Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations

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ABSTRACT: Satisfying the needs of mitigation for losses of habitat and biological resources demands further development of ecological theory to improve quantitative predictions of benefits of ecological restoration projects. Several limitations now exist in scaling compensatory restoration to match losses of ecosystem services. Scaling of restoration projects has historically been done by area of habitat, assuming that function follows. One recent development in compensatory mitigation uses a currency of secondary production, which has the important merit of specifying one measurable, functional goal against which to judge success. Future development of the fundamental basis for restoration ecology might profitably include: (1) identifying and quantifying important ecosystem services to serve as alternative goals of restoration; (2) discriminating among size classes in a population in estimating their contributions to ecosystem services; (3) re-evaluating the practice of restoring the populations of only a few representative or dominant species to replace a diversity of species losses; (4) contrasting the success of habitat restorations versus population enhancements; (5) incorporating more landscape-scale considerations into ecosystem-based restoration designs; (6) injecting more formal uncertainty analyses into scaling restoration projects; (7) enhancing the basic science of population, community, and ecosystem ecology to improve the capacity of the discipline to predict impacts of interventions; (8) integrating empirical and theoretical developments in food web dynamics to resolve contradictions in our models of how population changes propagate across trophic levels; and (9) incorporating the concept that populations, communities or ecosystems targeted for restoration may now be in alternative states and that restoration targets have been biased by shifting historical baselines. Forging partnerships between the practitioners of ecological restoration and basic ecologists holds a dual promise for testing ecological theory and for improving the effectiveness of environmental restoration.

KEY WORDS: Restoration ecology · Research needs · Ecosystem services · Secondary production · Scaling restoration projects · Conceptual challenges

INTRODUCTION

If ecological restoration is ever to approach the efficacy of conservation as a tool to combat the growing degradation of habitat (Vitousek et al. 1997) and depletion of living resources (Botsford et al. 1997), both of which are driven by pressures of expanding human populations, dramatic advances will be needed in the conceptual ecological foundation on which restoration relies (Allen et al. 1997, Young 2000). Both approaches, conservation and restoration, seem necessary because

while conservation is the typically more reliable and less costly means of sustaining ecosystem services, restoration is often required to respond to unexpected losses and to compensate for a long cumulative history (Jackson et al. 2001, Scheffer et al. 2001) of incremental degradation and destabilization of natural ecosystems.

In many ways, restoration ecology makes more demands on the discipline of ecology (e.g. Ewel 1987). This is not to argue that conservation comes easy: in fact, many of the biggest challenges in conservation biology involve developing novel techniques for recon-

ciling human uses of natural resources with a mandate to sustain provision of those resources indefinitely (e.g. Soule 1987, Wilson 1992). For example, recent growth in the conceptual basis for designing marine reserves may lead to management actions to sustain fishery stocks and harvest levels (Palumbi 2001, Lubchenco et al. 2003). In contrast to conservation, which involves managing human activities to reduce their influence on nature, restoration typically requires overt human intervention into degraded ecosystems to achieve a desired target (Jordan et al. 1987, NRC 1992). Restoration ecology depends on population, community, and ecosystem ecology to provide the conceptual basis for predicting not only direction but also magnitude of responses of ecosystems to restoration actions (Zedler 2000). Designing restoration projects and evaluating their subsequent success involves interdisciplinary science, including consideration of hydrology, hydrodynamics, sedimentary geology, biogeochemistry, and land-use planning (NRC 1992). The history of human interventions into ecosystems does not inspire high levels of confidence in our ability to design and engineer model ecosystems through intervention, raising skepticism about achieving restoration goals. Intentional introductions of non-native species have an especially poor record of achieving their predicted benefits. The practice of scaling to achieve compensatory restoration, despite its flaws and uncertainties, has the positive benefit of identifying an explicit functional goal of restoration against which success can be measured; this can force restoration ecology to become more focused, rigorous, and quantitative (Hobbs & Harris 2001).

This Theme Section on restoration scaling in MEPS (Peterson et al. 2003b, in this Theme Section) publicizes the recent development of alternative approaches to designing and scaling compensatory restorations in the marine environment. Specifically, the papers illustrate the application of ecological concepts to design restoration actions for the purpose of quantitatively enhancing ecosystem services to compensate for natural resource injuries (NOAA 1997). Agencies responsible for protecting and managing public trust resources are often required by law or policy to facilitate restoration as compensation for losses (Peterson et al. 2003b). This mandate has inspired original syntheses of available scientific evidence on population regulation of many affected species and their practical application to develop alternative designs for restoration actions. The requirement to achieve full quantitative compensation for the losses places a special burden on the discipline of ecology because of its explicit need to predict numerical responses (Ewel 1987). Here we identify important ecological considerations that still need to be addressed to improve the conceptual underpinnings for restoration scaling.

FUTURE CHALLENGES TO IMPROVE RESTORATION SCALING

Identifying and measuring ecosystem services. From its initiation, habitat restoration in the marine environment focused almost exclusively on developing the methods for re-establishing and sustaining the biogenic structural element, usually a plant, that defines the habitat and facilitates its function (NRC 1992). Successful culture methods have now been achieved for salt marsh grasses (Woodhouse et al. 1974), seagrasses (Fonseca et al. 1998), and oysters (Luckenbach et al. 1998). Many habitat restoration projects have been scaled based upon the simple metric of habitat area, assuming that function would follow structure (Lawton 1996). This assumption has been partially tested by evaluation of the rates of return of animal communities that depend upon the structure-providing (foundation) species (e.g. Cammen 1976, Fonseca et al. 1996, Grabowski 2002). Growing knowledge of the rate of return of associated animals has allowed this component of habitat function to be included in scaling some restoration projects. More recently, the movement towards quantifying success of restoration by functional measures has been accelerated by governmental mandates for compensatory replacement of injured or lost ecosystem services after environmental disasters (Peterson et al. 2003b).

