

## THEME SECTION

## Restoration scaling in the marine environment

*Coordination:* Charles H. Peterson, Ronald T. Kneib

*Contributors to Theme Section:* J. Catena, J. S. Cobb, J. T. DeAlteris, M. Donlan, D. F. French McCay, M. Gibson, J. H. Grabowski, C. Hebert, R. T. Kneib, W. J. Lindberg, R. N. Lipcius, C.-A. Manen, C. H. Peterson, S. P. Powers, J. J. Rowe, M. Sperduto

### Scaling restoration actions in the marine environment to meet quantitative targets of enhanced ecosystem services

Charles H. Peterson<sup>1,\*</sup>, Ronald T. Kneib<sup>2</sup>, Carol-Ann Manen<sup>3</sup>

<sup>1</sup>University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, North Carolina 28557, USA

<sup>2</sup>Marine Institute, University of Georgia, Sapelo Island, Georgia 31327, USA

<sup>3</sup>National Oceanographic and Atmospheric Administration, Damage Assessment Center, Silver Spring, Maryland 20910, USA

Recognition of the critical importance of the sustainable delivery of goods and services from natural ecosystems to human welfare, health, and economic systems is rapidly growing (e.g. Lubchenco et al. 1991, Daily 1996). Because the degradation of natural ecosystems is so pervasive both on land (Vitousek et al. 1997) and in the sea (Botsford et al. 1997), especially in coastal systems (Jackson et al. 2001), interest in restoration of natural resources, habitats, and services is also increasing (Thayer 1992, Wilson 1992). Restoration ecology may even become the dominant discipline in environmental science during the 21st century (Hobbs & Harris 2001).

Restoration ecology and conservation biology share the broad goal of managing human impacts on natural resources and ecosystems (Young 2000). Although seminal books on the 2 disciplines appeared almost simultaneously (Jordan et al. 1987, Soule 1987), subsequent conceptual growth in conservation biology has exceeded that of restoration ecology (Young 2000). Consequently, technical restoration activity in both terrestrial and marine environments has progressed faster than the fundamental conceptual support for it (Allen et al. 1997, Palmer et al. 1997, van Diggelen et al. 2001). A major goal of this Theme Section is to expose to wide review the conceptual bases for various types of restoration projects so as to stimulate further growth of the ecological theory required to advance and improve restoration practices.

One active and growing area of marine restoration ecology involves government-mandated restoration of natural resources injured by environmental incidents, such as oil and chemical spills, pollutant releases, or physical destruction of habitat (e.g. NOAA 1997). Federal laws in the USA, notably the Comprehensive Environmental Response, Cleanup, and Liability Act (CERCLA) of 1980, and the Oil Pollution Act (OPA) of 1990, dictate that restoration actions be taken to provide equivalent compensation for losses or injuries to natural resources held in public trust and to the services that those resources would have provided (Burlington 1999). Natural resources under public ownership include the air, water, and habitats, together with the plants and animals within them. The federal and state trustees of those resources are charged with the responsibility to assess losses and injuries, to restore, replace, rehabilitate or acquire their equivalent, and to obtain a monetary settlement from the responsible party to achieve this end. As an example of the development of such compensatory restoration, Fonseca et al. (2000) describe a process for quantitative matching of injury to seagrass habitat against benefits flowing from seagrass restoration projects.

Both CERCLA and OPA depend upon the natural science of ecology in 2 contexts: first for a natural resources damage assessment (NRDA) and second for a comprehensive restoration program that fully compensates for those damages. Scientific challenges exist for

\*Email: cpeters@email.unc.edu

each task. In damage assessment, the greatest challenges involve determining the metrics that best characterize the health and services provided by the ecosystem and then assessing the degree of departure from and rate of progression of natural recovery to conditions that would have prevailed in the absence of the environmental incident. Progress has been made in resolving many of the fundamental challenges in assessing impacts (e.g. Schmitt & Osenberg 1996). However, much new research is needed in developing rigorous and reliable scientific methods for restoring injured or lost natural resources and their ecosystem services to targeted levels. Predicting the quantitative consequences of any intervention into an ecosystem represents a challenge for the discipline of ecology (Lawton 1996). The demands for application of natural science to fulfill governmental mandates for compensatory restoration that is ecologically meaningful, scientifically sound, cost-effective, and reliable may drive further development of the conceptual foundation for restoration interventions and thereby enhance the capabilities of ecological science (Zedler 2000).

In this Theme Section, we intend to advance the conceptual basis of restoration ecology by publicizing recent analyses of restoration actions to achieve compensation for injuries to, and losses of, natural marine resources and the services that they provide. The papers illustrate multiple approaches to restoration, developing the conceptual basis for choosing specific restoration approaches and for scaling the intervention to match the quantitative injuries. The studies were conducted in response to 2 recent environmental incidents, the 1996 tanker barge 'North Cape' oil spill in Rhode Island and a 1997 process water spill from a phosphate plant into the Alafia River estuary near Tampa Bay in Florida.

Foci of the following papers in this Theme Section range from restoration of individual species populations to rehabilitation of entire communities and habitats. The contribution by French McCay et al. (2003a) uses the American lobster to illustrate how compensatory enhancement of a harvested (exploited) species can take advantage of a typically extensive body of research to determine the factor(s) that limit population size and also how changing fishery regulations provide unique opportunities for restoration. French McCay et al. (2003b) demonstrate for other exploited species, bivalve molluscs, how past scientific studies of resource enhancement, including development of hatchery technologies, permit juvenile seeding and adult transplantation to achieve compensation for losses. Donlan et al. (2003) assess the special challenges implicit in developing rigorous restoration options for a threatened or endangered species, the piping plover. Sperduto et al. (2003) synthesize avail-

able information on population limitation of loons, sea-ducks, and other seabirds in New England, and construct defensible restoration scaling. French McCay & Rowe (2003) develop a logical conceptual basis for scaling habitat restoration to compensate for the loss of several species at multiple trophic levels. Peterson et al. (2003) review available empirical data on quantitative enhancement of nekton populations by restoring oyster reefs in the southeast USA and apply demographic and growth models to estimate the species-specific augmentation of fish and crustacean production that is expected per unit area of oyster reef restoration. Powers et al. (2003) present an analogous synthesis and quantitative model to establish how installation of an offshore artificial reef is expected to affect fish production in the southeast USA. Kneib (2003) combines a bioenergetic approach with a landscape perspective to develop realistic expectations for augmentation of nekton associated with restoration of salt marsh habitat. Finally, Peterson & Lipcius (2003) use the preceding papers in the Theme Section to suggest how the discipline of restoration ecology has been and can further be advanced to better predict (e.g. Zedler 2000) the consequences of ecosystem interventions to restore natural living resources.

*Acknowledgements.* Development of this manuscript was supported by the NOAA Damage Assessment Center.

#### LITERATURE CITED

- Allen EB, Covington WW, Falk DA (1997) Developing a conceptual basis for restoration ecology. *Restor Ecol* 5:275
- Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. *Science* 277: 509–515
- Burlington LB (1999) Ten-year historical perspective of the NOAA damage assessment and restoration program. *Spill Sci Tech Bull* 5:109–116
- Daily GC (ed) (1996) *Nature's services: societal dependence on natural ecosystems*. Island Press, Chapel Hill, NC
- 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)
- 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 DP, 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 DP, 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 DP, Peterson CH, DeAlteris JT, Catena J (2003b) Restoration that targets function as opposed to structure: the feasibility of replacing lost bivalve production and filtration. *Mar Ecol Prog Ser* 264:197–212 (in this Theme Section)

- Hobbs RJ, Harris JA (2001) Restoration ecology: repairing earth's ecosystems in the new millennium. *Restor Ecol* 9: 239–246
- 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
- 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)
- Lawton JH (1996) Corncake pie and prediction in ecology. *Oikos* 76:3–4
- Lubchenco J, Olson AM, Brubaker LB, Carpenter SR and 12 others (1991) The sustainable biosphere initiative: an ecological research agenda. *Ecology* 72:371–412
- NOAA (1977) *Habitat equivalency analysis: an overview*. Policy and Technical Paper Series, No 95-1, Damage Assessment and Restoration Program, National Oceanographic and Atmospheric Administration, Silver Spring, MD
- Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community restoration ecology. *Restor Ecol* 5:291–300
- Peterson CH, Lipcius RN (2003) Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. *Mar Ecol Prog Ser* 264:297–307 (in this Theme Section)
- Peterson CH, Grabowski JH, Powers SP (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar Ecol Prog Ser* 264:249–264 (in this Theme Section)
- Powers SP, Grabowski JH, Peterson CH, Lindberg WJ (2003) Estimating enhancement of fish production by artificial offshore reefs: uncertainty exhibited by divergent scenarios. *Mar Ecol Prog Ser* 264:265–277 (in this Theme Section)
- Schmitt RJ, Osenberg CW (1996) *Detecting ecological impacts: concepts and applications in coastal habitats*. Academic Press, San Diego, CA
- Soule M (ed) (1987) *Conservation biology*. Sinauer, Sunderland, MA
- Sperduto M, Powers SP, Donlan M (2003) Scaling restoration actions to achieve quantitative enhancement of loon, sea duck, and other seabird populations. *Mar Ecol Prog Ser* 264:221–232 (in this Theme Section)
- Thayer GW (ed) (1992) *Restoring the nation's marine environment*. Maryland Sea Grant College Program, College Park, MD
- van Diggelen R, Grootjans AP, Harris JA (2001) Ecological restoration: state of the art or state of the science? *Restor Ecol* 9:115–118
- Vitousek PM, Mooney HA, Lubchenco J, Mellilo J (1997) Human domination of earth's ecosystems. *Science* 277: 494–499
- Wilson EO (1992) *Diversity of life*. Harvard University Press, Cambridge, MA
- Young TP (2000) *Restoration ecology and conservation biology*. *Biol Conserv* 92:73–83
- Zedler JB (2000) Progress in wetland restoration ecology. *Trends Ecol Evol* 15:402–407



# Scaling restoration of American lobsters: combined demographic and discounting model for an exploited species

Deborah P. French McCay<sup>1,\*</sup>, Mark Gibson<sup>2</sup>, J. Stanley Cobb<sup>3</sup>

<sup>1</sup>Applied Science Associates, 70 Dean Knauss Drive, Narragansett, Rhode Island 02882, USA

<sup>2</sup>Division of Fish and Wildlife, Rhode Island Department of Environmental Management, 3 Fort Wetherill Rd., Jamestown, Rhode Island 02835, USA

<sup>3</sup>Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA

**ABSTRACT:** Ecological theory does not currently allow precise predictions of the consequences of ecological restoration. Ecological restoration and species enhancement projects could be profitably used to test theoretically based predictions, but only if theory were first applied to develop quantitative predictions suitable for testing. Here, we review what is known about factors limiting population size and production of the American lobster *Homarus americanus*, and use that information to construct a demographic life-table model of population dynamics. We then use the model to evaluate alternative options for enhancing lobster population size and production. Because this species represents an example of a population subjected to intense human exploitation as a target of commercial fisheries, which has stimulated much research on its biology, demographic modeling is facilitated. Furthermore, intervention into the fishery provides a viable restoration option available only to exploited species. We apply the economic concept of discounting (of future pay-back in the form of restoration, analogous to being paid interest on a loan) to allow quantification of the scale of restoration needed to compensate for both the magnitude of the estimated loss of American lobsters and the time lags between loss and restoration following a major oil spill. Quantification of benefits is rarely performed for restoration projects to guide compensation for natural resource damages caused by environmental incidents. The methods and approach developed here can help address this past failure in order to provide compensating ecological and human services equal to those lost. The approach represents a significant step forward in conceptually and quantitatively addressing restoration needs. The methods may be applied to other species, especially those that are exploited by humans, but also others that can feasibly be restored to mitigate impacts of adverse environmental events.

**KEY WORDS:** Restoration · American lobster · Population model · Limiting factor · North Cape oil spill · Fishery · Natural resource damage assessment · Interim loss

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Widespread degradation of coastal marine ecosystems and the goods and services that they provide (Jackson et al. 2001, Peterson & Estes 2001) has stimulated great interest in the restoration of marine resources. Accordingly, restoration ecology has become perhaps the fastest-growing discipline in environmental sciences (Young 2000). Much of the practice of eco-

logical restoration and species enhancement is organized by government resource agencies rather than by research scientists, yet these projects represent interventions into natural ecosystems that could be used effectively to test and improve the ecological theory required to achieve the intended restorations. For example, in the United States, when natural resources are impacted by environmental incidents, such as oil and chemical spills, pollutant releases, or physical

\*Email: dfrench@appsoci.com

destruction of habitat, federal and state agents ('trustees') are legally mandated to recover damages from responsible parties and to use those funds for restoration (NOAA 1997). The restoration should, by law, provide ecological and human services equivalent to those that were lost. In practice, however, many restoration projects have been pursued with only limited confidence that they might restore the intended level of services. Quantification of benefits is a particular challenge and is required to ensure that the scale of the restoration project compensates for the estimated magnitude of the injuries to the natural resources (i.e. provides ecosystem and human services equivalent in value to those lost).

Species restoration plans are based either upon restoration of habitat, which can have positive consequences for a wide suite of species, or upon ecological intervention designed for a particular species to relieve some population bottleneck that limits its abundance (Peterson et al. 2003, in this Theme Section). Species-specific interventions demand substantial, detailed information on the ecology of the species. Nevertheless, to restore a species of particular value (ecologically and/or economically), it may be preferable to focus on species-explicit restoration options, because such plans may provide more confidence that the target species will benefit. Species-explicit restoration projects manipulate one or more limiting factors to population growth. Recovery plans for endangered and threatened species (Clark et al. 2002) represent examples of restoration projects that commonly include species-explicit intervention projects. When the species to be enhanced is the target of a fishery or is otherwise exploited, that species may often be best restored by developing a species-specific set of manipulations. Typically, management agencies maintain databases on catch and often on effort, as well as conduct research on commercially important species, thus providing unusually detailed information needed to develop a quantitative understanding of factors limiting population size and growth. In addition, because marine fish stocks are so severely exploited (Pauly et al. 1998), management of fishing pressure to lower fishing mortality provides a viable means of modifying population size, and thus a highly predictable tool of effecting desired restoration in exploited species.

The American lobster *Homarus americanus* is clearly representative of an exploited species of sufficient economic value and ecological importance, as a top predator, to have stimulated substantial research on its basic biology. The lobster fishery is the most valuable commercial fishery of the Northeast United States (ASMFC 2000). In addition, the lobster is heavily exploited and reduced to population levels lower than those which would provide the maximum sustainable yield

(Fogarty & Idoine 1988, ASMFC 2000). Thus, when an oil spill from the barge North Cape killed millions of lobsters in winter 1996, the responsible federal and state trustees developed a species-explicit plan for lobster restoration that considered manipulation of the fishery to compensate for the loss of the lobsters. This process of developing a quantitative model to guide lobster restoration serves as an example of how to advance restoration ecology in order to predict the quantitative benefits of restoration.

Here we describe the scientific bases for estimating the impact of the North Cape oil spill on the American lobster population along the Rhode Island (USA) coast, and for developing the restoration project that most reliably compensates for the loss. We first review the impact studies: estimated number of dead lobsters that washed ashore; use of field sampling to estimate impact by spatial and temporal contrasts of abundance of living lobsters; and ecotoxicological modeling of oil fates and the resulting acute mortality based on estimated pre-spill lobster abundance. We then review lobster life-history knowledge to identify factors that control population size and growth. For each of several potential restoration options based on known limiting factors, we use the population model to quantify the scale of the restoration required to match the lobster loss. Finally, we present the logical basis that led to the selection of the restoration choice deemed most feasible for the case and likely to be effective.

## ESTIMATING LOBSTER LOSSES

On 19 and 20 January 1996, during a severe winter storm, the barge North Cape spilled 828 000 gallons (3 134 000 l) of home heating oil (No. 2 fuel oil) into the surf zone on the southern coast of Rhode Island, USA. Most of the oil was mixed into the water column by the heavy surf, resulting in high concentrations of toxic components (i.e. polynuclear aromatic hydrocarbons, PAHs) in the shallow waters near shore (French McCay 2003). Mortality of near-shore marine organisms quickly became evident in the form of large numbers of American lobsters, surf clams *Spisula solidissima*, other invertebrates, and fishes washed up dead on the beaches. Counting these lobster strandings during the first 12 d after the spill provided one means of estimating the numbers of lobsters lost (Gibson et al. 1997a). Because this estimate included only those dead lobsters that washed ashore, and therefore underestimated total mortality, a second field method was employed that involved sampling of the under-water habitats to assess the difference in lobster populations between impacted and control areas just after the spill (Cobb et al. 1999).



A total of 18297 stranded lobsters were sexed and measured from transect and beach-sweep sampling to provide estimates of sex ratio (60% female, SE = 0.4%) and size-frequency distribution of dead lobsters by 5 mm carapace length (CL) intervals (Gibson et al. 1997a). Total number of oil-impacted and stranded lobsters was estimated by sampling 2 × 200 m transects parallel to the water line (along the deposition field of the last high-tide and including areas of high and low deposition and varying substrates) on each of 6 impact beaches, daily at low tide from 20 January to 2 February 1996 until new strandings had declined dramatically (to less than 10% of the minimum from any of the first 12 d). The transects were subsampled daily at 25 m intervals with 5 randomly placed 1 m<sup>2</sup> quadrats, with the width of the deposition zone estimated to enable expansion of the density data. After the quadrat-samples were taken, the entire 200 m beach section was swept clear of dead lobsters, and subsamples (by weight) of these sweep samples were sexed and sized. Sampling on control beaches (by sweeping the entire beach section clear due to very low incidence of lobster strandings) was also done to establish the relationship of the strandings to the spill. Daily mean quadrat densities of killed lobsters were estimated using a delta-distribution (Pennington 1983), due to the high frequency of null observations and the skewed distribution of the counts. Asymptotic mean quadrat density was estimated using a Weibull function applied to the cumulative daily means, to allow for additional strandings after the final day of sampling. The asymptotic quadrat densities were expanded to cover the entire beach area that accumulated stranded lobsters (area is estimated as impacted shoreline length times mean width of the depositional area), resulting in an estimate of 2.9 million dead lobsters stranded (Gibson et al. 1997a).

An estimate of the total kill of lobsters (9.0 million) was made by contrasting densities based on combined air-lift (<15 mm CL) and visual (>15 mm CL) samples conducted by divers soon after the spill in impacted and affected areas (Cobb et al. 1999). Side-scan sonar was used to map the boulder and cobble habitat that lobsters utilize within and nearby the area of the spill. The calculation of mortality involved assuming a pre-spill density of 1.76 lobsters m<sup>-2</sup> (from Wahle & Incze 1997) uniformly distributed over the rock and cobble reef area, developing a contour map of post-spill densities, and integrating numbers lost over the entire area where post-spill density was less than the assumed baseline (for a summary of the details of methods and calculations, see Cobb et al. 1999). This estimate of total lobster loss included a correction for 20% under-sampling of young-of-year (YOY: <15 mm CL) derived from tests of the airlift gear sampling effi-

ciency. Data from the beach strandings were used as the best estimate of size frequency of killed lobsters (Fig. 1). The strandings data underestimate YOY because these small lobsters are small and fragile and are likely to be lost or broken up in the surf. On the other hand, the strandings data provide a more reliable estimate of the size distribution of larger lobsters killed. The diver-conducted visual sampling from under water had a much smaller sample size, did not adequately capture the more mobile and evasive larger lobsters, and was done after the spill, so did not exactly match the dates of the mortality. If the ratio by number of YOY from airlift samples (corrected for 20% under-sampling) to lobsters 15–85 mm from visual density samples (i.e. from the pre-spill abundance distribution in Table 1) is used to correct the size-frequency distribution of stranded lobsters, the size distribution of the kill would be slightly further skewed toward the smaller sizes (Fig. 1).

Lobster mortality was strongly skewed towards the smaller size classes (Table 1) in the estimates derived from sampling their habitat (Cobb et al. 1999). Only ca. 15000 of the 9.0 million total lost lobsters were adults (defined as >85 mm CL and >5 yr of age); the vast majority were juveniles, indicating the great

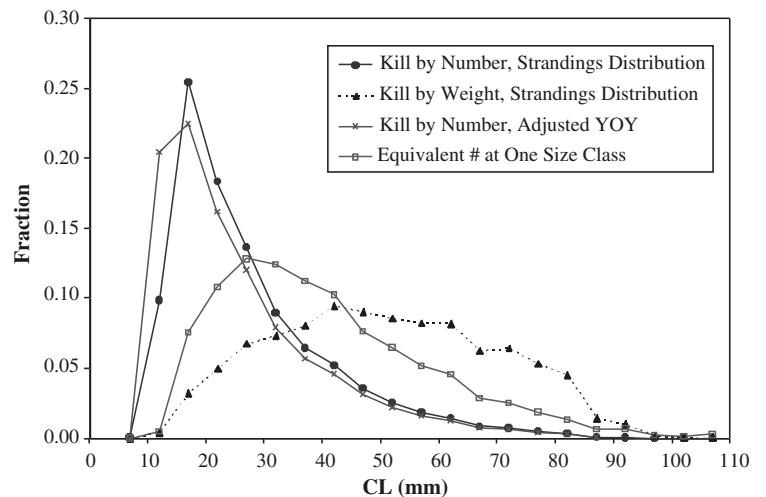


Fig. 1. *Homarus americanus*. Lobster mortality by size class for the North Cape oil spill. The size-frequency distribution of lobsters killed was based on measurements of 18297 killed lobsters collected from beach strandings after the spill. If % young of year (YOY) is adjusted using the ratio of <15 mm carapace length (CL) to 15–85 mm lobsters as the estimated pre-spill abundance size-distribution (Table 1), the size frequency distribution would be as indicated. The equivalent numbers at one (index) size class, which indicate the relative impacts by size, are calculated by multiplying (dividing) the number killed in a size class by the survival rate to (from) the index size class. The frequency distribution of the kill by weight is calculated by multiplying the numbers in each size class (based on the stranding-size distribution) by the wet weight per individual in that size class, derived from a length-weight relationship fit to data on Rhode Island lobsters

Table 1. *Homarus americanus*. Estimated pre-spill abundance and kill by carapace-length size class (CL in mm, midpoint of class) of the American lobster. The kill estimate was derived from comparisons of density inside and outside the spill area by air-lift and visual sampling soon after the spill (Cobb et al. 1999), combined with length and weight measurements of killed lobsters stranded after the spill

CL (mm)	Abundance (ind. m <sup>-2</sup> )	Kill (#)	Kill (kg)
7	0.0000	3436	1
12	0.3600	889894	1491
17	0.3953	2300217	10706
22	0.2849	1657647	16438
27	0.2119	1232654	22291
32	0.1396	812380	24183
37	0.1002	582972	26569
42	0.0812	472614	31241
47	0.0557	323872	29778
52	0.0393	228510	28265
57	0.0288	167335	27095
62	0.0224	130147	26970
67	0.0137	79468	20675
72	0.0113	65975	21200
77	0.0077	44985	17602
82	0.0055	31788	14960
87	0.0015	8696	4868
92	0.0009	5099	3364
97	0.0002	898	692
102	0.0001	299	267
107	0.0001	299	308
Total	1.7600	9039185	328963

importance of these near-shore reef habitats of less than 10 m depth as lobster nurseries. Using a CL (mm)-wet weight (g) relationship ( $W_1 = 0.001143 CL^{2.9337}$ ) derived from measurements of the Rhode Island lobsters (see 'Growth rate' below), the estimated lobster losses were converted by class to biomass, producing an estimated loss of 329000 kg of lobsters, comprised mostly of small size classes (Table 1, Fig. 1).

In addition to field studies, ecotoxicological modeling of oil fates and resulting acute mortality was performed (French McCay 2003) to estimate injuries to marine organisms, including lobsters. A physical fates model was used to predict water column PAH concentrations, which were validated by field sampling. The estimate of lobster mortality from the model serves as an alternative means of estimating the numbers of lobsters killed by the spill, although it is not fully independent because it is based on the same pre-spill abundance of Wahle & Incze (1997). The model produced an estimate of 8.3 million lobsters killed by the oil spill, consistent with that of 9.0 million based on airlift and visual quadrat sampling in the field. The quadrat- and modeling-based kill estimates are ca. 3 times the estimated number of stranded lobsters, which appears reasonable as many, but not all, killed lobsters would not have been washed up on beaches.

## DEVELOPMENT OF A DEMOGRAPHIC POPULATION MODEL

To scale the size of the restoration project in units that would allow quantitative compensation for the lost lobsters and their services, we developed a model of lobster demography for the spill region. The model is size- and age-structured (using 5 mm CL intervals indexed in the center of the interval), and based on counting females, reflecting their value to reproduction (Ricker 1975). We first modeled individual growth rate to be able to develop the dynamics of size- and age-dependent reproduction and mortality from natural factors and from fishing. Finally these estimated schedules of growth, survivorship, and mortality were combined into a life table, which was used to compute demographically equivalent numbers of individuals at different life stages.

### Growth rate

Lobster growth is a step function in which both the molt increment and frequency are functions of size (CL in mm). The growth increment is generally modeled as a linear regression of post-molt ( $CL_2$ ) on pre-molt length ( $CL_1$ ) (Ennis 1980). A regression was developed (Gibson et al. 1997b) for Rhode Island inshore lobsters using paired pre- and post-molt length measurements on 123 lobsters (of both sexes) > 60 mm CL collected from 1990 to 1996 (Angell & Lazar 1994, Angell 1995) and additional observations on smaller lobsters from Mauchline (1977), Hudon (1987), and James-Pirri (1996):

$$CL_2 = 1.744 + 1.094 CL_1 \quad (1)$$

where the SEs of the slope and intercept were 0.005 and 2.106, respectively. Residuals by sex indicated a slight tendency to overestimate post-molt size in larger females. However, large females made up only a small percentage of the kill (Fig. 1).

Molt frequency is higher in smaller lobsters (Mauviot & Castell 1976, Mauchline 1977, Fogarty & Idoine 1988) and varies by sex for mature lobsters, as females extrude and carry eggs between molts, extending the intermolt period (ASMFC 2000). A logistic curve relating intermolt duration in years ( $I_d$ ) to CL (Fogarty & Idoine 1988) for mature female lobsters, from South of Cape Cod to Long Island Sound from the latest stock assessment report (ASMFC 2000), was used:

$$I_d = \max(2, D) \text{ or } \min(7, D) \quad (2)$$

$$\text{where } D = 1 + e^{(-9.72 + 0.1032 CL)} \quad (3)$$

The limits of 2 to 7 yr serve to truncate the regression equation at the extremes, where the value of  $D$  does



not make biological sense. Whereas lobsters nearing maturity may molt annually, mature females molt, mate, wait a full year, and then extrude eggs. Thus, mature female lobsters generally have a minimum of a 2 yr molt cycle, although some small females in warmer waters may molt and spawn in the same summer. Tagging data indicate a maximum intermolt duration of ca. 7 yr (ASMFC 2000).

To depict lobster CL as a function of age (needed to estimate mortality), we used a rearrangement of the von Bertalanffy equation (a variation of the Brody growth equation: Ricker 1975):

$$CL_t = CL_\infty [1 - e^{-K(t-t_0)}] \quad (4)$$

where  $CL_t$  is length (in mm) at age  $t$ ,  $CL_\infty$  is the asymptotic maximum length,  $K$  is a constant called the Brody growth coefficient, and  $t_0$  is a constant. The value of  $CL_\infty$  (184.59 mm) is a general northwest Atlantic value from Russell (1980). The values of  $K$  and  $t_0$  were fit to molt increment and timing data for inshore Rhode Island lobsters of 15 mm CL:  $K = 0.135$ ,  $t_0 = -0.552$  (Gibson 1997b). As most Rhode Island lobsters are caught shortly after they enter the fishery at ca. 5 yr of age, uncertainty in  $CL_\infty$  has little influence on the life-table results developed here. While a seasonal growth model (e.g. Hoenig & Choudary Hanumara 1982, Pauly et al. 1992) might be used, the fit to local lobster size-at-age data allowed the computationally simpler annual model to be used in the present analysis, with little penalty in accuracy. To calculate weight from length:

$$W_t = aCL_t^b \quad (5)$$

where  $W_t$  is wet weight (g) at age  $t$  yr, and  $a$  and  $b$  are constants, estimated as  $a = 0.001143$  (SE = 0.3082 of  $\ln[a]$ ) and  $b = 2.9337$  (SE = 0.07347) from measurements on 297 lobsters collected from Rhode Island Division of Fish and Wildlife research trawls.

