *Estuarine landscapes, trophic spectrum, wetland restoration design.*

## INTRODUCTION

At the core of habitat restoration is the desire to return an ecosystem to a close approximation of its undisturbed state (NRC, 1992). Restoration science, and its recent manifestation, sustainability science (KATES *et al.*, 2001), are partly rooted in ecological fidelity; *i.e.*, those restoration goals characterized by structural replication, functional success, and durability (self-sustainability) (HIGGS, 1997). What has been generally missing in resto-

ration designs, however, is consideration of the functional linkages among habitat units in the estuarine landscape and the connectivity among system components. This is a form of ecological fidelity that has not received much attention but should, as many organisms benefit from functional processes of a habitat without ever occupying it.

Marine transients that utilize estuaries and the products of tidal salt marshes during their first year of life may fit the pattern of benefiting from an area without occupying it. Some are highly mobile, and tend to cross habitat boundaries in their quest for food and shelter. They are generally not

habitat specialists but rather are opportunistic in utilizing the resources of the estuarine landscape. Restoration planners should and must, therefore, view restoration goals in the context of the habitat mosaic and the exchange of materials and organisms between adjacent habitats (e.g., salt marshes and the open waters of the estuary). Stated simply, salt marshes do not function in isolation when supporting estuarine secondary production, but rather are integrated components of larger systems. Moreover, the open waters of the estuary may be donor-controlled systems, i.e., systems in which the rate of import, availability, or dynamics of allochthonous resources (such as products of the salt marsh), is controlled by external donor systems rather than by consumers. Indeed, consumers may be more abundant when supported by allochthonous resources than if supported solely by the *in situ* resources of open waters (POLIS *et al.*, 1995). The latter concept is critical in restoration ecology, because failure to account for trophic subsidies in the open estuary may result in restoration designs that have negative feedback on the recruitment success of numerous marine transients.

CHILDERS *et al.* (2000) captured these concepts in their description of the interaction among estuarine habitats in the support of fisheries. Their conceptual model posits integrated subsystems linked by an overlying water column that mediates functional processes across subsystem boundaries. Nutrient and organic matter flux associated with the movements of animals, especially juvenile marine transients, were also recognized as important vectors transcending system boundaries. The question of whether specific habitats confer disproportionate survival advantage to young marine transients is still rigorously debated (BECK *et al.*, 2001). In our view, trophic subsidies to donor-controlled systems may confer survival advantages on young nekton that depend on exported products from donor habitats. Thus the definition of nursery habitat by BECK *et al.* (2001) as places where the "contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur" may be a special case. Both the movements of animals and the flux of nutrients and organic matter by tidal action (including pulsed events) creates regionally specific nutrient "recipes" that marine transients can access virtually throughout the estuary. On a landscape scale, some marine transients appear to treat estuaries as fine-grained and readily utilize

all habitats. Others, including estuarine residents, may be obligate marsh dwellers that treat the landscape as increasingly coarse-grained (LEVINS, 1968; LITVIN and WEINSTEIN, 2003). In this paper, we discuss the integration of life history strategy and landscape scale considerations into restoration planning based on our previous research on marine transients and estuarine resident finfish in Delaware Bay, USA.

From a restoration ecology perspective, we pose two questions:

- Which geomorphological characteristics of tidal salt marshes promote exchange of material and organisms?
- Does the marsh invader *Phragmites australis* interfere with exchange processes in tidal salt marshes?

Addressing these questions will help focus future wetland restoration designs not only on functional elements of the habitat itself, but also on *promoting exchange* of materials and organisms between the habitat being restored and the adjacent estuary. Because our research has also focused on the invasive plant, *Phragmites australis*, and because this species has gained widespread attention in restoration projects, we use *Phragmites* to highlight certain restoration principles that apply to brackish wetland habitats.

Stable isotope data for marine transients from Delaware Bay are used to highlight the importance of individual life history strategies and to punctuate the argument for habitat connectivity in restoration designs. To illustrate this premise, we investigate the trophic spectrum of three species: an estuarine resident, *Morone americana* (white perch), and two marine transients, *Anchoa mitchilli* (bay anchovy) and *Cynoscion regalis* (weakfish). We included the marine transients to highlight the flow of nutrients from marsh primary producers to estuarine-dependent species on an estuary-wide (landscape) scale. The concept of the trophic spectrum was first described by DARNELL (1961) and reintroduced by POLIS and STRONG (1996) who commented that, with increasing diversity and reticulation in food webs, species often feed at multiple trophic levels rather than at individual levels, thereby blurring the latter into trophic spectra.

Finally, we ask the question, where do we go from here? In suggesting an answer, we will set forth some restoration design criteria that treat



Figure 1. Classic geomorphology for a relatively undisturbed mature tidal salt marsh. Photograph courtesy of R.T. Kneib, University of Georgia.

tidal salt marshes as part of interacting estuarine subsystems as depicted by CHILDERS *et al.* (2000).

#### WHICH GEOMORPHOLOGICAL CHARACTERISTICS OF TIDAL SALT MARSHES PROMOTE EXCHANGE OF MATERIAL AND ORGANISMS?

Several components of the geomorphological setting in Atlantic coast salt marshes are believed to be critical to the transfer of primary production to consumers and in determining the rates at which secondary productivity occurs in open waters of the estuary:

- The “classic” marsh drainage is a fourth- or fifth-order system characterized by high drainage density and high bifurcation ratios, extensive sinuosity, long stream lengths, and open water to intertidal marsh ratios of about 4:1 (Figure 1). The marsh surface is highly reticulated with plant tussocks interspersed with first-order streams (ZIMMERMAN *et al.*, 2000).

The small streams function much like a capillary network in the efficient exchange of materials (detritus, nutrients, dissolved organic matter [DOM], phytoplankton, fauna, etc.). Additionally, small nekton have access to virtually the entire vegetated marsh surface via first-order rivulets (ROZAS *et al.*, 1988).

- About 2% of the marsh surface in many Atlantic coast marshes consists of standing water in pools and ponds (RUBINO, 1991) and provides important nursery areas for marsh resident species (LITVIN and WEINSTEIN, 2003).
- Microtopography associated with high drainage density, sinuosity, and marsh surface reticulation is equated with extensive “edge,” thus enhancing material exchange and trophic relays (*i.e.*, the role of nekton in the transport of production across marsh landscapes to the open estuary; KNEIB, 1997).
- Depositional creek banks are common features of undisturbed marshes that may serve as predation refugia for the earliest life stages of nek-

ton (McIVOR and ODUM, 1998) and may be critical substrates for benthic microalgal production, especially during the summer and early fall when shading by the macrophyte canopy is at a maximum.