The fundamental assumption underlying most governmentally mandated attempts to scale restoration actions to achieve quantitative compensation for losses of living natural resources is the assumption that biomass production is an appropriate proxy for ecosystem services (e.g. NOAA 1997, Fonseca et al. 2000). Many processes of value and significance to the ecosystem clearly are enhanced as biological production grows. For example, a system in which production of an exploited species is augmented will typically sustain enhanced levels of exploitation. Yet choice of the trophic level at which to assess production can make an enormous difference to evaluation and quantification of ecological benefits of potential restoration options. For example, eutrophication is the process of nutrient loading in aquatic ecosystems that enhances primary production in the water column (Nixon 1995). This enhanced primary production can interfere with food-chain transfers to higher trophic levels by stimulating production of inedible nuisance algae, destroying nursery habitats such as rooted macrophytes and oyster reefs, killing benthic invertebrates by induction of bottom-water hypoxia and anoxia, and diverting energy flow away from consumers and into microbial loops (Elmgren 1989, Jackson et al. 2001, Baird et al. in press). Eutrophication is understandably viewed as a process that degrades the services provided by lakes,

estuaries, and coastal oceans (Carpenter & Lathrop 1999). Consequently, stimulating additional biological production at the level of phytoplankton would not serve as compensation for lost ecosystem services and benefits in eutrophic estuaries or coastal oceans.

Restoration design and scaling needs to consider not only the trophic level at which success should be measured, but also the species-specific responses within trophic level. For example, replacement of *Spartina alterniflora* marsh with *Phragmites communis* marsh is widely viewed as a failure to restore the functional value of the marsh habitat for animals (see Able et al. 2003) in large part because of difficulty in accessing the much denser *Phragmites*. Recent work in natural *Spartina* marshes, *Phragmites* marshes, and restored *Spartina* marshes in the Delaware Bay (New Jersey, USA) has demonstrated not only that juvenile fish (*Fundulus heteroclitus*) utilization is far greater in *Spartina* marshes but also that marsh restoration through *Phragmites* removal re-establishes the quantitative level of this particular nursery function (Able et al. 2003). Documenting and quantifying more such species-specific services of marine and estuarine habitats is a necessary step towards including species-level predictions in scaling restoration projects.

In principle, one could specify the important services provided by any given species or habitat and then design restoration actions to enhance one or more of them, with compensation computed as the sum of all such scaled benefits. Unfortunately, this procedure requires recognition and definition of the important services provided by the species or habitats that may serve as the target of restoration. Some benefits are known and widely acknowledged. However, others that are equally important may be unrecognized. For example, oyster reef habitat provides the ecosystem benefits of: (1) producing oysters of market value and of value to recreational fishermen; (2) filtering the estuarine waters, which can enhance their clarity and allow sufficient light penetration to support expansion of seagrass habitat, an important estuarine nursery; (3) promoting denitrification by concentrated deposition of feces and pseudofeces; (4) providing a hard substratum that enhances biodiversity and production of epibenthic invertebrates; (5) serving as emergent biogenic habitat that provides food and shelter to many demersal fishes and mobile crustaceans; (6) sequestering carbon in the calcium carbonate of shells, thereby reducing concentration of a greenhouse gas; (7) acting as a breakwater to protect the estuarine shoreline, including salt-marsh habitat, against erosive waves (Peterson et al. 2003a, in this Theme Section); and (8) diversifying the seascape to enhance the synergistic benefits of multiple habitat types, such as creating corridors between shelter and foraging grounds (Peter-

son et al. 2003a). Other benefits of oyster reef habitat doubtless exist without due recognition. Even after recognition of the suite of important benefits, converting them to a common comparable unit so as to sum them represents a major challenge to both ecology and natural resource economics. Scaling restoration so as to provide a sum of all benefits that will match a given loss represents a complex task certain to overlook some important ecosystem functions. Thus, the use of secondary production as proxy for ecosystem services may actually result in more accurate compensation from a restoration project. Nevertheless, this assertion is wishful thinking that deserves to be tested by actually enumerating ecosystem services, scaling them to production, and summing them in defensible ways to evaluate whether the procedure of matching gains and losses in secondary production suffices to achieve quantitative compensation in ecosystem services.

Few alternative metrics have been suggested to replace production as the scalar for compensatory restoration of ecosystem services. M. Buchman (unpubl.), however, has developed a metric for marine soft-sediment habitats to scale restoration of sediment chemistry through pollutant removal or capping. In several places, notably Chesapeake Bay (Weisburg et al. 1997) and the shallow shelf of the Pacific Ocean coast of North America (Word 1978), scientists have developed a site-specific index of benthic community health. M. Buchman (unpubl.) proposes a scaling method for quantifying the ecosystem benefits that scales benefits linearly to the increase in value of this index. Because an index like B-IBI (Benthic Index of Biotic Integrity: Weisburg et al. 1997) for the Chesapeake Bay includes several disparate components, such as categorical ratings for pollution-tolerant species and pollution-indicator species, and implicitly weights the multiple components in pooling them, it is unclear how scaling on such an index would compare to actual enhancement in production or to other explicit and quantifiable ecosystem services. This approach, however, represents a novel means of evaluating one component of the restoration process, specifically the quality of the restored resource. A necessary adjunct to this qualitative measure of restoration success is the integration of quantitative measures, such as estimates of secondary production, into a joint metric of ecosystem benefits of marine restoration.