### Reproductive rate

The relationship between CL and the proportion of female lobsters that are mature can be described by a logistic function (Fogarty 1995). The necessary egg production data were obtained from ASMFC (2000) for lobsters in the region south of Cape Cod to Long Island Sound. The proportion of females that are ovigerous ( $P_{\text{mat}}$ ) and fecundity ( $f$ : eggs per clutch) as a function of CL are described by:

$$P_{\text{mat}} = 1 / [1 + e^{(18.145 - 0.249CL)}] \quad (6)$$

$$f = 0.000605 CL^{3.7337} \quad (7)$$

Whereas fecundity does not vary regionally among northwest Atlantic stocks, the fraction of smaller

females that is ovigerous is higher in inshore southern New England than in the colder waters of the Gulf of Maine (Fogarty 1995). This geographic distinction has important implications for scaling restoration, because life-time egg production of newly-recruited southern New England lobsters is higher than it would be for similar-sized Gulf of Maine lobsters.

Mature female lobsters are assumed to produce eggs 1 or more times per molt cycle. ASMFC (2000) reports that lobsters > 120 mm CL spawn twice per molt cycle, and those > 200 mm CL extrude eggs every 2 yr. Most females < 120 mm CL produce eggs once per molt cycle. Intense fishing pressure has removed almost all lobsters over 100 mm CL, so egg production from larger females is negligible.

### Natural and fishing mortality rates

We adopted the basic fisheries population dynamics model of Ricker (1975). For lobsters of legal harvest size, the number at age  $t$  (yr),  $N_t$ , is a function of the number of new recruits to the fishery at age  $t_r$  years. For  $t \geq t_r$ :

$$N_t = R e^{-Z_A(t-t_r)} \quad (8)$$

$$Z_A = M + F \quad (9)$$

where  $Z_A$  is annual instantaneous total mortality (constant for ages  $t > t_r$ ),  $M$  is annual instantaneous natural mortality,  $F$  is annual instantaneous fishing mortality, and  $R$  is the number of lobsters that first recruited in the cohort (i.e.  $R$  = number at age  $t_r$  years). For  $t \leq t_r$ :

$$N_t = N_{t-1} e^{-Z_t} \quad (10)$$

where  $Z_t$  is the age-specific annual instantaneous natural mortality rate. The annual survival rate for age  $t$  ( $S_t$ ) is thus:

$$S_t = e^{-Z_t} \quad (11)$$

Based on State of Rhode Island data (Gibson et al. 1997b) and federal stock assessments (NMFS 1996), we used the mean  $F$  for the inshore Rhode Island lobster stock from 1992 to 1996 of 0.97. The assumed instantaneous natural mortality rate of recruited (legal-sized) lobsters,  $M$ , was set at 0.1, which is the typical value used for northwest Atlantic lobster stocks (Bannister & Addison 1986, Fogarty & Idoine 1988). The legal CL limit for lobsters from 1996 to 1998 (when the injury calculations were made) was 82.6 mm. The model assumes that lobsters fully recruit to the fishery at 82.6 mm (with  $F = 0$  and  $M$  including handling mortality for discards of sublegals).

The mortality of lobsters < 82.6 mm CL was estimated for 2 intervals:

$$Z_{\text{tot}} = Z_{e7} + Z_{\text{juv}} \quad (12)$$

where  $Z_{\text{tot}}$  is the mortality from egg to 82.6 mm CL,  $Z_{e7}$  is the mortality from egg to 7 mm CL, and  $Z_{\text{juv}}$  is the mortality from 7 to 82.6 mm CL (all instantaneous rates). Scaling of vital rates by body size is a general property of animal populations (Peters 1983, Dickie et al. 1987). Caddy (1986) suggested that natural mortality of lobsters is an inverse power-function of body size. His theoretical curve declined from  $Z_t > 1.0 \text{ yr}^{-1}$  for small lobsters to  $M = 0.1 \text{ yr}^{-1}$  for legal-sized lobsters. Wahle & Steneck (1992) confirmed the declining vulnerability to predation with size. Thus, an empirical relationship of  $Z_t$  to body size was developed for lobsters between 3 mm (larvae) and 82.6 mm (Gibson et al. 1997b). The data (Table 2) fit a linear relationship between  $\ln(Z_t)$  and  $\ln(W_t)$  in grams (Fig. 2):

$$\ln(Z_t) = -0.627 \ln(W_t) - 3.846 \quad (13)$$

Table 2. *Homarus americanus*. Estimates of lobster natural mortality rates ( $M$ ) at various life stages (EBP = early benthic-phase lobsters). CL: carapace length;  $CL_{\infty}$ : asymptotic maximum length

Stage	CL (mm)	Weight (g)	$M$ ( $\text{d}^{-1}$ )	Source
Larvae I–III	2.77	0.02	0.1234	Bibb & Hersey (1979)
Larvae I–IV	3.29	0.03	0.0984	Stasko (1980)
Larvae I–IV	3.29	0.03	0.2400	Harding et al. (1982)
Larvae I–IV	3.29	0.03	0.1253	Scarratt (1964)
Larvae I–IV	3.29	0.03	0.1460	Hudon et al. (1986)
EBP 5–13 mm	10	1.00	0.0394	James-Pirri (1996)
EBP 11–20	16	3.64	0.0174	James-Pirri (1996)
EBP 5–25 mm	15	3	0.0232	Hudon (1987)
EBP 25–60 mm	40	55	0.0033	Hudon (1987)
EBP V–70 mm	37	44	0.0006	Harding et al. (1982)
EBP 13–85 mm	49	100	0.0003	Bannister et al. (1994)
EBP new settlers, first month	13	2	0.0633	Wahle & Steneck (1992)
Prerecruits, 60–80 mm	70	284	0.0006	Angell (1995), 60–80 mm catch curve slope
Large RI adults, 83–185 mm	134	1920	0.0002	Hoenig (1983) longevity model with a maximum age of 50 yr and $CL_{\infty} = 185$ mm
Tagged legal lobsters, RI and MA	90	595	0.0004	Anthony (1980)

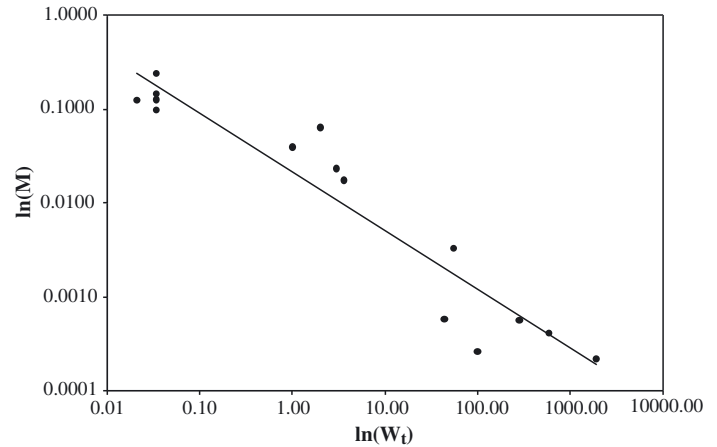


Fig. 2. *Homarus americanus*. Estimates of lobster natural mortality rates at various body weights, and regression line for log-transformed data

where  $r^2$  for the regression is 0.9078 (SE = 0.83,  $F = 128$ , 15 observations,  $p < 0.05$ ) and the SEs of the slope and intercept are 0.0554 and 0.2241, respectively. Translating body weight to CL, daily mortality rates were estimated by size class. Age-at-size estimates using the von Bertalanffy equation provided duration for each 5 mm CL increment in the model, from which  $Z$  for the increment was calculated (Table 3). The total mortality from 7 to 82 mm CL ( $Z_{\text{juv}}$ ) is 5.6, based on the empirical mortality-rate curve.

The loss of eggs between extrusion and hatching was estimated by Perkins (1971) to be 36%; thus, instantaneous egg mortality is ca. 0.45 (i.e. 64% of eggs hatch). The empirical mortality-rate curve implies  $Z_t = 0.147 \text{ (d}^{-1}\text{)}$  for the larval period (assumed 4 wk) and  $Z_t = 0.044 \text{ (d}^{-1}\text{)}$  from settlement to 7 mm ( $Z = 1.33$  for the interval), giving a total  $Z$  from hatching to 7 mm of 5.434, inferring that  $Z_{e7} = 5.88$  (0.3% survival from egg to 7 mm) and  $Z_{\text{tot}} = 11.5$ . However, the larval mortality estimates based on field data (Table 2, Fig. 2) indicate daily mortality is ca.  $0.1 \text{ d}^{-1}$ , or  $Z = 2.8$  for 28 d from hatch to settlement, implying  $Z_{e7} = 4.58$  (1% survival from egg to 7 mm) and  $Z_{\text{tot}} = 10.2$ . Thus, there is considerable uncertainty in  $Z_{e7}$  and particularly in the mortality rate for the period between hatching and settlement.

### Life table

To be able to compare the demographic value among age classes, and thereby compute such figures as the numbers of eggs equivalent to a given number of lobsters expected to recruit to the fishable population years later, we combined growth, mortality, and

Table 3. *Homarus americanus*. Estimated age and total instantaneous mortality rate ( $Z$ , from Gibson et al. 1997b) by carapace-length (CL) size class for American lobster. Age is calculated from length using a rearrangement of the von Bertalanffy growth equation fit to local lobster size-at-age data. Survival is calculated as  $e^{-Z_{7,i}}$ , where  $Z_{7,i}$  is the summed mortality rate from 7 mm to size class  $i$

CL (mm)	Age (yr)	Z to next size class (in increments of 5 mm)	Survival from 7 mm to size class
7	0.84	2.172	1.0000
12	1.05	1.006	0.1140
17	1.27	0.589	0.0417
22	1.49	0.393	0.0231
27	1.72	0.285	0.0156
32	1.96	0.219	0.0117
37	2.21	0.175	0.0094
42	2.46	0.145	0.0079
47	2.73	0.123	0.0068
52	3.00	0.106	0.0061
57	3.29	0.094	0.0054
62	3.58	0.084	0.0050
67	3.89	0.076	0.0046
72	4.21	0.070	0.0042
77	4.55	0.065	0.0039
82	4.90	0.359	0.0037
87	5.27	0.378	0.0026
92	5.66	0.399	0.0018
97	6.07	0.422	0.0012
102	6.51	0.449	0.0008
107	6.97	0.479	0.0005

reproduction relationships into a life table for the affected population (Table 4). The expected annual production of eggs per female of age class  $X$  in the population ( $M_X$ ) was calculated from  $P_{mat}$ ,  $f$ , and the proportion of females in the population that produces eggs during a given year ( $P_e$ ). We derive  $P_e$  from  $I_d$  in years and the number of clutches produced per molt cycle ( $C_m$ ):

$$M_X = P_{mat} f P_e \tag{14}$$

$$P_e = C_m / I_d \tag{15}$$

Our maturation equation implies that very young females produce eggs. However, we assumed that eggs are not produced by lobsters younger than 4 yr of age (67 mm). In southern New England, lobsters carry eggs for 10 to 11 mo before release, during which time they do not molt (Cobb et al. 1997). Thus, once lobsters mate and produce eggs, they begin a 2 yr molt cycle (ASMFC 2000). The intermolt duration in the life table reflects the molt cycles of egg-producing lobsters.

Table 4 presents expected lifetime egg production (LEP) per female of each size/age class, calculated for age  $X$ , as:

$$LEP_X = \frac{\sum_{n=X}^{n=X_{max}} (LX_n M_{X_n})}{LX_X} \tag{16}$$

where  $n$  is age in years (evaluated in the summation from age  $X$  to the maximum age  $X_{max}$ ),  $LX_n$  is the frac-

Table 4. *Homarus americanus*. Life table estimating lifetime egg production per female lobster of age  $X$  (yr). CL: carapace length in mm;  $P_{mat}$ : fraction ovigerous;  $f$ : fecundity (eggs per clutch);  $I_d$ : intermolt duration (yr);  $C_m$ : number of clutches per molt cycle;  $P_e$ : proportion of females in the population that are egg-bearing;  $M_X$ : eggs per female of age  $X$  in the population;  $S_X$ : survival rate at age  $X$ ;  $LX$ : survivorship from age 0.8 to age  $X$ ; LEP: lifetime egg production for age  $X$

$X$	CL	$P_{mat}$	$f$	$I_d$	$C_m$	$P_e$	$M_X$	$S_X$	$LX$	$LX M_X$	$X LX M_X$	LEP
0.8	7	0.00	1	1	0	0.00	-	0.114	1.00E+00	0	0	30
1.0	12	0.00	6	1	0	0.00	-	0.103	1.14E-01	0	0	266
2.0	32	0.00	243	1	0	0.00	-	0.516	1.17E-02	0	0	2584
3.0	52	0.01	1479	1	0	0.00	-	0.753	6.06E-03	0	0	5007
3.9	67	0.19	3799	2	1	0.50	357	0.810	4.56E-03	1.63	6.34	6652
4.9	82	0.91	8060	2	1	0.50	3653	0.379	3.69E-03	13.49	66.12	7773
6	96	1.00	14561	2	1	0.45	6536	0.379	0.00E+00	9.146	54.88	10868
7	107	1.00	21926	5	1	0.21	4504	0.379	0.00E+00	2.389	16.72	11427
8	117	1.00	30321	7	2	0.29	8663	0.379	0.00E+00	1.742	13.94	18263
9	126	1.00	39395	7	2	0.29	11256	0.379	1.40E-03	0.8580	7.72	25326
10	133	1.00	48825	7	3	0.43	20925	0.379	5.30E-04	0.6047	6.05	37116
11	140	1.00	58329	7	3	0.43	24998	0.379	2.01E-04	0.27384	3.01	42711
12	145	1.00	67684	7	3	0.43	29007	0.379	7.62E-05	0.12046	1.45	46724
13	150	1.00	76716	7	3	0.43	32878	0.379	2.89E-05	0.05176	0.673	46737
14	155	1.00	85303	7	3	0.43	36558	0.379	1.10E-05	0.02182	0.305	36558
Total = # of 7 mm offspring per 7 mm CL female = RO = $\sum(LX M_X)$										30.3		
Required survival from egg to 7 mm CL ( $S_{e7}$ ) for equilibrium = $2/RO$ =										0.066		
Generation time (yr) = $[\sum(X LX M_X)]/RO$												5.8

tion surviving to age  $n$ , and  $MX_n$  is the egg production at age  $n$ . For example, the lifetime production expected from a 7 mm female (RO) just settling to the benthic habitat is 30.3 eggs. The lifetime fecundity ( $F_n$ ) of an 82 mm female is estimated as 7773. Although larger, legally fishable females produce large numbers of eggs, few survive beyond 96 mm CL, making their contribution to the next generation insignificant. The generation time is 5.8 yr (calculated as:  $\sum XLXMX/RO$ ).

If it is assumed that the population (with the survival schedule in Table 4) is in equilibrium, such that a 7 mm lobster would just exactly replace herself plus 1 male after a lifetime of egg production, survival from egg to 7 mm is estimated as 6.6% (i.e.  $2/RO = 2/30.3$ ), implying that  $Z_{e7} = 2.72$ . This equilibrium survival estimate is much higher than the empirical data indicate (i.e. 0.3 to 1.0% survival from egg to 7 mm,  $S_{e7}$ ). If  $S_{e7}$  is 0.3 to 1.0%, in order for the population to sustain itself at the exploitation rate implied by  $F = 1$ , the lifetime egg-production of a 7 mm female would need to be 192 to 716 eggs. It has been suggested that the Rhode Island inshore population cannot sustain itself (based on similar analyses of survival rates and lifetime fecundity) and is supplemented by larval supply from offshore (Katz et al. 1994, Fogarty 1998), and this discrepancy between the empirical and equilibrium estimates indicates a very large offshore supplement. Annual (instantaneous) mortality of >82.6 mm lobsters would need to decrease to  $Z = 0.22$  for the inshore population to be self-sustaining, assuming  $S_{e7}$  is 1% and the survival schedule in Table 3. Alternatively, if survival to 82.6 mm is underestimated, lifetime egg production of a 7 mm female would be higher, perhaps high enough to be self-sustaining in the inshore area. Clearly, further data collection and analysis is needed to resolve the survival rates of <82.6 mm lobsters.

From an age-specific survival schedule, one can calculate how many lobsters of any given age are demographically equivalent to a number at any other age. This type of conversion is important in creating a restoration plan that achieves quantitative equivalence of lost and restored lobster numbers, because precise matching of age distributions will generally be impossible. This approach (typically with losses translated to equivalent adults) has been used for power plant impingement and entrainment assessments (following suggestion by Horst 1975, Goodyear 1977) and mitigation of dredging impacts (Wainwright et al. 1992, Dumbauld et al. 1993).

We compute (Table 5) the numbers of lobsters in each class that would be required by the mortality schedule in Table 3 to yield numbers of newly recruited lobsters (82.6 mm CL) equivalent to the total kill estimate (i.e. 'equivalent adults'). The total loss

of 9 million lobsters distributed among sizes, as in Table 1, is equivalent to the loss of 2.2 million new recruits from the legally fishable population (Table 5). Similarly, calculating backwards through the life stages, the observed kill translates into 608 million 7 mm lobsters (Table 5). We converted the equivalent numbers at 82.6 mm CL to fractions of the total recruit equivalents (Fig. 1), which shows that the greatest demographic impact of the oil spill was suffered by the second year class of juveniles (1.5 to 2 yr old), with a median CL of 27 mm. Note that the proportional distribution of demographic equivalents by size class is the same, regardless of the size class used as the basis of the calculations. Thus, this procedure normalizes the loss to a single unit of equivalent population value.

To proceed further backwards in the life history to estimate the number of egg equivalents, we used the estimated survival from egg to 7 mm ( $S_{e7}$ ) of: (1) 0.3 to 1% based on analysis of empirical data, and (2) 6.6% inferred by the life table for female lobsters, assuming equilibrium such that the inshore population is self-sustaining (Table 4). The number of lobsters killed in the spill originated from 59 to 219 billion eggs, assuming the empirical survival rates ( $S_{e7} = 1$  or 0.3%, respectively), and 9.2 billion eggs, assuming the life table and equilibrium ( $S_{e7} = 6.6\%$ , Table 5). Thus, there is great uncertainty in the number of egg equivalents lost, reflecting the uncertainty in egg to 7 mm survival.

#### LIMITATION OF LOBSTER POPULATION SIZE AND PRODUCTION

For restoration to be effective, the selected project(s) must increase the local lobster population at a scale that will provide augmented production to compen-

Table 5. *Homarus americanus*. Lobster loss from the North Cape oil spill in 1996 using age-specific survivorships converted into the demographic equivalents for each of several size classes.

$S_{e7}$ : survival from egg to 7 mm carapace length (CL)

Equivalent # at Stage	Total	Females	Males
82.6 mm	2 228 402	1 337 041	891 361
22 mm	14 046 329	8 427 797	5 618 531
7 mm (millions)	608	365	243
Postlarvae (millions)	7217	4330	2887
Eggs (millions), empirical ( $S_{e7} = 1\%$ )	58 940	35364	23 576
Eggs (millions), equilibrium ( $S_{e7} = 6.6\%$ )	9211	5527	3685

sate for loss of production. Consequently, restoration planning begins with identifying the factors that limit population size and productivity. Population size for any given species is unlikely to be limited by a single factor, unless a strong density-dependent bottleneck exists at some particular life stage. Different life stages are commonly controlled by different factors. In exploited marine fish and shellfish, over-harvesting generally has taken place to limit abundances in the larger size and age classes subject to fishing pressure (Pauly et al. 1998). Limiting factors can vary by location. For example, Lipcius et al. (1997) provide evidence that habitat availability limits recruitment of the spiny lobster *Panulirus argus* in some areas, while larval supply is limiting for other parts of the Bahamas. Evidence that may suggest habitat limitation for American lobsters comes from artificial reefs, which are quickly colonized by larger American lobsters (Scarratt 1968, Sheehy 1976, Castro et al. 2001), and YOY settlement increased when cobble habitat was provided in a formerly muddy area (Castro et al. 2001). Habitat availability, fishing pressure, and larval supply seem likely candidates as limiting factors for American lobster populations.

The literature on the biology of the American lobster characterizes its life history and ecological importance reasonably well. It has a long period of parental care and a short larval life (Cobb et al. 1997). Eggs are carried by the females for 9 to 12 mo before being released at hatching. Resulting larvae are planktonic, remaining in the water column for ca. 1 mo before settling to the bottom as postlarvae (Ennis 1995). Young juveniles (10 to 25 mm CL) seek shelter, usually in rocky cobbles and boulders, and remain secluded, feeding from within the shelter (Wahle & Steneck 1991). Older juveniles leave the shelter for feeding forays, but return frequently. As lobsters grow larger, they may leave shelters and move greater distances (Lawton & Lavalli 1995). These characteristics imply strong predatory control on early life-history stages, and indicate the dependence of at least early benthic stages on shelter (Wahle & Steneck 1991, 1992). However, the lower dependence of larger lobsters on shelters and high fishing rates (NMFS 1996) suggest that fishing limits population size in the larger size classes, possibly to the extent that larval supply is limiting to recruitment.

#### **Habitat availability and juvenile survival**

Inshore populations of juvenile and adult lobsters utilize cobble, rock, peat reefs and kelp beds, where the structure of the habitat provides shelter (Cobb 1971) and foraging habitat. Population densities in-

crease when artificial shelters are placed in the field (Scarratt 1968, Sheehy 1976, Lawton & Lavalli 1995, Castro et al. 2001). Lobsters are preyed upon by many bottom-feeding fish species, and addition of shelter likely reduces predation losses. Lobsters are omnivorous, acting mainly as predators, but also as scavengers (Herrick 1909, MacKenzie & Moring 1985, Hudon & Lamarche 1989, Lawton & Lavalli 1995). Calculations of prey production rates by Miller et al. (1971) suggest that lobster populations are not likely to be limited by food.

There have been many suggestions that the early benthic phase (EBP; ~5 to 40 mm CL) is structure-dependent and may act as a recruitment bottleneck to the fishable stock (Caddy 1986, Fogarty & Idoine 1986, Hudon 1987, Able et al. 1988, Wahle & Steneck 1991, 1992, Miller et al. 1992, Fogarty 1995, Lawton & Lavalli 1995). The availability of physical structures that provide refuge from predation affects survival rates of several crustaceans, resulting in increased densities in those habitats (Wahle & Steneck 1991, 1992, Dumbauld et al. 1993, Beck 1995, 1997). Wahle (1993) censused lobsters along 22 km within Narragansett Bay, finding that newly settled lobsters were absent from the prevailing sedimentary bottoms, which lack emergent structure and associated refuges, suggesting that structured habitat might be in short supply in Rhode Island waters. Wahle & Steneck (1991) similarly proposed that cobble habitats are preferred by the early benthic stages and limit population size. The potential for habitat limitation in early life history is also suggested by the study by Castro et al. (2001), who showed that when cobble reefs were placed in a muddy area, settlement of YOY lobsters increased from none to the equivalent of natural settlement in nearby rocky areas. However, Wahle & Inze (1997) ruled out habitat differences and implicated larval supply as being the mechanism behind the difference in recruitment on 2 sides of an island. They found that emigration by larger juveniles probably controlled the population size, suggesting that habitat limitation plays a role as body size increases. These studies, and those showing the effectiveness of addition of artificial habitat in enhancing lobster local abundance (Scarratt 1968, Sheehy 1976, Lawton & Lavalli 1995), suggest that an increase in cobble reef habitat in inshore waters of Rhode Island may enhance juvenile survival and increase local lobster populations.

#### **Fishing mortality**

Lobster stocks of the northwest Atlantic are known to be highly exploited (Fogarty & Idoine 1988, NMFS 1996, ASMFC 2000). The fishing mortality rate on



inshore Rhode Island lobsters is estimated at or above sustainable levels (Gibson et al. 1997b), with  $F = 1$  for the inshore population in the 1990s. Fogarty (1995) provided even higher estimates of  $F$  for southern New England and northeast USA stocks in general for previous years. From our life table (Table 4), it is clear that females that survive for more than 1 to 2 molt cycles after reaching fishable age and size contribute little egg production to the population. Thus, the population is dependent on egg production from smaller females and possibly on larval subsidy from offshore adults (Fogarty 1998). This implies that fishing pressure limits lobster population size, which in turn controls egg production. It follows that reduction in fishing mortality would increase adult population size and production, with enhancement of the next generation through increased egg production.

### Egg production and postlarval supply

Lobster management in the United States is based on egg production per recruit, on the assumption that populations are limited by egg production and resulting larval supply due to very high levels of exploitation on adult females (Fogarty & Idoine 1988, NMFS 1996). The relationship between stock size and recruitment has not been examined for *Homarus americanus*. However, the relationship between larval production and stock size and/or landings has been evaluated in detail (Fogarty 1995). Fogarty & Idoine (1986), using data for Northumberland Strait, concluded that the relationship was asymptotic, with a clear indication of density dependence. The relationship has a steep slope near the origin, indicating that larval supply may be limiting at low stock size, but at higher stock sizes there is some density-dependent control on the population, such as intraspecific competition for food or shelter resources (Fogarty 1995). Wahle & Incze (1997) present evidence that postlarval supply, determined by local hydrodynamic conditions, can limit settlement density of lobsters in cobble habitats. However, they suggest that as lobsters grow, crowding arises, causing emigration and smoothing annual variation in lobster density patterns, caused by differences in larval supply.

Benthic settlement is highly variable spatially and from year to year. Incze et al. (1997) found that postlarval supply and benthic settler density were significantly correlated in data sets from Rhode Island and Maine waters from 1989 to 1995. Postlarval supply explained 90% of the annual variation in settler density for the combined data set. Among-site differences in recruitment persisted for 1 yr after settlement, after which larger lobsters moved into areas of initially lower settlement. This implies that larval supply may

be limiting to settlement, but that subsequently habitat becomes limiting. Incze et al. (2000) showed that YOY recruitment was positively correlated with larval supply at a single site in Maine, and suggested that density-dependent effects may have been operating at times when recruitment was highest.

Thus, habitat availability, fishing pressure, and larval supply appear to be limiting to American lobster populations in southern New England via control on different life stages. However, given the very high fishing pressure and recent precipitous decline in the Rhode Island stock and catch (indicated by Rhode Island Division of Fish and Wildlife research trawl data and catch statistics from recent years), it seems clear that adult stocks are limited by fishing. The degree of limitation by larval supply and habitat for early benthic stages is much less certain. Thus, the choice of an appropriate restoration approach in this case was a matter of judgment based on uncertain outcomes and logistical constraints.

## ALTERNATIVES FOR LOBSTER RESTORATION

### Stocking with juveniles raised in hatcheries

If lobster populations are limited, in part, by larval supply, then rearing lobsters in a hatchery through to settlement size, and releasing them into nature, represents one restoration option. The techniques for rearing lobsters to the postlarval stage at a size suitable for release are well established, and lobster enhancement through this process has been performed many times (Addison & Bannister 1994). Unfortunately, no project has documented the stocking success of hatchery-reared *Homarus americanus*, primarily because of limitations in the collection tracking and monitoring data (Bannister & Addison 1998, Castro et al. 2001). Success has been evaluated in Europe with *Homarus gammarus* (Bannister et al. 1994, Phillips & Evans 1997), but the applicability of these results to the congeneric lobster in Rhode Island waters is questionable. Castro et al. (2001) stocked micro-wire tagged YOY lobsters directly onto artificial reefs in Rhode Island, but no increase in density over natural settlement of YOY was detected, and only one tagged individual was ever recovered. The authors suggested that hatchery-reared lobsters may be more susceptible to predation than naturally produced juveniles, based upon the lack of immediate shelter-seeking behavior upon release of hatchery-derived lobsters. This problem of abnormal behavior and high susceptibility to predation is common among other animals reared in captivity (Olla et al. 1998).

