

Reversing Two Centuries of Wetland Degradation: Can Science Better Inform Policy and Practice?

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Abstract Perhaps more than any other ecotone, the land–water interface has been “reclaimed” solely for human uses—living space, ports and harbors, and agriculture—essentially extirpating other goods and services that these ecosystems provide. Although the importance of ecosystem services associated with wetland transition zones has been increasingly recognized in the past 60 years, the approach to “restoration” and “rehabilitation” has largely lacked scientific rigor. The status of coastal wetland restoration science is discussed herein with specific attention to design criteria that attempt to restore wetland functions and ecological fidelity. Methods for better integration of restoration science and practice to inform policy, and the quantification of restored functions are described within the context of three case histories.

Keywords Restoration ecology • Linking structure with function • Essential fish habitat • Case histories

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Introduction

It is an open question whether ecosystem management will become a passing fad, an expansion of rigid bureaucratic procedures, or a sustaining foundation for learning to deal with interactions between people, nature, and economic activities (Holling 1996).

Restoration ecology straddles the interface of sustainability science and the reconciliation of human use of natural resources with the planet's ability to provide them. As the debate continues over whether humans have "escaped" the domination of natural laws or are still subject to them, Cairns (2000) expressed the concern that no matter how robust the science and technology of restoration ecology becomes, the science must enjoy societal acceptance of its dependence on ecosystem services as part of society's life support system. Unless this acceptance comes about, Cairns warns that the data will not be collected at the scale necessary to advance the science of restoration, and its development in a sustainability science framework will be hampered.

Restoration ecology also manages for change, fosters biodiversity and emphasizes the return of system functions, and goods and services to degraded ecosystems. An ecocentric framework for restoration is, therefore, an essential component of a transformation to global sustainability (Jackson and Hobbs 2009). Because humans dominate virtually all landscapes, the practice partially focuses on restoring ecosystem functions (e.g., flood storage capacity or storm buffering), that are not necessarily a return to "naturalness" (Stanturf et al. 2001; Weinstein and Reed 2005).

The science of restoration ecology also includes a body of theory for repairing damaged ecosystems (Palmer et al. 1997; Falk et al. 2006) and as these authors comment "the time is ripe for basic researchers to ask if current ecological theory is adequate for establishing the principles of restoration ecology." Yet, as Hildebrand et al. (2005) note, "the incredible complexity of nature forces us to simplify the systems we study in order to develop theory and generalities by reducing them to understandable subsets." Because ecosystems are inherently dynamic and exhibit nonlinearities and behavioral surprises, the ability to predict and manage restoration trajectories have been particularly vexing (Mitsch et al. 1998; Anand and Desrochers 2004; Ruiz-Jaen and Aide 2005). In addition, Hildebrand et al. (2005) assert that realistic goals should include multiple scientifically defensible endpoints of functional equivalence. In a thoughtful treatise, Ehrenfeld (2000) offered the following: (a) explicit recognition that no one-size-fits-all, goals have to be developed appropriately and individually for each project, and (b) that ecologists establish "probabilistic laws" to define the conditions under which it is desirable to address landscape-scale ecosystem processes; i.e., to determine the sets of conditions that mandate particular methods or goals for individual projects. Because wetlands are hydrologically, chemically, and biologically linked to the landscapes in which they occur, the "templates" for wetland restoration that comprise the various combinations of climate and hydrogeologic settings in a given geographic region, and cumulative alteration of landscapes therein, are likely the greatest constraint on successful restoration design (Bedford 1999). In addressing this particular issue, Kentula

(2000) described an emerging approach that develops a statistical representation or “model” of reference sites as the standard for comparison.

There are also questions related to community stability, resilience and persistence; all central to understanding/predicting whether a restored system will be self-sustaining. A primary challenge for restoration ecologists is to develop tools for assessing acceptable levels of variability in restored systems, most appropriately in a regional or landscape context and within some “bound of expectation” (White and Walker 1997; Weinstein et al. 1997; SER 2004; French 2005).

Thus, the evaluation of restored functions include measures of *processes* such as primary or secondary production, but may also reflect considerations of biogeochemical cycling, food web structure, food quality, habitat connectivity, biological interactions, refuge from predators, keystone species, donor control (Polis and Strong 1996), microhabitat structure, and access to resources. Many species exhibit complex life histories that place them in different parts of the landscape at different times, but their overall success may depend on the quality of specific habitats as critical “bottlenecks” in their life-history sequence. For example, marine transient finfish at mid-latitudes are characterized by life-history traits that evoke a “coastal conveyor belt” with adults spawning offshore and near estuaries, and young spending their first year of life in various estuarine habitats including tidal wetlands (Weinstein et al. 2009a). Young-of-year complete the cycle by accompanying adults offshore during their autumn migration to overwintering grounds. It is likely that the “quality” of the estuarine habitats, especially tidal wetlands and seagrass meadows is reflected in the growth and survival of young-of-year marine transients and is a critical aspect of their successful recruitment to adult stages. Restoration ecology should embrace these considerations.

Linking Structure to Function: The Salt Marsh Paradigm and Secondary Production

Teal’s (1962) mass balance model for a salt marsh near Sapelo Island, Georgia was soon followed by Odum’s (1968) outwelling hypothesis, and as a result, coastal wetlands and their detrital production were soon being depicted as the “great engine” driving much of the secondary production of near shore coastal waters (see also Turner et al. 1979; Weinstein 1981). The fundamental view of a detritus-driven system was soon challenged, however, by Haines (1979) who recognized that finfish, as well as, other primary producers (phytoplankton and benthic microalgae) also contributed substantially to nutrient flux from the salt marsh to open waters. Haines (1979) commented that the “true” nursery-ground of the estuary “was perhaps not so much the large open waters and sounds as the salt marshes and narrow tidal creeks.” She added that the major export of marsh plant production might occur “not as particulate detritus but as living organisms.” At about the same time, Weigert and Pomeroy (1981) stated that “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.” A year after Haines published her “emerging paradigm,” Nixon (1980) reviewed the concept of outwelling and concluded that the average passive export of organic matter (particulate and dissolved) was relatively small, amounting to between 100 and 200 gC m⁻² year⁻¹ for tidal wetlands on the mid-Atlantic and Gulf coasts of the United States.

Haines and Nixon’s views stimulated an era of intense research for refining our understanding of functional links between salt marshes and the estuary/coastal zone. Thus, the “outwelling” concept (Odum 1968) has become but a single component in an evolving view of marsh function and the links between primary and secondary production. Today, the Haines’ view is still undergoing modifications, and we are slowly unraveling the complexities of nutrient exchange, and the links between primary producers and the marsh/estuary fauna. The notion of the marsh drainage, especially the interface between tidal creeks and the marsh plain, serving as ecological “hotspots” (*sensu* Simenstad et al. 2000), and as a potential refugium from predators gained popularity in the 1970s (reviewed by Boesch and Turner 1984). *Spartina* spp. and many other marsh plants decompose relatively quickly, and this in situ production 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 are also readily and efficiently assimilated by many consumers (Currin et al. 1995; Sullivan and Moncreiff 1990). Although progress has been made in understanding how marshes “work,” we have also learned that the story is far more complicated than originally thought (Turner 1977; Peterson et al. 1994; Peters and Schaaf 1991; Mallin et al. 1992; Polis et al. 1997; Deegan et al. 2000; Winemiller et al. 2007; Dame and Christian 2008).