Size-dependent value of production. Current use of secondary production as the metric by which to scale restoration projects and achieve compensation for biological losses assumes that the ecosystem services provided by production are equal independent of the size class in which that production occurs. This is clearly false, at least for some readily specified ecosystem ser-

vices. For example, small size classes of bivalve molluscs such as surf clams and hard clams serve as prey largely for crabs but also for fishes, octopi, seastars, predatory gastropods, and other marine predators (Kraeuter 2001). As bivalves grow larger, they gradually reduce their risk of predation (e.g. Arnold 1984). On the other hand, they contribute more to reproductive output (e.g. Peterson 1986) and they filter water at much higher *per capita* rates. Consequently, quantifying restoration success by the enhanced production of juvenile clams, which would lead to greater trophic transfer to consumers, differs substantially from that measured by enhanced production of older clams, which would lead to greater release of gametes and reduction of turbidity. These ecosystem services are not equivalent and one may be preferred over the others depending upon the situation. For example, if recruitment limitation exists because of depletion of adult spawning stock (e.g. Peterson 2002), then enhancement of larger clams would be the more appropriate metric for restoration success than augmentation of juvenile abundance. On the other hand, for populations in which recruitment is not limited by spawning stock biomass, enhancement of juveniles may provide the more suitable measure of restoration success by supporting production at higher trophic levels. This issue arose but was not resolved in planning the compensatory restoration for loss of surf clams and other bivalves after the North Cape oil spill (French McCay et al. 2003b, in this Theme Section).

Enhancing one species to compensate for many. Frequently an environmental incident will cause losses distributed among many species within an ecological guild, such as the losses of benthic invertebrates in salt ponds (French McCay et al. 2003b) or seabirds (Sperduto et al. 2003, in this Theme Section) following the North Cape oil spill. Because it would seem impractical and disproportionately costly to design and conduct population restoration projects for each species separately, one species is commonly chosen for restoration to compensate for the total loss within the guild (Zedler 2000). This decision may imply an assumption of functional equivalence among guild members such that the total abundance within the guild, not the distribution of abundances among component species, dictates the level of ecosystem services provided. This may be reasonably accurate in some situations, but such a decision contradicts the usual management strategy and conservation position maintaining that biodiversity is important to sustaining ecosystem functions (Naeem & Li 1997, Tilman et al. 1997, Elmquist et al. 2003). One possible alternative to implicitly assuming that maintaining biodiversity is unimportant in conducting compensatory restoration may be to replace losses of guilds of species with a habitat restoration project designed to enhance many species rather than employing population restoration options.

Differing uncertainty in population versus habitat restoration. Designing a restoration project for a single species carries high uncertainty. Success requires deep understanding of the factors that control the species population at the site and time of the restoration. For many species, there exists little history of previous restoration attempts on which to base scaling computations or even on which to make accurate predictions of direction of population response to intervention in the ecosystem. Predicting the quantitative magnitude of enhancement and projecting that forward over years represents a form of ecological hubris of extraordinary dimensions. When such population restorations are chosen to compensate for losses of important public-trust resources, conducting well-designed monitoring and retaining financial resources for any necessary adaptive management of the restoration would seem advisable (NRC 1992). For some exploited resources, such as targets of fisheries, substantial information is available on population regulation and often also on the success of population enhancement programs (e.g. French McCay et al. 2003a,b, in this Theme Section). Such information can justify choosing a population-based restoration project for those resources. Furthermore, if an endangered or threatened species is affected by an ecological mishap, then for both legal and ethical reasons, choosing an action that is expected to restore that population is understandable, despite the practical difficulties that lie ahead (Donlan et al. 2003, in this Theme Section).

Alternatively, compensatory restoration might be achieved by habitat restoration instead of targeting a specific population (Soule 1987, Wilson 1992). Because of loss and degradation of so many important habitats (Jackson et al. 2001), actions taken to construct, revitalize, restore, or protect otherwise-doomed habitat of established value to critical living resources generally carry less uncertainty about success and performance. In estuarine and coastal environments, this approach would be represented by accelerated restoration of salt marsh, seagrass, mangrove, oyster reef, and other structured, biogenic habitats (Thayer 1992, Heck et al. 2003, Peterson et al. 2003a). It may not be prudent, however, based on the results of Powers et al. (2003, in this Theme Section), to construct offshore artificial reefs to compensate for lost fish production, given the high uncertainty about their ability to promote higher net production of associated fishes if fishing pressure targeting those reefs cannot be controlled.

When population enhancement is chosen as the means of achieving compensatory restoration, there arises a potential to flood the system with the enhanced species and thereby induce unanticipated den-

sity-dependent responses that limit or eliminate the enhancement pulse. For example, flooding the environment with large numbers of small organisms as part of a population enhancement project could induce either functional (prey switching in their feeding choices) or numerical (population increases) responses in predator populations such that survival of the target of restoration is negatively density-dependent and no net enhancement is achieved. Spreading out the enhancement over several years is one means of minimizing the impacts of this effect, but numerical responses in predators could result in persistent build-up of predator populations that could conceivably negate most or all of the benefits of enhancement.

Another density-dependent mechanism that could impede restoration efforts, particularly those involving modest population enhancements, involves the Allee effect (Allee 1931)—positive density dependence in fitness at low population size (Courchamp et al. 1999, Stephens et al. 1999). Allee effects may be manifested at the population level through: (1) reproductive activity, which often depends on adequate population densities to achieve effective egg fertilization or to locate a mate (Petersen & Levitan 2001): or (2) predation-induced mortality of juvenile stages. Allee effects generally have been ignored in restoration and conservation efforts (Gascoigne & Lipcius in press), with a few notable exceptions (e.g. Tegner & Dayton 1977, Quinn et al. 1993, Marshall & Lipcius unpubl.). Positively density-dependent survival due to predation (= inversely density-dependent predation) is a widespread attribute of marine predator-prey systems (Seitz et al. 2001), and could easily prevent the recovery of populations at low abundance (Gascoigne & Lipcius in press, Lipcius et al. in press a). In these cases, attempts at restoration would require information on the minimal level of population enhancement needed to overcome Allee effects due either to predation or to reproductive limitations. Furthermore, there may be interactive mechanisms between multiple juvenile and adult stages experiencing density-dependent predation. For instance, in queen conch the presence of older juveniles significantly increases the survival of young juveniles (Lipcius et al. in press a). Older juveniles provide a positive feedback on younger juveniles through modifying their susceptibility to predators, which apparently increases handling time and decreases attack rates on younger juveniles when older juveniles are available. Restoration of such stage-structured populations may therefore require attention not simply to a single life stage, but also to the interdependent stages that impinge on population recovery.