- *Spartina* spp. and many other marsh plants decompose relatively quickly and may be available to consumers by the end of the first growing season (FRY *et al.*, 1992; NEWELL, 1993). Benthic microalgae and many phytoplankton, with their high palatability and food chain efficiency, are also readily assimilated by many consumers (CURRIN *et al.*, 1995; SULLIVAN and MONTCREIFF, 1990).
- Typically, the intertidal low marsh is flooded for about 4–5 h during mean tides, thus allowing for extended access to the marsh plain by nekton and other consumers, and for the effective removal of toxins and the exchange of nutrients to support macrophyte growth. Alternatively, during low tides, the surface of the marsh sediments are exposed and aerated.

All of these traits of the intertidal marsh surface and the associated drainage network are critical to the efficient exchange of nutrients to the open estuary, where the preponderance of marine transients reside during their first year of life.

#### DOES *PHRAGMITES AUSTRALIS* INTERFERE WITH EXCHANGE PROCESSES IN TIDAL SALT MARSHES?

*Phragmites australis* (Cav.) Trin ex Steud, or common reed, is native to North America, but an introduced, highly invasive variety, most likely the “M” haplotype (SALTONSTALL, 2002), now occupies wetlands in large parts of the northeastern U.S. and all 48 conterminous states (CHAMBERS *et al.*, 1999). The introduced form of *P. australis* has dramatically expanded its range since the turn of the century and is now the dominant macrophyte in many brackish marshes, often forming extensive monocultures in the mid-Atlantic and New England states and along the Mississippi Delta region. Invasion success has appeared to accelerate in the past 40 years, and in many areas *P. australis* is now expanding its range at  $\sim 1\text{--}6\% \text{ y}^{-1}$ . Where extensive monocultures of *P. australis* cover the intertidal marsh surface, it is believed that changes in drainage density and other geomorphic features affect hydrology and hydroperiod. Over time, the marsh surface configuration departs more and more from the classic form described earlier (Fig-

ure 1), and perhaps with it, a deterioration of natural exchange processes. The near monocultures of *P. australis* in many meso-oligohaline marshes may have at least three physical effects on marsh function: 1) the normal hydroperiod of the marsh may be altered (WINDHAM, 1995, 1999), 2) reduced tidal exchange allows *P. australis* to extend its range into lower elevations and replace other macrophytes (WINDHAM and LATHROP, 1999), and 3) expansion of *Phragmites* results in isolated “islands” of remaining *Spartina* stands and other native species with diminished function (WEINSTEIN and BALLETO, 1999). Stands of *P. australis* that surround extensive portions of the marsh appear to restrict both sheet flow and the free movement of aquatic organisms into the marsh so that some portions of the marsh surface become virtual extensions of the uplands. The literal drying out of the marsh plain due to increased elevation tends to eliminate the smallest standing pools and rivulets that are critical habitat for larvae and early juveniles of marsh resident finfishes (ABLE and HAGAN, 2003). Because *Phragmites* is such a highly successful competitor it tends to form monocultures over extensive areas of marsh, reducing biodiversity and habitat complexity (CHAMBERS *et al.*, 1999). All of these factors have the potential to severely impact habitat quality in a *Phragmites*-dominated marsh and are in direct conflict with the perceived function of an undisturbed marsh system. *Phragmites* control, therefore, has become a central issue in the management and restoration of brackish marshes along much of the Atlantic seaboard.

#### PATTERNS OF NUTRIENT FLUX IN THE TROPHIC SPECTRUM OF ESTUARINE RESIDENT AND MARINE TRANSIENT FINFISHES IN DELAWARE BAY, A STABLE ISOTOPE APPROACH

In several respects, Delaware Bay (Figure 2) is an ideal system in which to investigate landscape-level trophic linkages between primary producers and consumers. Strongly light-limited (PENNOCK and SHARP, 1986), the Bay is largely devoid of submerged aquatic vegetation, and standing crops of macroalgae are low. *Phragmites australis*, a  $C_3$  plant with a unique stable isotope signature, occurs in vast monocultures in brackish wetlands covering approximately 32,000 ha of intertidal marsh in the meso-oligohaline zone. Because urbanization and commercialization of much of the

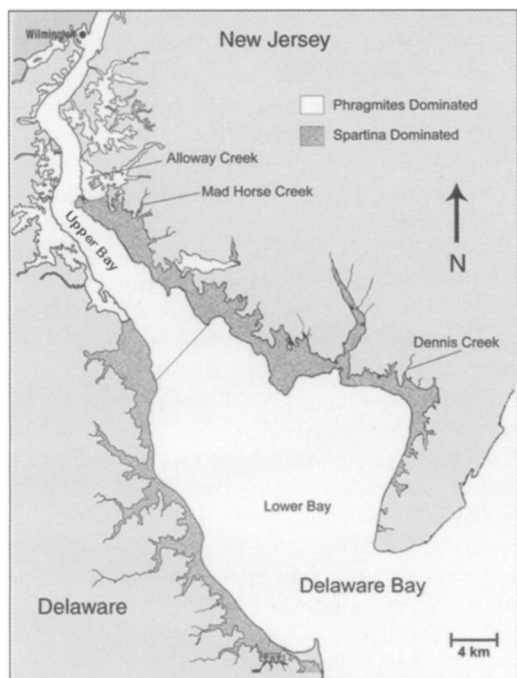


Figure 2. Fish collections were made at randomly selected stations in lower and upper Delaware Bay open water zones and in *Spartina*-dominated (Dennis Creek and Mad Horse Creek), and *Phragmites*-dominated (Alloway Creek) marshes. At each location, an attempt was made to capture *Cynoscion regalis* (weakfish), *Anchoa mitchilli* (bay anchovy), and *Morone americana* (white perch).

tidal fresh reach of the Delaware River shoreline results in greatly reduced terrestrial inputs from forested lands, *P. australis* serves as a primary source of nutrients in brackish areas of the estuary, and hence can be a critical biomarker for detecting the flow of nutrients from  $C_3$  macrophytes to local consumers in oligohaline waters. Although we have occasionally detected anthropogenic inputs of carbon and nitrogen, most likely from sewage, isotope signatures of finfish in Delaware Bay are primarily products of macrophyte (*Spartina* spp., *P. australis*), benthic microalgae and phytoplankton production (WAINRIGHT *et al.*, 2000; WEINSTEIN *et al.*, 2000; CURRIN *et al.*, 2003; LITVIN and WEINSTEIN, 2003).