Even if hatchery-reared lobsters were to survive introduction into the wild, this restoration option car-



ries some other risks common to hatchery-based stock enhancement. The introduced lobsters may compete with naturally produced individuals, introduce disease from the hatchery, or induce undesirable genetic changes in the native stock. The hatchery-raised lobsters may interact in some unnatural and undesirable fashion with the receiving ecosystem. Whereas analogous concerns have been exemplified in salmon stocks, they are less likely to be a problem in American lobsters, since the native populations are not at similarly depleted levels where the risks would be magnified. Nevertheless, hatchery stocking of *Homarus americanus* has not yet been demonstrated as a successful restoration strategy, so there is substantial uncertainty associated with this option.

### Habitat (rock reef) creation

If lobster populations are limited, in part, by the availability of refuges for juveniles, then construction of new rocky reefs represents another restoration option. Juvenile and adult American lobsters utilize artificial reefs constructed of concrete or stone, with the spacing and orientation of reefs having a significant effect on occupancy (Scarratt 1968, Sheehy 1976, Castro et al. 2001). Similar studies on *Homarus gammarus* in Europe, and other lobster species elsewhere, suggest that enhancement of local stocks is possible using appropriately designed reefs, in cases where structured habitat is limiting to the local population (Jensen et al. 1994, Spanier 1994). Structural habitat construction has been used to mitigate dredging-induced losses of Dungeness crab in an estuary in Washington, USA (Wainwright et al. 1992, Dumbauld et al. 1993). However, there is an on-going debate as to whether artificial reefs actually increase fish and invertebrate (or lobster) production, rather than merely attracting individuals already established in nearby natural habitat (Lindberg 1997, Castro et al. 2001, Powers et al. 2003, in this Theme Section).

Castro et al. (2001) monitored abundance, size, and sex of lobsters colonizing 6 experimental artificial reefs in Narragansett Bay, Rhode Island. They found that the density of YOY on artificial reefs matched that on control natural reefs. Although it is possible that the lobsters that settled and survived on the artificial reef would have done so at the same rates elsewhere on natural reefs had the new reef not been installed, the reef does represent new nursery habitat for lobsters. The work of Wahle and co-workers (Wahle & Steneck 1991, 1992, Wahle & Incze 1997, Casrto et al. 2001) indicates that postlarvae settle in cobble reef areas. Given the evidence for habitat limitation of EBP lobsters, placement of cobble reef containing mixed sizes

of cobble and boulders seems likely to enhance postlarval settlement, and possibly also adult production if larval supply is locally sufficient. Nevertheless, habitat enhancement for lobsters has not been shown experimentally to augment lobster stocks beyond the local reef area, and thus may not be an appropriate restoration strategy.

### Reduction in fishing mortality

Services provided by adult lobsters include supporting a fishery, producing eggs to support the next generation of lobsters, and providing ecological services within the food web. Given the existing high exploitation rate such that the lobster population is considered over-fished (as noted above), a restoration strategy with a high likelihood of success would be one which reduced fishing mortality, through modified management, to a level closer to that which would provide the maximum sustainable yield to the fishery. This would be the population level providing the most ecological production (production entering the food web) as well. Fisheries management is the focus of considerable professional effort (e.g. NMFS 1996). However, uncertainty prevails in the assessment of stock abundances and in determining the fishing rate that provides the maximum sustainable yield (Ludwig et al. 1993), making this approach difficult to implement, particularly in the face of resistance by the fishing industry. Furthermore, limitation of lobster catches would entail a loss of human use, at least in the short term. Consequently, choosing this option would induce another injury to human services, which would require compensation, thereby indirectly adding to the costs of the spill. In the particular case of compensation for injuries caused by the North Cape oil spill, there was a desire not to impact the fishery further. Thus, an alternative that accomplished a reduction in  $F$ , while not penalizing the fishermen in the local area, was pursued.

### Purchase and release of harvested females

One means of enhancing adult female lobsters without simultaneously diminishing the use of the resource by fishermen would be to purchase lobsters from fishermen and release them back to the wild population. The returned females can be v-notched (i.e. marked with a v-shaped cut in the tail), with a regulatory prohibition against taking or selling any v-notched lobster. This action would provide an immediate boost to adult lobster abundance over that which would otherwise prevail. Subsequently, the fishing mortality would be greatly reduced on those released adult female lob-

sters, thereby increasing lifetime egg production. If egg production and larval supply limit lobster settlement and ultimately constrain the abundance of adults, then this restoration option would have short- and long-term benefits of enhancing lobster abundance.

The fate of the eggs produced by these restocked adult females is uncertain. The dispersal of lobster larvae by currents during their 20 to 40 d larval life makes it difficult to predict settlement locations. In addition, it would be difficult to disentangle the effects of the restocking program from other factors that drive inter-annual variation in local larval abundances and adult lobster populations. Nevertheless, the present lobster management efforts by state and federal agencies target increasing egg production. Therefore, the proposed restocking project is consistent with current lobster management measures. Furthermore, the states of Massachusetts, Rhode Island, Connecticut, and New York have already passed a prohibition on the possession of v-notched female lobsters as part of the implementation of regional lobster management plans. Lobster harvesters holding a permit to fish in Federal waters are also prohibited from possessing v-notched lobsters. Given the lobsters' migratory behavior and the mobility of harvesters, a regionally recognized and enforceable marking system is critical to realizing the full measure of success from this restoration option.

#### METHODS FOR SCALING RESTORATION ALTERNATIVES

The use of ecological restorations to compensate for services lost because of injury to natural resources implies a need to scale the restoration to equal the loss. In our application, restoration should account for: (1) the sex ratio of killed lobsters; (2) the size distribution of killed lobsters; (3) the survivorship between life stages; (4) the delay between the kill and implementation of the restoration project; and (4) the time required for growth and maturation of lobsters into the age classes lost. The accounting involves population modeling, using the life table developed earlier. The same units and demographic parameters should be employed for measuring injury and benefits of restoration, such that the scale of the restoration is indeed compensatory. Compensation includes application of economic discounting, so that when restoration has been completed, its value matches the interim loss to the resource. In other words, the lag time is compensated by effectively paying interest, but in terms of additional restoration over-and-above that required to return the resource to the baseline population level had there not been a spill.

#### Stocking with juveniles raised in hatcheries

The total kill was equivalent to 7.2 billion postlarval lobsters, of which 4.33 billion were females (Table 5). Since females produce eggs to replenish the stock, if egg production limits the lobster population size, then replacement of lost females with males would not be entirely compensatory. Assuming that the hatchery produces equal numbers of males and females, the appropriate replacement number would need to be 8.66 billion postlarvae (twice the female loss). However, because it would take some number of years both to develop the hatchery program and for the lobsters to grow up to the ages lost, more than 8.7 billion females would be required to compensate for the loss and for the time gap between injury and restoration.

Delays between injury and instigation of restoration can be handled by an additional factor  $(1 + d)^\lambda$ , where  $\lambda$  is the number of years of lag (after 1996 when the injury occurred) before the restoration begins, and  $d$  is the annual discount rate, which is typically set at 3% ( $d = 0.03$ : NOAA 1997). In addition, the number of years required for postlarval lobsters to grow into each age class lost (i.e.  $t$  = the age of a size class in Table 3) needs to be compensated. The compensation number of post larvae ( $N_{PL}$ ) is calculated as

$$N_{PL} = \sum [PL_t (1 + d)^{\lambda+t}] \quad (17)$$

where  $PL_t$  is the number of postlarval equivalents for age class  $t$ . Thus, in this case,  $\sum PL_t = 8.7$  billion. Assuming, for example, that the hatchery stocking all occurred in 2001, 5 yr after the spill ( $\lambda = 5$ ),  $N_{PL} = 11$  billion (Table 6).

#### Habitat (rock reef) creation

Assuming that structural habitat is limiting to EBP lobsters, creation of new cobble reef would increase their numbers produced by the spawning adults present in the population. The scaling of the area of reef needed requires an estimate of the density of new lobsters provided per unit reef area. Quantifying the gain as 1.5 yr old lobsters that are 17 to 27 mm CL, a cobble reef in Rhode Island might be expected to produce 0.89 EBP  $m^{-2} yr^{-1}$  (Table 1). This production would be gained every year indefinitely over the lifetime of the reef, but future gains must be discounted 3% annually. Thus, the total production (TP) over  $n$  years of project life is:

$$TP = P \sum (1/(1 + d))^n \quad (18)$$

where  $P$  is the annual augmented production (0.89 EBP  $m^{-2} yr^{-1}$ ). If  $n$  exceeds 100 yr,  $TP$  levels off at 31.6  $P$ . Thus, assuming the reef to be permanent,  $TP = 28.2$  EBP per  $m^2$  of reef. The amount of reef needed for full compensation is computed as:

Table 6. *Homarus americanus*. Scale of hatchery stocking required for compensation of lobster loss due to the North Cape oil spill, incorporating economic discounting to account for the time-lag between the year the age class was killed and is replaced. In this example, it is assumed that the hatching of lobsters occurred entirely in the summer of 2001, 5.5 yr after the spill. CL: carapace length

CL (mm)	Required postlarval equivalents (millions)	LAG (yr)	Discount factor	Compensation # (millions)
7	0.05	5.8	1.3	0.06
12	111	6.0	1.3	133
17	787	6.3	1.4	947
22	1022	6.5	1.4	1238
27	1126	6.7	1.4	1374
32	987	7.0	1.4	1212
37	881	7.2	1.4	1091
42	851	7.5	1.4	1061
47	674	7.7	1.5	847
52	538	8.0	1.5	681
57	438	8.3	1.5	560
62	374	8.6	1.5	482
67	249	8.9	1.5	323
72	223	9.2	1.6	292
77	163	9.6	1.6	216
82	123	9.9	1.6	165
87	48	10.3	1.7	65
92	41	10.7	1.7	56
97	11	11.1	1.7	15
102	5	11.5	1.8	8
107	9	12.0	1.8	12
Total	8661			10779

$$\text{Compensation area (m}^2\text{)} = \left\{ \sum [\text{EBP}_t (1 + d)^{\lambda+t}] \right\} / \text{TP} \quad (19)$$

where  $\text{EBP}_t$  is the number of EBP equivalents for age class  $t$  (scaled as 22 mm CL and age 1.5 yr, the same size and age class as for TP) and  $\lambda$  is the number of years of lag after 1996 when the injury occurred before the reef is created. In this case,  $\sum \text{EBP}_t = 17$  million as 22 mm CL equivalents, after multiplying 14 million 22 mm equivalents of both sexes (Table 5) by 1.2 to account for the fact that 60% of the kill was female, and twice the female number is needed in compensation. Assuming, for example, that the reef was built in 2001, 5 yr after the spill ( $\lambda = 5$ ), the compensating amount of reef would be 0.74 km<sup>2</sup>.

### Reduction in fishing mortality

Scaling the required change in  $F$  to compensate for interim losses from a spill could be accomplished in several ways. One method would be to calculate the production foregone because of the spill (i.e. the lost biomass production in the dead individuals plus the

growth they would be expected to have undergone before death) and balance that with production gained by the change in fishing mortality rate. The methodology for these calculations is beyond the scope of the present analysis. Several production foregone models are available that could be used in scaling (e.g. Ricker 1975, Rago 1984, Jensen et al. 1988, Polacheck et al. 1993, Prager 1994).

An alternative approach is to use egg production as currency. Table 4 provides an estimate of lifetime egg production per 7 mm female in the population, assuming equilibrium and a self-sustaining inshore population. If the value of  $F$  is changed (for all females recruited to the fishable population), lifetime egg production per 7 mm female changes. The net gain in egg production per female times the number of 7 mm females in the stock represents the net gain of the restoration program. For example, in NMFS Area 539, there were approximately 1.4 million lobsters of fishable size in the late 1990s (Gibson et al. 1997b). Assuming that 50% of these are female (0.7 million legal females), and by summing  $LX$  for >82.6 mm females from Table 4, to obtain  $444 \times 7$  mm females per legal female in the stock, there were 311 million 7 mm females in Area 539. If the value of  $F$  in Area 539 changed from 0.97 to 0.755 for 10 yr, by recalculation of Table 4 (not shown) the net gain in 7 mm lobsters produced would just equal the number of 7 mm lobsters required for compensation (907 million, which is equal to twice the female equivalents lost, i.e. 729 million, times the discounting factors for each age class, as in Table 6, accounting for delay in realization of the gains). Thus, a modest reduction in  $F$  could increase the numbers of larger females in the population, providing a sufficient net gain in reproduction to offset losses from the spill. However, it should be noted that this calculation assumes a high survival rate from egg to 7 mm of 6.6%. If the survival rate from egg to 7 mm is actually 1% (or 0.3%), as indicated by the empirical analysis, the required  $F$  for a 10 yr program would be 0.47 (or 0.14). There are many possible scenarios involving changes in fishing mortality rate that could be scaled (and all are sensitive to the choice of egg-to-7mm survival rate). In the following section, the restoration plan used for the North Cape spill (NOAA et al. 1999) will illustrate scaling for a specific change in  $F$ .

### Purchase and release of harvested females

In a v-notching program, females returned to the sea have a lower fishing mortality than un-notched females. Scaling to calculate the required number of v-notched females involves use of the life table method

in Table 4, with egg production as the metric. The life-time egg production of a female from the size when it was v-notched is calculated with an altered value of  $F$  applied for the number of molt cycles where there is protection from harvest. Subsequent to that time, the value of  $F$  returns to that of the normal (un-notched) population. Thus, to estimate the numbers of lobsters required for a lobster-restocking program, one uses the total number of eggs demographically equivalent to the numbers killed summed over all age classes (Table 5). Because 60% of the killed lobsters were females, the compensating number of egg equivalents is twice the female loss: 11 billion eggs. (For clarity, only the results assuming the equilibrium-implied 6.6% survival from egg to 7 mm are followed through here. A much larger project would be required if egg-to-7mm survival rate is in fact 1% or lower.) The killed lobsters will be replaced (eventually) once that equivalent number of eggs is re-supplied through augmenting survival and egg production of notched females.

Economic discounting must still be applied to account for the delay between dates of loss and restoration. The total value for restoration gains over all years (TV), expressed as value in the year of the spill, is as follows, where  $V_n$  is value  $n$  years after the spill:

$$TV = \sum V_n [1/(1 + d)]^n \quad (20)$$

In this case, the value gained after  $n$  years results from future egg production and maturation to the size classes lost during the spill. The lag time for the gain,  $n$ , is the sum of the number of years before females are v-notched and restocked, the lag before eggs are produced, and the years required for eggs to mature into animals of each age killed. Example calculations are provided below.

#### SELECTED ALTERNATIVE FOR NORTH CAPE RESTORATION PLAN

Each of the 4 restoration alternatives was considered for restoring lobsters injured by the North Cape oil spill before one was selected. The number (11 billion) of post-larvae needed from a lobster hatchery to compensate for the loss was considered by the federal and state trustees as too great to be logistically feasible or economically reasonable. Furthermore, if all these lobsters were to be added simultaneously, or even spread out over a few years, there is real potential for density-dependent mortality through predation or interference competition for refuges. The ecological consequences of such a substantial pulse of small lobsters may not be desirable and may induce negative impacts that are difficult to anticipate. This problem is in fact unavoidable, as the spill induced a

perturbation to the population which will take time to recover via new settlement or a restoration project. There may be an over-shoot and density dependent compensation in the recovery curve, which could be magnified (or damped) by restoration. Our present knowledge of density-dependent adjustment of population parameters is rudimentary, at best, for most, if not all, fishery species.

The cobble reef area required to compensate for the lobster losses from the North Cape oil spill is 0.74 km<sup>2</sup>. When this option was considered by the trustees, given the assumption that habitat creation would in fact result in a net gain to the population, the main concern was where to locate a reef that large. The reef should presumably be placed in Block Island Sound near the spill impact zone so the compensation would occur in the area of impact. However, the reef would necessarily displace existing soft-bottom habitat (inducing another ecological loss that would need to be compensated) and disrupt fish trawling in the area, constituting a reduction in fishing grounds for the demersal fishery. Because fishermen had already suffered a large loss due to the spill, and given the uncertainty that habitat is limiting the local population, this option was not pursued.

The reduction of fishing effort and rates on either both sexes or on females (which would provide additional life-time egg production) would effectively restore the population, but would also represent a short-term loss to fishermen, who were not responsible for the impact caused by the spill. Given the large private losses to fishermen during the period after the North Cape oil spill, and the high uncertainty associated with estimating the appropriate compensation to the individual fishermen for additional losses imposed by such a prohibition, this option was not implemented. However, in a situation where restoration is not in compensation for injury caused by a private party (as in this oil spill) or where the fishermen's losses can be appropriately compensated, and particularly where a population is severely over-fished, the most effective restoration method would be reduction in fishing rate.

Restocking by release of adult female lobsters purchased from the fishery was the restoration option chosen for compensation in the North Cape case. This option effectively reduces fishing mortality ( $F$ ), but does not impose added restrictions on the fisherman's catch and profits. A 5 yr program of purchase, v-notching, and release was designed to minimize ecological perturbations and skewing of the sex ratio, as well as to avoid influencing market prices for lobsters. In addition, an extended time frame rendered the logistics of this restocking more feasible and less of a perturbation to the local lobster population.

### SCALE OF RESTORATION REQUIRED TO COMPENSATE FOR THE LOSS

The scaling calculations began with the development of size-specific survival rates (Table 3). We then converted the loss of lobsters across multiple size (age) classes into the numbers of eggs that had produced those animals lost, assuming this mortality schedule. Initial life-table assumptions differed from those presented here, resulting in an estimate that the spill mortality represented a loss of 18 billion eggs (Gibson 1998, French 1999). Based on new data compiled in ASMFC (2000), the killed lobsters derived from 9.2 billion eggs, 5.5 billion of which were female (Table 5). Assuming the same mortality schedule after restoration (Table 3), replacement of 11 billion eggs would be expected eventually to replace all lost females and thus their progeny, restoring both sexes in subsequent generations.

Our next step was to estimate the quantitative augmentation of egg production expected from the restocking program, and to calculate how many females were required to replace the numbers of eggs equivalent to the lobster kill. We assumed the following: (1) Female lobsters of legally fished sizes will be purchased from the fishery, v-notched, returned to the area where they were caught, and will receive regulatory protection from future harvest; (2) Handling losses will be 5%; (3) The fishing mortality on v-notched lobsters would be 50% of the normal rate; (4) The v-notch would last 1 to 2 molts, with 50% protection from fishing through the first molt and 25% after a second molt; and (5) Lobster demographic parameters will not change after restocking.

Using these assumptions, we computed a new life table for 90 mm CL v-notched lobsters (Table 7). For

the sake of clarity, and as a first step, the Table 7 calculations include discounting for the lag time in production of eggs after the date of restocking females, but not for the time lag between the kill and initiation of the 5 yr restocking program followed by development to the size classes lost. The resulting calculations indicate that each 90 mm female would be expected to produce 4260 eggs in her lifetime. Accounting for the time delays before the eggs are produced after v-notching, the egg production has a discounted value of 4083 eggs per female.

Complete discounting to compensate for the interim loss of lobsters and their services must include the following time lags: (1) the time between the kill, 1996, and the date of restocking of 90 mm females, from 2000 to 2004 (4 to 8 yr); (2) the time between restocking a 90 mm female and the production of eggs (1 yr plus discounting in Table 7); (3) the time required for eggs to develop to the ages of those lobsters killed (1 to 4 yr); and (4) correction for the fact that the v-notched females immediately replace the lost legal lobsters ( $\geq 5$  yr old). For example, 15 to 35 mm lobsters are ca. 2 yr old. This age class of lobsters killed would have reached legally fishable size in 2000. They were eggs in 1994. Restocking of females in 2000 would produce eggs in 2001. Consequently, there is a 7 yr lag in the replacement of juvenile lobsters that were ca. 2 yr old in January 1996. Similarly, there is an 8 yr time lag for the 2 yr-olds killed, and so on.

The computations that discount for all these time lags are relatively straightforward. The demographically equivalent number of eggs for each age class to be produced by restocked females is discounted annually over the number of years of lag, from the year the killed lobsters were eggs to the year eggs replacing them will appear. Using a 3% annual discount rate ( $d$ ),

Table 7. *Homarus americanus*. Eggs produced per v-notched 90 mm CL female, assuming that restocking occurred in 1996. Molts: number of molts after 90-mm stage; CL: carapace length in mm;  $I_d$ : intermolt duration (yr); Age is calculated from length using relationship from Gibson (1998);  $F$ : instantaneous fishing mortality rate; Survival (to next molt) is calculated as  $e^{-(F+M)\Delta t}$ , where  $M$  is instantaneous natural mortality rate, 0.1, and  $\Delta t$  is years from that size class to the next;  $P_{mat}$ : fraction ovigerous;  $f$ : fecundity (eggs per clutch);  $M_X$ : eggs per female at age  $X$ . Number (#) of eggs for each CL class is calculated as the fraction of v-notched females surviving to that class multiplied by  $M_X$ . Discounting at 3%  $yr^{-1}$  for the number of years after 1996 when eggs would be produced is applied, to calculate discounted numbers of eggs by class, assuming females are v-notched in 1996

Molts	CL (mm)	$I_d$	Age (yr)	Fraction protected	$F$ realized	Survival	$P_{mat}$	$f$	$M_X$	# eggs	# eggs discounted
0	90	2.0	5.5	0.500	0.49	0.310	0.986	11398	11240	3314	3217
1	100	2.9	7.5	0.500	0.49	0.188	0.999	17000	16981	939	859
2	111	6.9	10.4	0.250	0.73	0.00334	1.000	25189	36198	7	6
3	124	7.0	17.3	0.00	0.97	0.00056	1.000	37106	54200	0.006	0.004
4	137	7.0	24.3	0.00	0.97	0.00056	1.000	54377	79427	0.000	0.000
5	152	7.0	31.3	0.00	0.97	0.00056	1.000	79320	115859	0.000	0.000
6	168	7.0	38.3	0.00	0.97	0.00056	1.000	115225	168305	0.000	0.000
Total										4260	4083



the number of females required to replace that age class  $L$  years after the spill ( $N_{A,L}$ ) is calculated as:

$$N_{A,L} = N_A[(1 + d)^L] \quad (21)$$

where  $N_A$  is the number of adult females needed to produce the necessary egg equivalents for Age Class A. Table 8 presents calculations of adjustment factors (the discounting term in the equation), assuming that all restocking were to occur in 2000 or from 2000 to 2004 in equal numbers over the 5 yr period. Computationally, the required adjustments for discounting can be simplified by applying a single factor derived from integrating over all age classes, 1.26 for restocking in 2000 and 1.33 for restocking from 2000 to 2004 (Table 8). Thus, if all v-notching occurred in 2000, the number of 90 mm CL females required would be 3.4 million [= 1.26(11 billion eggs/4083 eggs per female)]. Assuming a 5 yr restoration program, the compensation number is 3.6 million v-notched 90 mm CL females [= 1.33(11 billion eggs/4083 eggs per female)]. Again, these results are assuming egg-to-7mm survival is 6.6%. If this survival is only 1%, 23 million females would be required in a 5 yr program.

The compensation number is very sensitive to assumptions made in the scaling calculations within the range of uncertainty. Most of the uncertainty is related to the survival schedule assumed for lobsters less than legal size, particularly for the egg-to-7mm

survival rate (which undoubtedly varies by environmental conditions, both spatially and annually). Given a survival schedule, the results are most sensitive to the level of fishing protection assumed for v-notched females. For example, assuming the equilibrium-inferred 6.6% survival for egg to 7 mm, if the 50% protection assumption were changed to 88%, the compensation number for the 5 yr program would be about one quarter as high, and equivalent to that of the restoration plan actually undertaken (1.2 million females v-notched over 5 yr, NOAA et al. 1999). In order of sensitivity, the remaining assumptions of most importance are the maturation schedule relative to the size of the v-notched females, the size of the v-notched females, and intermolt duration. Each of these factors relates indirectly to how well the introduced lobsters are protected from fishing mortality. The very high fishing mortality of unprotected females limits the egg production to the first 2 molt cycles, while more protection increases egg production. To illustrate how geographic origin affects maturation schedule, only 42% of 90 mm lobsters from the Gulf of Maine, USA, are mature and able to produce eggs in the first and most important molt cycle, whereas 99% of Rhode Island females are mature. Similarly, stocking smaller lobsters, even from Rhode Island waters, reduces realized egg production because a smaller fraction is ovigerous during the protected molt cycles. For example, the compensation number of 83 mm CL females taken from Rhode Island would be 4.3 million (for a 5 yr program), as compared to 3.6 million 90 mm CL lobsters. The intermolt duration influences egg production because it determines how many clutches can be produced before the stocked female is taken by the fishery. This demographic parameter is not well characterized, providing uncertainty in our computations.

The compensation number of 3.4 million 90 mm CL females (as well as the 1.2 million females to be v-notched in the implemented restoration plan, NOAA et al. 1999) is greater than the total number of legal females in NMFS Area 539 at any given time (0.7 million; Gibson et al. 1997b). Thus, the v-notching has to be implemented over a number of years (e.g. the implemented plan was to v-notch 246 000 for each of 5 yr). The revised compensation number of 3.4 million estimated here, applied to a 5 yr plan, infers that no female lobsters could be taken in the harvest ( $F = 1$ , so annual catch of females is equal to

Table 8. *Homarus americanus*. Computation of effects of discounting by 3% yr<sup>-1</sup> for time lags between lobster loss and restoration. Discounting accounts for time lag between the kill, initiation of restocking, the time after restocking before females begin to produce eggs (1 yr), and development to each size class of lobster lost (if <5 yr). Legal lobsters ≥ 5 yr are replaced immediately at the time of v-notching. Lags are weighed by the proportion of egg-equivalents killed in each age class, and summed for all age classes to develop correction factors (1/summed discounted value) to account for the lag before replacement

Age when killed (yr)	Fraction of egg equivalents	Year were eggs	Years of lag to replace if all v-notched in 2000	Discounted value if all v-notched in 2000	Discounted value for 5 yr v-notching program
0.5	0.0129	1995	6	0.0108	0.0102
1.5	0.4528	1994	7	0.3682	0.3474
2.5	0.2779	1993	8	0.2194	0.2069
3.5	0.1559	1992	9	0.1195	0.1127
4.5	0.0732	1991	10	0.0545	0.0514
5.5	0.0197	1990	4	0.0175	0.0165
6.5	0.0048	1989	4	0.0042	0.0040
7.5	0.0012	1988	4	0.0011	0.0010
8.5	0.0006	1987	4	0.0006	0.0005
9.5	0.0010	1986	4	0.0009	0.0008
Total	1.0000			0.797	0.752
Factor to account for lag before replacement				1.255	1.331



standing stock, 0.7 million, a value equivalent to 1/5 the compensation number). In reality, a restoration project of this size would need to occur over a longer time period than 5 yr, to allow for handling losses and less than 100% protection by the v-notch. Moreover, given such a large compensation requirement, the most effective restoration approach would be to reduce fishing effort directly, as opposed to v-notching, and so reduce the handling and non-compliance losses. This would require appropriate compensation to the fishing industry, related to their lost catch, livelihood and profits due to the initial spill-caused injury and the restoration-induced changes.

A harvest that is highly biased towards males suggests that the sex ratio might be affected enough that mating and sperm availability for fertilization of eggs would become a limitation. The expected change in the sex ratio was evaluated under 2 assumptions: (1) that the v-notched females would mix over the entirety of Area 539, and (2) the v-notched females would be returned to Rhode Island waters, ca. 25% of Area 539. Under the plan that was actually implemented, the sex ratio would be expected to change over 5 yr from 50% female to 56% under Assumption (1), or to 67% under Assumption (2). Assuming no harvest of females for 5 yr, the sex ratio would change to 63% under Assumption (1) or to 80% under Assumption (2). If the initial sex ratio is >50%, the sex ratios would become more skewed. In addition, the females would be larger than the males, which may cause some difficulties in mating (Cobb 1995). In the implemented plan, the return of v-notched females was wide-spread to minimize focusing of returns and skewing of the sex ratio. For larger projects, these calculations indicate that a much longer time frame than 5 yr would be needed, and the compensation number would need to be increased 3% annually for each year of delay before benefits are accrued.