Landscape effects of project siting and ecosystem-based restoration. In estimating the quantitative enhancement expected from alternative restoration pro-

jects, each project is often considered independently. Ecosystem benefits of paired or multiple projects can exceed the sum of projects done in isolation. These extra benefits typically are derived through landscape effects of proximity of restorations (NRC 1992). For example, salt marsh restoration has the well-appreciated benefit of providing additional subsidy of the detrital food chains of estuaries, leading to enhanced production of many important estuarine organisms, such as penaeid shrimps and their consumers (Haines & Montague 1979, Zimmerman et al. 2000). Benthic micro-algal production is high in salt marshes (Pinckney & Zingmark 1993) and leads to secondary production of many marsh animals (Sullivan & Moncreiff 1990, Currin et al. 1996, Deegan & Garritt 1997). The structure provided by salt marsh grasses is also important as habitat for many birds, such as rails, and invertebrates, including marsh periwinkles and mussels. Oyster reef restoration enhances production of fishes and mobile crustaceans by providing habitat for recruiting larvae, shelter for juveniles, and prey for all life stages (Peterson et al. 2003a). Kneib (2003, in this Theme Section) estimated the quantitative benefits of salt marsh restoration by computing the likely enhancement of tertiary production by small fishes and crustaceans that are the major beneficiaries of the increased primary production. Nevertheless, if a salt marsh restoration were paired in proximity to a restored oyster reef, interactions between the 2 habitats would be likely to provide additional ecosystem benefits that derive from landscape-level synergism between the habitats and that would not normally be included in the 2 independent scaling exercises. For example, demersal predators that seek structural habitat as shelter from their own enemies are likely to be better able to utilize the restored salt marsh if there is a corridor of biogenic oyster reef habitat connecting the restored marsh in the intertidal zone to subtidal refuge habitat (Micheli & Peterson 1999). Low-tide exposure of salt marshes forces aquatic consumers to retreat to the subtidal, where availability of structural refuges, such as seagrass beds or subtidal oyster reefs, may determine the capacity of these mobile consumers to use the resources available at high tide in the salt marsh. Moreover, marsh-associated nutritional subsidies apparently enhance the abundance of benthic prey in the subtidal zone bordering salt marshes (R. Seitz & R. Lipcius unpubl.), such that additional food would also be available to epibenthic predators, in addition to the shelter provided by the oyster reef. Furthermore, as sea level continues to rise through effects of greenhouse warming of the earth's atmosphere, erosion and destruction of salt-marsh habitat will likely grow at an increasing pace. Fringing oyster reefs serve as a biogenic breakwater that can not only reduce the erosive

energy of waves striking the marsh shoreline but also can grow vertically at rates that exceed sea-level rise. With adequate sources of sediments from rivers, the elevation of the salt marsh could also be maintained in depositional environments. Consequently, pairing of salt-marsh restorations with oyster reef restorations has the potential to extend the longevity of the marsh and thus enhance the long-term delivery of ecosystem services. This sort of ecosystem-based based restoration can be considered part of 'integrated resource management' and is strongly encouraged (NRC 1992).

The decision about where to locate a restoration project has many implications for its subsequent functioning and value to the ecosystem. The primary consideration in locating a restoration project is to place it in an environment suitable for sustaining the restoration over a long time. This requires assessing and then matching the environmental conditions required to support development and success. Often historical presence of the targeted restoration habitat guides siting decisions, although environmental changes do occur and may render past knowledge obsolete (see 'Alternative stable states and shifting baselines in populations and ecosystems'). However, even within the range of physically suitable conditions, habitat functions can vary with physical setting. For example, seagrass habitat located in high-energy environments is patchier and utilized by fishes and invertebrates in different ways than seagrass beds in low-energy settings (Fonseca & Bell 1998).

There can be advantages to designing restoration projects in a fashion that creates a network of habitat patches along an environmental gradient, similar to that being proposed as a solution to the problems posed by environmental uncertainty (Allison et al. 2003) and by unknown complexities of metapopulation source-sink dynamics (Lipcius et al. in press b) in the effective design of marine protected areas. Then, if environmental conditions deteriorate in one part of the gradient, habitat at the remaining portions of the gradient could serve as a refuge for mobile organisms to survive what otherwise could become a widespread mortality event. This process has been documented by Lenihan et al. (2001) for oyster reefs restored along a depth gradient in an estuary subject to bottom-water hypoxia; by placing reefs in shallow as well as deep water, fish possessed a refuge during a major hypoxic event that eliminated their sessile invertebrate prey on deep-water reefs. Reefs in shallow waters are, alternatively, more vulnerable to storm damage. In addition, survivors in one habitat patch could become a source population for recruits to sink habitats where populations have been extirpated by environmental (e.g. hypoxia) or biotic (e.g. disease) catastrophes (Lipcius et al. in press b). The potential impact of source-sink

dynamics on the effectiveness of population restoration efforts in marine reserves has been recognized (Crowder et al. 2000, Lipcius et al. 2001, Botsford et al. 2003) and integrated into conceptual models that synthesize the multiple pathways by which metapopulation structure may drive restoration success in marine reserves (Lipcius et al. in press b). Similarly, for habitat and population restoration efforts, whether dealing with plants or animals, it is imperative to examine the impact of spatially explicit processes and metapopulation implications on the efficacy of restoration.