During 1998 and 1999, bay anchovy, white perch, and juvenile weakfish were captured with otter trawls at various locations throughout the Delaware Bay in salt marsh creeks and open waters (Figure 2). Because bay anchovy and white

perch were collected in a separate study from juvenile weakfish, it should be noted that not all species were targeted for collection at each location. Salt marsh habitats sampled included Dennis Creek, located in polyhaline waters; Mad Horse Creek, a meso-oligohaline site adjacent to the upper bay; and Alloway Creek, a meso-oligohaline *Phragmites* degraded marsh in the upper bay. Two open water areas were also sampled, designated Lower Bay and Upper Bay (Figure 2), and demarcated by the polyhaline-mesohaline transition zone. Primary producers, including dominant macrophytes, benthic microalgae, and phytoplankton, were also collected in spring and fall (during senescence) in both years. Details of the fish and vegetation collections and analyses have been reported previously and are not repeated here (WAINRIGHT *et al.*, 2000; WEINSTEIN *et al.*, 2000; LITVIN and WEINSTEIN, 2003).

#### The Use of Stable Isotopes in Salt Marsh Research

The elements carbon, nitrogen, and sulfur occur in multiple forms in nature, commonly as  $^{12}C$ ,  $^{14}N$ , and  $^{32}S$ , but much more rarely as stable  $^{13}C$ ,  $^{15}N$ , and  $^{34}S$ . The ratios of "heavier" isotopes to the common, lighter forms,  $^{13}C/^{12}C$ ,  $^{15}N/^{14}N$ , and  $^{34}S/^{32}S$ , in plant and animal tissues have been used to study the structure of terrestrial and aquatic food webs. Because of differences in photosynthetic chemical pathways and species-specific discrimination between the two isotopic forms of each element, some plants are "heavier" due to the presence of a greater proportion of the heavy isotope, while others are "lighter" by virtue of a smaller proportion of the heavy isotope. Consequently, plant or animal tissues are described as either "enriched" or "depleted" in their relative ratios of heavy-to-light isotopes.

It is also known that the ratios are either conserved or fractionated in predictable ways as these elements move through food webs to higher trophic levels (MICHENER and SHELL, 1994). Thus, the isotopic composition of an animal feeding at any level in the food web can be traced back to the primary producers at the base of the food web. If more than one food is available (the typical case), consumers will have isotopic signatures that are intermediate between the proportions of foods they eat.

The stable isotopes of C, N, and S have been used to advance our understanding of food-web re-

relationships and energy flow in estuaries, and to examine trophic linkages between producers and consumers. Despite the physical mixing of end members, the conservative nature of isotopic ratios allow for discrimination among carbon and other nutrient sources, and helps determine the origin of organic matter in natural systems (FRY and SHERR, 1984; CIFUENTES *et al.*, 1988; PHILLIPS and GREGG, 2001).

Isotopic composition for carbon, nitrogen, and sulfur is generally expressed in  $\delta$  notation where a negative sign ( $-$ ) indicates depletion and a positive sign ( $+$ ) enrichment of the heavy isotope relative to the lighter isotope according to the following relationship:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X =  $^{13}\text{C}$ ,  $^{34}\text{S}$ , or  $^{15}\text{N}$ , and R =  $^{13}\text{C}/^{12}\text{C}$ ,  $^{34}\text{S}/^{32}\text{S}$ , or  $^{15}\text{N}/^{14}\text{N}$  of the samples and the standards.

Because measurements are subject to day-to-day variations in sample preparation and instrument performance, the isotopic ratio in a given sample is typically compared to a "reference standard."

The  $\delta^{13}\text{C}$  range is generally widest among phytoplankton and algae that depend on variable sources of dissolved inorganic carbon (MABERLY *et al.*, 1992; LAJTHA and MARSHALL, 1994). Benthic microalgae tend to be enriched in  $^{13}\text{C}$  because of boundary layer effects and the greater diffusional resistance of  $\text{CO}_2$  or  $\text{HCO}_3^-$  in water (FRANCE, 1995a), whereas marsh macrophytes and terrestrial plants are more tightly constrained because their primary source of  $^{13}\text{CO}_2$  is atmospheric. In contrast, variability in  $\delta^{34}\text{S}$  is highest in macrophytes (ranging from  $-10\text{‰}$  to  $+13.05\text{‰}$ ) because they utilize S from variable sources including the pool of lighter sulfur in marsh sediments (STRIBLING and CORNWELL, 1997).

Taken together,  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  can distinguish phytoplankton signatures from among terrestrial, marsh, and benthic algal signatures. Although marsh-derived isotopic signatures from organic matter sources are generally distinct, seasonal overlap in the signatures can sometimes be a confounding factor, especially in brackish reaches of the estuary (FOGEL *et al.*, 1992; CURRIN *et al.*, 2003; but see LITVIN and WEINSTEIN, 2003). Variability of  $\delta^{34}\text{S}$  is observed to be lowest in macroalgae and phytoplankton ( $\delta^{34}\text{S} \approx +18\text{‰}$ ) because they use seawater sulfate.  $\delta^{34}\text{S}$  values for microphytobenthos are intermediate (4 to 14‰) depending upon the proportions of reduced sulfur and seawater sulfate at the sediment/water interface (SULLIVAN

and MONTCRIEFF, 1990; CURRIN *et al.*, 1995; STRIBLING and CORNWALL, 1997). Thus, stable sulfur and carbon isotopes can be used to differentiate between benthic versus pelagic nutrient sources, and rooted macrophyte versus algal nutrient sources.

The degree of discrimination among nutrient sources can be further refined by use of stable isotopes of nitrogen, with the recognition that shifts (and variability) in isotope ratios of N occur with each trophic step ( $\sim 2$  to  $4\text{‰}$  for  $\delta^{15}\text{N}$  versus  $<1\text{‰}$  for  $\delta^{13}\text{C}$ ) (PETERSON and FRY, 1987; MICHENER and SHELL, 1994). Dual isotope plots of C and N are particularly useful in distinguishing among terrestrial plants and *in situ* sources of plant matter in estuaries (FRY and SCHERR, 1984; FRANCE, 1995a,b). In earlier studies, it was noted that the natural range of  $\delta^{15}\text{N}$  in plants is smaller than that of  $\delta^{13}\text{C}$  (GEARING, 1988) and that within estuaries the difference in  $\delta^{15}\text{N}$  between primary producers are relatively small while terrestrial organic matter signatures are significantly lighter ( $\sim 0 \pm 2\text{‰}$ ).