## DISCUSSION

Our treatment of how restoration of lobsters following a Rhode Island oil spill can be quantitatively matched to compensate for the discounted loss demonstrates a process that can render restoration ecology a more quantitative science. The process of developing an effective restoration plan, and scaling it to fit the quantitative goal, has several components. A review of the life history and ecology of the target species is critical to identify factors likely to be limiting to the injured population. Restoration interventions are effective if they can relieve the influence of one or more limiting factors. Demographic models need to be developed for calculating the scale of restoration needed

and for developing a common currency to compare injury and benefits of restoration. The results are very sensitive to the life-history parameters assumed; thus, these need to be quantified carefully to represent the injured population. The concept of discounting so as to compensate for the interim loss of the resource, its ecosystem and human services, represents an important consideration in scaling any restoration project. Lag times inevitably exist between loss and full restoration. These lags include the time between the loss and the initiation of restoration actions, and the time for the project to reproduce the life stages lost.

Many assumptions about the effectiveness of restoration have great uncertainty associated with them. For example, in the absence of previous data, we were forced to estimate handling losses and the effectiveness of regulations prohibiting take of v-notched lobsters. In addition, survival rates of larval and juvenile lobsters are highly uncertain. Restoration ecology possesses a number of tools with which to deal with uncertainty. For example, at the cost of greater effort in restoration planning, a formal uncertainty analysis could be conducted as part of contrasting alternative-restoration options. Such uncertainty information played a role in the rejection of some options by the North Cape trustees, but this was not based on quantitative uncertainty analyses. In environmental management, uncertainty is often handled by enhancing the scale of restorations to better protect public trust resources. Wetland, marsh, and seagrass restorations are commonly conducted over larger areas than the areas removed so as to include uncertainty in the performance of the projects. The replacement ratios used typically increase with the level of uncertainty. Probably the most certain way of handling doubts about the effectiveness of restoration would be to require monitoring of the projects and subsequent adjustments if restoration targets were not met. The quantitative scaling computations that we develop here are best treated as hypotheses and predictions to be tested directly through monitoring of this sort. In the present case of the North Cape, monitoring is being performed and v-notch incidence among females has increased, but complications, such as a dramatic decrease in the stock size since 2000, increasing incidence of shell disease, and delays in the v-notching program, preclude analysis of the success of the restoration program at this time.

The lobster restoration plan that we present here provides a model for a species that is long-lived and which is exploited. The importance of the lobster fishery has led to enough research on the population processes of lobsters to be able to develop a reasonable demographic model to guide restoration scaling for the southern New England stock. For most marine species

that do not form the basis of a fishery, that information will be inadequate to construct a predictive quantitative demographic model. Furthermore, the intensity of fishing pressure in the lobster fishery and in other fisheries (Pauly et al. 1998) provides several viable and highly effective opportunities for restoration actions not available for species that are not fished. Consequently, the analysis that we present of options to restore lobsters has generic applicability to a large group of marine fish and shellfish that often will represent the most valuable resources, deserving of special attention in restoration. To some degree, special focus on restoring exploited species may stress value to human uses more than value to the ecosystem. However, the decline in fisheries is itself perhaps the greatest conservation challenge in the sea (Botsford et al. 1997, Jackson et al. 2001), so the 2 needs tend to coincide. However, concerns about the broader ecological impacts of enhancing one target species in the system are justified and deserve attention in considering restoration choices. The capability of ecology to make correct predictions is more limited at the level of the community and ecosystem than at the level of individual species populations. Consequently, effectiveness of restoration and conceptual development in ecology can both benefit from developing a full suite of predictions and testing them through monitoring of well-designed restoration projects.

*Acknowledgements.* This work was supported by NOAA, Damage Assessment Center (DAC), Silver Spring, MD. The biological considerations and scaling calculations were developed after discussions with, and obtaining considerable input from, Saul Sails of the University of Rhode Island, Mike Fogarty of NMFS, Michael Clancy of the University of Rhode Island (now of Boston University), John Catena of NMFS Restoration Center, Carol-Ann Manen of NOAA-DAC, and Steve Moran of RIDEM. Charles (Pete) Peterson of the University of North Carolina at Chapel Hill provided critical guidance, editing, and review of the manuscript, as did 3 anonymous reviewers who provided insightful comments that improved our analysis. We thank Mike Donlan of Industrial Economics for advice and encouragement.

#### LITERATURE CITED

- Able K, Heck KL, Fahay MP, Roman CT (1988) Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. *Estuaries* 11:83–86
- Addison AT, Bannister RCA (1994) Re-stocking and enhancement of clawed lobster stocks: a review. *Crustaceana* 67:131–155
- Angell TE (1995) Rhode Island lobster research and management project. 1994 Annual/Completion Report (NOAA Grant No. NA46FI0084. Project No. 3-IJ-77), Rhode Island Division of Fish and Wildlife, Wickford
- Angell TE, Lazar NB (1994) Rhode Island lobster research and management project. 1991–1993 Annual/Completion Report (NOAA Grant No. NA36FI0117-01. Project No. 3-IJ-43-3), Rhode Island Division of Fish and Wildlife, Wickford, RI
- Anthony VC (1980) A review of lobster mortality estimates in the United States. In: Anthony VC, Caddy JF (eds) Proc Canada-US Workshop Status of Assessment Science for NW Atlantic lobster (*Homarus americanus*) Stocks. Can Tech Rep Fish Aquat Sci 932:17–26
- ASMFC (Atlantic States Marine Fisheries Commission) (2000) American lobster stock assessment report for peer review. Stock Assessment Report No. 00-01 (Supplement), ASMFC, Washington, DC
- Bannister RCA, Addison JT (1986) Effect of assumptions about the stock-recruitment relationship on a lobster (*Homarus americanus*) stock assessment. *Can J Fish Aquat Sci* 43:2353–2359
- Bannister RCA, Addison JT (1998) Enhancing lobster stocks: a review of recent European methods, results, and future prospects. *Bull Mar Sci* 62:369–387
- Bannister RCA, Addison JT, Lovewell SRJ (1994) Growth, movement, recapture rate and survival of hatchery-reared lobsters (*Homarus gammarus* Linnaeus, 1758) released into the wild on the English east coast. *Crustaceana* 67:156–182
- Beck MW (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* 7:968–980
- Beck MW (1997) A test for the generality of the effects of shelter bottlenecks in four stone crab populations. *Ecology* 78:2487–2503
- Bibb BG, Hersey R (1979) Distribution and abundance of lobster larvae in Block Island Sound, 1978. Final Report to New England Power, Raytheon Environmental Services, Portsmouth, RI
- Botsford LW, Catilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. *Science* 277:509–515
- Caddy JF (1986) Modeling stock-recruitment processes in Crustacea: some practical and theoretical perspectives. *Can J Fish Aquat Sci* 43:2330–2344
- Castro KM, Cobb JS, Wahle RA, Catena J (2001) Habitat addition and stock enhancement for American lobsters, *Homarus americanus*. *Mar Freshw Res* 52:1253–1261
- Clark JA, Hoekstra JM, Boersma PD, Kareiva P (2002) Improving US Endangered Species Act recovery plans: key findings and recommendations of the SCB recovery plan project. *Conserv Biol* 16:1510–1519
- Cobb JS (1971) The shelter-related behavior of the lobster, *Homarus americanus*. *Ecology* 52:108–115
- Cobb JS (1995) Interface of ecology, behavior, and fisheries. In: Factor JR (ed) *Biology of the lobster Homarus americanus*. Academic Press, New York, p 139–151
- Cobb JS, Booth JD, Clancy M (1997) Recruitment strategies in lobsters and crabs: a comparison. *Mar Freshw Res* 48:797–806
- Cobb JS, Clancy M, Wahle RA (1999) Habitat-based assessment of lobster abundance: a case study of an oil spill. *Am Fish Soc Symp* 22:285–298
- Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecol Monogr* 57:233–250
- Dumbauld BR, Armstrong DA, McDonald TL (1993) Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. *Can J Fish Aquat Sci* 50:381–390
- Ennis GP (1980) Recent and current Canadian research on growth of lobsters in the wild. In: Anthony VC, Caddy JF (eds) Proc Canada-US Workshop Status of Assessment Science for NW Atlantic lobster (*Homarus americanus*) Stocks. Can Tech Rep Fish Aquat Sci 932:9–15

- Ennis GP (1995) Larval and postlarval ecology. In: Factor JR (ed) *Biology of the lobster *Homarus americanus**. Academic Press, New York, p 23–46
- Fogarty MJ (1995) Populations, fisheries, and management. In: Factor JR (ed) *Biology of the lobster *Homarus americanus**. Academic Press, New York, p 111–137
- Fogarty MJ (1998) Implications of migration and larval interchange in American lobster (*Homarus americanus*) stocks: spatial structure and resilience. *Proc North Pacific Symp Invertebrate Stock Assessment and Management*. *Can Spec Pub Fish Aquat Sci* 125:273–283
- Fogarty MJ, Idoine JS (1986) Recruitment dynamics in an American lobster (*Homarus americanus*) population. *Can J Fish Aquat Sci* 43:2368–2376
- Fogarty MJ, Idoine JS (1988) Application of a yield and egg production model based on size to an offshore American lobster population. *Trans Am Fish Soc* 117:350–362
- French DP (1999) North Cape oil spill: synthesis of injury quantification and restoration scaling for lobsters. Report to NOAA Damage Assessment Center, Silver Spring, MD (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- French McCay DP (2003) Development and application of damage assessment modeling: Example assessment for the North Cape oil spill. *Mar Pollut Bull* 47:341–359
- Gibson MR (1998) Potential egg production from lobsters killed in the North Cape oil spill and replacement estimates using recycled commercial catch. Division of Fish and Wildlife, Rhode Island Dept of Environmental Management, Wickford (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- Gibson MR, Angell TE, Lazar NB (1997a) Estimation of lobster strandings following the North Cape oil spill in Block Island Sound. Research Reference Document 97/1, Division of Fish and Wildlife, Rhode Island Dept of Environmental Management, Wickford (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- Gibson MR, Angell TE, Lazar NB (1997b) Equivalent adult estimates and stock status of lobster involved in the North Cape oil spill in Block Island Sound. Research Reference Document 97/2, Division of Fish and Wildlife, Rhode Island Dept of Environmental Management, Wickford (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- Goodyear CP (1977) Mathematical methods to evaluate entrainment of aquatic organisms by power plants. Report FWS/OBS-76/20.3, US Fish Wildl Serv, Washington, DC
- Harding GC, Vass WP, Drinkwater KF (1982) Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. *Can J Fish Aquat Sci* 39:1117–1129
- Herrick FH (1909) Natural history of the American lobster. *Bull US Fish Comm* 29:147–408
- Hoenig J (1983) Empirical use of longevity data to estimate mortality rates. *Fish Bull* 82:898–903
- Hoenig J, Choudary Hanumara R (1982) A statistical study of seasonal growth models for fishes. Tech Rep Dept Comp Sci Stat, University of Rhode Island, Kingston
- Horst TJ (1975) The assessment of impact due to entrainment of ichthyoplankton. In: Saila SB (ed) *Fisheries and energy production: a symposium*. Lexington Books, Lexington, MA, p 107–118
- Hudon C (1987) Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Îles de la Madeleine (Quebec). *Can J Fish Aquat Sci* 43:2243–2247
- Hudon C, Lamarche G (1989) Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. *Mar Ecol Prog Ser* 52:155–168
- Hudon C, Fradette P, Legendre P (1986) La répartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des Îles de la Madeleine, Golfe du Saint-Laurent. *Can J Fish Aquat Sci* 43:2164–2176
- Incze LS, Wahle RA, Cobb JS (1997) Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. *Mar Freshw Res* 48:729–743
- Incze LS, Wahle RA, Palma AT (2000) Advection and settlement rates in a benthic invertebrate: recruitment to first benthic stage in *Homarus americanus*. *ICES J Mar Sci* 57:430–437
- Jackson JBC, Kirby MX, Berge WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- James-Pirri MJ (1996) The influence of settlement time on post-settlement growth in the American lobster (*Homarus americanus*). PhD thesis, University of Rhode Island, Kingston
- Jensen AC, Collins KJ, Free EK, Bannister RC (1994) Lobster (*Homarus gammarus*) movement on an artificial reef: the potential use of artificial reefs for stock enhancement. *Crustaceana* 67:198–211
- Jensen AL, Reider RH, Kovalak WP (1988) Estimation of production foregone. *North Am J Fish Manage* 8:191–198
- Katz CH, Cobb JS, Spaulding M (1994) Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Mar Ecol Prog Ser* 103:265–273
- Lawton P, Lavalli KL (1995) Postlarval, juvenile, adolescent, and adult ecology. In: Factor JR (ed) *Biology of the lobster *Homarus americanus**. Academic Press, New York, p 47–88
- Lindberg WJ (1997) Can science resolve the attraction-production issue? *Fisheries* 22:10–13
- Lipcius RN, Stockhausen WT, Eggleston DB, Marshall LS Jr, Hickey B (1997) Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: source-sink dynamics? *Mar Freshw Res* 48:807–815
- Ludwig D, Hilborn R, Walters C (1993) Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17–18
- MacKenzie C, Moring JR (1985) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—American lobster. US Fish Wildl Serv Biol. Rep 82(11.33), US Army Corps of Engineers, TR EL-82-4
- Mauchline J (1977) Growth of shrimps, crabs, and lobsters—an assessment. *J Cons Int Explor Mer* 37:162–169
- Mauviot CJ, Castell JD (1976) Molt-and growth-enhancing effects of bilateral eyestalk ablation on juvenile and adult American lobsters (*Homarus americanus*). *J Fish Res Board Can* 33:1922–1229
- Miller RJ, Mann KH, Scarratt DJ (1971) Production potential of a seaweed-lobster community in eastern Canada. *J Fish Res Board Can* 28:1733–1738
- Miller RJ, Campbell A, Sharp GJ, Hudon C (1992) Are small juvenile lobsters habitat limited? *Can Tech Rep Fish Aquat Sci* 1390:55–61
- NMFS (National Marine Fisheries Service) (1996) Stock assessment review committee (SARC) consensus summary of assessments. 22nd Northeast Regional Stock Assessment Workshop, NEFSC Ref Doc 96-13. NMFS, Woods Hole
- NOAA (National Oceanic and Atmospheric Administration) (1997) Natural resource damage assessment guidance

- document: scaling compensatory restoration actions (Oil Pollution Act of 1990). NOAA Damage Assessment Center, Silver Spring
- NOAA (National Oceanic and Atmospheric Administration), Rhode Island Department of Environmental Management (RIDEM), US Department of the Interior (USDOI), and US Fish and Wildlife Service (USFWS) (1999) Restoration plan and environmental assessment for the January 19, 1996 North Cape oil spill, revised draft for public comment, March 31, 1999. NOAA, Silver Spring, MD
- Olla BL, Davis MW, Ryer CH (1998) Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bull Mar Sci* 62:531–550
- Pauly D, Soriano-Bartz M, Moreau J, Jarre-Teichmann A (1992) A new model accounting for seasonal cessation of growth in fishes. *Aust J Mar Freshw Res* 43:1151–1156
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. *Science* 279: 860–863
- Pennington M (1983) Efficient estimators of abundance for fish plankton surveys. *Biometrics* 39:281–286
- Perkins HC (1971) Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). *Fish Bull* 69: 451–453
- Peters RH (1983) The ecological implications of body size. *Cambridge studies in ecology*. Cambridge University Press, Cambridge
- Peterson CH, Estes JA (2001) Conservation and management of marine communities. In: Bertness MD, Gaines SD, Hay, ME (eds) *Marine community ecology*. Sinauer, Sunderland, MA, p 469–507
- Peterson CH, Kneib RT, Manen C-A (2003) 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)
- Phillips BF, Evans LH (1997) Aquaculture and stock enhancement of lobsters: report from a workshop. *Mar Freshw Res* 48:899–902
- Polacheck T, Hilborn R, Punt AE (1993) Fitting surplus production models: comparing methods and measuring uncertainty. *Can J Fish Aquat Sci* 50:2597–2607
- Powers SP, Grabowski JH, Peterson CH, Lindberg WJ (2003) Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios. *Mar Ecol Prog Ser* 264:265–277 (in this Theme Section)
- Prager MH (1994) A suite of extensions to a non-equilibrium surplus-production model. *Fish Bull* 92:374–389
- Rago PJ (1984) Production foregone: an alternative method for assessing the consequences of fish entrainment and impingement losses at power plants and other water intakes. *Ecol Model* 24:79–111
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1–382
- Russell H (1980) The determination of growth rates for American lobsters. *Can Tech Rep Fish Aquat Sci* 932. In: Anthony VC, Caddy JF (eds) *Proc Canada-US Workshop Status of Assessment Science for NW Atlantic Lobster (*Homarus americanus*) Stocks*. *Can Tech Rep Fish Aquat Sci* No 932:141–150
- Scarratt DJ (1964) Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. *J Fish Res Board Can* 21:661–680
- Scarratt DJ (1968) An artificial reef for lobsters. *J Fish Res Board Can* 25:2683–2690
- Sheehy DJ (1976) Utilization of artificial shelters by the American lobster (*Homarus americanus*). *J Fish Res Board Can* 33:1615–1622
- Spanier E (1994) What are the characteristics of a good artificial reef for lobsters? *Crustaceana* 67:173–186
- Stasko AB (1980) Lobster larval surveys in Canada. In: Anthony VC, Caddy JF (eds) *Proc Canada-US Workshop Status of Assessment Science for NW Atlantic Lobster (*Homarus americanus*) Stocks*. *Can Tech Rep Fish Aquat Sci* No 932:141–150
- Wahle RA (1993) Recruitment to American lobster populations along an estuarine gradient. *Estuaries* 16:731–738
- Wahle RA, Incze LS (1997) Pre- and post-settlement processes in recruitment of the American lobster, *Homarus americanus*. *J Exp Mar Biol Ecol* 217:179–207
- Wahle RA, Steneck RS (1991) Recruitment habitats and nursery grounds of the American lobster (*Homarus americanus* Milne Edwards): a demographic bottleneck? *Mar Ecol Prog Ser* 69:231–243
- Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *J Exp Mar Biol Ecol* 157:91–114
- Wainwright TC, Armstrong DA, Dinnel PA, Orensanz JM, McGraw KA (1992) Predicting effects of dredging on a crab population: an equivalent adult approach. *Fish Bull* 90:171–182
- Young TP (2000) Restoration ecology and conservation biology. *Biol Conserv* 92:73–83

*Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA*

*Submitted: February 10, 2003; Accepted: October 26, 2003  
Proofs received from author(s): December 9, 2003*



# Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration

Deborah P. French McCay<sup>1,\*</sup>, Charles H. Peterson<sup>2</sup>,  
Joseph T. DeAlteris,<sup>3</sup> John Catena<sup>4</sup>

<sup>1</sup>Applied Science Associates, 70 Dean Knauss Drive, Narragansett, Rhode Island 02882, USA

<sup>2</sup>Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA

<sup>3</sup>University of Rhode Island, Building 50, East Farm, Kingston, Rhode Island 02881, USA

<sup>4</sup>National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Restoration Center, 1 Blackburn Drive, Gloucester, Massachusetts 01930, USA

**ABSTRACT:** Abundant suspension-feeding bivalves have a dominant organizing role in shallow aquatic systems by filtering overlying waters, affecting biogeochemical processing, and diverting production from the water column to the benthos. In degraded aquatic systems where bivalve populations have been reduced, successful restoration of ecosystem functions may be achieved by targeting the revival of bivalve populations. The 'North Cape' oil spill on the coast of Rhode Island (USA) provides an opportunity to demonstrate the feasibility of scaling bivalve restoration to meet quantitative goals of enhanced production. After this oil spill, mortalities of bivalves were estimated by impact assessment modeling of acute toxicity, and results were confirmed by comparisons with counts of dead and moribund animals on local beaches. Computation of lost bivalve production included future production expected from affected animals, had they lived out their expected life spans. This calculation of production forgone required a demographic model that combined age-specific mortality with individual growth. Application of this modeling approach to surf clams *Spisula solidissima*, the species that comprised 97% of the total loss of bivalve production from the spill, illustrates the detailed implementation of scaling restoration to match estimates of losses. We consider the factors known to limit abundance and production of surf clams and other marine bivalves (hard clams, American oysters and bay scallops) and review the advantages of hatchery stocking, transplantation, habitat restoration, and reduction of fishing pressure in selecting a reliable and efficient restoration action. Age-specific estimates of the scale of population enhancement required to restore production showed that fewer additional animals were needed when larger (older) animals were added, but at the expense of greater grow-out requirements. Relaxation of fishing was most effective for hard clams. Accurate scaling of restoration was most sensitive to mortality rate, and the most efficient restoration involving seeding of small bivalves would be accomplished using surf clams. Monitoring of the restoration option chosen to compensate for the bivalve loss following the 'North Cape' oil spill can serve to test the underlying demographic assumptions and accuracy of the restoration scaling.

**KEY WORDS:** Bivalves · Loss · Limiting factors · Natural resource damage assessment · 'North Cape' oil spill · Population modeling · Restoration

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Restoration ecology has focussed mostly on replenishing species that provide physical structure to the habitat, typically the larger plants (Jordan et al. 1987).

In the marine environment, this approach explains the overwhelming dominance of restoration projects and studies that are devoted to salt marsh grasses and sea-grasses (Thayer 1992). The restoration of structure has compelling justification in that the function and value

of a habitat are usually determined by its structural integrity (e.g. Wilson & Peters 1988) and the defining structure of many marine habitats is provided by the larger plants and reef-building animals. Nevertheless, provision of habitat structure does not necessarily guarantee the return of normal function and the rate of return of function may often lag structural restoration by many years (Zedler 1995, Fonseca et al. 1996, 1998). Consequently, the field of restoration ecology could benefit and grow from greater appreciation of the functional organization of the biological communities within ecosystems and from targeting some restoration efforts directly towards re-establishment of the limited number of functionally significant species that are the strong interactors in the system (Paine 1980).

Within estuaries and other relatively shallow aquatic ecosystems, suspension-feeding bivalve molluscs can dictate the character of the entire system through their water filtration function (Kremer & Nixon 1978, Cloern 1982). The significance of bivalves in clarifying the waters, in driving energy flows from pelagic to benthic food chains, and in promoting growth of light-limited benthic macrophytes, which themselves serve as critical habitat, can be clearly displayed through observing the consequences of unplanned perturbations of bivalve populations. The ecosystem consequences of zebra mussel *Dreissena polymorpha* invasions in the Great Lakes and the introduction of the Asian clams *Potamocorbula amurensis* to San Francisco Bay have resulted in dramatic changes in the aquatic ecosystem, consistent with their functional roles as filters (Nichols et al. 1990, MacIsaac et al. 1999). Where natural bivalve populations have been reduced (e.g. oysters in the Chesapeake Bay and other estuaries) turbidity of estuarine waters has increased, promoting pelagic jellyfish explosions, and leading to widespread sea-grass loss (Newell 1988, Jackson et al. 2001). This ecosystem service of water filtration serves as a top-down grazing control on algal blooms, perhaps the most serious direct symptom of eutrophication, one that leads indirectly to oxygen depletion and mass mortalities of invertebrates and fish. Bivalve filtration also counteracts eutrophication by inducing higher rates of denitrification (Newell et al. 2002).

In addition to their ecosystem role as biological filters, harvested populations of bivalves are a source of food and recreation for humans. The over-exploitation of abundant estuarine bivalves is in large measure responsible for their decline in estuaries and for recent collapses of estuarine ecosystems (Jackson et al. 2001). However, because of their economic value, there also is a wealth of information about bivalve population dynamics and technologies developed to sustain and enhance stocks. All of this is useful in restoring depleted populations and here we consider potential

opportunities for estuarine restoration through enhancing suspension-feeding bivalves and thus their filtration function in the system. As an example, we use a restoration assessment performed to replace the loss of ecosystem services of surf clams and other bivalve molluscs following the 'North Cape' oil spill in Rhode Island, USA, and develop a quantitative demographic model for growth, survival, and production of surf clams. When coupled with estimates of clam density, the model allows quantitative estimation of surf clam biomass-production lost after the spill. We then illustrate by application of analogous demographic models of bivalve production how a bivalve enhancement project can be quantitatively scaled to compensate for the loss in ecosystem services caused by loss of surf clams and other bivalves after exposure to oil or other pollutants.

## MATERIALS AND METHODS

**Loss of production by bivalves.** After the barge 'North Cape' grounded on the south coast of Rhode Island (USA) during a severe winter storm on 19 January 1996, most of the 2682 metric tons (828 000 gallons or 3130 m<sup>3</sup>) of No. 2 fuel oil that was spilled became rapidly entrained into the water column by the heavy surf (French McCay 2003). This mixing process resulted in high concentrations of polynuclear aromatic hydrocarbons (PAHs) throughout the water column, sufficient to induce mass mortality of benthic marine animals suffering from narcosis. The induction of acute toxicity became evident as numerous lobsters *Homarus americanus*, surf clams *Spisula solidissima*, blue mussels *Mytilus edulis*, rock crabs *Cancer* spp., sea-stars, ampeliscid amphipods, hard clams *Mercenaria mercenaria*, and demersal fishes washed up dead or moribund on beaches for several days beginning immediately after the spill (Gibson 1997). These dead animals had occupied either the sand-bottom or the cobble-boulder habitats in the shallow subtidal shelf contiguous with the beach. Oil was also transported into coastal lagoons (termed salt ponds), where additional losses of benthic invertebrates such as soft-shell clams *Mya arenaria*, eastern oysters *Crassostrea virginica*, and bay scallops *Argopecten irradians* followed (French & Rines 1998).

Losses of bivalve molluscs were quantified by integrating several studies. Field sampling was conducted on 2 dates after the oil spill to quantify local post-spill abundance of surf clams by size (age) class in and out of the spill-affected zone. Physical fates modeling was used to predict water column PAH concentrations, which were validated with observed PAH concentrations in the water column at multiple locations. Based on known acute toxicity levels for appropriate taxa and



estimates of pre-spill abundances, an ecotoxicological impact assessment model was employed to estimate mortalities of species, including surf clams and other bivalves, in the marine and salt pond environments. The estimated surf clam mortality was compared to the estimated number stranded on beaches near the impact site after the spill. We converted the loss of surf clams to an estimated loss of biomass from size frequency distributions of killed clams and the applicable size-weight relationship. Finally, we developed a demographic model of surf clam individual growth and mortality to compute the production forgone because of the additional lifetime growth that would have been expected had those dead animals survived to complete their natural expected life spans. The biomass of the immediate kill and the production forgone were combined to yield the total loss of production caused by the oil spill.

**Minimum estimate of surf clam mortality.** Sampling of stranded surf clams was conducted daily at low tide from 20 to 22 January 1996 on 6 impacted beaches (Fig. 1). Two control beaches west (Westerly) and east (Newport) of the impact zone were sampled to quantify purely storm-induced strandings (Gibson 1997). On each impacted beach, 2 × 200 m-long transects were established parallel to the shore at low tide, from which dispersed sets of randomly placed quadrats were used to quantify densities and size frequency distributions of bivalves. The total area covered by strandings was also estimated on each affected beach. Since logistics precluded sweeping the transects clear of stranded animals, the overall mean density (3.65, SE = 1.08) for the 3 d of sampling, less the mean (0.04, SE = 0.03) for the

control beaches, was multiplied by mean width (5.73 m, SE = 0.77) and length (15955 m) of the impacted beach to estimate a minimum number of 330300 surf clams stranded on the shoreline (Gibson 1997). Although more surf clams came ashore on subsequent days, they were not counted. Gibson (1997) estimated total surf clam strandings at 1.8 million. This estimate does not represent total surf clam mortality because not all clams killed became stranded on the beaches. Specifically, smaller clams were absent from the strandings: no clam <3.6 cm in length, and few <7 cm, were observed on the beaches. A 3.6 cm surf clam would be in its second year of life (Weissberger 1998), meaning that none of the young-of-the-year (YOY; and few 1 yr-olds) were included in the strandings. Thus, the estimated number of surf clams stranded represents the minimum loss of clams >1+ yr of age.