Evaluation of the significance of ecosystem setting to the functional role and value of estuarine habitats is an active current focus of ecological research (e.g. Irlandi & Crawford 1997, Grabowski 2002, Hovel et al. 2002). Ecology may not be capable yet of providing confident predictions of the interactive benefits of landscape pairing of natural or restored habitats because study of trophic subsidies and connectivities from one system to another are still in their infancy (Polis et al. 1997). However, as ongoing research is completed, this current focus in ecosystems ecology can contribute to more complete and accurate valuation of restoration projects.

Uncertainty analyses. In rigorous ecological modeling, it is customary to provide formal uncertainty and sensitivity analyses to provide quantitative indications of how much risk of error is associated with various model predictions. Uncertainty analyses have not yet been formally incorporated into the practice of restoration scaling. Uncertainty is typically acknowledged and even used by employing qualitative rankings of restoration options to help guide choices for compensatory mitigation of natural resource losses (e.g. Powers et al. 2003). Yet trustees of natural living resources would be able to make more informed decisions about future compensatory restoration actions if they were armed with explicit estimates of the probabilities of a suite of alternative outcomes associated with each restoration alternative (e.g. Reckow 1999, Kinzig et al. 2003). If quantitative estimates of uncertainty were available, they could conceivably be used to modify the scale of restoration effort required for compensatory restoration, applying a replacement ratio for resource or habitat lost that grows with uncertainty. This principle is already regularly used by management agencies in scaling mitigation projects required as conditions of various construction permits (Fonseca et al. 2000). Perhaps the most reliable means of insuring quantitative replacement of a lost public-trust resource involves monitoring of the resource(s) of interest and then adaptively modifying the scale or even type of restoration in response to documented performance of the restoration (Fonseca et al. 1998). Such monitoring and adaptive management could

legitimately be included among the costs of restoration. Similarly, knowledge gained about the efficacy of alternative restoration actions, which has value for planning future restoration and adaptive management actions, could be credited as a benefit of restoration. At present, most monitoring of compensatory restoration projects seems rudimentary, incomplete, and inadequate to advance restoration science. Knowledge enhancement is not presently included as one of the credits in conducting compensatory restoration.

Building the science of restoration ecology. Compensatory restoration projects occasionally involve large-scale experimental interventions that represent ideal, and perhaps otherwise unaffordable, opportunities to test basic ecological hypotheses involving dynamics of populations, communities, and ecosystems (Zedler 2000). Yet, there is insufficient collaboration between restoration agents in government and agencies charged with supporting basic science (Carpenter & Lathrop 1999, Hobbs & Harris 2001). After an extended period of denigration by mainstream academia, terminated by bold syntheses (e.g. Lubchenco et al. 1991), conservation biology became academically accepted as part of the science of ecology. Restoration ecology is, however, still typically viewed with suspicion by academia and often characterized as applied horticulture with inadequate fundamental foundation in theory (e.g. Palmer et al. 1997). The ability to render accurate predictions about interventions into ecological systems indeed represents an acid test of the capabilities of the science of ecology. The practice of restoration can be greatly enhanced by further developing the conceptual foundation of restoration ecology, which could be achieved by forging partnerships between ecosystem restoration and basic ecology.

Unresolved conflicts in habitat paradigms and food-web dynamics. Basic ecological understanding of the functioning of important biogenic habitats in estuarine and coastal marine environments is still incomplete. Presently prevailing models for the functioning of the most important biogenic habitats such as seagrass beds and salt marshes contain largely unrecognized and thus unresolved conflicts. For example, the presumption that seagrass beds serve as an obligate nursery habitat for juvenile fishes does not stand up to rigorous scrutiny: other structured habitats are populated by similar densities of juvenile fishes and mobile invertebrates (Heck et al. 2003). One of the most important unrecognized conflicts in our present paradigms for the functioning of important biogenic habitats relates directly to estimation of production at higher trophic levels and thus to the ability to accurately scale restoration projects. Specifically, seagrass beds and salt marshes are commonly assumed to provide enhanced food availability and simultaneously enhanced refuge from predation. This dual function of the habitat can pose an unresolved contradiction. A refuge from predation implies inhibition of energy flow up the food chain to higher-order predators, not enhancement of energy flow to apex consumers. Consequently, the quantitative production enhancement achieved by establishment of restored seagrass or salt-marsh habitat may be expected to vary dramatically by trophic level. Secondary producers, the herbivorous and detritivorous marine benthic invertebrates, may experience dramatically enhanced production through energy subsidies in seagrass and salt-marsh habitat. However, structural refuges provided by the emergent plants and their subsurface roots may block high rates of transfer of energy to their predators, the tertiary producers (Coen et al. 1981, Peterson 1982). Integration of these 2 processes of bottom-up enhancement of secondary production and provision of structural refuges from predation could be achieved in restoration scaling by appropriately modifying the ecological transfer efficiency between the second and third trophic levels. However, ecologists have not yet recognized this contradiction in prevailing concepts of energy flow through vegetated estuarine habitats and thus have not provided estimates of how the refuge action modifies these transfer efficiencies. Even when transfer efficiencies can be confidently assigned to reflect refuge functions, computation of the benefits of habitat restoration will still vary between the second and third trophic levels. Thus, application of the approach of French McCay & Rowe (2003, in this Theme Section) that synthesizes all ecosystem injuries and benefits by conversion to a single trophic level would yield different answers at different levels.