#### Life History Traits of Species that Utilize Estuaries

We have previously defined four life history strategies among the nekton that utilize tidal salt marshes directly or appear to otherwise benefit from primary production in marshes (LITVIN and WEINSTEIN, 2003). Type I species are marsh residents who spend their entire life cycle within the confines of the marsh, which consists of the intertidal marsh surface and intertidal and subtidal marsh creeks (MINELLO *et al.*, 2003). Common mummichog (*Fundulus heteroclitus*) and sheepshead minnow (*Cyprinodon variegatus*) do not have marine life stages and may be marsh obligates. Type II species are marine-transient or estuarine-resident species, such as the spot (*Leiostomus xanthurus*) and white perch, which take up seasonal residence in subtidal marsh creeks for extended periods and exhibit some of the highest rates of seasonal production measured for estuarine fauna (WEINSTEIN, 1983). Type III species include juvenile weakfish, which we have studied extensively. They are marine transients that are seasonally abundant in salt marshes but appear to be relatively short-term residents in marshes compared to Type II taxa. Finally, Type IV species are the larger marine nekton that are mostly or entirely marine as adults, but which may periodically

make feeding forays into estuaries and benefit indirectly from marsh production (e.g., via “trophic relays”, KNEIB, 1997) or export of marsh products into coastal food webs. Obviously, these categories are artificial constructs, and their distinctions are matters of degree rather than strictly exclusive classifications. Nevertheless, they provide a convenient way of tracking the nature and duration of trophic linkages between the marsh and the consumers that benefit from them.

While all of the taxa studied (and others) appear to take advantage of the organic matter produced in salt marshes, we will demonstrate that the relative contribution to their diet varies as a function of their relative mobility, ontogenetic factors, feeding strategy, and seasonal patterns of habitat use. Type III marine transients, for example, appear to use the entire estuary without specific ties to a particular habitat type. They are abundant throughout Delaware Bay during their first year—in tidal creeks, shoals, and open waters. From a life history perspective, this makes sense, because these highly mobile taxa can readily “sample” habitat units for abundant food or suitable refuge and move on to the next habitat patch when an area becomes unsuitable or when food supplies are reduced or exhausted. However, there seems to be a general pattern of movement superimposed upon the more random sampling of habitat patches. Early in the year some marine transients tend to accumulate in upper or lateral (i.e., tributary) reaches of the estuary, and as they grow (to some critical size?), tend to move down estuary to the lower reaches (CHAO and MUSICK, 1977; LITVIN and WEINSTEIN, in press, but see PAPERNO *et al.*, 2000). The latter authors noted that the primary nurseries for juvenile weakfish in Delaware Bay were located at salinities < 20 psu where density, growth, and survival were generally at a maximum. Juveniles tended to remain in this region of the estuary until August, when down-bay emigration ensued.

Superimposed upon the patterns described above are the proximate uses of the water column by each species. Whereas white perch tend to be mainly demersal, weakfish appear to feed throughout the water column, and bay anchovy appear to be the most pelagically oriented of the three species (ABLE and FAHAY, 1998; LITVIN and WEINSTEIN, 2003). As will be demonstrated below, these behavioral traits are directly linked to the contributions of specific primary producers to the food webs of each species.

### Trophic Linkages in White Perch, Bay Anchovy, and Juvenile Weakfish

A comparison of stable isotope signatures in the tissues of white perch, bay anchovy, and juvenile weakfish (Figure 3a, b; for detailed statistical analyses of the data, see LITVIN and WEINSTEIN 2003; LITVIN and WEINSTEIN, in press) suggests that local sources of organic matter are the primary drivers of nutrient flux in the food webs of these species (see also DEEGAN and GARRITT, 1997). Moreover, the consistency of the signatures suggest that there is considerable site fidelity exhibited by these taxa in that their isotopic composition, on average, reflected the unique recipe of nutrients in the habitats in which they were captured.

Several patterns emerged in the data. In salt marshes, there was a transition in whole-body isotopic composition in all three species that could be associated with the change in the dominant macrophytes from *Spartina* spp. in the lower bay through a transition zone to the upper bay where *Phragmites australis* formed virtual monocultures over extensive areas (Figure 2; Figure 3A). Superimposed on the vegetation dominance pattern was the relative contribution of benthic microalgae in the order of white perch > juvenile weakfish > bay anchovy. This pattern mirrored the increasing benthic-to-water column orientation of the three taxa. Conversely, and as expected, phytoplankton (as SPM) contributed more to bay anchovy and weakfish biomass than did benthic microalgae, although the latter appeared to make a greater contribution to weakfish than to bay anchovy (Figure 3a). These patterns generally held in open waters with bay anchovy and weakfish separated by the relative contributions of *Spartina* spp. and *Phragmites australis* in the transition from lower to upper Bay. (White perch were not collected in the open bay.) However, juvenile weakfish appeared to be less dependent on benthic microalgae when in open waters where they utilized phytoplankton to approximately the same degree as bay anchovy (Figure 3b).

It is clear from the results described above, and our earlier work (WAINRIGHT *et al.*, 2000; WEINSTEIN *et al.*, 2000; CURRIN *et al.*, 2003; LITVIN and WEINSTEIN, 2003), as well as that of others (DEEGAN and GARRITT, 1997), that marine transients benefit from the presence of salt marshes without necessarily having to occupy them. Thus the estuarine “commisary” serves up different recipes