**Density of surf clams.** Surf clams were sampled in and out of the spill-affected area, providing density data for input to the ecotoxicological impact assessment model and improving estimation of production forgone by providing site-specific growth and survivorship information. In May/June 1997, 17 mo after the oil spill, surf clams were sampled using 2 different sampling devices along 1 transect in the impacted (W) and 1 in the adjacent control area (FW) to the west (Fig. 1). Each transect contained 5 stations and was oriented perpendicular to shore, extending out to a depth of 10 m, the limit found to be minimally impacted in the ecotoxicological model. One sampler was an 8.4 cm diameter core sieved through a 2 mm mesh; the other was a suction dredge that passed contents of a 1 m<sup>2</sup>

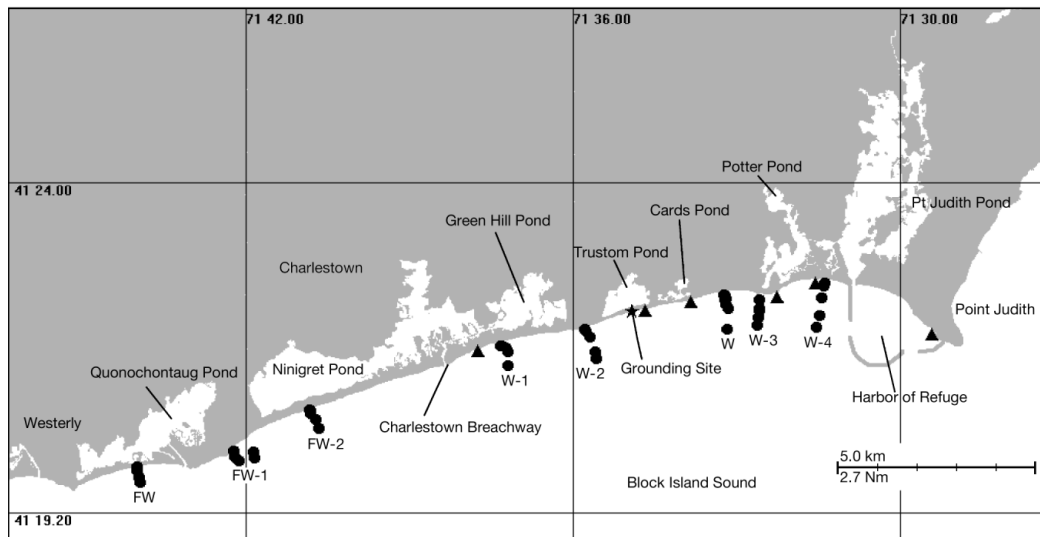


Fig. 1. Transect locations on the south coast of Rhode Island (USA) for sampling surf clams *Spisula solidissima*: (1) stranded on beaches (triangles), conducted daily at low tide 20 to 22 January 1996; and (2) densities in subtidal sediments (circles), taken by core and dredge in May/June 1997 and December 1997 to February 1998. The 'North Cape' grounding site is indicated by the star. The impact zone extended along the shore to 10 m deep water (i.e. at the outer station of each W transect) from Point Judith to the Charlestown Breachway. W: impacted sites; FW: adjacent control areas

sample frame through a mesh bag with 4 × 6 mm openings. These 2 sampling devices produce largely complementary information, in that the dredge sample did not fully retain YOY clams, whereas the core could not capture larger clams approaching the diameter of the tube. At each station, 30 core and 15 dredge samples were randomly placed and collected clams were counted and measured (shell length; Tables 1 & 2).

Surf clams were sampled a second time from December 1997 to February 1998, 24 mo after the spill, using only the dredge sampler at 3 original stations and 30 new stations (Fig. 1, Table 2). Because the dredge sampler missed the smallest YOY clams, we used a correction factor for that undercounting to render the December 1997 to February 1998 density estimates for YOY comparable with previous densities estimated by coring. In the May/June 1997 samplings along the FW transect, the ratio of YOY density in cores (Table 1) to that in dredge samples (Table 2) was 17.0 (SD = 14.7). For the period of December 1997 to February 1998, YOY density was estimated as 17.0 × the measured dredge-sample density (in Table 2) to correct for the under-sampling of those size clams. Clams were found in fine to coarse sand, but not at locations where granules or rock boulders were present.

#### Surf clam recruitment response after the oil spill.

The surf clam samples provide some insight into the likely loss of clams from the oil spill and into the population dynamics of surf clams. Dredge sampling 17 mo after the spill uncovered no surf clams large enough to have been present before the spill (>3.6 cm length) in the impact area and only 1 clam (15.1 cm long) in the control area (Table 2). Thus, this information is consistent with the assumption of mass mortality of surf clams in the spill area (1 to 40% mortality was computed by and applied in the biological effects model, French McCay 2003). Nevertheless, the similarly low density of older surf clams in the presumptive control area to the west raises questions. The core sampling in

May/June 1997 revealed numerous surf clams of 1.4 to 1.9 cm in length in the control area (mean = 12.0 m<sup>-2</sup>; SD = 7.0 m<sup>-2</sup>) but far more on the impacted transect at stations with sand (mean = 672 m<sup>-2</sup>; SD = 311 m<sup>-2</sup>), but not granular (>1 mm) sediments (Table 1). This size class presumably reflects animals of ca. 1 yr of age (Weissberger 1998). Consequently, these clams had settled in the first summer (1996) after the oil spill. Based on dredge sampling for both sampling periods, and the correction factor 17.0 for under-sampling, the YOY (Year Class 0) clams exhibited a mean density of 6.2 m<sup>-2</sup> (SD = 7.0 m<sup>-2</sup>) in the control area and 1231 m<sup>-2</sup> (SD = 2584 m<sup>-2</sup>) in the impact zone (Table 2). The far higher recruitment in the spill area could be explained as a consequence of: (1) greater survival after settlement where predators like sea stars, moon snails, and rock crabs had been decimated by the spill; (2) a serendipitous consequence of patchiness in recruitment and the lack of replication of transects in this study; or (3) evidence of a geographic cline in settlement rate from highs near the point of land at the east where grounding occurred to lows toward the west where the control area was located. We used surf clam density data from the control area to estimate pre-spill densities in estimation of mortality. To the degree that clam recruitment to this western area is systematically lower than to the spill area, this decision resulted in conservative estimates of surf clam losses.

**Survivorship of young clams.** Subsequent sampling from December 1997 to February 1998 (ca. 2 yr post-spill) provided further insight into the surf clam demography in this area of the Rhode Island coast. Dredge samples contained the previously detected cohort of now 1.5 yr-old clams (2.5 to 7.5 cm in length with a mean of 5.6 cm) plus a new cohort of presumably 0.5 yr-old recruits (<2.5 cm). By comparing densities only in re-sampled stations in the control area of almost 1 yr-olds in May/June 1997 to 1.5 yr-olds from December 1997 to February 1998 (Table 2), we computed a 7-mon survival rate of 6.3 %, which translates to an annual rate of 0.88 %. We rounded that value up for our subsequent demographic modeling and assumed a 1% annual survival rate for surf clams from Age 0.5 to 1.5, or 10% per half year in this period (Table 3). The sampling data provided a separate confirmation of this early life-stage mortality rate. Multiplying by the correction factor (17) to adjust for undercounting of YOY clams in dredge samples at the 3 control area stations that were re-sampled from December 1997 to February 1998 yielded an estimated YOY (0.5 yr-old) density of 2.72 m<sup>-2</sup> (Table 3). Application of a 1% annual survival rate would yield an expected 1.5 yr-old density in this cohort of 0.027 m<sup>-2</sup>. The actual density of 1.5 yr-olds in the December 1997 to February 1998 sampling was 0.04 m<sup>-2</sup>.

Table 1. Mean grain size (mm) and density (ind. m<sup>-2</sup>) of surf clams *Spisula solidissima* along impacted (W) and control (FW) transects (see Fig. 1), based on 8.4 cm-diameter core samples (30 replicates per station) taken in the spring of 1997

Transect	Depth (m)	Date sampled (dd/mm/yy)	Grain size (mm)	Density Mean (SD)
W	3	19/05/97	0.1	763.9 (438.7)
W	4	18/05/97	0.1	926.3 (539.8)
W	6	18/05/97	0.1	324.8 (352.7)
W	8	19/05/97	1.1	0 (0)
W	10	20/05/97	2.1	0 (0)
FW	3	24/05/97	0.3	6.0 (33.0)
FW	4	24/05/97	0.2	30.1 (68.4)
FW	6	25/05/97	0.1	18.1 (55.1)
FW	8	27/05/97	0.1	0 (0)
FW	10	27/05/97	0.1	6.0 (33.0)

Table 2. Mean grain size (mm) and measured surf clam *Spisula solidissima* density (ind. m<sup>-2</sup>) along the indicated transects (see Fig. 1) in dredge samples (15 replicates per station) taken in the spring of 1997 and winter 1997/98. Transects designated by W are in the impacted area, whereas FW indicates the control area. Transect W-R is a re-sampling of the W transect

Transect	Depth (m)	Date sampled (dd/mm/yy)	Grain size (mm)	Density Mean (SD)	Year class
W	3	28/05/97	0.1	472.9 (93.0)	0 (1996)
W	4	08/06/97	0.1	337.9 (94.6)	0 (1996)
W	6	12/06/97	0.1	254.6 (42.3)	0 (1996)
W-R	3	12/01/98	0.1	110.5 (31.8)	1 (1996)
W-R	4	21/12/97	0.1	13.80 (7.4)	1 (1996)
W-R	6	15/01/98	0.2	3.30 (1.6)	1 (1996)
W	8	29/05/97	1.1	2.44 (1.3)	0 (1996)
W	10	31/05/97	2.1	0.80 (1.3)	0 (1996)
W1	3	10/12/97	0.1	1.00 (0.9)	0 (1997)
W1	4	15/12/97	0.1	1.80 (1.3)	0 (1997)
W1	6	11/12/97	0.6	1.50 (1.4)	0 (1997)
W1	8	12/12/97	1.1	0.00 (0)	
W1	10	13/12/97	1.0	0.00 (0)	
W2	3	03/12/97	0.2	0.90 (1.1)	1 (1996)
W2	4	05/12/97	0.3	0.00 (0)	0 (1997)
W2	6	06/12/97	0.4	0.80 (0.9)	0 (1997)
W2	8	08/12/97	0.8	3.70 (2.0)	0 (1997)
W2	10	09/12/97	1.0	1.60 (1.3)	0 (1997)
W3	3	25/11/97	1.6	0.00 (0)	
W3	4	26/11/97	0.8	0.00 (0)	
W3	6	28/11/97	1.2	0.00 (0)	
W3	8	29/11/97	1.0	1.30 (0.7)	0 (1997)
W3	10	30/11/97	1.7	0.10 (0.2)	0 (1997)
W4	3	11/11/97	0.2	8.30 (3.3)	1 (1996)
W4	4	12/11/97	0.2	17.10 (7.2)	1 (1996)
W4	6	18/11/97	0.1	11.80 (9.2)	1 (1996)
W4	8	19/11/97	0.8	3.90 (1.4)	0 (1997)
W4	10	24/11/97	0.4	2.50 (2.3)	0 (1997)
FW	3	15/06/97	0.3	1.33 (1.5)	0 (1996)
FW	4	16/06/97	0.2	1.07 (1.2)	0 (1996)
FW	6	14/06/97	0.1	0.53 (0.6)	0 (1996)
FW	8	17/06/97	0.1	0.07 (0.3)	0 (1996)
FW	10	18/06/97	0.1	0.33 (0.6)	0 (1996)
FW1	3	20/01/98	0.8	0.00 (0)	
FW1	4	21/01/98	0.6	0.00 (0)	
FW1	6	22/01/98	0.3	0.10 (0.2)	0 (1997)
FW1	8	02/02/98	0.7	0.20 (0.4)	0 (1997)
FW1	10	03/02/98	0.4	0.00 (0)	
FW2	3	20/12/97	0.3	0.30 (0.5)	0 (1997)
FW2	4	20/02/98	0.4	0.80 (0.9)	0 (1997)
FW2	6	22/02/98	0.6	0.30 (0.5)	0 (1997)
FW2	8	21/02/98	0.5	0.40 (0.5)	0 (1997)
FW2	10	23/02/98	0.8	0.00 (0)	

#### Numbers of clams by age class at the time of the spill.

We used results of post-spill sampling (Tables 1 & 2) and our age-specific mortality schedule (see 'Survival' below) to estimate, by size and age class, the densities of surf clams present at the time of the 'North Cape' oil spill. To form our best estimate of densities of surf clams in each age (size) class, we used only the YOY data for each sample year from the control (presumably unaffected) site west of the spill area, computed numbers for older clams using a survivorship schedule based on mortality

rates taken from the literature (see below), and averaged the 2 yr of data. From the May/ June 1997 sampling, we chose the mean abundance of YOY clams from the core sampling (Table 1) and projected that backwards in time by 0.5 yr to provide one estimate of YOY clam abundance for the date of the spill. Across all the control core samples, YOY density averaged 12 m<sup>-2</sup>, which after application of a half-year survivorship of 10% represents survivors expected from 120 0.5 yr-olds in January 1996 (Table 3). Based on this YOY abundance and estimated survivorship rates, the control area contained an estimated 5.52 older clams m<sup>-2</sup>, with the size distribution shown in Table 3. Similarly, the observed density of 0.5 yr-old clams sampled in the control area from December 1997 to February 1998 was 2.72 m<sup>-2</sup> (corrected for dredge sampler error as explained above). Assuming the survivorship schedule and stable age distribution in Table 3, the density of older clams during this second period was 0.13 m<sup>-2</sup>. To derive our estimate of surf clam densities by age (size) class at the time of the spill (January 1996), we averaged across these 2 yr the densities in each age class, weighting by sampling effort (Table 3). This weighting had the effect of undervaluing the clams that settled in the year just after the oil spill, perhaps appropriate if residual negative effects of the spill persisted.

The resulting average densities computed from the site-specific sampling data (Table 3) match available published data in the literature reasonably well. Weighted averages of the 2 samplings yield a YOY density of 41.8 m<sup>-2</sup> and a density of 1.9 older clams m<sup>-2</sup>, totaling 43.7 m<sup>-2</sup> (Table 3). Abundance of older clams (>3.6 cm) was similar to

Olsen's (1970) observed mean of 1.8 m<sup>-2</sup> for that same size class in nearby Rhode Island waters. Franz (1976) observed 25 to 125 YOY m<sup>-2</sup> in August on the south coast of eastern Long Island, ca. 50 km from the spill site, with the greater numbers farther to the west toward the Rhode Island coast.

**Ecotoxicological impact assessment modeling.** Mortality of surf clams and other bivalves was estimated by application of ecotoxicological impact assessment modeling (French & Rines 1998, French McCay 2002,

Table 3. *Spisula solidissima*. Age-specific growth and mortality of surf clams used to develop predictions of abundances prior to the 'North Cape' oil spill in Rhode Island. Projections are made for the half-year to match the season (winter) of the oil spill. Length-weight relationships were from Weinberg & Hesler (1996). Survival rates were taken from a literature review and cohort analysis (see 'Survival' in text). The first column of density estimates is based upon core sampling data of 1 yr-old clams taken in May/June 1997, and the second column on dredge sampling data of 0.5 yr-old clams taken in December 1997 to February 1998. Actual observations are presented in **bold** while others are projected by applying the age-specific survivorship schedule. The final column is the effort-weighted mean of the first 2 estimates. YOY: young-of-the-year (0.5 yr-old at time of spill)

Age (yr)	Shell length (cm)	Meat weight (g)	Survival to next class	Density estimates (ind. m <sup>-2</sup> )		
				May/June 1997	Dec 1997 to Feb 1998	Weighted mean
0.5	1.0	0.130	0.10	120	<b>2.72</b>	<b>41.8</b>
1	1.5	0.371	0.10	<b>12</b>	0.272	4.18
1.5	3.6	3.54	0.50	1.20	0.027	0.42
2.5	6.2	14.2	0.905	0.60	0.014	0.21
3.5	8.2	29.6	0.905	0.54	0.012	0.19
4.5	9.8	47.0	0.905	0.49	0.011	0.17
5.5	11.1	64.5	0.905	0.44	0.010	0.15
6.5	12.1	80.8	0.861	0.40	0.009	0.14
7.5	12.9	95.3	0.861	0.35	0.008	0.12
8.5	13.5	107.9	0.861	0.30	0.007	0.10
9.5	14.1	118.6	0.861	0.26	0.006	0.09
10.5	14.5	127.6	0.861	0.22	0.005	0.08
11.5	14.8	134.9	0.861	0.19	0.004	0.07
12.5	15.0	140.9	0.861	0.16	0.004	0.06
13.5	15.2	145.8	0.861	0.14	0.003	0.05
14.5	15.4	149.8	0.861	0.12	0.003	0.04
15.5	15.5	153.0	0.861	0.10	0.002	0.04
YOY at time of spill				120.0	2.72	41.8
Total >3.6 cm at time of spill				5.52	0.13	1.92
Total at time of spill				125.5	2.85	43.7

2003), which involved coupling a temporal physical fates model of transport and degradation of PAHs with a biological effects model to predict acute toxic mortality for different taxa. Field sampling of PAH concentrations in the water column was conducted to validate the model's time-dependent predictions of exposure. Side-scan sonar was used to map the areas of soft-bottom (which is all fine-to-coarse sand) and rocky reef habitats in the spill-affected area, which allowed modeling to be stratified by location and amount of habitat (French McCay 2003). Published information on variation in acute mortality with exposure (French McCay 2002) was then applied together with available information on natural pre-spill densities and size distributions to predict total loss of abundance and biomass for key taxa (French & Rines 1998, French McCay 2003).

Exposure concentrations of PAHs in bottom water were validated and the biological effects model originally validated for lobsters (French McCay 2003) was applied to bivalves offshore from the beach (French McCay 2003) and in salt ponds (French & Rines 1998)

because bivalves and juvenile lobsters suffer similar toxic effects by narcosis (French McCay 2002). Computation of initial loss of biomass from acute mortality required estimates of pre-spill abundance, size distribution, and size-biomass relationships for each bivalve, while subsequent computation of production forgone required estimates of expected growth and mortality rates (French McCay 2003). The modeling for the salt ponds included a separate but linked model of temporal change in PAH concentrations (Hinga 1997) in which source PAH concentrations were provided by the ocean model (French McCay 2003) and the rate of decline of concentrations were fitted to pond observations (Hinga 1997). Then exposure and mortality of bivalves was estimated from application of the same biological effects model used for the ocean to salt-pond abundance estimates derived from literature reviews (French & Rines 1998, French McCay 2003).

Results of this ecotoxicological impact assessment modeling exercise (Table 4) demonstrated that surf clams comprised the vast majority (ca. 88% by number and 96% as biomass) of the bivalves killed after the 'North Cape' oil spill. Contributions from other species (blue mussels, hard clams, soft-shell clams, oysters, and bay scallops) were all relatively small. When the estimated surf clam density (Table 3) was entered into the biological effects model, the total number of older (>1 yr) dead surf clams predicted by the ecotoxicological impact assessment was 2.6 million (Table 4), which is larger than Gibson's (1997) computed value of 1.8 million stranded surf clams. Not all dead surf clams would be stranded on the beaches, so the larger number of dead predicted by the model is reasonable. The model predicted a total loss (all ages) of 150 million surf clams, representing a biomass of 193 000 kg (Table 4). All other bivalves added only another 8000 kg of additional biomass losses at the time of the spill.

**Demographic modeling to compute production forgone.** Estimates of age-specific growth, the relationship of clam size to biomass, age-specific mortality schedule, and the numbers of clams killed in each age class were required to estimate production forgone. For most of the individual and population demographic parameters, a synthesis of available literature provided



Table 4. Summary of estimates of bivalve losses resulting from the 'North Cape' oil spill. Losses are based upon application of ecotoxicological impact assessment modeling: marine (French McCay et al 2003) and salt pond (French & Rines 1998). Production forgone is the expected summed somatic growth in the absence of the spill. Total loss is biomass killed plus production forgone, with future losses discounted at 3% annually. YOY: young-of-the-year (0.5 yr-old at time of spill)

Location Species category	Numbers killed (thousands)	Biomass killed (kg)	Production forgone (kg)	Total loss of production (kg)
<b>Coastal marine</b>				
Hard clam <i>Mercenaria mercenaria</i>	37	7	798	805
Surf clam <i>Spisula solidissima</i> (total)	150 588	192 496	171 516	364 013
YOY	148 010	19 241	64 963	84 204
>1 yr	2 578	173 255	106 554	279 809
Blue mussel <i>Mytilus edulis</i>	20 247	879	1 203	2 082
Total bivalves	170 872	193 382	173 517	366 900
<b>Salt pond</b>				
Soft-shell clam <i>Mya arenaria</i>	499	5 712	3 888	9 600
American oyster <i>Crassostrea virginica</i>	149	1 857	905	2 762
Bay scallop <i>Argopecten irradians</i>	0.159	5	0	5
Total bivalves	649	7 573	4 794	12 367
Total	171 521	200 955	178 311	379 267

appropriate values, while others were from analysis of samples collected in the spill area (Tables 1 & 2). Estimation of the numbers killed by age (size) class came from application of the biological effects ecotoxicology model (French McCay 2003) after estimation of the numbers of clams in each age (size) class present at the time of the oil spill (Table 3).

**Growth.** We chose to describe length as a function of age by using the traditional von Bertalanffy growth curve (Ricker 1975):

$$L_t = L_\infty \{1 - e^{-K(t-t_0)}\} \quad (1)$$

where  $L_t$  is shell length (cm) at age  $t$  (yr),  $L_\infty$  is the asymptotic maximum length,  $K$  is the Brody growth coefficient, and  $t_0$  is a constant. Based on Weinberg & Hesler (1996), we used the following values for surf clams:  $L_\infty = 15.99$  cm,  $K = 0.232$ , and  $t_0 = -0.099$ . However, insertion of these parameter values indicates a length of 3.6 cm at  $t = 1$  yr. Based on Weissberger (1998), 3.6 cm clams would be well into their second year of life, and we assumed that age  $t$  represents a nominal age (actual age in years minus 0.5) in our application of the von Bertalanffy growth curve. This calibration also had the advantage of assessing abundances at mid winter (the half birthdays), coinciding

with when the spill occurred. Conversion of shell length to weight was achieved by applying the following equation with parameters from Fay et al. (1983):

$$W_t = a L_t^b \quad (2)$$

where  $W_t$  is wet meat weight at age  $t$  (yr) and  $a$  and  $b$  are constants ( $a = 0.0001304$  and  $b = 2.578$ , for surf clam length in cm and weight in kg, Table 3).

**Survival.** To describe age-specific survival, we adopted the basic exponential fisheries population dynamics model of Ricker (1975). For surf clams of legally harvestable size, the number at age  $t$  (yr),  $N_t$ , is a function of the number of new recruits to the fishery at age  $t_r$  years. For  $t > t_r$ :

$$N_t = R e^{-Z_A(t-t_r)} \quad (3)$$

$$Z_A = M + F \quad (4)$$

where  $Z_A$  is annual instantaneous total mortality (assumed constant for ages  $t > t_r$ ),  $M$  is annual instantaneous natural mortality,  $F$  is annual instantaneous fishing mortality, and  $R$  is the number of individuals in this cohort that first recruited to the fishable population (i.e.  $R =$  number at age  $t_r$  yr). For  $t \leq t_r$ :

$$N_t = N_{t-1} e^{-Z_t} \quad (5)$$

where  $Z_t$  is the age-specific annual instantaneous natural mortality rate. The annual survival rate for age  $t$  ( $S_t$ ) is thus:

$$S_t = e^{-Z_t} \quad (6)$$

We estimated rates of age-specific mortality of Rhode Island surf clams using information from several sources. Grosselin & Qian (1997) analyzed the early survival of newly settled clams and determined that only about 1% of the new settlers would still be alive by winter. Thus, we assumed survival of surf clams from age 0 to 0.5 yr to be 1%. Based on analysis of sampling data for surf clams at the spill site and detailed above, an annual survival rate of 1%, or 10% per 0.5 yr, is assumed to apply from 0.5 to 1.5 yr (Table 3). Instantaneous mortality rates of harvestable-sized surf clams (>12.1 cm or > 6 yr old) in southern New England have been estimated by NMFS (1995) to be  $M = 0.05$  and  $F = 0.1$ , giving a total mortality rate  $Z = 0.15$ . Estimated mortality rates for smaller clams are higher, but empirical data are not readily available. Clams reach a size refuge from predation at 5 cm in length (MacKenzie et al. 1985), or ca. 2 yr of age. Thus,

we assumed that mortality rates for 2.5 to 5.5 yr olds are  $M = 0.1$  (twice the rate of larger clams), with  $F = 0$  (no fishing). For surf clams from 1.5 to 2.5 yr old (3.6 to 6.2 cm length), we chose an annual survivorship of 50%, halfway between that of younger and older age classes (Table 3).

**Computation of production forgone.** In addition to the estimated direct kill of 148 million YOY plus 2.6 million older clams, weighing (without shells) a total of 192 500 kg (Table 4), the total production loss must also include production forgone, which is the somatic growth those clams would be expected to have achieved over their remaining natural lifespan. The equations used to calculate the expected remaining lifetime production ( $P_L$ ) are:

$$P_L = \sum \sum N_{i,y} S_{i+y} (W_{i+y+1} - W_{i+y}) / (1 + d)^y \quad (7)$$

$$N_{i+1,y+1} = N_{i,y} S_{i+y} = N_{i,y} e^{-(M_i+y+F_i+y)} \quad (8)$$

where  $N_{i,y}$  is the number of Age Class  $i$  expected to have remained alive at the beginning of year  $y$  after the spill,  $S_{i+y}$  is the expected portion of Age Class  $i$  surviving from Age  $i+y$  to  $i+y+1$ ,  $W_{i+y}$  is the weight per individual for Age Class  $i$  at  $y$  years after the spill,  $M_{i+y}$  is instantaneous annual natural mortality rate,  $F_{i+y}$  is instantaneous annual fishing mortality rate (both for Age  $i+y$ ), and  $d$  is the discount rate ( $d = 0.03$ : NOAA 1997). Before the age of recruitment, fishing mortality is 0. The discount factor,  $1/(1 + d)^y$ , decreases the value of the production by 3% for each year that passes before that production would have been realized. This follows the economic model that losses, or gains of restoration, in the future are less valued than present production. Including identical discounting on both the injury and restoration sides of the equation allows time lags in both losses and benefits to be appropriately treated so as to measure values lost and gained fixed to a common year.

## RESULTS

### Injury

The total loss of surf clam production from the 'North Cape' oil spill was 364 000 kg (192 500 kg killed directly and 171 500 kg in production foregone). Injuries to all bivalves in the marine environment and the salt ponds were computed in an identical fashion (French & Rines 1998, French McCay 2003) and are summarized in Table 4. Although these projections of injuries for other bivalve species did not have benefit of site-specific sampling data, the dominance of the surf clam loss means that the total loss of bivalve production is not greatly biased by errors in estimating

pre-spill densities of rare species. The total loss of bivalve production caused by the 'North Cape' oil spill was thereby estimated to be 379 000 kg (Table 4). This represents the injury that restoration should be scaled to replace.

### Scale of compensatory restoration

The quantitative benefits of restoration, whether it be via hatchery stocking, transplantation, reduction of fishing, or habitat restoration, can be estimated by the net bivalve production that is added to the ecosystem. Use of this metric to establish the scale of the restoration project required to compensate for the loss must use the same currency (bivalve production discounted to a common year) that was used to quantify the loss. Secondary production represents one fundamental ecosystem process, so using this as a proxy for all ecosystem services has some justification. Furthermore, production of suspension-feeding bivalves correlates with their important filtration and biochemical processing functions. Other important ecosystem functions of bivalves may not be well measured by production alone. For example, the size structure of the lost animals is not necessarily reproduced in a restoration that matches the loss using production as the sole criterion. Smaller individuals provide an ecosystem service of feeding demersal predators, especially crabs, whereas older bivalves find substantial refuge from predation (e.g. Kennedy et al. 1996, Kraeuter 2001). Thus biasing the restoration action by using larger bivalves could add stability to the population dynamics by serving as a long-lasting spawning sanctuary and would provide similar filtration on phytoplankton but at the expense of failing to pass the energy produced up the food chain.

The process of estimating gains in production from any of the potential restoration approaches involves use of the same computations developed to estimate production forgone. In this case, we apply the identical equations derived above to project demographics and individual growth into the future, not to quantify production that would have occurred absent losses but instead to predict production that will occur through augmentation of abundance of one or more age (size) classes. Again analogous to the method for quantifying loss of production, we add the biomass of any individuals added to start the restoration to the discounted future production expected before they die to compute the total net enhancement of production. Using the identical method for estimating both the loss and gain is appropriate to insure that the scaling of restoration matches, and thus compensates for, the magnitude of the injury.