Marsh Physiography

From a restoration standpoint, the physiography of the salt marsh is a critical link in the dynamics and transfer of primary production to consumers. The physiographic features of the marsh that contribute to primary and secondary production include: elevation, drainage characteristics and surface rugosity that expands “edge” and influences the hydroperiod (Kneib 1997; Zimmerman et al. 2000; Larkin et al. 2008); access to the intertidal marsh for fauna (Rozas et al. 1988); predation refugia (McIvor and Odum 1988; Beck et al. 2001, 2003); and interspersed standing water for foraging by resident fishes and wading birds, and resting areas for waterfowl (Rubino 1991).

“Donor Control” and Restoration Planning

Marine transients may also benefit from tidal salt marshes and their production *without directly occupying these habitats*. Many are highly mobile, and tend to cross habitat boundaries in their quest for food and shelter. They are generally not

habitat specialists but are rather opportunistic in utilizing the resources of the estuarine landscape. Restoration planners should and must, therefore, view restoration goals within 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 are integrated components of larger systems (Weinstein et al. 2005). Moreover, the open waters of the estuary may be donor-controlled, i.e., they are 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 the context of 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 supporting 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.

Essential Fish Habitat, Restoration Design, and Higher Order Metrics of Restoration Success

Restoration efforts can also be evaluated within the context of essential fish habitat (EFH) by integrating the factors affecting fish survival and well-being during their life cycle (Able 1999). The degree to which a natural or restored habitat is utilized is presumed dependent on its value. In restored sites, habitat value is maximized once it has reached its restoration asymptote (Weinstein et al. 1997). The application of EFH to fishery management and restoration design necessitates the analysis of habitat information in a hierarchical or matrix fashion. At the least informative level (Tier I), the presence or absence information may be used to infer the potential value of habitats, albeit with a high level of uncertainty. At increasingly complex levels, habitat value becomes a function of the relative abundance or density of individuals at different locations (Tier II). At the next level, growth, reproduction, and survival rates, if available, are used with the assumption that the habitats

contributing most to productivity should be those supporting the highest levels of these parameters (Tier III). Finally, production rates can be used to directly relate species or life stages to types, quantity, quality, and location of essential habitats (Tier IV). There has been a relatively slow evolution of restoration success criteria to include the upper tiers of EFH (III and IV).

In the remainder of this chapter, we focus on the integration of life-history strategy and landscape scale considerations in restoration planning based on our previous research on marine transients and estuarine resident finfish in the Delaware Bay, and Hudson River estuaries, USA. We adopt, but go beyond the premise introduced by Simenstad and Cordell (2000), that “the fundamental approach we recommend is ‘self-monitoring,’ letting the fish test whether the occupation of a restored habitat provides residence time, foraging success, or growth equivalent to that achieved in a comparable reference habitat.” Rather, we address secondary production and Tier III and IV EFH parameters as potential endpoints to measure the outcome and success of restoration practices. The three case histories we present do not make direct comparisons between reference and restored habitats (although we have done this), but from a restoration ecology perspective are intended to assist future wetland restoration designs, not only to consider specific processes, but also to *promote exchange* of materials and organisms between the habitat being restored and the adjacent estuary; i.e., the donor control function of wetlands. Case History I focuses on the growth and survival of a marsh resident finfish, the common mummichog, *Fundulus heteroclitus* and stresses the deposition of energy reserves for overwintering survival at the end of the first year (Tier III, EFH). Case History II uses bioenergetics modeling in a “whole estuary” approach to estimate the nursery value of estuarine regions comprised of marsh and open waters for young-of-year weakfish, *Cynoscion regalis* (Tier III, EFH), and Case History III addresses the response of macroscale tidal salt marsh restoration within the context of secondary production of species that depend on these habitats and/or their products (Tier IV, EFH). Together, the three case histories demonstrate advances in the science of restoration ecology that go far beyond structural characteristics of degraded and restored tidal marshes to address the components of functional equivalency of restored sites.

Case History I (EFH Tier III): Biochemical Condition of a Marsh Resident Finfish, *Fundulus heteroclitus*

Carnivorous fishes are reliable indicators of the condition of complex ecosystems because they are the tertiary link in the food web. Thus, the magnitude of protein and fat deposition and the level of fat reserves can be used to not only assess the “degree of well-being” of fishes but can also serve to integrate the overall value of habitats in their production. Using this premise, we examined the concept of habitat quality for a marsh resident, the mummichog, *F. heteroclitus*, in relatively undisturbed and *Phragmites australis*-dominated tidal salt marshes along the mid-Atlantic

Coast of the United States. In addition to our earlier work on the trophic spectrum of this species (Wainright et al. 2000; Currin et al. 2003), an interesting “natural experiment” was available to us because (1) the species spends its entire life cycle within the confines of the marsh and has an extremely small home range (Valiela et al. 1977; Meredith and Lotrich 1979; Teo and Able 2003), and (2) many tidal salt marshes, particularly those with brackish salinities, are dominated by virtual monocultures of the invasive variety of the *P. australis* that is perceived to reduce habitat quality for *F. heteroclitus*, and general access to the marsh plain by nekton (Weinstein and Balletto 1999; Saltonstall 2002; Hagan et al. 2007). By adopting a whole system approach, we essentially had a “captive audience,” one in each of two isolated marsh complexes located on the Hudson River estuary (Weinstein et al. 2009b), a polyhaline system dominated by *Spartina alterniflora* and a meso-oligohaline system dominated by an invasive variety of *P. australis*. In addition to others, the following questions were addressed in our work: (1) were there any differences in biochemical condition, principally the deposition of energy reserves, in mummichogs captured seasonally in the *S. alterniflora*-dominated “natural” and the *P. australis*-invaded salt marshes (Tier III EFH analysis); (2) were any differences related to size distributions of individuals in the populations; and (3) could biochemical condition ultimately serve as a success criterion to evaluate the functional success of wetland restoration?

The Use of Biochemical Condition as a Metric of Restoration Success

Biochemical condition of individual *F. heteroclitus* was evaluated on the basis of triacylglycerol (TAG), free fatty acid (FFA), and phospholipid (PL) composition and concentration. Other lipid classes such as cholesterol, fatty alcohols, and wax esters were not examined in detail but were included in the calculation of total lipid mass. It is generally accepted that the size of lipid stores and their composition can be used to predict whether a fish is ready to migrate, preparing to overwinter, or is likely to have future reproductive success (Ackman 1980; Shulman and Love 1999). Previous results of lipid class dynamic studies in young teleosts suggest that TAG is the primary form of lipid used in energy storage; therefore, this lipid class was selected as an important indicator of biochemical condition (Ackman and Eaton 1976; Lochmann et al. 1995, 1996; Lochmann and Ludwig 2003; Heintz et al. 2004; Weinstein et al. 2010). FFAs and phospholipids, however, can also contribute to energy metabolism (Ross and Love 1979; Yuneva et al. 1991; Henderson and Tocher 1987) and may be important in the reproductive cycle (Ackman 1980). We examined these in individual fish. TAG, FFA, and PL, all expressed in milligrams per gram dry weight for whole fish was extrapolated from extracted subsamples and converted to total storage quantities by adjusting to the dry weight of each fish.