A related role of emergent structure in restored habitats is also not adequately incorporated into present energetics-based estimations of production benefits from restoration. Energetics-based methods of computation combine knowledge of gains in primary productivity, trophic structure of subsequent energy flow, and conversion efficiencies to compute the enhancement of secondary or tertiary production (e.g. French McCay & Rowe 2003, Kneib 2003). However, secondary and tertiary production is also enhanced by mere provision of structural habitat for species that do not feed on primary producers in that habitat. For example, the emergent culms of *Spartina alternifora* baffle currents and wave energy sufficiently to stabilize the sediment surface and allow occupation by oysters. Those oysters feed largely on microalgae, phytoplankton and benthic diatoms (Haines & Montague 1979, Riera & Richard 1996, Page & Lastra 2003), and do not derive much nutritional benefit from the vascular plants whose production is directly enhanced by marsh-habitat restoration. In addition, clumps of oysters provide habitat for

mussels, barnacles, and other filter feeders energetically dependent to some large degree on phytoplankton, which are not enhanced by the marsh. Consequently, when enhancement of secondary production through restoring salt marshes is estimated by tracking the fate of the enhanced primary production in the marsh, the mechanism of enhancement of secondary production by habitat provision is not included. Similarly, in seagrass-bed habitat, water currents are baffled by emergent vegetation projecting into the water column. This deceleration of flow induces deposition of larvae of marine benthic invertebrates and deposition of suspended organic food particles (Peterson et al. 1984, Eckman 1987, Wilson 1990). Thus, secondary production in restored seagrass beds is also enhanced through physical effects of the provision of habitat for organisms that are not fully, or in some cases even partially, nourished by the enhanced primary production of that habitat. Like the salt marsh, scaling calculations for the seagrass habitat that are based solely upon bottom-up enhancement of production would miss this contribution from provision of structural habitat and thus underestimate ecosystem benefits (see French McCay & Rowe 2003).

Successful enhancement of populations by restoration efforts will also be shaped by food-web interactions because secondary production in restored habitats is dictated by size-dependent growth and survival within the habitat, which depend on predator-prey interactions (see Lipcius et al. in press b for examples from population restoration using marine reserves). The manner in which food web interactions will determine the size structure and abundance of individuals within a restored habitat may be predictable to some degree based on fundamental relationships between the life-history features of the target species and the geometry of the restored habitat (Walters 2000). As the abundance of predators increases within a restored habitat, the abundance of their major prey may decline, which can result in trophic cascades that further modify community structure. For instance, in population restoration projects using marine reserves in New Zealand, abundance and size of a predatory demersal fish (sparid snapper *Pagrus auratus*) and spiny lobster (palinurid lobster *Jasus edwardsii*) increased significantly, which decreased abundance of an invertebrate grazer (sea urchin *Evechinus chloroticus*), and subsequently permitted re-establishment of vigorous kelp forests dominated by the laminarian *Ecklonia radiata* (Babcock et al. 1999). Changes in food-web and trophic structure allow some species to increase, but cause others (notably prey species) to decline, which may lead to lower production and slower biomass accumulation in restored habitats than expected. Similarly, establishment of reserves in kelp beds led to sub-stantial increases in the abundance of sea otters *Enhydra lutris*, which subsequently reduced the abundance, size and microhabitat use of the targeted restoration species, red abalone *Haliotis rufescens*, even more than fishery exploitation (Fanshawe et al. 2003). Various features of restored habitats will interact with life-history characteristics of target species to determine restoration effectiveness, and these must be addressed to increase the likelihood of restoration success.

Success of restoration projects will therefore depend, in part, upon the incorporation of multispecies management approaches, based predominantly on food-web dynamics (e.g. Pauly et al. 1998). For instance, in coastal salt marshes, reductions in blue crab abundance (Lipcius & Stockhausen 2002), partly through heavy fishing pressure, may have allowed marsh snails *Littoraria irrorata* to increase in abundance and subsequently injure salt marsh grasses through their feeding activities, ultimately leading to reduction of the marsh habitat (Silliman & Bertness 2002). If such an interaction were strong in restored marshes, it could easily retard or preclude recovery of the salt marsh and its community. Hence, it is imperative to incorporate an ecosystem-based approach in restoration ecology. Admittedly, there is considerable debate over the reliability of predictions about changes in the abundance of target species derived from multispecies approaches (Yodzis 2001). Thus, restoration ecology must incorporate multispecies approaches, preferably as testable hypotheses to be evaluated during monitoring and, if supported, acted upon through adaptive management of the restoration.

Alternative stable states and shifting baselines in populations and ecosystems. A significant potential difficulty for restoration efforts arises from the possibility that populations and ecosystems may exhibit alternative stable states (Scheffer et al. 2001, Carpenter 2002). Given that many food webs and ecosystems have undergone dramatic, historical alterations due to both anthropogenic (e.g. overfishing and eutrophication: Jackson et al. 2001) and natural (hurricanes: R. Lipcius & R. Seitz unpubl.) disturbances, it is possible that restoration attempts will fail to restore habitats or communities to their 'pristine' state. Even when there is agreement among restoration biologists on the preferred state of a habitat or community, its composition, and its biomass structure, that habitat or community may be unattainable due to the 'stability' of the degraded ecosystem or distorted community (Scheffer et al. 2001, Carpenter 2002). 'Stability' refers to the situation wherein a disturbed or degraded ecosystem is an 'alternative stable state' (Scheffer et al. 2001, Carpenter 2002), one not easily shifted back to the undisturbed state due to feedback mechanisms maintaining the status quo. The characteristic of stability is not lim-

ited to pristine systems; it is also a feature of disturbed systems (Scheffer et al. 2001, Carpenter 2002), which is one of the factors that may render restoration of disturbed ecosystems difficult. Restoration biologists should therefore consider the possibility that some desired habitat or community configurations may not be readily achievable, at least in the short term, without massive intervention (Carpenter 2002). For instance, the seaside lagoons of the Eastern Shore of Chesapeake Bay harbored extensive seagrass beds that supported a lucrative bay scallop fishery until the Storm King hurricane of 1933 devastated the ecosystem. The resultant turbid conditions have not only precluded restoration of seagrass beds, but also prevented the re-establishment of a productive bay scallop fishery in the seaside lagoons for over 6 decades (R. Lipcius & R. Seitz unpubl.). Alternative stable states of ecosystems are a very real possibility in disturbed ecosystems that must be considered in planning and scaling restoration efforts.