The choice of species to use in the bivalve restoration does not affect the method of estimation of quantitative gain in production, just the parameter values used in the projection. Many considerations enter into this choice, including reliability of the technology for each species, availability of a source (for stocking or seed production), cost effectiveness, and the distribution of losses among species. Assuming that all suspension-feeding bivalves are equivalent and interchangeable in restoring losses may compensate for lost production, filtration, and biogeochemical processing but does not necessarily replace those functions in the same habitat (here coastal ocean vs. salt pond). In addition, not all bivalves are of equal value to the ecosystem or to humans in fisheries. We scaled the restoration required for several alternative choices of bivalve species and size class within species (Table 5). We considered the American oyster *Crassostrea virginica*, bay scallop *Argopecten irradians*, hard clam *Mercenaria mercenaria*, and soft-shell clam *Mya arenaria*, as well as the surf clam *Spisula solidissima*. The same demographic model described above was used for each species, but different specific life-history parameters were used (Tables 5 & 6). For hard clams and oysters, we also made these scaling projections with and without fishing pressure to quantify the contributions of establishing fishing sanctuaries. Each alternative was scaled to compensate for the loss of 379 000 kg of bivalves, providing the numbers of individuals initially required to seed, transplant, protect from the fishery, or produce by habitat restoration. Each of the life-history parameters is estimated with uncertainty and a thorough analysis of benefits of restoration could include a formal uncertainty analysis to aid in choosing the most appropriate restoration option. We do not do so here because we use these results merely to illustrate general patterns. For oysters, we employ several different natural mortality rates (Table 5) because our estimates of their demographic rates are the most uncertain, fluctuating with disease incidence and severity.

The results of these computations to scale restoration options reveal several patterns. First, the larger the individuals added through seeding (or stocking, protecting, etc.), the fewer are needed. This outcome is illustrated best by hard clam results, where numerous starting sizes were modeled (Table 5). The numbers required do not decrease linearly with size but instead show a sharp early increase and then a far slower change for larger, older clams which experience lower natural mortality rates (e.g. Peterson et al. 1995). If the animals are from a hatchery, the costs of rearing seed to larger size are far higher, so cost efficiency would require survivorship gains to be balanced against increased costs to choose the optimal size to add. Sec-

ond, for hard clams, protection from fishing can enhance the expected benefits of the restoration more than for any other species modeled (Table 5). This result follows from the longer natural life span of this species, which allows for greater expected growth in the future. Third, the calculations reveal that future production of oysters is highly sensitive to mortality rate. For oysters subject to fishing pressure, the number of seed oysters required to provide 179 000 kg of production increased from 29 to 122 million as  $M$  was increased from 0.223 to 0.50 yr<sup>-1</sup> (Table 5). Fourth, if seeding is restricted to relatively small (and less expensive) individuals (e.g. <3.3 cm in length), the most efficient restoration can come from choosing surf clams, requiring only 5.3 million as compared to 16 to 75 million hard clams, 25 to 122 million oysters, 32 million bay scallops, and 26 to 218 million soft-shell clams (Table 5).

## DISCUSSION

Accomplishment of the compensatory net gain in bivalve production requires that the restored species is limited by factors addressed by the restoration actions and that restoration is successful. These issues, along with practical matters concerning logistics, were considered in developing the restoration plan for providing the required compensation for the effects of the oil spill considered here as an example. In the following sections, we briefly discuss what is known about limitations to bivalve production and the effectiveness of the 4 specific restoration approaches that were considered.

### Limitation of bivalve population size and production

Because of their commercial value, there is a substantial body of scientific information on such species as surf clams *Spisula solidissima*, hard clams *Mercenaria mercenaria*, American oysters *Crassostrea virginica*, and bay scallops *Argopecten irradians*. They are appealing candidates for restoration because of their general historical decline in abundance in the southern New England region, their value as natural biological filters of over-fertilized and eutrophied systems, their human use value for exploitation, and their ecological importance as prey for marine predators like crabs and bottom fishes. While surf clams experienced the greatest loss in production from the 'North Cape' oil spill, enhancement of these ecologically similar species was considered because they provide analogous filtration services and other functions within the ecosystem.

Table 5. Numbers of additional individuals required to compensate quantitatively for production lost (379267 kg) from the oil spill. Results are derived from application of the age-specific survivorship and growth models (see 'Survival' in text). Computations vary bivalve species, size class added, fishing pressure, and (for oysters) mortality rate.  $M$  is instantaneous exponential rate of natural mortality,  $F$  is instantaneous exponential rate of fishing mortality (French et al. 1996). Mortality rate from Age 0 to 1 yr is assumed to be 10% (Grosslein & Qian 1997). Length at age and length-weight parameters ( $L, W$ ) are from: (1) Weinberg & Hesler (1996) and Fay et al. (1983); (2) French et al. (1996); and (3) Rice et al. (1989)

Species	$M$ ( $\text{yr}^{-1}$ )	$F$ ( $\text{yr}^{-1}$ )	Age of recruit- ment to fishery	Length (cm)	Meat weight (g)	Age ( $\text{yr}^{-1}$ )	Lifetime production (kg/kg)	Lifetime production + initial biomass (kg ind. $^{-1}$ )	Nos. of ind. required for compensation (millions)	Source for $L, W$
Surf clam <i>Spisula solidissima</i>	0.12	0.03	6	3.0	1.42	1	49.61	0.0719	5.3	(1)
Surf clam <i>Spisula solidissima</i>	0.12	0.03	6	1.5	0.065	0	107.3	0.0070	54	(1)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0.3	3	2.0	1.1	0	4.235	0.0058	66	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	2.0	1.1	0	7.131	0.0090	42	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0.3	3	2.0	1.1	0	19.94	0.0231	16	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	5.8	22.4	4	1.305	0.0517	7.3	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	7.5	46.4	7	0.291	0.0599	6.3	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	8.5	66.2	>18	0.010	0.0668	5.7	(2)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	7.8	50.9	17	0.383	0.0704	5.4	(3)
Hard clam <i>Merccenaria mercenaria</i>	0.1	0	3	8.5	66.0	17	0.164	0.0768	4.9	(3)
American oyster <i>Crassostrea virginica</i>	0.223	0	2	2.0	0.40	1	36.62	0.0150	25	(2)
American oyster <i>Crassostrea virginica</i>	0.223	0.3	2	2.0	0.40	1	31.51	0.0130	29	(2)
American oyster <i>Crassostrea virginica</i>	0.357	0	2	2.0	0.40	1	27.35	0.0113	33	(2)
American oyster <i>Crassostrea virginica</i>	0.357	0.3	2	2.0	0.40	1	24.48	0.0102	37	(2)
American oyster <i>Crassostrea virginica</i>	0.5	0.3	2	2.0	2.00	0	0.552	0.0031	122	(2)
Bay scallop <i>Argopecten irradians</i>	0.1	1	1	5.4	24.90	1	0.185	0.0295	13	(2)
Bay scallop <i>Argopecten irradians</i>	0.1	1	1	2.0	10.00	0	0.194	0.0119	32	(2)
Soft-shell clam <i>Mya arenaria</i>	0.1	0.6	2	1.5	0.35	0	4.040	0.0017	218	(2)
Soft-shell clam <i>Mya arenaria</i>	0.1	0.6	2	3.3	3.07	1	3.758	0.0146	26	(2)

***Spisula solidissima***. Although surf clams are targeted in commercial fisheries, less is known about factors that control their abundance and productivity compared with other exploited bivalve species. Its habitat along the high-energy ocean beaches limits access of researchers and challenges ecologists to define the scales of important population processes.

Surf clams have planktotrophic pelagic larvae that are transported as part of the plankton for about 2 wk before settlement begins (Fay et al. 1983). Thus, it is likely that physical flow regimes could limit the abundance of successful settlers and they almost certainly help dictate the patchy spatial patterns of settlement (Olsen 1970, Franz 1976). There is also potential for

recruitment limitation at low adult densities, but no evidence is available to test this hypothesis. However, the high abundance of settlers that appeared in the impact zone after the 'North Cape' spill suggests that recruitment may not be limiting in that locality.

Like other benthic bivalves settling into soft sediments (Grosselin & Qian 1997), surf clams suffer very high losses to predators until they reach a length of about 5 cm, which does not occur until around Age 2 yr (MacKenzie et al. 1985). The predators that are most important in controlling survival and thus production of surf clams are naticid gastropods and various crabs (Weissberger 1998). Demersal fishes may have important effects in reducing abundance of juvenile surf clams in some situations, whereas flounders act to limit growth rates by nipping siphons of larger clams, forcing them use energy for regeneration. High local *Spisula* density also acts to reduce growth rate, presumably by grazing down food concentrations in the benthic boundary layers (Weinberg & Hesler 1996). Fishing mortality ( $F$ ) begins at ca. Age 6 yr and is estimated to be  $\leq 0.1$  (NMFS 1995, Table 5), not as intense as some other fisheries. Thus, the intense predation on juvenile clams up to ca. Age 2 yr appears to represent the strongest control on surf clam abundance and production. This suggests that stocking with small clams (Table 5) would increase surf clam production. Protection from predation might also increase clam production, but at a loss to the food web.

***Mercenaria mercenaria*.** The hard clam is the most similar of the candidate bivalve species considered for restoration in the 'North Cape' case to the surf clam, which made up the bulk of the losses, and so was evaluated in some detail. A recent book (Kraeuter & Castagna 2001) synthesizes knowledge of hard clam biology, including factors that limit abundance and

production. Gamete production in hard clams increases with size, as in most free-spawning marine invertebrates (Peterson 1986a). Because of their high fecundity, most managers of hard clam fisheries assume no spawner-recruit relationship and so even a small number of spawning adults will be sufficient to provide adequate numbers of larvae to sustain the next generation (e.g. Hancock 1973). However, in North Carolina declining recruitment as a result of reduced spawning stock biomass caused by fishery exploitation implies that hard clams may become recruitment limited when adult spawners fall below some critical biomass (Peterson 2002). Little is known about the control of larval survival and success in hard clams, but the North Carolina case suggests that if density-dependent mortality exists, it is not strong enough to overcome a reduction of around 50% in spawning stock biomass.

At the time of settlement to bottom sediments, hard clams are susceptible to predation by infaunal predators like flat worms (Watzin 1983), small crustaceans like snapping shrimp (Beal 1983), suspension feeders that filter them from the water column, and deposit-feeding invertebrates (Hunt et al. 1987). At natural densities, adult and juvenile hard clams do not effectively limit the success of settlement in their local vicinity through filtration (Peterson 2002). Predation rates are high after settlement up to a length of ca. 2.5 cm, where blue crabs, a major predator, begin to experience lowered efficiency in crushing the shell (Arnold 1984, Peterson 1990, Kraeuter 2001). As larger individuals, hard clams continue to have enemies but predation by whelks (Peterson 1982), stone crabs, and rays (Kraeuter 2001) does not lower overall abundance except in certain habitats and under special conditions. Fishing exploitation is intense on natural populations

of hard clams and clearly represents an important control on abundance (Peterson 2002) and population structure (Rice et al. 1989).

Bottom habitat causes very important indirect control of hard clam abundance, operating both on the hydrodynamics of the settlement process and, even more importantly, on risk of predation after settlement. Emergent vegetation in seagrass beds slows currents and induces deposition of suspended particles, including invertebrate larvae (Peterson et al. 1984). After settlement, the seagrass root system provides some structural refuge from burrowing and digging predators, thereby further enhancing hard clam abundance (Peterson 1982, 1986b, Wilson 1990). Conse-

Table 6. Bivalve growth parameters used in restoration model calculations. Length at age and length (cm) versus weight (g) parameters ( $L, W$ ) are from: (1) French et al. (1996); and (2) Rice et al. (1989).  $L_{\infty}$ : asymptotic maximum length;  $K$ : Brody growth coefficient;  $t_0$ : constant (see 'Growth' in text)

Species	$L_{\infty}$ (cm)	$K$	$t_0$ (yr)	a ( $L, W$ )	b ( $L, W$ )	Source for $L, W$
Hard clam <i>Mercenaria mercenaria</i>	8.5	0.333	0.594	0.155	2.83	1
Hard clam <i>Mercenaria mercenaria</i>	8.5	0.333	0.594	0.0723	2.81	2
American oyster <i>Crassostrea virginica</i>	13.7	0.551	-0.365	0.087	2.21	1
Bay scallop <i>Argopecten irradians</i>	6.4	1.950	0.058	0.00018	2.93	1
Soft-shell clam <i>Mya arenaria</i>	8.6	0.356	-0.337	0.1100	2.82	1

quently, the extent of seagrass habitat limits the abundance of hard clams indirectly. Even more effective than seagrass as a barrier to predation by the hard clam's most significant enemy, the blue crab, is shell bottom habitat provided by oysters (Castagna & Kraeuter 1985, Peterson et al. 1995) and other mollusc species. Declines in oyster reefs and oyster shell habitats (Rothschild et al. 1994, Lenihan & Peterson 1998) have been even greater than the declines in seagrass habitat (Orth & Moore 1983) over the past century. Consequently, hard clam populations are almost certainly reduced regionally because of this loss in an important refuge from intense predation. However, in Narragansett Bay, *Crepidula fornicata* covers large areas forming a shell bottom (French et al. 1991), which may in part mitigate the losses of seagrass and oyster reefs and explain the greater abundance of hard clams in that estuary as compared to other New England waters.

Thus, as for surf clams, stocking (or other action to increase abundance) of small hard clams (Table 5) would increase production. Protection from predation, perhaps by habitat restoration, might also increase clam production, but potential loss to the food web should be considered as clams also provide this ecological service.

***Crassostrea virginica*.** The American oyster is sufficiently important to have stimulated a huge body of research, including a recent book (Kennedy et al. 1996) that synthesizes the present scientific knowledge of oyster biology. Populations of American oysters are grossly depleted throughout the Atlantic estuaries of North America (Rothschild et al. 1994, Lenihan & Peterson 1998), even to the point of functional extinction in most estuaries north of Delaware Bay. Production of sufficient numbers of gametes limits oyster settlement where adult spawning stock biomass is low, such as in lower-salinity waters of the Chesapeake Bay where reconstructed oyster reef habitat fails to receive repeatable settlement. In Southern New England embayments, oyster populations are almost surely recruitment limited as well, given the low size of the oyster populations. Because of the habitat-destroying fishing practice of oyster dredging, which removes the shell reef along with living oysters, habitat for oysters is also limiting (Rothschild et al. 1994). Even the reefs that remain are degraded by reduction of their height, which reduces oyster growth rates and exposes them to catastrophic mortality during hypoxic events (Lenihan & Peterson 1998). Such hypoxic events are enhanced by eutrophication, meaning that reef habitat degradation and eutrophication interact to help limit oyster abundance and production in deeper areas of stratified estuaries (Lenihan & Peterson 1998). As juveniles, oysters fall prey to blue crabs and to drilling gas-

tropods. Oyster drills can eliminate oyster sets in high-salinity waters and restrict adults to locations higher in the estuary. Two introduced protozoan parasites, Dermo and MSX (*Haplosporidium nelsoni*), now also kill American oysters before they reach their second birthday, thereby limiting abundance and production of the oysters. Oysters that do find suitable reef habitat and survive the parasites are typically harvested by fishermen. Thus, there are many opportunities for restoration to increase oyster abundance and production that might be used to compensate a spill-induced injury or other loss.

***Argopecten irradians*.** Since the bay scallop is essentially an annual, living for only ca. 18 mo (Belding 1910, Gutsell 1930), abundance typically fluctuates dramatically from year to year because of the absence of multiple older age classes to stabilize interannual fluctuations. The high interannual variation in recruitment of bay scallops implies that reproductive success acts as a major limitation to bay scallop abundance. If adult spawning stock biomass falls below a threshold level within a hydrographically isolated water basin, bay scallop recruitment will be reduced or fail (Peterson & Summerson 1992, Peterson et al. 1996). Even at densities higher than this presumed threshold, variation in settlement success probably explains much of the temporal variation in annual cohorts of bay scallops.

Bay scallop larvae must encounter suitable habitat for metamorphosis and settlement, which involves attachment to structures such as seagrass (Thayer & Stuart 1974) or cobbles in some New England estuaries (Belding 1910). Consequently, while settlement habitat almost certainly helps control bay scallop abundance and thereby production, the habitat limitation in New England bays is probably less strong than in the southern lagoons. However, predation on juvenile bay scallops by crabs and demersal fishes is intense enough to exert a strong control on abundance, with seagrass providing a vital service in elevating juvenile scallops up above the seafloor where crabs forage more readily (Pohle et al. 1991). Thus, seagrass restoration would likely benefit bay scallops where recruitment is sufficient.

At all life stages bay scallops are sensitive to physiological stressors like low salinity, sedimentation, and temperature extremes (e.g. Tettelbach et al. 1985). Even as adults, bay scallop densities are reduced by predators such as gulls (Prescott 1990) and rays (Peterson et al. 2001). Fishing is prosecuted on bay scallops throughout their range of high abundance. Because the year class of bay scallops that is fished has already spawned in late summer and is fated to die from senescence before another late summer spawning, fishing pressure is allowed to be extremely high (Peterson 1990). Consequently, the bay scallop possesses not one

but several factors that act to limit its abundance and production, making it an appealing candidate for restoration. However, its vulnerability to predation and life history characteristics make it less reliable than other bivalve species for mitigating a loss of primarily more robust species.

### Effectiveness of bivalve restoration

Owing to their fishery value and successful use in aquaculture, technologies have been developed to allow artificial propagation of bivalves in hatcheries and subsequent growth in nurseries to a size appropriate for introduction into the field. Thus, stocking of bivalves is feasible, although most reliably and inexpensively for those species whose seed is commercially produced in existing hatcheries, e.g. hard clams, oysters, soft-shell clams, and bay scallops. Surf clams are not commercially raised for aquaculture, but they too should present few challenges given their close taxonomic and ecological similarities to hard clams. Stocking shellfish with seed holds the promise of enhancing abundance and production for species whose settlement is limited by spawning stock biomass or whose abundance is controlled by high mortality during the early post-settlement life stage. Bivalve seeding would not immediately restore the full size and age distribution of the bivalve losses from the oil spill. In addition, successive stocking over several years may be necessary to avoid or counteract any induced density-dependent mortality from predators targeting a rich new food resource. Despite this potential for compensatory mortality to reduce or eliminate the stocking effort, there are good examples of the success of such bivalve seeding (e.g. Beal 1993, Peterson et al. 1995). For shellfish species that have been depleted by overharvest, the benefits of stock enhancement by seeding would be expected to continue for successive generations, especially if the seed areas were protected as spawner sanctuaries. Consequently, this option of seed stocking from hatcheries has many advantages and was included in the 'North Cape' oil spill restoration plan (NOAA et al. 1999, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm)).

Transplantation of larger bivalves into an impacted area could enhance abundance at the impact site, but potentially induces an equivalent loss at the donor area. Nevertheless, there are multiple scenarios by which transplantation, which is readily tolerated by soft-sediment bivalves (e.g. Peterson et al. 1996), could enhance net production. For those species whose spawning stock biomass limits recruitment and ultimate population size, transplantation into a spawner sanctuary could serve to increase population abun-

dance and production (e.g. Peterson & Summerson 1992). To avoid a loss at a donor area, the adults chosen for transplantation could be purchased from the fishery markets. Nevertheless, to enhance net production, the spawner sanctuary would need to be protected from human exploitation and located in an area that is a viable source site (Crowder et al. 2000) from which larvae would be effectively transported to habitat now depleted by exploitation.

If relief from recruitment limitation is not the objective, there are alternative scenarios whereby bivalve transplantation may enhance production. For example, if the species suffers depressed individual growth rates at the donor site because of density-dependent competition or otherwise suboptimal growth conditions, then transplantation to the impact area could enhance production by increasing individual growth rates. For the suspension-feeding bivalve molluscs of estuarine and coastal marine soft sediments, however, competition for resources is only rarely an important determinant of individual growth, especially in today's conditions of enhanced eutrophication (Peterson & Beal 1989).

In considering bivalve restoration options for the 'North Cape' case, plans for dredging in the nearby Providence River involved an unmitigated loss of many hard clams, which could serve as donor individuals for transplantation into the oil-impacted area. However, mitigation for this dredging activity itself is indicated, as the clams in the dredged area are public trust resources. Such a mitigation for dredging impacts on Dungeness crab was pursued in Grays Harbor, Washington, using similar restoration scaling methods involving demographic modeling (Wainwright et al. 1992, Dumbauld et al. 1993). The restoration was to provide structural habitat (shell reef) as juvenile nursery area, resulting in a net gain in crab numbers equivalent to those lost via the dredging.

For several benthic bivalves, evidence is compelling that habitat destruction and modification has reduced their productivity. Shell reef (Luckenbach et al. 1999, Breitburg et al. 2000, O'Beirn et al. 2000) and seagrass (Fonseca et al. 1998) have been restored in many areas to enhance productivity. However, there is no evidence or even indication that surf clams, the species that suffered the vast majority of the injury from the oil spill, are limited by habitat quantity or quality.

For the large majority of species that are targets of commercial fisheries, fishing exploitation occurs at such high levels that their productivity is depressed (Botsford et al. 1997, Pauly et al. 1998). Thus, one very effective restoration action for such species would be to reduce fishing pressure. The detailed models already produced to guide fisheries management provide methods for scaling the reduction in fishing to match the quantitative injury estimate. Furthermore,



data already maintained on fisheries landings could be used to monitor the effectiveness of the actions taken to reduce fishing pressure such that adaptive corrections could be employed to insure full compensation. However, limitation of bivalve catches as a restoration action would entail a loss of human use and economic losses to the industry. The restoration chosen should not in principle pass on new injuries and costs without applying restoration funds to compensate for these new injuries. The public's use of the resource is compensated by the restoration itself, and the discounting effectively includes the paying of interest for the delay in repayment of services. However, lost profits by private parties are not necessarily compensated. Such compensation of private parties may pose legal barriers, depending on legislation constraining restoration, and would incorporate the need to determine how the injury is distributed across each fishing entity. Documentation of who truly suffered this injury and to what degree would represent a challenging task.

### CONCLUSIONS

Our quantitative calculations of production gains achievable through bivalve restoration are best viewed as hypotheses to be tested. There is substantial uncertainty associated with such projections. In mitigating for environmental injuries, uncertainty is often handled by requiring the scale of mitigation to exceed what is necessary to replace the loss by some mitigation ratio that increases with uncertainty. For example, ratios of 2 to 3 acres of restoration for each acre of salt marsh lost are common (Thayer 1992). Alternatively, monitoring can be done to confirm the effectiveness of any restoration action when combined with any subsequent intervention if necessary to replace lost public trust resources. Choosing this alternative would provide for empirical tests of the accuracy of the modeling done to scale the restoration projects and thus lead to improved understanding of the basic demographic processes and reducing uncertainty in future applications.

We developed our quantitative scaling of bivalve restoration purely on the basis of production. We justify that choice on grounds that it represents one important ecosystem process that correlates well with the ecosystem services of water filtration and biogeochemical processing of materials (Kremer & Nixon 1978, Newell 1988). Nevertheless, compensatory restoration might benefit from more extensive identification and quantification of the full range of ecosystem services provided by bivalves (and other groups) so that restoration projects could be designed to replace the actual ecosystem functions that were damaged or lost. Perhaps the greatest failure of an approach based

on production alone is the absence of a constraint on the size class(es) in which the replacement production is to occur. Small bivalves have great value as prey for higher trophic levels, so if restoration were to involve only larger individuals, then the function of transfer of energy up the food chain may not be adequately restored. In addition, the implicit treatment of all suspension-feeding bivalves as functionally equivalent can be challenged. Here, surf clams occupy an entirely different habitat, the coastal ocean, than oysters, soft-shell clams, and bay scallops, which live in the protected estuarine waters. Thus, their ecosystem contributions are made to different systems, where they may not be of equal value or importance. Furthermore, assumptions of equivalence in value of ecosystem services across species of bivalves can lead to decisions to use but one species to restore losses of many. In the 'North Cape' oil spill example used here, this is not an issue because the vast majority of the injury occurred to a single species. However, future application of this approach to situations where several species contributed heavily to the injury raises concern over maintaining biodiversity within the ecosystem. Sustaining biodiversity is an important goal of environmental conservation (Wilson & Peters 1988). Current theory and empirical data tend to support the view that redundancy of species within functional groups provides greater stability of functions like production under varying environmental conditions (Naeem et al. 1994). Embracing that principle in restoration of ecosystem services would imply more diverse efforts spread among several species rather than the choice of a single most cost-efficient, expedient, or reliable species.

*Acknowledgements.* Support for this work was provided by the National Oceanographic and Atmospheric Administration, Damage Assessment Center (NOAA DAC), Silver Spring, MD. We thank C. A. Manen for her guidance and all the 'North Cape' oil spill trustees for thoughtful contributions. M. Donlan provided administrative assistance. Comments from B. Beal, H. Bloom, H. Gempp, C. Judy, J. Kraeuter, R. Krauss, S. Malinowski, R. Mann, C. McKenzie, R. Rheault, J. Weinberg, and J. Wesson are gratefully acknowledged.