Findings and Conclusions

The tradeoffs between energy allocation for growth, reproduction, and the laying down of sufficient storage reserves for periods of resource scarcity as “competing demands” in prereproductive organisms living in seasonal environments have been described by numerous authors (Walters and Juanes 1993; Fullerton et al. 2000; Post and Parkinson 2001). This is especially important in north-temperate fishes because experimental and field data suggest that energy availability is often limiting, i.e., fish in their natural environments tend to grow at less than their physiological optimum at a given temperature (Post and Parkinson 2001).

Although our comparisons on a dry weight (morphometric; EFH tier II evaluation) basis alone *did not detect differences* in somatic condition of *F. heteroclitus* populations in the two marshes (Fig. 1a), the examination of energy reserves in these fish after removing the potential confounding influences of the reproductive cycle and parasitization clearly indicated that significant differences occurred in TAG and FFAs levels (Fig. 1b).

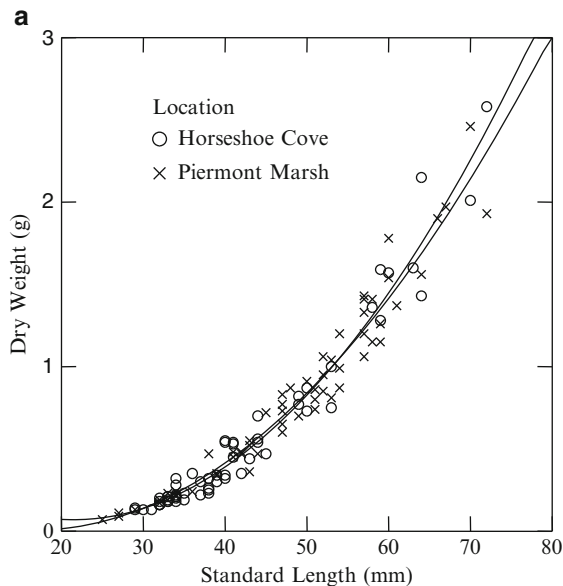


Fig. 1 (a) The relationship between length (mm) and somatic condition (dry weight in g) by location for mummichogs *Fundulus heteroclitus* captured in two tidal salt marshes, Horseshoe Cove and Piermont Marsh on the Hudson River estuary. (b) Total free fatty acids, triacylglycerol (TAG), and phospholipids vs. standard length (mm) in individual mummichogs (*F. heteroclitus*) captured at Horseshoe Cove (H) and Piermont (P) Marshes. All lipid values expressed in milligrams (mg)

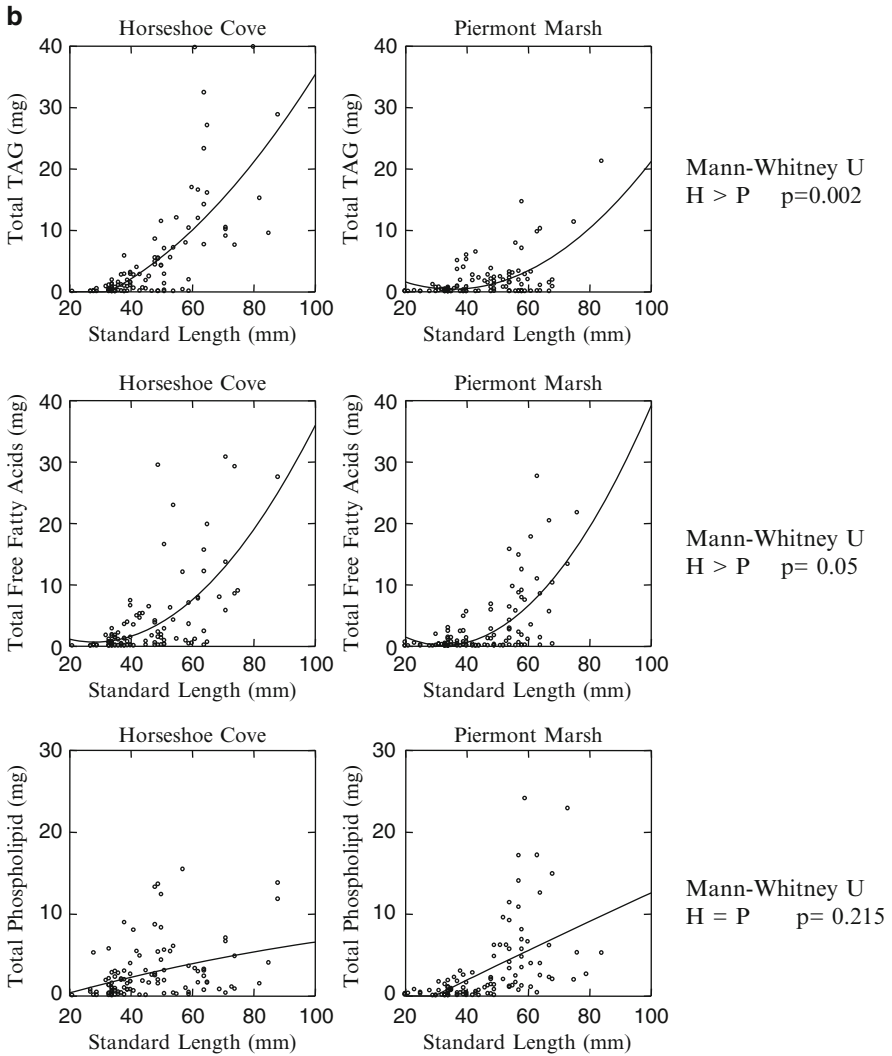


Fig. 1 (continued)

Supplementing tier II data with a tier III biochemical condition approach was, therefore, a more sensitive measure of the condition of individuals produced in these habitats. This conclusion is supported by Mommensen (1998) who suggested that a 100 g fish acquiring 1 g of lipid was unlikely to change in length, and although its weight gain was hardly detectable in the statistical noise, the fish had added a statistically significant amount of energy.

By focusing on energy reserves, principally TAG, we have been able to demonstrate that mummichogs residing in a polyhaline *S. alterniflora*-dominated tidal salt marsh were better able to acquire energy reserves for reproduction and overwintering survival than fish residing in a *Phragmites*-dominated marsh. Thus, *Phragmites* invasion and its consequent habitat impacts may be contributing to lower quality EFH for mummichogs (Weinstein and Balletto 1999; Hagan et al. 2007; Weinstein et al. 2009b).

Case History II (EFH Tier III): Use of Bioenergetics Models to Estimate the Nursery Value of Estuarine Habitats, Young-of-Year Weakfish (*C. regalis*)

Spatially explicit models of fish growth have been used to measure the quality of habitats for nekton production in a variety of species and aquatic systems by integrating variability in biotic and abiotic factors across habitats within a bioenergetics framework (Brandt et al. 1992; Brandt and Kirsh 1993; Mason et al. 1995; Demers et al. 2000; Luo et al. 2001). In this example, a mechanistic growth model, Fish Bioenergetics 3.0 (Hanson et al. 1997), was applied to a series of habitat “regions” within Delaware Bay (upper, middle and lower Bay; Fig. 2). Each region consisted of a marsh to open water gradient, and each had its own set of unique environmental conditions. While most models estimate growth from environmental conditions and the availability of prey, the approach adopted here was to estimate prey consumption from detailed growth estimates in juvenile weakfish that were recruited to the Bay in 1999 and 2001. The calculated rates of consumption (“realized” consumption) were compared to those expected if individuals were feeding at their maximum rate (“optimum” consumption), under ad libitum prey density. The goal was to understand how temporal and spatial variability in availability of food resources and temperature regime governed habitat use and value for juvenile weakfish.