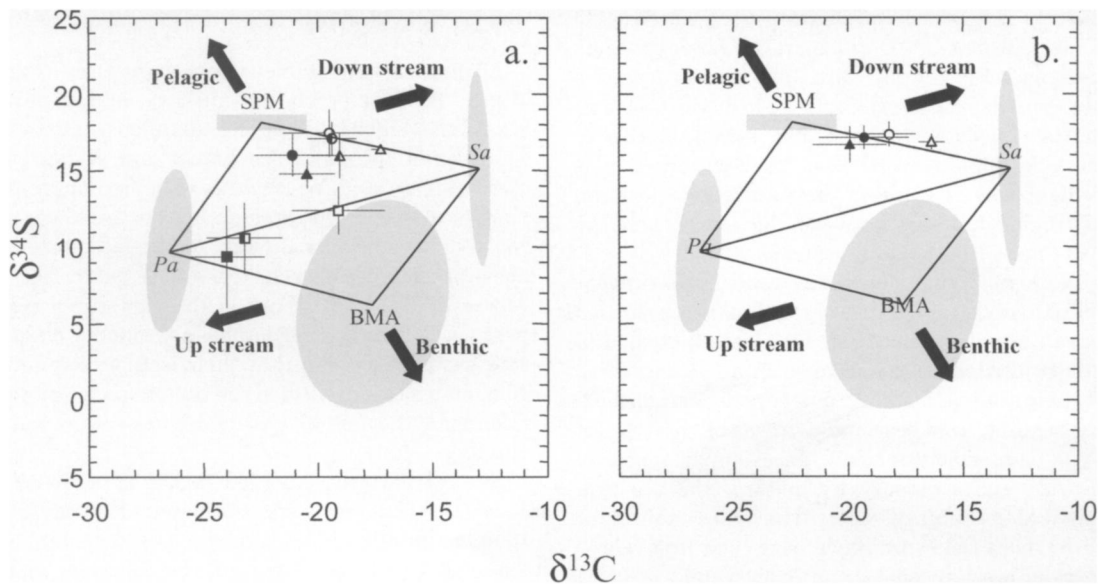


Figure 3. Dual isotope plots for  $\delta^{34}\text{S}$  on  $\delta^{13}\text{C}$  for a) *Cynoscion regalis* (juvenile weakfish) (triangles), *Anchoa mitchilli* (bay anchovy) (circles) and *Morone americana* (white perch) (squares) collected in salt marshes (Dennis Creek (open symbols), Mad Horse Creek (half filled symbols), and Alloway Creek (filled symbols)), and b) *Cynoscion regalis* (juvenile weakfish) (triangles) and *Anchoa mitchilli* (bay anchovy) (circles) collected in lower (open symbols) and upper (filled symbols) Delaware Bay open waters. All error bars shown are  $\pm$  one standard deviation (LITVIN and WEINSTEIN, 2003). Primary producers collected in salt marshes are presented as  $\pm$  one standard deviation ellipses (suspended particulate matter [SPM], benthic microalgae [BMA], *Phragmites australis* [Pa], and *Spartina alterniflora* [Sa]; WEINSTEIN *et al.*, 2000). Arrows indicate primary direction of nutrient flux influence from each primary producer category to the three finfish species.

in different regions, and the many estuarine-dependent species apparently take full advantage of these varied combinations of primary producers when seeking energy for rapid growth and survival. Of course, the estuary as a whole is characterized by gradients in available organic matter, a boundary-less state, rather than sharp transitions from one food source to the next (Figure 4). For bay anchovy and juvenile weakfish, both marine transients, we have observed a gradual change in whole body stable isotope composition, trending from higher proportions of marsh macrophytes and benthic microalgae in and near tidal creeks to higher proportions of phytoplankton organic sources as one moves towards open waters (LITVIN and WEINSTEIN, 2003). Similarly, along the long axis of

the estuary, *Phragmites australis* tends to supply a greater proportion of the nutrition of marine transients in and near brackish salt marshes, whereas *Spartina alterniflora* and benthic microalgae dominate the nutrition of these taxa in and near marshes in the mid and lower estuary (at salinities greater than about 10‰). Yet there is rarely a time when the signatures of virtually all primary producers are *not* detected in most taxa whether they are marsh resident (WAINRIGHT *et al.*, 2000; CURRIN *et al.*, 2003), estuarine resident, or marine transient (WEINSTEIN *et al.*, 2000; LITVIN and WEINSTEIN, 2003). We are not fully certain of the specific export routes for salt marsh primary production—as tidal flux of particulate organic matter, as dissolved organic carbon (especially in

Figure 4. Conceptual diagram of nutrient gradients developed from data on primary producer sources in Delaware Bay. Primary colors (blue, red, yellow) are used to depict the main *local* source of organic matter: blue, *Spartina* spp.; red, *Phragmites australis*; yellow, phytoplankton; and diagonal hatching, benthic microalgae (PETERSON *et al.*, 1985; DEEGAN and GARRITT,

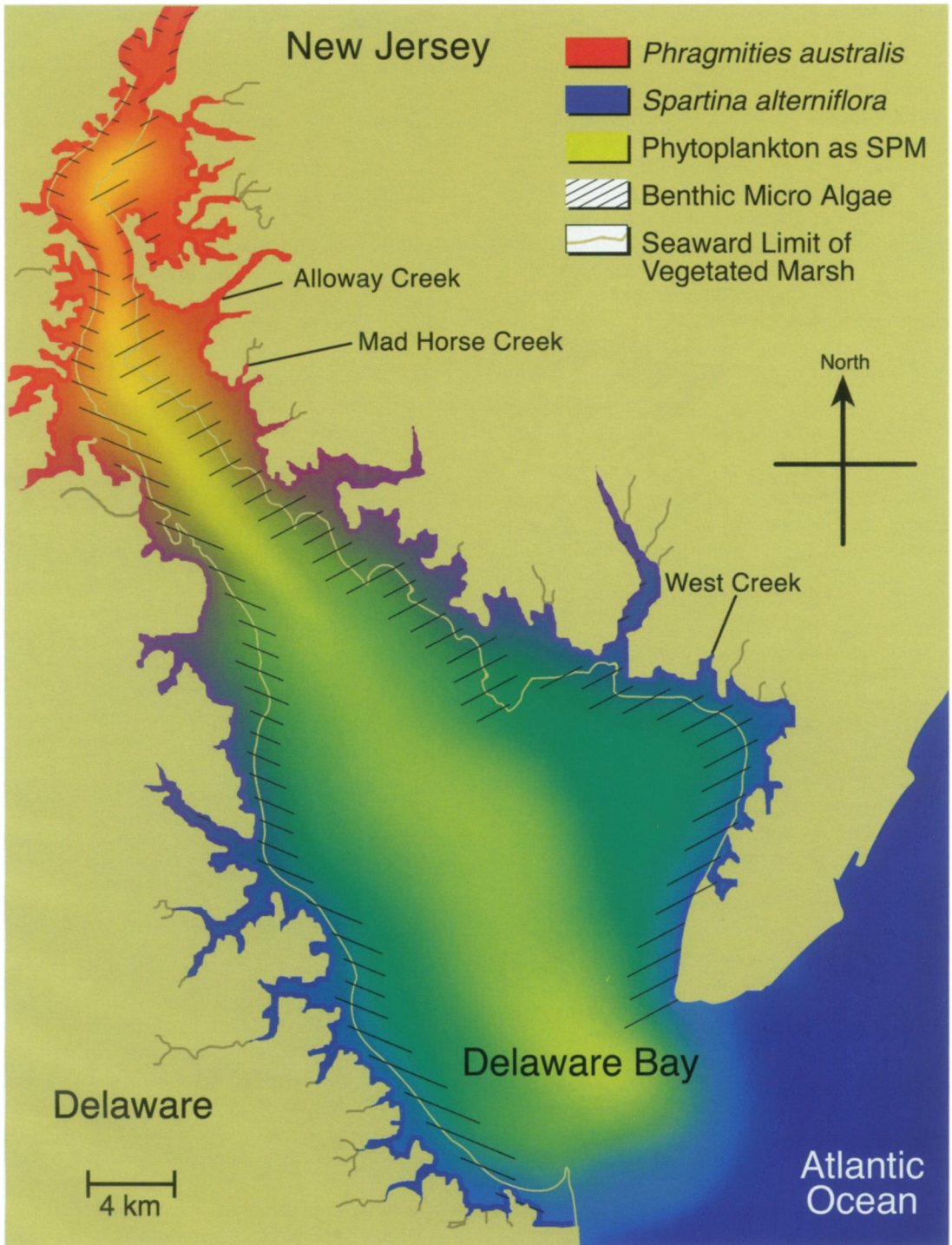


Figure 4. Continued. 1997; CHANTON and LEWIS, 2002). Each organic matter source is “blended” with the others to depict the gradients of general availability to secondary consumers in the food web as reflected in the results of this study. Nutrient flux and the establishment of the gradients likely result from a combination of pulsing events, trophic relays, spawning migrations, dissolved organic matter export, and detrital infusion.

those portions of the estuary where the marsh: open water ratio  $> 0.8$  (ELDRIDGE and CIFUENTES, 2000), as allochthonous inputs, in pulsed events, or in the tissues of emigrating marine transients themselves. It is clear that by whatever route, nutrients from the marsh are reaching marine transients *whether or not they spend time in the marsh*.