In summary, the process of scaling restoration projects to compensate for natural resource injuries has served to identify important unresolved questions that may help direct new basic research in the science of restoration ecology and promote partnerships between habitat restoration and basic ecology.

LITERATURE CITED

Able KW, Hagan SM, Brown SA (2003) Mechanisms of marsh habitat alteration due to *Phragmites*: responses of young-of-the-year mummichog (*Fundulus heteroclitus*) to treatment for *Phragmites* removal. Estuaries 26(2B):484–494

Allee WC (1931) Animal aggregations: a study in general sociology. University of Chicago Press, Chicago

Allen EB, Covington WW, Falk DA (1997) Developing a conceptual basis for restoration ecology. Restor Ecol 5:275

Allison GW, Gaines SD, Lubchenco J, Possingham HP (2003) Enduring persistence of marine reserves: catastrophes require adopting an insurance factor. Ecol Appl 13:S8–S24

Arnold WS (1984) The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne). J Exp Mar Biol Ecol 80: 207–219

Babcock RC, Kelly S, Shears NT, Walker JW, Willis TJ (1999) Changes in community structure in temperate marine reserves. Mar Ecol Prog Ser 189:125–134

Baird D, Christian RR, Peterson CH, Johnson GA (in press) Consequences of hypoxia on estuarine food web and ecosystem function: energy diversion from consumers to microbes. Ecol Appl

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509–515

Botsford LW, Micheli F, Hastings A (2003) Principles for the design of marine reserves. Ecol Appl 13:25–31

Cammen LM (1976) Abundance and production of macroinvertebrates from natural and artificially established salt marshes in North Carolina. Am Midl Nat 96:244–253

Carpenter SR (2002) Ecological futures: building an ecology of the long now. Ecology 83:2069–2083

Carpenter SR, Lathrop RC (1999) Lake restoration: capabilities and needs. Hydrobiologia 396:19–28

Coen LD, Heck KL, Able LG (1981) Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62:1484–1493

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends Ecol Evol 14:405–410

Crowder LB, Lyman SJ, Figueira WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. Bull Mar Sci 66:799–820

Currin CA, Newell SY, Paerl HW (1996) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple isotope analysis. Mar Ecol Prog Ser 121:99–116

Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. Mar Ecol Prog Ser 147:31–47

Donlan M, Sperduto M, Hebert C (2003) Compensatory mitigation for injury to a threatened or endangered species: scaling piping plover restoration. Mar Ecol Prog Ser 264: 213–219 (in this Theme Section)

Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within seagrass meadows. J Exp Mar Biol Ecol 106:165–191

Elmgren R (1989) Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. Ambio 18:326–332

Elmquist T, Folke C, Nystrom M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494

Ewel J (1987) Restoration is the ultimate test of ecological theory. In: Jordan W, Gilpin M, Aber J (eds) Restoration ecology: a synthetic approach to ecological research, Cambridge University Press, New York, p 31–33

Fanshawe S, Van Blaricom GR, Shelly AA (2003) Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. Conserv Biol 17: 273–283

Fonseca MS, Bell SS (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar Ecol Prog Ser 171:108–121

Fonseca MS, Meyer DL, Hall MO (1996) Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components. Mar Ecol Prog Ser 132:141–156

Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. Decision Analysis Series No. 12, NOAA Coastal Ocean Program, Silver Spring, MD

Fonseca MS, Julius BE, Kenworthy WJ (2000) Integrating biology and economics in seagrass restoration: how much is enough and why? Ecol Engineer 15:227–237

French McCay DF, Rowe JJ (2003) Habitat restoration as mitigation for lost production at multiple trophic levels. Mar Ecol Prog Ser 264:233–247 (in this Theme Section)

French McCay DF, Gibson M, Cobb JS (2003a) Scaling restoration of American lobsters: combined demographic and discounting model for an exploited species. Mar Ecol. Prog Ser 264:177–196 (in this Theme Section)

French McCay DF, Peterson CH, DeAlteris JJ, Catena J

(2003b) Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration. Mar Ecol Prog Ser 264:197–212 (in this Theme Section)

Gascoigne J, Lipcius RN (in press) Allee effects in marine systems. Mar Ecol Prog Ser

Grabowski JH (2002) The influence of trophic interactions, habitat complexity, and landscape setting on community dynamics and restoration of oyster reefs. PhD thesis, University of North Carolina at Chapel Hill, NC

Haines EB, Montague CL (1979) Food sources of estuarine invertebrates analyzed by $^{13}C/^{12}C$ ratios. Ecology 60:48–56

Heck KL Jr, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123–136

Hobbs RJ, Harris JA (2001) Restoration ecology: repairing earth's ecosystems in the new millennium. Restor Ecol 9: 239–246

Hovel KA, Fonseca MS, Myer DL, Kenworthy WJ, Whitfield PE (2002) Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Mar Ecol Prog Ser 243:11–24

Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:231–236

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638

Jordan WR, Gilpin ME, Aber JD (1987) Restoration ecology. Cambridge University Press, Cambridge

Kinzig A, Starrett D, Arrow K, Aniyar S and 17 others (2003) Coping with uncertainty: a call for a new science-policy forum. Ambio 32:330–335

Kneib RT (2003) Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. Mar Ecol Prog Ser 264:279–296 (in this Theme Section)

Kraeuter JN (2001) Predators and predation. In: Kraeuter JN, Castagna M (eds) Biology of the hard clam. Elsevier, Amsterdam, p 441–589

Lawton JH (1996) Corncake pie and prediction in ecology. Oikos 76:3–4

Lenihan HS, Peterson CH, Byers JE, Grabowski JH, Thayer GW, Colby DR (2001) Cascading effects of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol Appl 11:764–782