Trawl survey data were used to estimate growth from the changes in the mean monthly weight of juvenile weakfish (Litvin 2005). A separate model was constructed for each cohort identified by length frequency analysis within each Delaware Bay region/year combination and analyzed for the duration that the cohort persisted. Fixed parameters of the model included prey energy density and the *initial* wet weight of individuals within cohorts (derived from the empirical data). The variable parameters included were: in situ temperature, energy density of juvenile weakfish and diet composition (shift from specialization on mysids in early recruits to >90% piscivory in larger individuals; Greccay and Targett 1996; Nemerson 2001).

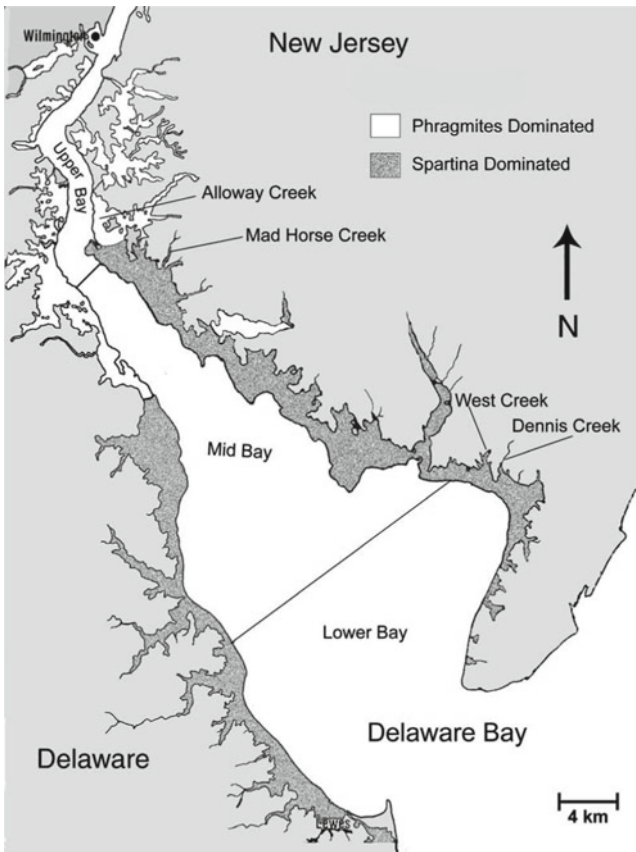


Fig. 2 Weakfish (*Cynoscion regalis*) sampling regions in Delaware Bay comprised of lower, middle (“mid”), and upper Bay and their associated tidal marshes

We modeled (1) realized consumption, which is estimated prey consumed under in situ temperature and empirical estimates of growth (“realized growth” derived from the trawl surveys), (2) optimal growth, which is the theoretical maximum growth under in situ temperature and ad libitum feeding conditions; and (3) optimal consumption, which is the prey consumed under optimal growth. From these results we calculated the excess demand, the proportional difference between the cumulative optimum, and the realized consumption over the period the cohort persisted (which is a relative measure of the suitability of a given habitat for fish production). The calculated realized and optimal growth and consumption and excess demand were compared to determine if food availability, temperature or other factors determined

the production rates of young-of-year weakfish. In addition, these measures were compared among cohorts, Bay region and years to elucidate how habitat values varied both spatially and temporally.

Findings

Not surprisingly, the relationship between optimum and realized consumption varied both spatially and temporally (Figs. 3 and 4). Analyzed in terms of the cumulative consumption of prey (g individual⁻¹), it is important to note that optimum and realized consumption rates are equal when the slopes of their curves are equal over a given period. For the first cohort in 1999, optimum consumption increased steadily over the summer and fall in the middle and lower Bay but remained flat between days 200 and 240 in the upper Bay, before rising for a brief period (Fig. 3). The realized consumption in the upper Bay exceeded optimum consumption in the early summer (July) then mirrored optimum consumption until the cohort was no longer detected. The optimum and realized consumption in the middle and lower Bay regions were approximately equal in July and August with optimum consumption exceeding realized consumption during the remaining months. The optimum consumption for cohort 2 quickly outstripped the realized consumption, except in the lower Bay (Fig. 3). Optimum consumption in 2001 increased throughout the summer in the lower and middle Bay for cohort 1, and was followed by a slight decrease in the fall (Fig. 4). Optimum consumption in the upper Bay rose in June through July, fell in August, and then increased steadily during the remainder of the growing season. The realized consumption in all regions fell vastly short of optimum throughout the season. For the second cohort, the difference between optimum and realized consumption was substantial in the middle, but not the lower, Bay (Fig. 4). The excess demand (grams prey consumed per individual) for the first cohort varied substantially between regions and years (Fig. 5). The excess demand in 1999 ranged from -81% (the realized exceeded optimum consumption) through 78% in the middle Bay, and rose to 131% in the upper Bay, respectively. The surplus consumption in 2001 was markedly higher (407–505%), with peak values occurring in the upper Bay. This was driven both by changes in the estimated growth rates in the field (realized growth) and changes in optimum growth which rose from the upper through the lower bay in both years and was higher in 2001 in all regions (Fig. 5).