### LITERATURE CITED

- 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
- Beal BP (1983) Predation of juveniles of the hard clam *Mercenaria mercenaria* (Linne) by the snapping shrimp *Alpheus heterochaelis* Say and *Alpheus normanni* Kingsley. *J Shellfish Res* 3:1–9
- Beal BP (1993) Effects of initial clam size and type of protective mesh netting on survival and growth of hatchery-raised individuals of *Mya arenaria* in eastern Maine. *J Shellfish Res* 12:138–139

- Belding DL (1910) A report upon the scallop fishery of Massachusetts. Commonwealth of Massachusetts, Boston
- Botsford LW, JC Castilla, CH Peterson (1997) The management of fisheries and marine ecosystems. *Science* 277:509–515
- Breitburg, D, Coen LD, Luckenbach MW, Mann R, Posey M, Wesson JA (2000) Oyster reef restoration: convergence of harvest and conservation strategies. *J Shellfish Res* 19: 371–377
- Castagna M, Kraeuter JN (1985) *Mercenaria* culture using stone aggregate for predator protection. *Proc Natl Shellfish Assoc* 67:1–6
- Cloern JE (1982) Does the benthos control phytoplankton biomass in south San Francisco Bay? *Mar Ecol Prog Ser* 9: 191–202
- Crowder LC, Lyman SJ, Figuiera WF, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. *Bull Mar Sci* 66:799–820.
- Dumbauld BR, Armstrong DA, McDonald TL (1993) Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. *Can J Fish Aquat Sci* 50:381–390
- Fay CW, Neves RJ, Pardue GB (1983) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic). Surf clam, Report FWS/OBS-82/11.13, US Fish Wildl Serv, Washington, DC
- 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. NOAA Coastal Ocean Program Decision Analysis Series No 12. NOAA Coastal Ocean Office, Silver Spring, MD
- Franz DR (1976) Distribution and abundance of inshore populations of the surf clam *Spisula solidissima*. *Am Soc Limnol Oceanogr Spec Symp* 2:404–413
- French DP, Rines H (1998) Estimation of losses in the salt ponds resulting from water column and sediment acute toxicity from the North Cape oil spill. NOAA Damage Assessment Center, Silver Spring, MD (part of case administrative record, available at <http://www.darp.noaa.gov/neregion/ncape.htm>)
- French DP, Rines H, Boothroyd J, Galagan C and 9 others (1991) Habitat inventory/resource mapping for Narragansett Bay and associated coastline. Final Report, Narragansett Bay Project, New England Interstate Water Pollution Control Commission, US Environmental Protection Agency, Boston
- French DP, Reed M, Jayko K, Feng S and 16 others (1996) The CERCLA type A natural resource damage assessment model for coastal and marine environments (NRDAM/CME), technical documentation, Vol. I–V. Final Report, Contract No. 14-0001-91-C-11, Office of Environmental Policy and Compliance, US Department of the Interior, Washington, DC
- French McCay DP (2002) Development and application of an oil toxicity and exposure model, OilToxEx. *Environ Toxicol Chem* 21:2080–2094
- French McCay DP (2003) Development and application of damage assessment modeling: Example assessment for the North Cape oil spill. *Mar Pollut Bull* 47:341–359
- Gibson MR (1997) Estimated strandings of surf clams and other species following the North Cape oil spill in Block Island Sound. Division of Fish and Wildlife, Rhode Island Dept of Environmental Management, Wickford (part of case administrative record, available at <http://www.darp.noaa.gov/neregion/ncape.htm>)
- Grosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. *Mar Ecol Prog Ser* 146:265–282
- Gutsell JS (1930) Natural history of the bay scallop. *Bull US Bur Fish* 46:569–632
- Hancock DA (1973) The relationship between stock and recruitment in exploited invertebrates. *Rapp p-v Reun Cons Int Explor Mer* 164:113–131
- Hinga KR (1997) Concentrations over time of North Cape oil in water and sediments in Rhode Island's south shore ponds. Report by University of Rhode Island, Narragansett, to NOAA Damage Assessment Center, Silver Spring, (part of case administrative record, available at <http://www.darp.noaa.gov/neregion/ncape.htm>)
- Hunt JH, Ambrose WG Jr, Peterson CH (1987) Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve, *Mercenaria mercenaria* (L.), on larval settlement and juvenile recruitment of infauna. *J Exp Mar Biol Ecol* 108:229–240
- 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
- Kennedy VS, Newell RIE, Eble AF (1996) The eastern oyster. *Crassostrea virginica*. Maryland Sea Grant, College Park
- Kraeuter JN (2001) Predation on hard clams. In: Kraeuter JN, Castagna M (eds) *Biology of the hard clam*. Pergamon Press, Oxford
- Kraeuter JN, Castagna M (eds) (2001) *Biology of the hard clam*. Pergamon Press, Oxford
- Kremer JN, Nixon SW (1978) A coastal marine ecosystem: simulation and analysis. Springer-Verlag, Berlin
- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Luckenbach MW, Mann R, Wesson JA (eds) (1999) Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point
- MacIsaac HJ, Johannsson OE, Ye J, Sprules WG, Leach JH, McCorquodale JA, Gingorovich IA (1999) Filtering impacts of an introduced bivalve (*Dreissena polymorpha*) in a shallow lake: application of a hydrodynamic model. *Ecosystems* 2:338–350
- MacKenzie CL Jr, Radosh DJ, Reid R (1985) Densities, growth, and mortalities of juveniles of the surf clam (*Spisula solidissima*) (Dillwyn) in the New York Bight. *J Shellfish Res* 5:81–84
- Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737
- Newell RIE (1988) Ecological changes in the Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: Lynch MP, Krome EC (eds) *Understanding the estuary: advances in Chesapeake Bay research*. Publication No. 129 CBP/TRS 24/88, Chesapeake Bay Research Consortium, Gloucester Point, VA, p 536–546
- Newell RIE, Cornwell JC, Owens MS (2002) Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. *Limnol Oceanogr* 47:1367–1379
- NMFS (National Marine Fisheries Service) (1995) Status of fishery resources off the northeastern United States for 1994. NOAA Tech Mem NMFS-NE-108
- Nichols FH, Thompson JK, Schemel LE (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. *Mar Ecol Prog Ser* 66:95–101

- NOAA (National Oceanic and Atmospheric Administration) (1997) Natural resource damage assessment guidance document: scaling compensatory restoration actions (Oil Pollution Act of 1990). NOAA Damage Assessment Center, Silver Spring, MD
- O'Beirn FX, Luckenbach MW, Nestlerode JA, Coates GM (2000) Toward design criteria in constructed oyster reefs: oyster recruitment as a function of substrate type and tidal height. *J Shellfish Res* 19:387–395
- Olsen SB (1970) Some aspects of the ecology of *Spisula solidissima solidissima* (Dillwyn). MSc thesis, University of Rhode Island, Kingston
- Orth RJ, Moore KA (1983) Chesapeake Bay — an unprecedented decline in submerged aquatic vegetation. *Science* 222:51–53
- Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. *J Anim Ecol* 49:667–685
- Pauly D, Cristensen V, Dalsgaard J, Froee R, Torres F Jr (1998) Fishing down marine food webs. *Science* 279:860–863
- 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 (1986a) Quantitative allometry of gamete production by *Mercenaria mercenaria* into old age. *Mar Ecol Prog Ser* 29:93–97
- Peterson CH (1986b) Enhancement of *Mercenaria mercenaria* densities in seagrass beds: Is pattern fixed during settlement season or altered by subsequent differential survival? *Limnol Oceanogr* 31:200–205
- Peterson CH (1990) On the role of ecological experimentation in resource management: managing fisheries through mechanistic understanding of predator feeding behavior. In: Hughes RH (ed) Behavioural mechanisms of food selection. Springer-Verlag, Berlin, p 821–846
- 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, Beal BP (1989) Bivalve growth and higher order interactions: importance of density, site, and time. *Ecology* 70:1390–1404
- Peterson CH, Summerson HC (1992) Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Mar Ecol Prog Ser* 90:257–272
- 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, Summerson HC, Huber J (1995) Replenishment of hard clam stocks using hatchery seed: combined importance of bottom type, seed size, planting season, and density. *J Shellfish Res* 14:293–300
- Peterson CH, Summerson HC, Luettich RA Jr (1996) Response of bay scallops to spawner transplants: a test of recruitment limitation. *Mar Ecol Prog Ser* 132:93–107
- Peterson CH, Fodrie FJ, Summerson HC, Powers SP (2001) Site-specific and density-dependent extinction of prey by schooling rays: generation of a population sink in top-quality habitat for bay scallops. *Oecologia* 129:349–356
- Pohle DG, Bricelj VM, Garcia-Esquivel Z (1991) The eelgrass canopy: an above-ground refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. *Mar Ecol Prog Ser* 74:47–59
- Prescott RC (1990) Sources of predatory mortality in the bay scallop *Argopecten irradians* (Lamarck): interactions with seagrass and epibiotic coverage. *J Exp Mar Biol Ecol* 144:63–83
- Rice MA, Hickox C, Zehra I (1989) Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (Linnaeus 1758), in Narragansett Bay. *J Shellfish Res* 8:345–354
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can* 191:1–382
- Rothschild BJ, Ault JS, Gouletquer P, Heral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39
- Tettelbach ST, Auster PJ, Rhodes EW, Widman JC (1985) A mass mortality of the northern bay scallop, *Argopecten irradians irradians*, following a severe spring rainstorm. *Veliger* 27:381–385
- Thayer GW (ed) (1992) Restoring the Nation's marine environment. Maryland Sea Grant College Program, College Park
- Thayer GW, Stuart HH (1974) The scallop makes its bed of eelgrass. *US Natl Mar Fish Serv Mar Fish Rev* 36:27–39
- Wainwright TC, Armstrong DA, Dinnel PA, Orensanz JM, McGraw KA (1992) Predicting effects of dredging on a crab population: an equivalent adult approach. *Fish Bull* 90:171–182
- Watzin MC (1983) The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. *Oecologia* 59:163–166
- Weinberg JR, Hesler TE (1996) Growth of the Atlantic surf clam, *Spisula solidissima*, from Georges Banks to the Delmarva Peninsula, USA. *Mar Biol* 126:663–674
- Weissberger EJ (1998) The effects of predation on the recruitment of the surf clam *Spisula solidissima*. PhD thesis, Rutgers University, New Brunswick, NJ
- Wilson EO, Peters FM (eds) (1988) Biodiversity. National Academy Press, Washington, DC
- Wilson FS (1990) Temporal and spatial patterns of settlement: a field study of molluscs in Bogue Sound, North Carolina. *J Exp Mar Biol Ecol* 139:201–220
- Zedler JB (1995) Salt marsh restoration: lessons from California. In: Cairns J (ed) Rehabilitating damaged ecosystems. Lewis Publishers, Boca Raton, FL, p 75–95

Editorial responsibility: Ronald Kneib,  
Sapelo Island, Georgia, USA

Submitted: June 13, 2003; Accepted: November 24, 2003  
Proofs received from author(s): December 9, 2003

# Compensatory mitigation for injury to a threatened or endangered species: scaling piping plover restoration

Michael Donlan<sup>1,\*</sup>, Molly Sperduto<sup>2</sup>, Charlie Hebert<sup>3</sup>

<sup>1</sup>Industrial Economics, 2067 Massachusetts Avenue, Cambridge, Massachusetts 02140, USA

<sup>2</sup>United States Fish and Wildlife Service, 70 Commercial St, Suite 300, Concord, New Hampshire 03301, USA

<sup>3</sup>United States Fish and Wildlife Service, 911 NE 11th Ave, Portland, Oregon 97232, USA

**ABSTRACT:** Conducting natural resource damage assessments and adopting compensatory restoration plans for endangered and threatened species have special constraints. These constraints are illustrated by the agency responses to evaluate impacts of the North Cape oil spill on piping plovers *Charadrius melodus* in Rhode Island, and to establish appropriate compensatory restoration. Adopting a precautionary principle implies that strict adherence to an  $\alpha$ -value of 0.05 in formal tests for injury on endangered species, where rarity implies low statistical power, would result in overlooking many true impacts. Criteria for concluding that injury took place must nonetheless exist, including (1) existence of a conceptually valid mechanism to link exposure to the stressor and the documented negative responses; (2) field data supporting the existence of the stressor-response link; and (3) sampling designs that consider impacts of potentially confounding factors such as natural temporal change. Choosing restoration options is also challenging for endangered species because ethical considerations and risks associated with some interventions preclude otherwise acceptable actions for common species. For the piping plover, a synthesis of population limitations done for the species recovery plan was used to design compensatory restoration of protection of nesting on newly colonized beaches, an action difficult to scale in advance to match the estimated injury from oil, but adaptively adjustable if monitoring shows a need.

**KEY WORDS:** Restoration · Compensatory mitigation · Habitat protection · Piping plover · Oil spill · Endangered species · Threatened species

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Conservation biologists tend to express a strong preference for preserving or restoring habitat, instead of taking actions designed to benefit particular target species. This attitude is based upon recognition that habitat destruction and degradation are responsible for the majority of losses to the natural biota (Soule 1986). In addition, oil spills and other pollution events frequently affect a broad range of biota present in the area of impact. Actions taken to benefit habitat will contribute to the welfare of several species simultaneously, and not just one. Furthermore, simply enhancing numbers of

new recruits of a target species will fail to achieve a sustainable increase in the population if the carrying capacity of the environment required to support them is inadequate (Meffe et al. 1997). Nevertheless, endangered and threatened species represent a special group for which explicit legislation or ethical concerns may often dictate that protection, restoration, and enhancement efforts be focused at the level of the individual species (Peterson et al. 2003, in this Theme Section).

Establishing the scientific basis for supporting restoration of rare and declining species is a challenge for ecologists and conservation biologists because of several constraints. Rarity itself implies low sample



sizes for most ecological studies, and therefore high uncertainty in estimating abundance or in evaluating the success of alternative intervention options designed to benefit the population. This concern has generated the development of statistical methods explicitly designed to deal with rare species (e.g. Green & Young 1993, Strayer 1999). Occasionally, research will be done on a more abundant surrogate species (Caro & O'Doherty 1999), but this approach requires establishing, with confidence, that the factors responsible for the large demographic differences between the conservation target and the surrogate species do not prevent rigorous transfer of results from one to the other (Bevill & Louda 1999). Of the many causes for rarity, some imply intrinsic incompatibilities between even closely related species (Kunin & Gaston 1993). Ethically, restoration options that entail risk to the threatened population cannot be justified, thereby closing the door to some actions that may indeed have been beneficial. Ethics further dictate that where data are sparse and uncertainty high, a precautionary approach be taken in evaluating evidence of injury to a threatened or endangered species and in adopting restoration plans to compensate for that injury (Gerber et al. 1999).

In the US, recovery plans for many listed species have been developed and implemented by federal agencies charged with administration of the Endangered Species Act. Such plans are helpful in developing compensatory restoration because they review the causes of population limitation for the target species and identify potential restoration actions.

Here we illustrate how the constraints of rarity and the existence of an established recovery plan affect the process of choosing, scaling, and implementing compensatory restoration through the example of a federally threatened shorebird, the piping plover *Charadrius melodus*. Known nesting grounds for piping plovers were extensively polluted by the 1996 North Cape oil spill in Rhode Island. This oil spill precipitated studies of the impacts on the Moonstone Beach breeding population of piping plovers, and led to the development of compensatory restoration actions. By describing the process of injury assessment and restoration development, we communicate insights of value to restoration of other threatened or endangered species.

#### **THE BIOLOGY OF PIPING PLOVERS AND RISKS FROM THE OIL SPILL**

The piping plover is a shorebird, once described as common along Atlantic beaches, that became greatly diminished in abundance by 1900 through hunting and egg gathering (Haig & Oring 1987). Numbers partially

rebounded after passage of the Migratory Bird Treaty Act in 1918, but declined again after World War II with the increase in coastal development and recreation (Raithe 1984). Rhode Island and other New England states provide summer nesting habitat on coastal beaches. Birds arrive in Rhode Island in late March or early April. By late April, pairs are established and nest construction has begun (MacIvor 1990, Keane 2002). Nests are constructed above the high-tide line on coastal beaches, with preferences exhibited for wide beach, sand spits, overwash areas, and other disturbed habitat with sparse vegetation and proximity to protected, moist foraging habitats (Burger 1987, Elias et al. 2000, Keane 2002). Egg laying and chick rearing typically take place from May through June, with most chicks fledging in late June and July. Chicks are precocial but cannot fly for their first month after hatching. Chicks spend a high proportion of their time feeding, leading to a tripling of weight in their first 2 wk. Any that fail to achieve at least 60% of adult weight by Day 12 are unlikely to survive (Cairns 1977). Piping plovers feed on invertebrates from intertidal pools, wrack lines on beaches, sand and mud flats, overwash areas, and shorelines of coastal ponds, lagoons, and salt marshes (Goldin 1993, US Fish and Wildlife Service 1996).

On 19 January 1996, the barge North Cape grounded on the Rhode Island shoreline, causing a subsequent oil spill. A nearby beach, Moonstone Beach, known to provide consistently used nesting and brood habitat for the piping plover, was oiled. Because this oiling occurred well before the seasonal return of breeding plovers, acute mortality from oiling was not an issue. However, the loss of invertebrate prey, with subsequent increased foraging costs and risks, and consequent reductions in energy intake, growth, and survival of chicks, represented a potential injury to the local population. To evaluate this hypothesis, studies were undertaken to (1) identify any spill-related impacts on plover prey abundance at impact and reference beaches, and (2) document piping plover behavior and productivity at impact and reference beaches during the breeding season following the spill, and compare this information to historical data.

#### **IMPACT OF THE OIL SPILL ON PIPING PLOVERS**

##### **Prey abundance at oiled and reference beaches.**

Piping plovers consume infaunal, epifaunal and flying prey. To measure prey abundance in the wrack and dune foraging habitats, standard pitfall traps were utilized at the oiled (Moonstone Beach), and a nearby unoiled (East Beach), plover nesting areas (Gould 1996). This methodology targeted surface crawling invertebrates, including amphipods, because they are



an important component of piping plover diets (Shaffer & Laporte 1994, Staine & Burger 1994). While the wrack line generally comprises a small amount of barrier beach habitat, studies have shown it to be a very important and preferred foraging habitat, where bay-side intertidal or ephemeral pool habitats are not available (Hoopes et al. 1989, Goldin 1993, Elias et al. 2000). Ten 1 gallon (3.8 l) pitfall traps were established at each beach, 5 along the wrack and 5 along the dune. Wrack samples were collected seaward of plover nests, 100 ft (30 m) away (along the water line) to minimize disturbance to nest sites. Traps were set on 29 May 1996 and collected approximately 24 h later. Trap contents were preserved and tabulated using standard laboratory procedures. The dominant macroscopic organism by weight and volume in the wrack areas of both beaches was the amphipod *Talorchestia longicornis*. Mean volume and wet weight of the amphipods at the oiled and unoled beach wrack were significantly different based on *t*-test results (volume:  $3.58 \pm 1.95$  ml [mean  $\pm$  SD] vs  $20.28 \pm 9.94$  ml [mean  $\pm$  SD],  $\alpha = 0.01$ , respectively; weight  $1.70 \pm 1.06$  mg [mean  $\pm$  SD] vs  $13.24 \pm 7.23$  mg [mean  $\pm$  SD],  $\alpha = 0.01$ , respectively).

To measure prey abundance in the intertidal zone, invertebrates were sampled on 27 and 28 June 1996 at Moonstone Beach and at a different reference beach (Goosewing Beach) using cores (10 cm in diameter and 10 cm deep) (SAIC 1996). Samples were collected from 10 stations systematically placed across the face of each beach. Samples were sieved with 2.0 and 1.0 mm mesh screens. Sample material was preserved with a solution of buffered formalin and rose Bengal and then identified and enumerated. While average invertebrate abundances (based on number of organisms) at Moonstone and Goosewing Beaches were not significantly different ( $\alpha = 0.05$ ), species composition varied between the beach intertidal zones (SAIC 1996). Only 2 *Amphiporeia virginiana* were found at Moonstone Beach sample sites, compared to 456 at Goosewing Beach sites (the most common invertebrate, by more than 1 order of magnitude). The predominant organism (in terms of numeric abundance) at Moonstone Beach was *Marionina subtarranea*. According to the SAIC authors, 'the virtual absence of *A. virginiana* from Moonstone Beach is consistent with the hypothesis that this habitat was exposed to oil. It is well known that amphipods are the first group of organisms to disappear and one of the last to recolonize habitats exposed to oil spills (e.g. Dauvin 1979, Sanders et al. 1980)' (SAIC 1996, p. 3). These data suggest that the piping plovers' food supply may have been reduced due to the spill.

**Reproductive success at the oiled beach.** As a means of testing the impacts of oiling Moonstone Beach, piping plover nesting, chick rearing, and chick foraging

activities were monitored during 1996 at the oiled beach and compared to similar data from previous years. Management activities undertaken in 1996 for plover protection included all those conducted annually since 1992: erection of symbolic fencing (a cord of yellow rope attached to posts anchored in the beach) to warn intruders, predator controls, nest enclosures, and beach-user educational efforts. One additional management activity (trapping of predators) was added in 1995 and repeated in 1996. A local trapper was contracted to trap along the barrier beach, and removed 1 coyote and 2 mink from the area in 1996. Predator removal data from 1995 are unavailable, although the level of trapping effort was believed to be similar in both years.

Piping plover productivity proved lower in 1996 than in the previous year, and differences in chick foraging behavior may explain the lower productivity. As shown in Table 1, in 1996 an average of 1.0 fledgling was produced per nesting pair, as compared to 1.6 in the previous year, a reduction of 37% (Casey 1996). Plovers reuse nesting sites with a high degree of faithfulness over years (MacIvor et al. 1987, Strauss 1990), and the nesting in 1996 was indeed within the same general area as in 1994 and 1995. Nevertheless, the average daily distance traveled for foraging by chicks in 1996 was substantially greater than in 1994 and 1995 (Casey 1996). Quantitative daily distance data are available for multiple years at nests in 4 locations. Average daily distances traveled by chicks nesting in the 1st location were 290.5 (1996) vs 128.9 m (1994); 124.1 (1996) vs 44.5 m (1994) in the 2nd location; 87.2 (1996) vs 14.0 m (1995) in the 3rd location; and 39.6 (1996), 21.0 (1995) vs 23.4 m (1994) in the 4th location.

Thus, the productivity decline from 1995 to 1996 could be attributed to the oiling of the beach reducing invertebrate prey in the wrack (preferred foraging habitat) and intertidal habitat, causing plovers to travel longer distances and expend more energy during foraging, with likely costs of slower growth and perhaps higher mortality. Although combining the information on oiling intensity, prey abundances in the wrack, foraging behavior, and productivity provides a consistent mechanistic indication of injury to plover populations from the oil spill, one additional anomaly in the productivity patterns over the years needs mention. The 1.0 fledgling per nesting pair in 1996 exceeded or equaled the documented productivity on this beach from 1991 through 1994 (Casey 1996). To conclude that the drop from 1995 to 1996 represents an indication of a spill impact requires the additional assumption that the predator trapping initiated in 1995 and continued in 1996 was indeed successful in setting a new baseline productivity of 1.6 fledgling per nesting pair in 1995. This is a reasonable, but untested, assumption.

Table 1. *Charadrius melodus*. Results of piping plover reproductive success at reference and impact area beaches. Source of data: McGourty (1996), Table 2 and Casey (1996, Appendix E)

Year	Sites	Pairs	Nests	Eggs	Hatched	Hatched (%)	Fledged (%)	Fledged per pair	Fledglings
<b>Reference area beaches</b>									
1996	6	20	22	87	75	86	42	56	2.1
1995	4	13	18	63	46	73	24	52	1.9
1994	4	9	10	39	31	80	22	71	2.4
1993	3	9	11	45	32	71	23	72	2.6
1992	2	5	6	23	15	65	12	80	2.4
<b>Impact area beach</b>									
1996	1	9	16	53	22	42	9	41	1.0
1995	1	9	9	35	31	89	14	45	1.6
1994	1	8	9	33	17	52	8	47	1.0
1993	1	8	10	38	33	87	7	21	0.9
1992	1	6	6	19	7	37	4	57	0.7

#### Reproductive success at nearby reference beaches.

To test whether the 1996 change in piping plover productivity on the oiled Moonstone Beach was simply a consequence of natural year-to-year dynamics in this general geographic area, piping plover nesting and foraging were also monitored in 1996 at 6 reference beaches in southern Rhode Island (McGourty 1996), and comparisons made to historical data available from 4 of those locations (Table 1). The reference beaches are similarly oriented (facing Block Island Sound in a generally SSE direction), within approximately 25 km of the oiled beach, and so likely comparably exposed to storms and broader-scale environmental conditions that could affect productivity. Sparsely vegetated beach face, sand spit and/or overwash areas preferred by the piping plover were available, and plovers successfully nested at oiled and reference beaches (Casey 1996, McGourty 1996). Predation and disturbance by humans and pets are important threats to plover populations (US Fish and Wildlife Service 1996). Reference and oiled beaches were subjected to similar management protections (generally including the use of symbolic fencing, predator exclosures and volunteers to help monitor nests, educate the public and discourage disturbance of plover nesting areas), and management actions taken at reference beaches in 1996 were similar to those applied in previous years.

Records were kept on numbers of nesting pairs, hatching success, chick mortality, productivity, nest failure/abandonment, territory size, and chick movement. The numbers of fledglings per plover pair increased on average at reference beaches from 1.9 in 1995 to 2.1 in 1996 (an increase of approximately 10%) (Table 1). Compared with the 37% decrease observed at the oiled beach in that same year, plover reproductive success on reference beaches did not show a decline from 1995 to 1996. This further supports the

inference of spill-induced impacts on Moonstone Beach. However, average productivity per nesting pair at the reference beaches in 1995 (1.9) and 1996 (2.1) was less than the range of 2.4 to 2.6 fledglings produced on average in the 1992 to 1994 period. Thus, the 1996 productivity at these beaches was compared to a 'base' year (1995) with relatively low productivity levels.

**Injury quantification.** With only 9 nesting pairs at the impact beach, factors unrelated to the spill cannot be ruled out as a cause of the observed productivity decline using traditional standards of statistical significance. For example, variation in physical environmental factors could produce a change in productivity of 37% without any impact from oil. Piping plovers suffer losses of fledglings and reductions in productivity from several factors that were not, and cannot, all be monitored, such as pedestrian disruptions (Burger 1991), loose dogs (Cairns & McLaren 1980), predation (Burger 1987, MacIvor 1990, Elias-Gerken & Fraser 1994), and storms. However, analysis of temporal trends in productivity at oiled and reference beaches and documented differences in plover prey and changes in foraging behavior, combined with a synthesis of the literature on processes that affect productivity of piping plovers, lend support to the case for spill-related injury to Moonstone Beach plovers. Adoption of a precautionary approach for threatened and endangered species (e.g. Gerber et al. 1999) dictates that compensatory restoration be done: conceptually valid mechanisms can explain impacts to the population; field data establish a credible link between the hypothesized source of harm and the impact; and empirical field observations comparing temporal trends at oiled and reference areas reduce (but do not eliminate) the likelihood that any observed changes were due to chance or larger-scale factors affecting multiple nesting beaches.

To estimate the approximate magnitude of injury to this plover population, we adopted a simplified approach. We assumed that in the absence of the spill, productivity in 1996 would have equaled productivity in 1995. Then, lost piping plover productivity in 1996 can be approximated by:

$$(1995 \text{ productivity} - 1996 \text{ productivity}) \times \text{number of plover pairs in 1996} = \text{lost chicks} (1.56 \text{ chicks per pair} - 1.00 \text{ chicks per pair}) \times 9 \text{ pairs} = 5.0 \text{ fledged chicks}$$

To this loss in 1996 chick production, we must add impacts to future productivity, assuming that plovers are not limited by available overwintering, foraging, or nesting habitat, but rather by numbers of recruits surviving to enter the breeding population. Using a chick over-winter survival rate of 48% (Melvin & Gibbs 1994), 2.4 of those 5 missing chicks would have been expected to survive the winter and return to breed the following year. Assuming a 1997 productivity equal to that of 1995 (1.56 chicks per pair), the chicks lost because of the spill would be expected to have produced 1 to 2 (1.87) fledglings of their own in 1997. This process could be extended to several generations. However, this more elaborate calculation seemed unjustified for 2 reasons. First, we do not know for certain that piping plovers are limited by recruitment to the breeding population instead of habitat (US Fish and Wildlife Service 1996). Second, if a restoration action could be designed to enhance the piping plover numbers by at least 5 chicks, then their subsequent contributions to the future generations will be expected to match what would have been provided by the lost chicks. This approach avoids the need to quantify demographic consequences of chick loss, although it does ignore the time lag between injury and restoration by failing to apply a discount factor. Such precision was judged unnecessary, given the uncertainty in quantifying the compensatory restoration action selected.

## RESTORATION OPTIONS AND SCALING

Identifying compensatory restoration options for a threatened or endangered species requires the same in-depth review of demographic limitations to population growth, as is required for developing restoration plans for any species. This task is made easier for those federally listed species in the US that have recovery plans. The piping plover recovery plan (US Fish and Wildlife Service 1996) served to guide compensatory restoration planning after the North Cape oil spill. A careful review of this piping plover recovery plan, and the management actions already in place in Rhode Island, led to the selection of an unimplemented restoration action to serve as compensation for the likely loss of 5 or more plovers from the oil spill. The trustees of public trust resources decided upon a compensatory restoration action that involved identifying potential breeding beaches in the vicinity of the spill area that were newly colonized by young adults, which exhibit much greater propensity than experienced breeders to colonize new breeding sites (Wilcox 1959). By immediately extending management protections to them, similar to the management already in place at historic breeding beaches, productivity could be enhanced. This option is not novel. It was used to compensate for plover losses after a previous oil spill in Rhode Island, the World Prodigy in 1989. Consequently, the documented success in fledging of additional chicks from that program could be used to scale the area of beach surveyed and the amount of protection required to compensate for the 5 or more chicks lost to this North Cape spill in 1996.

Table 2 provides productivity data at the 4 beaches affected by the World Prodigy piping plover restoration (Napatree Point, Ninigret east beach, Quononchontaug, and Watch Hill east beach). Monetary compensation received as a result of the World Prodigy spill funded management protection efforts at these beaches in 1992,

Table 2. *Charadrius melodus*. Comparison of piping plover reproductive success at beaches affected by the 1992 to 1994 World Prodigy restoration project before and during project implementation. na: not available. Source of data: Suzanne Paton, RI National Wildlife Refuge Complex, pers. comm.

Year	Napatree Point		Ninigret CA (east beach)		Quononchontaug		EB Watch Hill (east beach)	
	Pairs	Fledges	Pairs	Fledges	Pairs	Fledges	Pairs	Fledges
1994	2	0	2	6	1	3	4	13
1993	4	4	1	3	0	0	4	16
1992	1	0	0	0	1	1	4	11
Mean (1992–1994)	2.33	1.33	1.0	3.0	1	1.33	4	13.33
1991	3	0	1	0	1	0	4	2
1990	2	0	na	na	na	na	4	0
1989	1	0	na	na	na	na	4	2
Mean (1989–1991)	2.0	0	na	na	na	na	4	1.33

1993 and part of 1994. Productivity data were available for 3 yr prior to implementation of the World Prodigy restoration at Napatree Point and EB Watch Hill. As shown in Table 2, productivity increased substantially at EB Watch Hill during 1992 to 1994, despite no change in the number of nesting pairs (4). At least 11 chicks fledged during each year that protection was in place; in the 3 yr prior to protection, no more than 2 chicks fledged in any year. However, at Napatree Point, no fledglings were produced during 2 of the 3 yr that World Prodigy-funded protections were in place. Such comparisons at the other 2 beaches are difficult to make given the availability of only 1 yr of pre-restoration productivity data. Overall, precise quantification of restoration benefits attributable to the World Prodigy is not possible, due to the many factors that affect fledgling survival and the small number of plover pairs at these beaches. Nevertheless, available data suggest that a World Prodigy-scale restoration project is capable of producing several fledglings per year, although inter-beach and inter-year variability is likely to be high.