Lipcius RN, Stockhausen WT (2002) Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar Ecol Prog Ser 226:45–61

Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation dynamics. Mar Freshw Res 52:1589–1598

Lipcius RN, Schreiber SJ, Marshall LS Jr, Gascoigne J (in press a) Density-dependent predation and alternative states in stage-structured populations: theory and field evidence in the queen conch. Ecol Lett

Lipcius RN, Crowder LB, Morgan LE (in press b) Conservation of populations and metapopulations by marine reserves: caveats, conceptual framework, and an opportunity for optimality. In: Norse E, Crowder LB (eds) Marine conservation biology. Island Press, Chapel Hill, NC

Lubchenco J, Olson AM, Brubaker LB, Carpenter SR and 12 others (1991) The sustainable biosphere initiative: an ecological research agenda. Ecology 72:371–412

Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecol Appl 13:S3–S7

Luckenbach MA, Mann R, Wesson JE (eds) (1998) Oyster reef restoration: a symposium and synthesis of approaches. Virginia Institute of Marine Sciences Press, Gloucester Point, VA

Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. Conserv Biol 13: 869–881

Naeem S, Li SB (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509

Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41:199–219

NOAA (National Oceanographic and Atmospheric Administration) (1977) Habitat equivalency analysis: an overview. Policy and Technical Paper Series, No 95–1, Damage Assessment and Restoration Program, NOAA, Silver Spring, MD

NRC (National Research Council) (1992) Restoration of aquatic ecosystems. National Academy Press, Washington, DC

Page HM, Lastra M (2003) Diet of intertidal bivalves in the Ria de Arosa (NW Spain): evidence from stable C and N isotope analysis. Mar Biol 143:519–532

Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community restoration ecology. Restor Ecol 5:291–300

Palumbi SR (2001) The ecology of marine protected areas. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Publishing, Sunderland, MA, p 509–530

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. Science 279: 860–863

Petersen CW, Levitan DR (2001) The Allee effect: a barrier to recovery by exploited species. In: Reynolds JD, Mace GM, Redford KH, Robinson JG (eds) Conservation biology. Cambridge University Press, Cambridge

Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar Biol 66:159–170

Peterson CH (1986) Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. Mar Ecol Prog Ser 29:93–97

Peterson CH (2002) Recruitment overfishing in a bivalve mollusc fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. Can J Fish Aquat Sci 59:96–104

Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. J Mar Res 42:123–138

Peterson CH, Grabowski JH, Powers SP (2003a) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar Ecol Prog Ser 264:249–264 (in this Theme Section)

Peterson CH, Kneib RT, Manen CA (2003b) Scaling restoration actions in the marine environment to meet quantitative targets of enhanced ecosystem services. Mar Ecol Prog Ser 264:173–175 (in this Theme Section)

Pinckney J, Zingmark RG (1993) Biomass and production of benthic microalgal communities in estuarine habitats. Estuaries 16:887–897

Polis G, Anderson WB, Holt RD (1997) Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 29:289–316

Powers SP, Grabowski JH, Peterson CH, Lindberg WJ (2003) Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent sce-

narios. Mar Ecol Prog Ser 264:265–277 (in this Theme Section)

Quinn JF, Wing SR, Botsford LW (1993) Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. Am Zool 33:537–550

Riera P, Richard P (1996) Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine bay of Marennes-Oleron. Estuar Coast Shelf Sci 42:347–360

Reckow KH (1999) Water quality prediction and probability network models. Can J Fish Aquat Sci 56:1150–1158

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Seitz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82:2435–2451

Silliman BR, Bertness MD (2002) A trophic cascade regulates salt marsh primary production. Ecology 99:10 500–10 505

Soule M (ed) (1987) Conservation biology. Sinauer Publishing, Sunderland, MA

Sperduto M, Powers SP, Donlan M (2003) Scaling restoration actions to achieve quantitative enhancement of loon, seaduck, and other seabird populations. Mar Ecol Prog Ser 264:221–232 (in this Theme Section)

Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? Oikos 87:185–190

Sullivan MJ, Moncreiff CA (1990) Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. Mar Ecol Prog Ser 62:149–159

Tegner MJ, Dayton PK (1977) Sea urchin recruitment patterns and implications of commercial fishing. Science 196: 324–326

Thayer GW (ed) (1992) Restoring the nation's marine environment. Maryland Sea Grant College Program, College Park, MD

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Vitousek PM, Mooney HA, Lubchenco J, Mellilo J (1997) Human domination of earth's ecosystems. Science 277: 494–499

Walters CJ (2000) Impact of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bull Mar Sci 66:745–758

Weisburg SB, Ranasinghe JA, Dauer DM, Schaffner LC, Diaz RJ, Frithsen JB (1997) An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. Estuaries 20: 149–158

Wilson EO (1992) Diversity of life. Harvard University Press, Cambridge, MA

Wilson FS (1990) Temporal and spatial patterns of settlement: a field study of mollusks in Bogue Sound, North Carolina. J Exp Mar Biol Ecol 139:201–220

Woodhouse WW Jr, Seneca ED, Broome SW (1974) Propagation of *Spartina alterniflora* for substrate stabilization and salt marsh development. Coastal Engineer Research Center, US Army Corps of Engineers, Fort Belvoir, VA

Word JQ (1978) The infaunal trophic index. S Calif Coastal Water Res Project Ann Rep, El Segundo, CA, pp 19–39

Young TP (2000) Restoration ecology and conservation biology. Biol Conserv 92:73–83

Yodzis P (2001) Must top predators be culled for the sake of fisheries? Trends Ecol Evol 16:78–84

Zedler JB (2000) Progress in wetland restoration ecology. Trends Ecol Evol 15:402–407

Zimmerman RJ, Minello TJ, Rozas LP (2000) Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer, Dordrecht, p 293–314