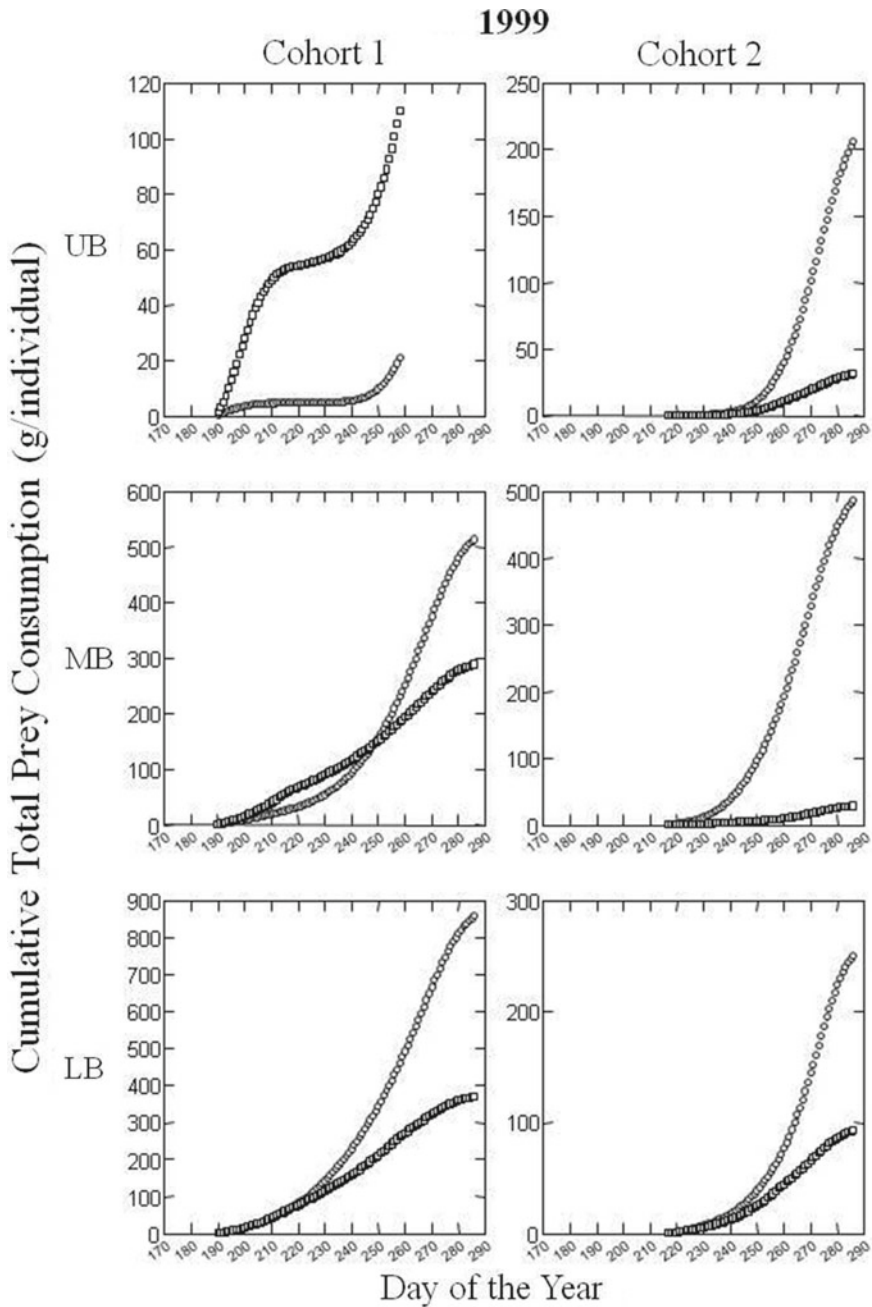


Fig. 3 The relationship between realized (*open squares*) and optimum (*open bullets*) consumption for juvenile weakfish captured in 1999, Delaware Bay, USA. LB, MB, and UB are lower, middle, and upper Bay, respectively

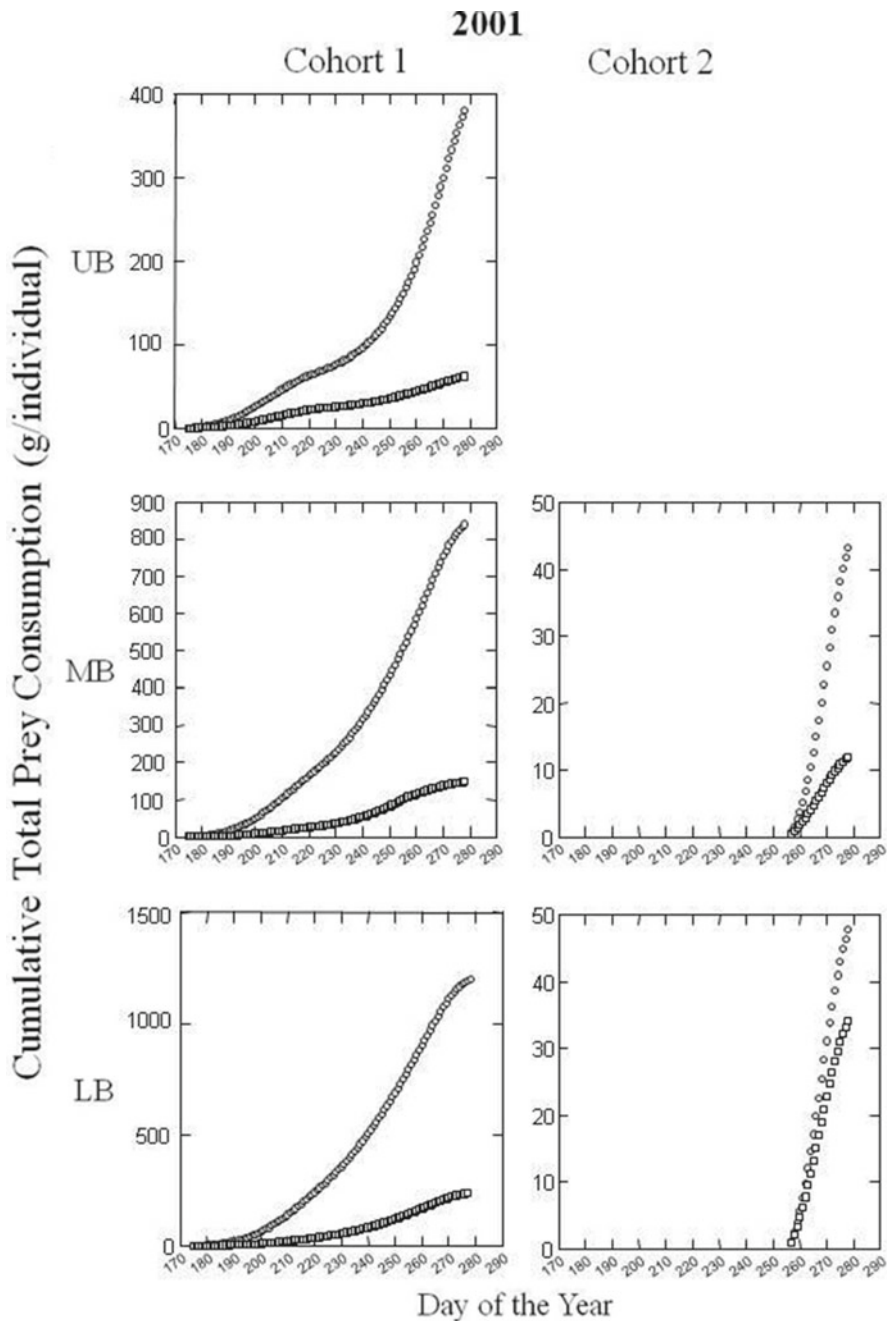


Fig. 4 The relationship between realized (*open squares*) and optimum (*open bullets*) consumption for juvenile weakfish capture in 2001, Delaware Bay, USA. LB, MB, and UB are lower, middle, and upper Bay, respectively

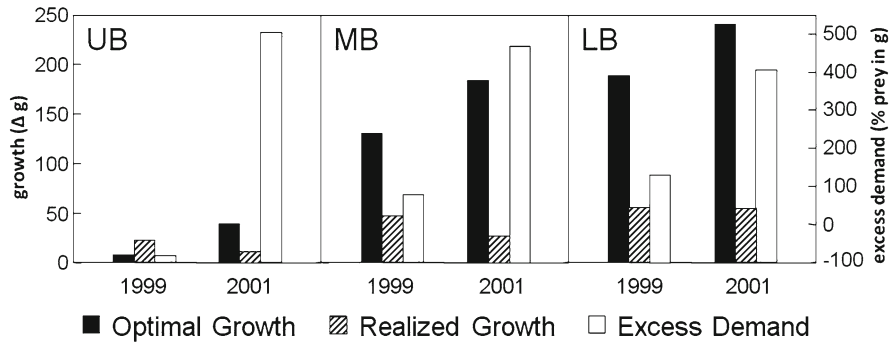


Fig. 5 Optimal growth, realized growth, and excess demand for cohort 1 from each Bay region (lower LB; mid MB; upper Bay UB) for 1999 and 2001

Summary and Conclusions

The trends in optimum consumption and excess demand provided insights into the relative suitability of the different segments of Delaware Bay for juvenile weakfish. In both years, estimates of optimum consumption suggested that the region with the physiological conditions most suitable for potential growth varied temporally. In July and August, optimum consumption estimates were higher in the lower Bay than those from the middle Bay, and both possessed higher values than the upper Bay region. This disparity in potential habitat quality dissipated as temperatures fell through September and October, with the optimal zone shifting to the upper Bay in the final days modeled. Between years, the differences in the mean estimates of excess demand (~100% and ~450% for 1999 and 2001, respectively) suggested that the value of Bay regions for the production of young weakfish was considerably lower in 2001. While it is difficult to determine if the variability in estimated habitat suitability between habitats and among years is driven by differences in prey supply, the expected reduction in juvenile weakfish foraging success due to high turbidity encountered in oligohaline habitats, or physiochemical considerations not accounted for in the model (see below), these results parallel the spatial patterns in juvenile weakfish condition and growth previously reported for this estuary and its marshes (Greco and Targett 1996; Paperno et al. 2000; Litvin and Weinstein 2003; Litvin 2005).