We appear to have come full circle. Perhaps TEAL (1962) was correct all along when he suggested that 45% of the primary production in Georgia salt marshes was available to estuarine consumers. However, rather than detrital export driving the mechanics of the process, as Teal suggested, we postulate the process is far more complex, and as noted earlier, these considerations need to be incorporated into restoration planning and designs.

#### WHERE DO WE GO FROM HERE?

A daunting challenge in modern ecology is to determine how changes through time and space influence population and community dynamics. Like other natural systems, salt marshes are open entities and may be influenced substantially by factors from outside the local system, *i.e.*, influences between habitats can exceed internal, within-habitat factors (POLIS *et al.*, 1995). This argues for the whole estuary, or landscape scale, approach that we have adopted in our research to examine multi-habitat dynamics (LITVIN and WEINSTEIN, in press). If we consider a Type III species like the weakfish in salt marsh restoration designs, it quickly becomes obvious that we are dealing with a species that lives in a dynamic mosaic of different patches and habitats that varies in productivity and in the composition and abundance of resources (the "recipes" that we have alluded to). Moreover, as manifested in isotopic signatures of the three taxa studied, the production and availability of resources change depending on scales. They change through space on scales from meters (within the water column in tidal creeks) to kilometers (in the marsh transition from *Spartina*-dominated to *Phragmites*-dominated plant communities and in the open estuary from the lower to upper bay) (Figures 3 and 4; LITVIN and WEINSTEIN, in press), and they change temporally on diel, seasonal, and inter-annual scales (LITVIN and WEINSTEIN, in press). Weakfish survival during their first year is likely influenced by spatial dynamics of the entire estuarine mosaic and the resources therein, rather than on habitat specialization. Except for a rela-

tively brief period ( $\sim 30$  days) early in recruitment where there is measurable site fidelity based on stable isotope signatures unique to certain areas of the estuary (LITVIN and WEINSTEIN, 2003), larger juveniles seemed to have little direct dependence on salt marshes. Thus, juvenile weakfish may do well in various combinations of habitat patches, taking advantage of the trophic resources therein and then moving on to other segments of the mosaic where suitable food (and perhaps refuge from predators) is found. The Type III strategy is likely common in marine transients that have evolved life history strategies adapted to rapid temporal and spatial changes in resource availability and environmental harshness (WINEMILLER and ROSE, 1992). The metapopulation dynamics of Type III marine transients suggests that *estuaries*, not necessarily the specific habitats therein, are important to these species, and that salt marshes do not necessarily function as primary nurseries (WEINSTEIN, 1979; BECK *et al.*, 2001). Instead, salt marshes simply provide trophic subsidies to increase estuary-wide secondary production. Future research should focus on the means by which salt marsh production reaches open waters; in this sense we have indeed come full circle to the importance of marshes as exporting systems.

Based on our previous experience with one of the largest estuarine wetland restoration projects ever undertaken (more than 8000 ha) (WEINSTEIN *et al.*, 1997; TEAL and WEINSTEIN, 2002; WEINSTEIN *et al.*, 2001; WEINSTEIN and WEISHAR, 2002), we offer the following design parameters to facilitate tidal exchange and access by fauna between the marsh and adjacent open waters.

- (1) A fourth- or fifth-order drainage system characterized by high drainage density and sinuosity should be engineered to maximize edge (WEINSTEIN *et al.*, 2001).
- (2) Average marsh plain elevations should lie slightly below mean high tide so that the marsh surface hydroperiod is characterized by an inundation cycle of approximately 4.5 h and areas above mean tide are flooded approximately 50% of the time (TEAL and WEINSTEIN, 2002).
- (3) Ideally, sites should be selected where a ready supply of plant propagules are located nearby. If such conditions exist, and the marsh plain elevations are suitable, rapid recolonization will be realized without the expensive neces-

sity of planting desirable vegetation (WEINSTEIN *et al.*, 2001).

- (4) Subtidal creeks should be constructed in a way that provides refugia for Type I and Type II species (marsh residents and marsh facultative marine transients; LITVIN and WEINSTEIN, 2003).
- (5) An intertidal marsh-to-subtidal water ratio of about 4:1 should be constructed, with the marsh surface inundated by approximately 2–4% standing water in shallow pools.
- (6) In brackish marshes, a management plan should be developed to break up any *Phragmites australis* monocultures, and restore first-order tidal creeks to at least 80% of the marsh plain.

We also strongly recommend that the initial restoration plan include adaptive management follow-up of at least five years, with funding for this activity included in the project permit. Similarly, multidisciplinary teams of ecologists, fishery scientists, and botanists, geologists, and engineers should be established early in the restoration design phase and perhaps be made mandatory. The combined experience of the team will help ensure the most relevant set of design criteria for the specific project under development.

If tidal elevation and surface elevations are correct, much will follow that will ensure efficient exchange of organisms and materials to and from the marsh. The importance of the drainage system and its components cannot be overly emphasized, and was recognized long before marsh restoration became the vogue:

“The true nursery ground of the estuary is not so much the large open water rivers and sounds as the salt marshes and narrow tidal creeks (HAINES, 1979).”

“Our present view of the food web of the marsh and estuary suggests that the preservation of fisheries depends as much upon the protection of the smaller tidal creeks as upon protection of the marsh and its *Spartina* production (WEIGERT and POMEROY, 1981).”

These early observations were ultimately supported by subsequent research conducted on first-order drainages. For example, KNEIB (1997) used flume weirs to focus on access to forage sites by young nekton and demonstrated that not only were fish densities at high tide greater at high-drainage-density sites, but that fish were also sig-

nificantly more abundant in high- than in low-intertidal habitats at high-drainage-density sites. Similarly, ROZAS *et al.* (1988) noted that fishes were on average three times more abundant in rivulets (first-order streams) than at creek bank access sites. Also, marsh residents (Type I) used the intertidal marsh extensively, arriving with an average of < 10% of their stomach volume filled, but leaving with between 60% and 80% gut fullness (ROZAS *et al.*, 1988). The importance of edge has been cited by numerous authors (see TEAL and WEINSTEIN, 2002; recently summarized by MINELLO *et al.*, 2003).