Two factors, both attributable to the high river discharge rates in June and July of 2001, likely drove inter-annual differences in habitat suitability (USGS¹). Juveniles recruited to the upper Bay in June through the early fall of 2001 faced increased physiological stress and lower potential growth rates than those from other regions

¹USGS New Jersey Monthly Streamflow Statistics for Trenton, NJ (Site # 01463500); <http://waterdata.usgs.gov/nl/nwis>.

due to the interaction of high temperatures and low salinity (Lankford and Targett 1994; Greco and Targett 1996; Paperno et al. 2000). In addition, an increase in the flow rates might have led to “compression” of the meso and polyhaline regions and resulted in the increased density of piscivorous marine predators that might normally be restricted from oligohaline waters (Weinstein et al. 1980; Taylor 1987; Martino and Able 2003). Therefore, juvenile weakfish moving down Bay in 2001 into meso and polyhaline waters with superior physiochemical conditions likely faced increased predation risk, relative to low flow years, which in turn might affect acquisition of prey and growth (Walters and Juanes 1993; Sogard 1997).

A significant purpose of any modeling effort is to identify data needs and suggest future directions for research. We developed several recommendations based on this work. It is important to examine the interactive effects of temperature and salinity on the scope of growth to parameterize future bioenergetics models intended to gauge habitat value for estuarine fish. Knowing the choices in prey, aside from their energy density may also be important. The variability of postconsumptive constraints based on prey type, known to occur in young weakfish (Lankford and Targett 1997), were not considered although they may lead to consumption-dependent systematic errors in estimates of growth (Bajer et al. 2004). Although labor-intensive, obtaining estimates of spatial and temporal variability of prey from stomach content analysis, and the incorporation of this information into bioenergetic variables (that represent postconsumptive processes), would further increase model accuracy. Also, the methods to account for seasonal changes in habitat utilization patterns, e.g., estimating movements out of marsh habitats and downstream migration rates as individuals grew (Litvin and Weinstein 2004), should be accounted for when determining spatially explicit growth. Stable isotope analyses have demonstrated great utility as “biomarkers” for discerning habitat utilization patterns in juvenile weakfish and other species from Delaware Bay and the employment of this technique in conjunction with field measures of length and weight will improve the accuracy of growth estimates (Weinstein et al. 2000; Litvin and Weinstein 2003, 2004). These three considerations are also particularly important when using bioenergetics models to move beyond the “regional” approach utilized here to determine the value of specific marsh habitats for juvenile nekton in the context of the greater estuary. Estuarine and marsh habitats, even those separated by small distances, should be expected to have different environmental regimes as well as abundance and diversity of food resources. For restored marsh habitats, their position in the restoration trajectory may heavily influence these factors (Weinstein et al. 2005). In addition, understanding the habitat utilization patterns of species, like juvenile weakfish, potentially using a wide variety of estuarine habitats is critical to understanding the relative value of marsh habitats for fish production. For example, the physiochemical conditions in open waters of the Bay region in 2001 were sub-par, and so the biotic conditions in marsh habitats may have resulted in higher optimum and realized growth for juvenile weakfish. This may both increase the value of marsh habitats for juvenile fish production in a given year, and buffer individuals leaving marshes to migrate toward the bay mouth from the depressed conditions in the open estuary. Together, these two situations would

ultimately increase the relative contribution (per unit area) from marsh habitats to overall estuarine production. While the exclusion of these considerations does not preclude the use of the model to help understand the variables governing the demonstrated spatial and temporal stochasticity in the nursery value of estuarine habitats for young weakfish and other species, their incorporation into models would help to improve both their accuracy and utility as a tool for both ecologists and natural resource managers.

Case History III (EFH Tier IV): Estimating the Response of the Delaware Bay Ecosystem to Tidal Marsh Restoration

During the 1990s, 45.5 km² of wetland habitat were restored in the Delaware Bay ecosystem to offset mortality caused by power plant cooling water intakes (Teal and Weinstein 2002). The restoration effort resulted in a 3% increase in marsh habitat (Balletto et al. 2005; Hinkle and Mitsch 2005) and provided scientists with the opportunity to assess changes to system productivity and structural changes before and after restoration. A series of baseline and monitoring studies were conducted to quantify nekton assembly composition and usage of restored and reference marshes (Kimball and Able 2007; Nemerson and Able 2005; Jivoff and Able 2003; Able et al. 2008). These studies documented the impact of restoring habitat and demonstrated that the nektonic assemblage responded favorably to restoration. These studies, however, did not address overall system productivity and the structural changes resulting from restoration efforts.

In the following section, we summarize the approach and results reported in Frisk et al. (2011) who estimated the increment of new secondary production that resulted in the entire Delaware Bay ecosystem following restoration. Estimating system-wide impacts required distinguishing between the impacts of restoration and background variability in spatiotemporal patterns of productivity and ecosystem structure. The latter effort entailed estimating system productivity after restoration and simulating the proportion of biomass that would have been lost if restoration efforts had not taken place. To achieve this result required the development and parameterization of a mass-balanced time-dynamic ecosystem model fitted to observed time series of key species and then simulating a nonrestored system.

Assessing Restoration Using Ecopath with Ecosim

Details regarding the model structure of Ecopath with Ecosim (EwE) can be found in Christensen and Pauly (1992), Walters et al. (1997), and Pauly et al. (2000), and, for the model presented here, in Frisk et al. (2011). Ecopath was used to develop a mass-balanced network of trophically-linked biomass pools representing a static

description of the ecosystem from detritus to upper-trophic level species. The Ecopath model provided the initial parameters used to fit the dynamic Ecosim model to time series of data for the Delaware Bay ecosystem. Ecosim uses a series of coupled delay-difference age/size-structured equations to model all species in the system. The flows between species are linked by both predator and prey consumption rates.

Parameter Inputs

The times series data are derived from long-term biological studies and harvest records used to estimate biomass and landings and for the development of stock assessments for key species in Delaware Bay (DNREC 1966–2003; NOAA Fisheries 2011). The demographic and diet data were derived from the literature or inferred from adjacent systems when necessary.

Measuring Habitat Restoration

Changes to ecosystem structure and productivity following restoration were reflected in the biological time series conducted in the Bay during 1996–2003. Therefore, the biomass gains resulting from restoration were captured in a model fitted to these data. To estimate the lost productivity had restoration not occurred, a second model was run that assumed a 3% decrease in the available marsh habitat. This was achieved by fitting the Ecosim model for 1966–2003 and applying forcing functions to decrease the production rates for marsh meiofauna and macrofauna for the years following restoration, 1996–2003. The difference between the two models' total system biomass was used to estimate the gains associated with restoration.