We hope that future wetland restoration designs will reverse the earlier problems inherent in the Clean Water Act, Section 404 program (TURNER *et al.*, 2001), and gone forever will be success criteria like “85% survival of planted vegetation after three years.” The field of restoration science has progressed far beyond the woefully inadequate restoration design criteria of most Section 404 permits.

#### ACKNOWLEDGMENTS

Without the support of J. H. Balletto of the PSEG Corporation, none of the research leading to this synthesis would have been possible. We thank J. M. Teal and two anonymous reviewers for their insightful comments on earlier drafts of the manuscript. Thanks also to M. Samuels for preparing the color figures, and to R. Kneib for providing the photograph used in Figure 1. This study was partially supported by grants 98-NER-027 (NOAA; Saltonstall-Kennedy) and # NA 17RG1396 (NOAA-Aquatic Nuisance Species). This paper is contribution # NJSG-03-537, of the New Jersey Sea Grant College Program.

#### LITERATURE CITED

- ABLE, K.W. and FAHAY, M.P., 1998. *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. New Brunswick: Rutgers University Press, 342p.
- ABLE, K.W. and HAGAN, S.M., 2003. The impact of common reed, *Phragmites australis*, on essential fish habitat: influence on reproduction, embryological development, and larval abundance of mummichog (*Fundulus heteroclitus*). *Estuaries*, 26, 40–50.
- BECK, M.W.; HECK, K.L., JR.; ABLE, K.W.; CHILDERS, D.L.; EGGLESTON, D.B.; GILLANDERS, B.M.; HALPERN, B.; HAYS, C.G.; HOSHINO, L.; MINELLO, T.J.; ORTH, R.J.; SHERIDAN, P.F. and WEINSTEIN, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bio-science*, 51, 633–641.
- CHAMBERS, R.M.; MEYERSON, L.A. and SALTONSTALL, K.,

1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany*, 64, 261–273.
- CHAO, L.N. and MUSICK, J.A., 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *Fishery Bulletin, U.S.*, 75, 57–702.
- CHILDERS, D.L.; DAY, J.W., JR. and MCKELLAR, H.N., JR., 1980. Twenty more years of marsh and estuarine flux studies: revisiting Nixon. In: WEINSTEIN, M.P. and KREEGER, D.A. (eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Dordrecht, The Netherlands: Kluwer Academic, pp. 391–424.
- CIFUENTES, L.A.; SHARP, J.H. and FOGEL, M.L., 1988. Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. *Limnology and Oceanography*, 33, 1102–1115.
- CURRIN, C.A.; NEWELL, S.Y. and PAERL, H.W., 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series*, 121, 99–116.
- CURRIN, C.A.; WAINRIGHT, S.A.; ABLE, K.W., WEINSTEIN, M.P. and FULLER, C.M., 2003. Determination of food web support and trophic position of the mummichog (*Fundulus heteroclitus*) in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*), and restored salt marshes. *Estuaries*, 26, 495–510.
- DARNELL, R.M., 1961. Trophic spectrum of an estuarine community, based upon studies of Lake Ponchartrain, Louisiana. *Ecology*, 42, 553–568.
- DEEGAN, L.A. and GARRITT, R.H., 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series*, 147, 31–47.
- ELDRIDGE, P.M. and CIFUENTES, L.A., 2000. A stable isotope model approach to estimating the contribution of organic matter from marshes to estuaries. In: WEINSTEIN, M.P. and KREEGER, D.A. (eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Dordrecht, The Netherlands: Kluwer Academic Publishers, pp. 495–514.
- FOGEL, M.L.; CIFUENTES, L.A.; VELINSKY, D.J. and SHARP, J.H., 1992. Relationship of carbon availability in estuarine phytoplankton to isotopic composition. *Marine Ecology Progress Series*, 82, 291–300.
- FRANCE, R.L., 1995a. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine Ecology Progress Series*, 124, 307–312.
- FRANCE, R.L., 1995b. Nitrogen isotopic composition of marine and freshwater invertebrates. *Marine Ecology Progress Series*, 115, 205–207.
- FRY, B. and SHERR, E.B., 1984.  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science*, 27, 13–47.
- FRY, B.; HULLAR, M.; PETERSON, B.J.; SAUPE, S. and WRIGHT, R.T., 1992. DOC production in a salt marsh estuary. *Archives fur Hydrobiologia Beih*, 37, 1–8.
- GEARING, J.N., 1988. The use of stable isotope ratios for tracing the nearshore-offshore exchange of organic matter. In: JANSSON, B.O. (ed.), *Lecture Notes on Coastal and Estuarine Studies, Coastal Offshore Ecosystem Interactions*. Berlin: Springer-Verlag, pp. 69–101.
- HAINES, E.B., 1979. Interactions between Georgia salt marshes and coastal waters: a changing paradigm. In: LIVINGSTON, R.J. (ed.), *Ecological Processes in Coastal and Marine Systems*. New York: Plenum, pp. 35–46.
- HIGGS, E.S., 1997. What is good ecological restoration? *Conservation Biology*, 11, pp. 338–348.
- KATES, R.W.; CLARK, W.C.; CORELL, R.; HALL, J.M.; JAEGER, C.C.; LOWE, I.; MCCARTHY, J.J.; SCHELLNHUBER, H.J.; BOLIN, B.; DICKSON, N.M.; FAUCHEUX, S.; GALLOPIN, G.C.; GRUBLER, A.; HUNTLEY, B.; JAGER, J.; JODHA, N.S.; KASPERSON, R.E.; MABOGUNJE, A.; MATSON, P.; MOONEY, H.; MOORE, B., III; O'RIORDAN, T. and SVEDIN, U., 2001. Sustainability science. *Science*, 292, 641–642.
- KNEIB, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology Annual Reviews*, 35, 163–220.
- LAJTHA, K. and MARSHALL, J.D., 1994. Sources of variation in the stable isotopic composition of plants. In: LAJTHA, K. and MICHENER, R.H. (eds.), *Stable Isotopes in Ecology and Environmental Science*. London: Blackwell Scientific Publications, pp. 138–157.
- LEVINS, R., 1968. *Evolution in Changing Environments: Monographs in Population Ecology*. Princeton: Princeton University Press, 181p.
- LITVIN, S.Y. and WEINSTEIN, M.P., 2003. Life history strategies of estuarine nekton: the role of marsh macrophytes, benthic microalgae, and phytoplankton in the trophic spectrum. *Estuaries*, 26, 552–562.
- LITVIN, S.Y. and WEINSTEIN, M.P., 2004. Multivariate analysis of sulfur, carbon, and nitrogen stable isotopes as an indicator of nutrient flow from primary producers to juvenile weakfish (*Cynoscion regalis*) in the Delaware Bay estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, in press.
- MABERLY, S.C.; RAVEN, J.A. and JOHNSTON, A.M., 1992. Discrimination between  $^{12}\text{C}$  and  $^{13}\text{C}$  by marine plants. *Oecologia*, 91, 481–492.
- MCIVOR, C.C. and ODUM, W.E., 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology*, 69, 1341–1353.
- MICHENER, R.H. and SCHELL, D.M., 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: LAJTHA, K. and MICHENER, R.H. (eds.), *Stable Isotopes in Ecology and Environmental Science*. London: Blackwell Scientific, pp. 138–157.
- MINELLO, T.J.; ABLE, K.W.; WEINSTEIN, M.P. and HAYS, C., 2003. Salt marsh nurseries for nekton: testing hypotheses on density, growth, and survival through meta-analysis. *Marine Ecology Progress Series*, 246, 39–59.
- NEWELL, S.Y., 1993. Decomposition of shoots of a salt-marsh grass: methodology and dynamics of microbial assemblages. *Advances in Microbial Ecology*, 13, 301–326.
- NATIONAL RESEARCH COUNCIL (NRC), 1992. *Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy*. Washington: National Academy Press, 121p.
- PAPERNO, R.; TARGETT, T.E. and GREY, P.A., 2000. Spatial and temporal variation in recent growth, overall growth, and mortality of juvenile weakfish (*Cynoscion regalis*) in Delaware Bay. *Estuaries*, 23, 10–20.
- PENNOCK, J.R. and SHARP, J.H., 1986. Phytoplankton production in the Delaware Estuary: temporal and

- spatial variability. *Marine Ecology Progress Series*, 34, 143–155.
- PETERSON, B.J. and FRY, B., 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18, 293–320.
- PETERSON, B.J.; HOWARTH, R.W. and GARRITT, R.W., 1986. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science*, 227, 1361–1363.
- PHILLIPS, D.L. and GREGG, J.W., 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia*, 127, 171–179.
- POLIS, G.A. and STRONG, D.R., 1996. Food web complexity and community dynamics. *American Naturalist*, 147, 813–846.
- POLIS, G.A.; HOLT, R.D.; MENGE, R.A. and WINEMILLER, K., 1995. Time, space, and life history: influences on food webs. In: POLIS, G.A. and WINEMILLER, K. (eds.), *Food Webs: Integration of Patterns and Dynamics*. New York: Chapman & Hall, pp. 435–460.
- ROZAS, L.P.; McIVOR, C.C. and ODUM, W.E., 1988. Intertidal rivulets and creek banks: corridors between tidal creeks and marshes. *Marine Ecology Progress Series*, 47, 303–307.
- RUBINO, G.D., 1991. Chronocycling Geologic Processes on a Tidal Marsh from Aerial Photography. Newark, Delaware: University of Delaware, Masters thesis, 107p.
- SALTONSTALL, K., 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences*, 99, 2445–2449.
- STRIBLING, J.M. and CORNWELL, J.C., 1997. Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries*, 20, 77–85.
- SULLIVAN, M.J. and MONCREIFF, C.A., 1990. Edaphic algae are an important component of salt marsh food webs; evidence from multiple stable isotope analyses. *Marine Ecology Progress Series*, 62, 149–159.
- TEAL, J.M., 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43, 614–624.
- TEAL, J.M. and WEINSTEIN, M.P., 2002. Ecological engineering, design, and construction considerations for marsh restorations in Delaware Bay, USA. *Ecological Engineering*, 18, 607–618.
- TURNER, R.E.; REDMOND, A.M. and ZEDLER, J.B., 2001. Count it up by acre or function—mitigation adds up to net loss of wetlands. *National Wetlands Newsletter*, 23, 5–16.
- WAINRIGHT, S.A.; WEINSTEIN, M.P.; ABLE, K.W. and CURRIN, C.A., 2000. Relative importance of benthic microalgae, phytoplankton, and detritus of smooth cordgrass (*Spartina*) and the common reed (*Phragmites*) to brackish marsh food webs. *Marine Ecology Progress Series*, 200, 7–91.
- WEIGERT, R.G. and POMEROY, L.R., 1981. The salt-marsh ecosystem: A synthesis. In: POMEROY, L.R. and WEIGERT, R.G. (eds.), *The Ecology of a Salt Marsh*. New York: Springer Verlag, pp. 219–230.
- WEINSTEIN, M.P., 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin, U.S.*, 77, 339–357.
- WEINSTEIN, M.P., 1983. Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*) along a tidal creek-seagrass meadow coenocline. *Canadian Journal of Fisheries and Aquatic Sciences*, 40, 1633–1638.
- WEINSTEIN, M.P. and BALLETO, J.H., 1999. Does the common reed, *Phragmites australis*, reduce essential habitat for fishes? *Estuaries*, 22(3B), 793–802.
- WEINSTEIN, M.P. and WEISHAR, L.L., 2002. Beneficial use of dredged material to enhance the restoration trajectories of formerly diked lands. *Ecological Engineering*, 19, 187–201.
- WEINSTEIN, M.P.; BALLETO, J.H.; TEAL, J.M. and LUDWIG, D.F., 1997. Success criteria and adaptive management for a large-scale wetland restoration project. *Wetlands Ecology and Management*, 4, 111–127.
- WEINSTEIN, M.P.; LITVIN, S.Y.; BOSLEY, K.I.; FULLER, C.M. and WAINRIGHT, S.C., 2000. The role of tidal salt marsh as an energy source for juvenile marine transient finfishes: a stable isotope approach. *Transactions of the American Fisheries Society*, 129, 797–810.
- WEINSTEIN, M.P.; TEAL, J.M.; BALLETO, J.H. and STRAIT, K.A., 2001. Restoration principles emerging from one of the world's largest tidal marsh restoration projects. *Wetlands Ecology and Management*, 9, 387–407.
- WINDHAM, L., 1995. Effects of *Phragmites australis* Invasion on Aboveground Biomass and Soil Properties in Brackish Tidal Marsh of the Mullica River, New Jersey. New Brunswick, New Jersey: Rutgers University, Master's thesis, 61p.
- WINDHAM, L., 1999. Effects of an Invasive Reedgrass (*Phragmites australis*) on Nitrogen Cycling in Brackish Tidal Marshes of New York and New Jersey. New Brunswick, New Jersey: Rutgers University, Ph.D. thesis, 170p.
- WINDHAM, L. and LATHROP, L.G., JR., 1999. Effects of *Phragmites australis* (common reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. *Estuaries*, 22, 927–935.
- WINEMILLER, K.O. and ROSE, K.A., 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218.
- ZIMMERMAN, R.J.; MINELLO, T.M. and ROZAS, L.P., 2000. In: WEINSTEIN, M.P. and KREEGER, D.A. (eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Dordrecht, The Netherlands: Kluwer Academic, pp. 293–314.