Model development. The modeling approach used 47 functional groups including: 27 fish species, 5 invertebrate groups, 4 multi-species benthic groups, 6 multi-species fish groups, 3 plankton groups, 1 shorebird group, and 1 marine mammal group (Frisk et al. 2011). The static mass-balanced Ecopath food-web model was developed for 1966 and served as the initial parameter estimates for the time-dynamic Ecosim model for the period 1966–2003. The Ecopath model required estimates of biomass (B), the ratio of production to biomass (P:B), consumption to biomass (Q:B), ecotrophic efficiency (EE), and diet data for all model groups. The Ecosim models were parameterized using catch, biological survey, diet, and demographic data. Time series of biomass (catch per unit effort) for eight species, catch time series for six species and fishing mortality for five species were fitted in Ecosim (Table 1).

Table 1 Data used for fitting the Ecosim model included time series of catch (C), biomass (B), and fishing effort (F) where numbers represent the length of time series in years

Species	C_{fitted}	$C_{\text{subtracted}}$	B	F
American eel		38		
Atlantic croaker	38		38	38
Atlantic menhaden	38		38	38
Blue crab	38			38
Bluefish	38		38	38
Clearnose skate			27	
Dogfish			27	
Horseshoe crab		30		
Oyster		38		
Spot		38		
Striped bass	38		23	38
Summer flounder	38			
Weakfish		38	27	
White perch		38		

Catch was statistically fitted (C_{fit}) or subtracted from model estimated biomass (C_{sub}). Stock assessments were conducted on Atlantic croaker, Atlantic menhaden, and bluefish providing biomass (CPUE) and fishing effort (fishing exploitation rate). Other biomass estimates were derived from the DNREC surveys except striped bass which came from ASMFC (2004)

The catches were subtracted from the estimated biomass for eight key species that did not have prior estimates of fishing mortality to ensure that the model produced stock sizes large enough to support the historical fisheries.

Findings

The results of the model runs indicated that restoration resulted in a net gain of 47.7 tons km⁻² year⁻¹ in system biomass. The biomass change was seen across a wide range of species and biomass groups, and had an average percent change of 1.2%, ranging from 4.3% for macrozooplankton to 1.3% decrease in blue crab (Fig. 6).

Restoration also resulted in 41 species increasing in biomass and four species showing slight decreases. The decreases likely resulted from food web interactions with groups that increased. Proportionally, consumer trophic species such as Atlantic menhaden, resident striped bass, macrozooplankton, and summer flounder showed the greatest gains.

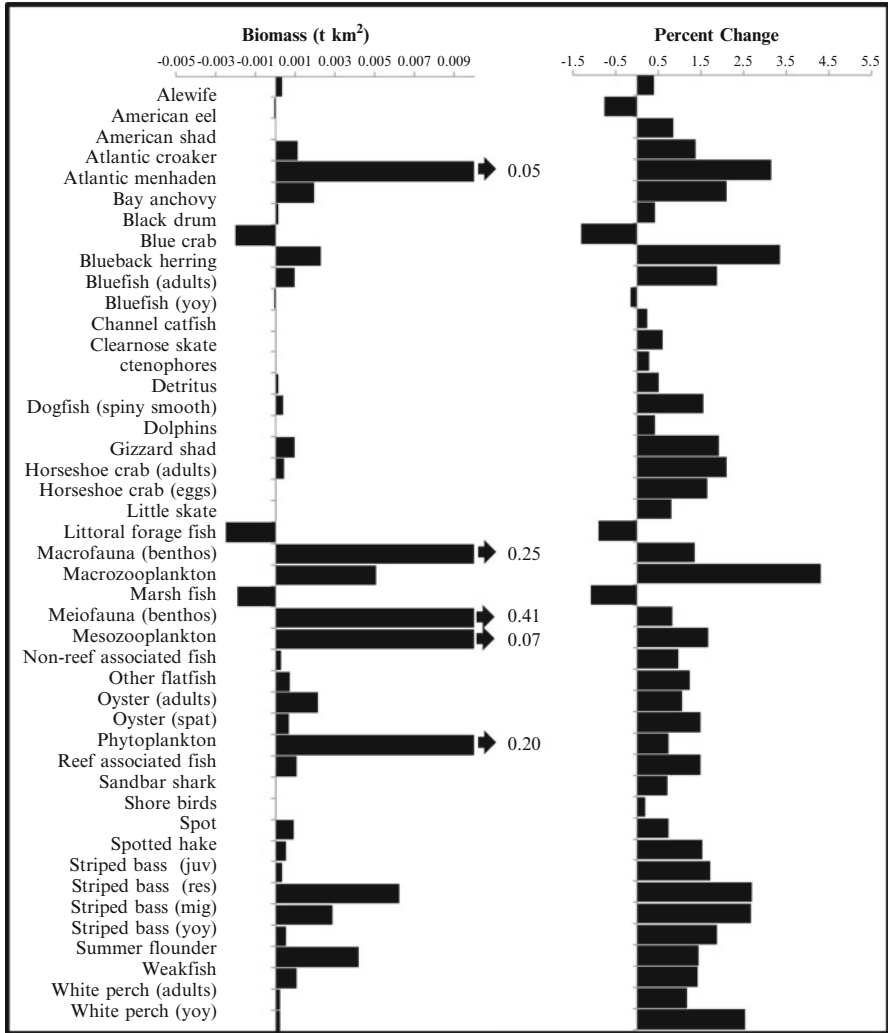


Fig. 6 Change in species' annual abundance resulting from restoration for the period 1996–2003 reported in biomass and percent change, where “yoy” indicates young of the year staged fish, “juv” is juvenile staged fish, “res” is a resident contingent, and “mig” is a migratory contingent

Summary and Conclusions

As with any modeling attempt, ecosystem complexities are not completely captured in the model structure. Ecosystem models require large amounts of information, and the reliability and availability of data varies by species and biological group. The Delaware Bay model is a compromise among realism, parameteriza-

tion, and data limitations. Estimating restoration impacts utilizing data collected continually before and after restoration does not allow for direct comparisons of an ecosystem with and without restoration. Instead, the statistically fitted model was altered to reflect a simulated no-restoration system to estimate the loss of biomass had the marsh habitat not been created. The approach allows for a total system evaluation of restoration; however, the simulation approach may add uncertainty to the results.

Large-scaled restoration efforts require an enormous investment of time and money. The success and justification of these efforts should be judged by whether or not the degraded ecosystems can ultimately be rehabilitated to provide basic ecological goods and services. In Delaware Bay, researchers conducted numerous field studies documenting the success of newly created marsh habitat for use by native species and general production of finfish and shellfish (Kimball and Able 2007; Jivoff and Able 2003; Able et al. 2008). More broadly, Frisk et al. (2011) were able to show that the overall ecosystem biomass increased including several important commercial finfish. The results supported previous field estimates and demonstrated increases throughout the entire food web that were dependent on the increased marsh habitat. The results from the Frisk et al. (2011) mass-balanced time-dynamic ecosystem model of Delaware Bay were used to address the following questions: (1) Has restored habitat resulted in changes to the productivity of the ecosystem?; (2) Is there evidence that restoration can impact the structure and health of the Delaware Bay ecosystem?

The model results indicated that many species increased in biomass including ecologically important lower trophic groups such as macrofauna, macro-meso zooplankton, and higher trophic groups consisting of striped bass, Atlantic croaker, and summer flounder. The model estimates indicated that restoration of marsh habitat resulted in increased biomass throughout the food web. These results, when combined with previous field studies indicated that the restoration of 45.5 km² of marsh habitat increased productivity and restored ecologically meaningful amounts of goods and services to the Bay.

In addition to biomass gains, the model results indicated that restoration has the potential to alter the structural composition of Delaware Bay, and that there were slight changes in several ecosystem properties including productivity and system maturity metrics (see Frisk et al. 2011, for details). This has important implications for stemming over a century's loss of wetland habitat. Network analyses indicated that the Delaware Bay is in an immature state and suffers from decades of nutrient enrichment and pollution (Sharp 2010). It is encouraging that these model results indicate that restoration can reduce the impact of long-term alteration of estuarine ecosystems and potentially increase system maturity. The changes, however, were slight and even larger-scaled restoration efforts integrated with management strategies covering the entire drainage basin may be needed to further restore ecosystem function.

Synthesis

The need for linking restoration ecology, ecological restoration, and sustainability science are a *sin qua non* of the global sustainability transition. In this Age of Humans (Crutzen 2002), they form what Aronson and Vallejo (2006) term our “survival strategy” where “nonscientists and scientist work together in transdisciplinary efforts to imagine, develop, test and apply new methods, tools and approaches to the enormous [sustainability] challenges ahead.” Moreover, managing our life support systems will require stewardship “from the inside” in ways that recognize our dependence on, and responsibility to, sustainably manage the systems that we are an integral part of. Aronson and Vallejo (2006) suggest that restoration projects should adopt broad suites of relevant, reliable and complementary traits or ecosystem attributes that when combined, reflect the structural and functional dynamics of the system.

The discipline of restoration ecology has now matured to where knowledge of natural systems can define a better pathway to the desired restoration outcomes (Larkin et al. 2008). Whether it is considering individual habitats in a system-wide integrated framework (Childers et al. 2000; Weinstein et al. 2005), reestablishing the physiographic heterogeneity (and concomitant physical access) of a salt marsh that we have set forth above, or other “landscape” features—hydrology/hydroperiod (Rozas et al. 1988), edge or “critical transition zones” (Baltz et al. 1993; Kneib 2003), drainage density (Kneib 1994, 1997), area of vegetated marsh (and its relationship to secondary production; Turner 1977; Zimmerman et al. 2000)—and organism interactions; trophic access (*sensu* Kneib 2003), predator–prey interactions (Boesch and Turner 1984; Deegan et al. 2000), ecological and engineering criteria can be combined into a much more quantitative approach to achieving “success” (or whatever we choose to call it; Zedler 2007). Despite the current debate over the issue of attaining habitat equivalency of marsh *functions*, we agree with Kneib (2003) that the rubric “build it and they will come” has a degree of validity with respect to organisms utilizing the restored habitat. Kneib notes that “early indications suggest that fishes do not discriminate between natural and excavated wetland channels,” and that “there should be every expectation that nekton production from the restored created site has potential to rapidly match that of natural systems.” But Kneib (2003) also noted that “site-specific bioenergetic and landscape constraints [while setting upper limits to production] should guide the development of realistic expectations and success criteria for marsh restoration designed to enhance estuarine nekton production.” The simple underlying question then is: yes, we have restored a marsh, but what kind of marsh have we restored and will it fulfill our expectations with respect to secondary production goals for targeted species?

What seems clearly lacking in today’s purview is a policy and practice that goes beyond developing the status and trend inventories for coastal wetlands (Stedman and Dahl 2008), or the promulgated guidelines for conservation, restoration and management that lack rigorous ecological criteria for meeting design goals. Clearly, the importance of coastal wetlands as EFH is recognized by

resource agencies: “coastal wetlands provide valuable habitat for the vast majority of commercially and recreational marine species” (Stedman and Dahl 2008). Although more than \$28 million has been allocated by the National Oceanographic and Atmospheric Administration’s (NOAA) for habitat restoration (J. Rapp, personal communication) there seems to be a great paucity of process and function criteria, in general, and especially at higher levels of EFH analysis. In NOAA’s “Science-Based Restoration Monitoring of Coastal Habitats” guidelines for developing a monitoring plan (Thayer et al. 2003), explicit recognition is given to the need to develop testable hypotheses to “determine progress toward restoration goals,” yet the examples given of postimplementation monitoring are large structural criteria, and no functional criteria are proposed above the level of Tier II, EFH; i.e., density and composition of organisms. A cursory review of Progress Reports submitted under the NOAA Restoration Center’s Community-based Restoration Program (CRP), Progress Report Narrative Formats includes only biological inventories (restricted at or below EFH, Tier II) and/or topographical/structural parameters.

We can and must do better. Simenstad et al. (2006) note that “while desirable functions may result from the structure of ecosystems, it is typically the dynamics of ecosystem processes that sustain the structure at the landscape scale or in some cases may even be the underlying mechanism behind the function.” Further, the relationship between salt marsh restoration and attributed functions is highly scale-dependent, nonlinear, and dictated by thresholds (Simenstad et al. 2006). We agree that the long-term performance of a restored site depends on reintroducing natural dynamics and disturbances into the system (Middleton 1999), also within the context of life-history requirement of extant flora and fauna. Perhaps these restoration efforts should be approached as “natural experiments” to be quantified for their return of desired ecosystem goods and services, and, as Simenstad et al. (2006) note, be treated in a manner that enables learning from the results. Performance criteria should include more process-based metrics to help ensure success.

Virtually all restoration scientists agree that tidal marshes are complex systems that require the best applications of science and engineering principles (Weinstein et al. 1997) to achieve the goals of a particular restoration design; especially when these are systems whose physiographic province affecting virtually every component of secondary production support is measured in centimeters (Vivian-Smith 1997). As noted above, the progress we have made in understanding how marshes “work” is far from complete, and research should not become subordinate to practice in advancing the goals of restoration. Ongoing research can provide important perspectives on the results achieved, and will allow us to correct mistakes, and suggest new approaches for defining success (Kentula 2000).

It is beyond the scope of this chapter to attempt a comprehensive review of the application of restoration science to the design and success of tidal wetland restorations in supporting secondary production except to say that quantitative studies are far and in-between in the published literature. A relatively recent review by Borde et al. (2004) helps make the point. Beginning in 1998, more than 550 citations from

scientific journals, books, technical reports and proceedings were surveyed for “innovations” in coastal restoration. This effort supported NOAA’s attempts “to advance the science of restoration ecology” including research on coastal ecosystem structure and function. Although the review of the literature suggested that restored salt marshes were functioning to increase the growth, production, and resilience of fish populations, there were no specific recommendations to incorporate these functional criteria into goal setting and success criteria, nor have we seen inclusion of parameters like EFH Tier III and IV criteria built into restoration planning. Rather, the authors’ summary of “innovative methods and techniques” to our knowledge have yet to find their way into NOAA Restoration Center design protocols, monitoring techniques, nor project success. We are not saying it will be easy, but simply recognizing that it should and must be done.

Finally, we leave the reader with a research approach proposed by Choi (2004). It serves both as a useful take home message and template for future progress. In synthesizing the need for a “futuristic approach” to restoration, Choi proposed that we:

1. Set realistic and dynamic (rather than static) goals for future, instead of past, environments
2. Assume multiple trajectories acknowledging the unpredictable nature of ecological communities and ecosystems
3. Take an ecosystem or landscape approach, instead of ad hoc gardening, for both structure and function
4. Evaluate restoration progress with explicit criteria
5. Maintain long-term monitoring of restoration outcomes

Of course, we recommend further that these efforts be supported by strong ongoing and fully funded restoration science research!

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