## DISCUSSION

The evaluation of impacts of the North Cape oil spill on the piping plover population of Rhode Island beaches, and the process of deciding upon a restoration option and scaling it to the injury, provide some generic guidance for endangered and threatened species. Here the concern for Type II error of not detecting a true impact of the spill (Fairweather 1991) was sufficient to lead to a conclusion of likely impact of the oil spill, despite the lack of evidence that would meet the standard test of statistical significance at an  $\alpha$ -value of 0.05. Specialized statistical methods (e.g. Green & Young 1993, Strayer 1999) and other approaches (e.g. Caro & O'Doherty 1999) have been developed to establish a scientific basis for restoration decision-making with rare species. The most rigorous analytic approach possible must be implemented; in circumstances where sufficient data simply cannot be obtained, cautious application of statistical hypothesis testing seems an appropriate response to the special importance that endangered and threatened species have, and an appropriate application of the precautionary principle (Peterman & M'Gonigle 1992, Gerber et al. 1999). With both intrinsic difficulties in detecting effects on small and rare populations (Green & Young 1993) and also high societal importance of any negative impacts that do exist, managerial inaction based on absence of statistical significance may not be appropriate. The piping plover example described here provides a reasonable set of minimum criteria for deciding that evidence is sufficient to trigger compensatory res-

toration actions for threatened and endangered species in the absence of sufficient data for statistical evaluation: a conceptually valid mechanism of harm should exist, and field data should link the stressor to the response(s) and provide evidence of a negative impact based on a reasonable sampling design including, to the degree possible, temporal and reference-area comparisons.

Our description of the decision-making process of development of a compensatory restoration program also has broad generic application to endangered, threatened, or simply rare species of concern. The existence of carefully considered recovery plans for federally listed species in the US and species of concern in other countries gives a jump-start to planning for compensatory restoration after any environmental incident. However, development of a viable restoration option may be challenging in cases where significant actions have already been taken by managers of endangered species. Furthermore, the ethical and biological constraints in manipulation of endangered species preclude selection of some reasonable restoration actions that involve unacceptable risks. Application of the concept of compensatory restoration to endangered species will also commonly require relaxation of the quantification standards that are typically applied to scale restoration in order to provide a quantitative match to the injury. Instead, subsequent monitoring of the effectiveness of restoration and adaptive adjustment of the restoration program, if necessary, can serve to insure the conservation mandate of the trustees of natural resources.

*Acknowledgements.* Support for this work was provided by the NOAA (National Atmospheric and Oceanographic Administration) Damage Assessment Center and the US Fish and Wildlife Service. C. H. Peterson provided editorial guidance. Input from L. D'Anna, L. von Oettingen and A. Hecht was helpful.

## LITERATURE CITED

- Bevill RL, Louda SM (1999) Comparisons of related rare and common species in the study of plant rarity. *Conserv Biol* 13:493–498
- Burger J (1987) Physical and social determinants of nest selection in piping plover in New Jersey. *Condor* 98: 811–818
- Burger J (1991) Foraging behavior and the effect of human disturbance on the piping plover (*Charadrius melodus*). *J Coast Res* 7:39–52
- Cairns WE (1977) Breeding biology and behaviour of the piping plover *Charadrius melodus* in southern Nova Scotia. MSc thesis, Dalhousie University, Halifax
- Cairns WE, McLaren IA (1980) Status of the piping plover on the east coast of North America. *Am Birds* 34:206–208
- Caro TM, O'Doherty G (1999) On the use of surrogate species in conservation biology. *Conserv Biol* 13:805–814

- Casey JK (1996) Assessment of the North Cape oil spill impacts to the 1996 piping plover breeding season at Trustom Pond NWR. US Fish and Wildlife Service Report, Ninigret National Wildlife Refuge, Charlestown, RI
- Dauvin JC (1979) Impact des hydrocarbures de l'Amoco Cadiz sur le peuplement infralittoral des sables fins de la Pierre Noire (Baie de Morlaix). *J Rech Oceanogr* 4:28–29
- Elias SP, Fraser JD, Buckley PA (2000) Piping plover brood foraging ecology on New York barrier islands. *Wildl Manag* 64:346–354
- Elias-Gerken SP, Fraser JD (1994) Piping plover foraging ecology on Pike's Beach, Southampton, New York. Report to US Fish and Wildlife Service. USFWS, Sudbury, MA
- Fairweather PG (1991) Statistical power and design requirements for environmental monitoring. *Aust J Mar Freshw Res* 42:555–567
- Gerber LR, DeMaster DP, Karieva PM (1999) Gray whales and the value of monitoring data in implementing the US Endangered Species Act. *Conserv Biol* 13:1215–1219
- Goldin MR (1993) Piping plover (*Charadrius melodus*) management, reproductive ecology, and chick behavior at Goosewing and Briggs Beaches, Little Compton, Rhode Island, 1993. The Nature Conservancy, Providence, RI
- Gould R (1996) A comparison of invertebrate pit-trap samples from Trustom Pond and East Beaches, Rhode Island, USA following an oil spill. Report to US Fish and Wildlife Service, Concord, NH
- Green RH, Young RC (1993) Sampling to detect rare species. *Ecol Appl* 3:351–356
- Haig SM, Oring LW (1987) The piping plover. In: DiSilvestro R (ed) Audubon Wildlife Report. National Audubon Society Academic Press, New York, p 503–519
- Hoopes EM, Griffin CR, Melvin SM (1989) Effects of human recreation on piping plover foraging ecology and chick survival at Ninigret National Wildlife Refuge. Report to US Fish and Wildlife Service, Newton Corner, MA
- Keane SE (2002) Effects of herring gulls and great black-backed gulls on breeding piping plovers, South Monomoy Island, Massachusetts. MSc thesis, Virginia Tech, Blacksburg, VA
- Kunin WE, Gaston KJ (1993) The biology of rarity: pattern causes, and consequences. *Trends Ecol Evol* 8:298–301
- MacIvor LH (1990) Population dynamics, breeding ecology, and management of piping plovers on outer Cape Cod, Massachusetts. MSc thesis, University of Massachusetts, Amherst, VA
- MacIvor LH, Griffin CR, Melvin SM (1987) Management, habitat selection, and population dynamics of piping plovers on outer Cape Cod, Massachusetts: 1985–1987. Report to the National Park Service, Cape Cod National Seashore, South Wellfleet, MA
- McGourty E (1996) Rhode Island piping plover restoration project 1996. Ninigret National Wildlife Refuge, Charlestown, RI
- Meffe GK, Carroll GR (1997) Principles of conservation biology, 2nd edn. Sinauer, Sunderland, MA
- Melvin SM, Gibbs JP (1994) Viability analysis for the Atlantic coast population of piping plovers. Report to US Fish and Wildlife Service, Sudbury, MA
- Peterman RM, M'Gonigle M (1992) Statistical power analysis and the precautionary principle. *Mar Pollut Bull* 24: 231–234
- Peterson CH, Kneib RT, Manen C-A (2003) 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)
- Raithel C (1984) The piping plover in Rhode Island. Rhode Island Natural Heritage Program, Providence, RI
- SAIC (Science Applications International Corp) (1996) Potential impact of the North Cape Oil Spill on piping plover and shorebird prey species in intertidal and beach/pond shore habitats: interpretation of benthic data. Report to Beak Consultants, Kirkland, WA
- Sanders HL, Grassle JF, Hampson GR, Morse LS, Garner-Price S, Jones CC (1980) Anatomy of an oil spill: long-term effects from the grounding of the barge Florida off West Falmouth, Massachusetts. *J Mar Res* 38:265–380
- Shaffer F, LaPorte P (1994) Diet of piping plovers on the Magdalen Island, Quebec. *Wilson Bull* 106:531–536
- Soule M (1986) Conservation biology. Sinauer, Sunderland, MA
- Staine KJ, Burger J (1994) Nocturnal foraging behavior of breeding piping plovers (*Charadrius melodus*) in New Jersey. *Auk* 111:579–587
- Strauss E (1990) Reproductive success, life history patterns, and behavioral variation in a population of piping plovers subjected to human disturbance (1982–1989). PhD thesis, Tufts University, Medford, MA
- Strayer DL (1999) Statistical power of presence-absence data to detect population declines. *Conserv Biol* 13: 1034–1038
- US Fish and Wildlife Service (1996) Piping plover (*Charadrius melodus*) Atlantic coast population: revised recovery plan. US Fish and Wildlife Service, Hadley, MA
- Wilcox L (1959) A twenty year banding study of the piping plover. *Auk* 76:129–152

Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA

Submitted: July 25, 2003; Accepted: October 30, 2003  
Proofs received from author(s): November 27, 2003





# Scaling restoration to achieve quantitative enhancement of loon, seaduck, and other seabird populations

Molly B. Sperduto<sup>1,\*</sup>, Sean P. Powers<sup>2</sup>, Michael Donlan<sup>3</sup>

<sup>1</sup>United States Fish and Wildlife Service, 70 Commercial Street, Suite 300, Concord, New Hampshire 03301, USA

<sup>2</sup>Department of Marine Sciences, University of South Alabama and Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, Alabama 36528, USA

<sup>3</sup>Industrial Economics, 2067 Massachusetts Avenue, Cambridge, Massachusetts 02140, USA

**ABSTRACT:** The 1996 'North Cape' oil spill along the Rhode Island coast led to the deaths of at least 2292 birds, resulting in an estimated 6275 bird-years lost (adjusted by expected longevity and productivity). We synthesize information on bird population dynamics to develop an appropriate restoration strategy. Marine birds (seaducks, loons, grebes) with natural recovery periods estimated to exceed 1 yr accounted for 87% of the total bird-years lost. Marine birds (gulls, cormorants, alcids, gannets) with recovery estimated to be less than a year accounted for 10% of injuries. Common loons *Gavia immer* and common eiders *Somateria mollissima* were selected as targets for restoration because of regional concern over their population status and the magnitude of lost bird-years. Three restoration options were evaluated for loons: nest site protection; nest site enhancement; and public education/outreach. Nest site enhancement opportunities were limited and benefits from public education/outreach efforts were uncertain. Nest site protection was preferred for both loons and eiders because nest site availability and/or quality currently limit(s) productivity. This option assumes that preventing future productivity loss compensates for productivity loss that resulted from the 'North Cape' oil spill. This assumption is supported by regional productivity estimates for the 2 target species, is consistent with scientific literature, and represents the consensus of expert opinions. Based on a series of scaling calculations, protection of 25 nest sites for a 100 yr period is expected to balance the loss of 2920 loon-years. Protection of 315 eider nest sites over a 100 yr period would replace 2605 bird-years lost (remaining marine bird injury). Calculations adjust future production credit through economic discounting of 3% yr<sup>-1</sup>. Our analysis provides a means of quantifying the level of breeding habitat protection required to restore injured populations of marine birds.

**KEY WORDS:** Restoration · Habitat protection · Marine birds · Oil spill · Seabird · Habitat equivalency analysis

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Direct and indirect population losses resulting from pollution (Burger & Gochfeld 2001), habitat destruction or degradation (Boersma et al. 2001), and overexploitation of prey resources by humans (Montevecchi 2001) are common in many bird species that rely on coastal habitats. These and other threats result in a need for effective mechanisms to conserve and restore coastal

bird populations. Although a relatively wide range of potential restoration options exists for many injured and declining marine resources, practical constraints limit their suitability for marine birds. For example, unlike restoration opportunities for many species of marine fishes and invertebrates, it is not practical, nor in many cases possible, to replace dead, injured or missing birds directly through captive breeding programs. Although the creation of some types of new

\*Email: molly\_sperduto@fws.gov

habitat is possible and may be an effective mechanism for enhancing fish and invertebrate populations (Peterson et al. 2003a, in this Theme Section), creating shoreline for coastal bird species would typically be enormously expensive. In contrast to many marine fish and invertebrate species, however, considerable efforts to conserve bird populations have been conducted for decades by government and private entities. Such initiatives can provide 'blueprints' for practical, cost-effective restorations of injured bird populations.

Significant seabird mortalities are common after oil spills in coastal areas because marine birds frequently occur in large aggregations, rafting, floating, and feeding on the water surface (e.g. Piatt & Lensink 1989, Burger 1997, Irons et al. 2000, Peterson 2001). Oil-induced matting of feathers causes loss of insulation and water repellency functions, leading to hypothermia, starvation, or drowning (Burger & Gochfeld 2001). Ingestion of oil, primarily through preening, can result in further mortality of birds (Coon & Dieter 1981, Burger & Gochfeld 2001). Chronic effects from exposure to hydrocarbons remaining after the spill may be expressed as lowered breeding success (Grau et al. 1977, Fry et al. 1986, Hoffman 1990), reduced fledgling growth and survival (Trivelpiece et al. 1984, Hoffman 1990), developmental and behavioral abnormalities (Burger & Gochfeld 2001) and reduced adult survival for several years (Esler et al. 2000). Indirect negative effects of oil spills on marine birds may occur from habitat degradation or reduction in prey resources (Agler et al. 1999, Peterson 2001).

Here we use information about population-limiting factors in loons, seaducks and other marine birds to develop appropriate restoration methods for injured bird resources. First we review the methodology used to quantify injury to marine birds resulting from the 1996 'North Cape' oil spill. Of particular significance to marine birds was the timing of the 'North Cape' oil spill: the January release of a large quantity of home heating oil along the Rhode Island coastline coincided with the concentration of many wintering waterbird species in nearshore areas. We evaluate 3 restoration options intended to enhance populations of marine birds to offset losses: protection of habitat from future development, nest-site enhancement, and public outreach/education designed to decrease human-related mortality. In addition, we present the methodology used to quantitatively evaluate the favored restoration option.

## MATERIALS AND METHODS

**Injury quantification.** The basis for quantifying the total injury of seabirds, salt pond birds, and non-water birds is the recovery of dead or dying birds, application

of a multiplier to account for the proportion of dead birds not recovered, and calculation of production foregone by these dead birds and their progeny. The number of marine birds (salt pond birds and seabirds) found dead during and after a spill typically underestimates total mortality resulting from an oil spill (Hlady & Burger 1993). Therefore a multiplier is appropriately used to account for the birds that sink, drift out to sea, or are scavenged. Our search of the literature found that the maximum multiplier used in poorly documented spills was 10 (Burger 1993). The mean multiplier from a review of 45 oil spills (Burger 1993) was 4 to 5. A multiplier of 6 was applied to marine and salt-pond birds for the 'North Cape' spill because currents and wind speeds were sufficiently strong to disburse oil over a great area and to transport large numbers of birds offshore. A multiplier was not used for non-water birds because recovery rates for carcasses of these species are generally high. Only 12 non-water birds were found dead.

To estimate the interim loss of birds resulting from the spill (the loss from the time of the injury until injured resources recover), the number of each bird species killed was multiplied by its estimated recovery period (defined as the time necessary for the population to reach pre-spill, baseline levels), resulting in bird-years lost. To estimate recovery periods, we reviewed data on production of fledglings, survival rates, maximum lifespan, and current population abundances for each species (Table 1), as well as the numbers of each species or taxon that suffered losses from the spill (Table 2). Based on this information, we divided the injured species (taxa) into 2 groups, corresponding to those whose recovery would likely be complete during the first breeding season vs. those whose recovery would require a longer time period. For species in this first group, data on current population levels, survival rates and productivity support a conclusion that natural compensatory mechanisms would restore population levels during the first breeding season. Species (taxa) with recovery times estimated to be greater than 1 yr, generally breed at older ages, have lower reproductive success, and, in this instance, suffered high spill-related mortality. Recovery periods in this group were estimated to equal their expected lifetimes in the absence of the spill. This simplification was used as a proxy for return to baseline levels, although clearly compensatory mechanisms could result in 'replacement' of these birds sooner. Alternatively, if populations are in decline, recovery could take longer.

The calculation of recovery time for species judged to require more than the first breeding season required information on age structure of the bird populations killed by the spill, and on natural mortality rates. Due

Table 1. Biological parameters for marine birds whose recovery is estimated to require more than 1 breeding season

Species	Fledgling (1st year) survival rate	Post-fledgling survival rate	Max age (yr)	Breeding age (yr)	Young/individual	Source
Scoters (black <i>Melanitta nigra</i> and surf <i>M. perspicillata</i> )	0.40	0.75	15	2	1.3	Johnsgard (1975), Bordage & Savard (1995)
Red-breasted merganser <i>Mergus serrator</i>	0.15	0.60	15	2	1.3	Johnsgard (1975)
Goldeneye <i>Bucephala clangula</i>	0.27	0.64	15	3	0.9	Eadie et al. (1995)
Bufflehead <i>Bucephala albeola</i>	0.39	0.59	15	2	1.1	Johnsgard (1975), Gauthier (1993)
Common eider <i>Somateria mollissima</i>	0.20	0.68	21	2 to 4	0.64	Johnsgard (1975), Bellrose (1976), Blumton et al. (1988), Goudie et al. (2000), B. Allen pers. comm.
Grebes (horned <i>Podiceps auritus</i> and red-necked <i>P. griseogen</i> )	0.60	0.62	24	2	0.91	Fjeldsa (1973), Clapp et al. (1982), Johnsgard (1987), French et al. (1996), G. Neuchterlein pers. comm.
Loons (common <i>Gavia immer</i> and red-throated <i>G. stellata</i> )	0.76	0.88	24	5	0.27	Belant & Anderson (1991), Croskery (1991), Evers (1993, 2001), French et al. (1996), McIntyre & Barr (1997), Taylor & Vogel (1998)

to the inability to age bird carcasses found during the recovery effort, we used the simplifying assumption that birds killed by the spill were of average age for their respective populations. To estimate average age, we first determined age-specific survival rates and the maximum attainable age for each taxon through review of available literature (Table 1). To the extent possible, several literature estimates were averaged for each parameter. For all taxa, a fledgling survival rate was applied for the first year and a constant rate of annual survival applied to each subsequent year (post-fledgling to adult) up to the maximum attainable age (Table 1). The number of age classes was dictated by the maximum attainable age, whereas the age distribution was computed by applying the annual survival rates. Average age was then determined by calculating a weighted average age.

Using the weighted average age for those taxa whose recovery was estimated to exceed 1 breeding season, the number of additional years that an average-aged bird would have been expected to live in the absence of the spill can be calculated. This time period is estimated by simple demography. For example, the average-aged scoter of 3.8 yr killed by the spill could have lived 11 additional years, given a maximum age of 15 (Table 1). The probability of surviving 1 more year in the absence of the spill is 0.75, the annual survival rate for post fledgling scoters (Table 1). The probability of surviving both a first and second year is the survival rate raised to the second power, and so on. Summing the probabilities of survival for each remain-

ing age class beyond the calculated average age gives the number of additional years an average-aged bird would be expected to survive. For scoters this equation is  $(0.75)^1 (1 \text{ yr}) + (0.75)^2 (1 \text{ yr}) + (0.75)^3 (1 \text{ yr}) \dots + (0.75)^{11} (1 \text{ yr}) = 2.87 \text{ yr}$ . Thus, an average-aged scoter would likely live 2.87 additional years if the spill had not occurred. Total bird-years lost for birds that died as a result of the spill was then estimated by multiplying the additional years a bird would have lived in the absence of the spill by the number of individuals killed by the spill.

The use of a 'bird-years' metric to calculate the scale of injury and restoration offers several advantages. A primary advantage to the 'bird-years' approach is that it corrects for the fact that some bird species have a much longer lifespan than others. This often is an important consideration when injuries to several species are 'combined' into a single habitat project that restores these injuries through productivity increases to a smaller number of bird species. In those circumstances, if scaling is done using 'birds lost' instead of 'bird-years', some long-lived birds killed by the spill will be inappropriately 'replaced' by short-lived birds or vice-versa. For injury quantification purposes, this method involves estimation of the number of years injured birds would have lived if the spill had not occurred. From a restoration perspective, credit reflects the number of years that birds produced by the proposed restoration are expected to live. Another potential benefit of the bird-years approach is that it can help correct for disparities related to the age distri-

Table 2. Injury quantification for birds killed by the 'North Cape' oil spill

		Number recovered	Total kill	Discounted life expectancy (yr)	Direct mortality (bird-years)	Fledgling production lost (bird-years)	Total bird-years lost
<b>Marine birds—long term impact likely</b>							
Common loon	<i>Gavia immer</i>	67	402	5.46	2196	639	2835
Common eider	<i>Somateria mollissima</i>	59	354	1.93	685	168	853
Grebes (horned, red-necked)	<i>Podiceps auritus</i> , <i>P. grisegena</i>	38	228	1.51	345	360	705
Goldeneye	<i>Bucephala clangula</i>	32	192	1.64	314	94	408
Red-breasted merganser	<i>Mergus serrator</i>	34	204	1.39	284	53	337
Bufflehead	<i>Bucephala albeola</i>	11	66	1.34	88	37	125
Scoters (black, surf)	<i>Melanitta nigra</i> , <i>M. perspicillata</i>	3	18	2.60	47	64	111
Red-throated loon	<i>Gavia stellata</i>	2	12	5.46	66	19	85
Subtotal		246	1476		4025	1434	5459
<b>Marine birds—long term impact unlikely</b>							
Gulls (great black-backed, herring)	<i>Larus marinus</i> , <i>L. argentatus</i>	74	444	1.00	444	0	444
Cormorant	<i>Phalacrocorax auritus</i>	16	96	1.00	96	0	96
Murre	<i>Uria aalge</i>	5	30	1.00	30	0	30
Gannet	<i>Morus bassanus</i>	3	18	1.00	18	0	18
Razorbill	<i>Alca torda</i>	2	12	1.00	12	0	12
Dovekie	<i>Alle alle</i>	1	6	1.00	6	0	6
Subtotal		101	606		606		606
<b>Salt-pond birds—long term impact unlikely</b>							
Great blue heron	<i>Ardea herodias</i>	6	36	1.00	36	0	36
Canada goose	<i>Branta canadensis</i>	6	36	1.00	36	0	36
Black duck	<i>Anas rubripes</i>	5	30	1.00	30	0	30
Scaup	<i>Aythya affinis</i>	4	24	1.00	24	0	24
Mute swan	<i>Cygnus olor</i>	4	24	1.00	24	0	24
Mallard	<i>Anas platyrhynchos</i>	3	18	1.00	18	0	18
Pintail	<i>Anas acuta</i>	2	12	1.00	12	0	12
Ruddy duck	<i>Oxyura jamaicensis</i>	2	12	1.00	12	0	12
Coot	<i>Fulica americana</i>	1	6	1.00	6	0	6
Subtotal		33	198		198		198
<b>Non-water birds—long term impacts unlikely</b>		12	12	1.00	12	0	12
<b>Total</b>		<b>392</b>	<b>2292</b>		<b>4841</b>	<b>1434</b>	<b>6275</b>

bution of injured and restored birds. In some cases, environmental insults may kill birds that are near the end of their natural lives while restoration projects replace them with birds that have their entire lifespans ahead of them. In most cases there are no field data available concerning the ages of birds killed by the perturbations.

For species (taxa) whose recoveries were estimated to exceed 1 breeding season, the loss in bird-years expected from first-generation fledglings that would have been but were not produced by breeding adults killed by the 'North Cape' oil spill was added to the mortality injury. For this computation, we first estimated the percentage of birds killed by the 'North Cape' spill that would have produced young in the absence of the spill. For grebes, mergansers, goldeneye, buffleheads, scoters and eiders (this group constitutes all of the taxa whose recoveries were estimated to exceed 1 breeding season,

with the exception of loons), we assumed that all birds of breeding age would have maintained breeding territories and would have attempted to produce young had the spill not killed them. This assumption is supported by information obtained from Eadie et al. (1995), which indicates that over 90% of breeding-age common goldeneyes breed in a given year. For these species (taxa), we calculated the proportion of the population in each age class using the survival rates. We then summed over all age classes equal to or greater than the breeding age identified in the literature (Table 1) to determine the proportion of breeding birds killed by the spill. Finally, to estimate the bird-years lost by fledglings-never-hatched for grebes, mergansers, goldeneyes, buffleheads, scoters, and eiders, the number of fledglings produced per breeding individual per season (Table 1) was multiplied by the average life span of a fledgling. These calculations were repeated for each breeding season that a



killed bird would have been expected to produce fledglings in the absence of the spill. The average life span of fledglings was calculated using the age-specific survival probabilities previously described. Using scoters as an example, approximately 1.58 bird-years are expected from each fledgling over the course of its lifetime with a fledgling survival of 0.4, an adult survival rate of 0.75, and a maximum life span of 15 yr. For scoters, the total fledgling production foregone per year was 27.7 bird-years lost based on 75% of the 18 individuals killed by the spill of breeding age and 1.3 fledglings produced per breeder and a fledgling life expectancy of 1.58 bird-years (i.e.  $18 \text{ scoters} \times 0.75 \times 1.3 \text{ fledglings per scoter} \times 1.58 \text{ bird-years lost per fledgling}$ ). Next, we used the estimate of how long an average-aged bird would have lived had the spill not occurred to compute the number of breeding seasons foregone as a result of the spill. For scoter this value is 2.87 yr, and so we assumed that an average-aged bird would have been expected to produce fledglings for 3 breeding seasons following the spill. Each season's fledgling production foregone by loss of the birds killed by the spill was summed to calculate the total fledgling production foregone as a portion of the injury.

For loons, computing loss of fledglings requires a more complex conceptualization of loon nesting behavior. Based on information from a 22 yr database from New Hampshire established by the Loon Preservation Committee (Taylor & Vogel 2000), 66% of the loons killed by the spill were estimated to be 'breeding' loons, while 20% comprised non-breeder adults and the remaining 14% represented the young-of-the-year cohort. If an established territory is vacant due to death or divorce of the breeding adults, non-breeding adults regularly and quickly fill that void (Piper et al. 2000; Evers 2001). Decreases in fledgling production as a result of 'breeding' loon deaths may be partially offset by the otherwise non-breeding adults because pre-spill loon populations consisted of a number of reproductively competent birds that did not breed (i.e. up to 20%). However, due to decreased experience and fitness of these otherwise non-breeding adults, fewer fledglings are produced by the replacement loons in the first few years (for birds: Owen & Black 1989, Wooller et al. 1989, for loons: D. Evers pers. com.). To account for the role of these non-breeding loons in post-spill recovery, we estimated that their fledgling production would be reduced for 2 yr. The production losses expected for the remaining 4 yr in which a breeding adult killed by the spill would have been expected to produce young were not included, since otherwise non-breeding adults in the population were expected to have filled the available territories. It is important to note that spills especially destructive to loon populations could effectively eliminate the 'non-breeding' as well as the 'breeding' cohort,

thereby preventing immediate occupancy of vacant breeding territories, resulting in little or no off-setting production of fledglings.

**Restoration scaling.** Restoration focused on marine birds adversely affected by the spill, and whose recovery period was estimated to exceed 1 breeding season (loons, grebes, mergansers, goldeneyes, buffleheads, scoters, and eiders). The magnitude of injury to loons required that restoration include specific actions to off-set the loon injury. The cost and the logistic difficulty of developing and implementing multiple, small restoration projects for each of the other injured bird species led us to seek a single project that would restore the remaining injured species. The focus of this second component was restoration of sea duck populations with particular attention to eiders.

Life history data for common loons *Gavia immer* and common eiders *Somateria mollissima* were used to scale appropriate restoration (Table 3). Loons display strong territorial behaviors during nest occupation, which occurs along shorelines of freshwater lakes (Piper et al. 2000). Eiders breed primarily along shorelines of coastal islands, where they do not generally exhibit territorial behavior, but show some degree of cooperation among female breeders during nesting (Kilpi & Lindstrom 1997). Both taxa are monogamous with loons forming durable pair bonds (i.e. multiple seasons) and eiders pairing briefly for breeding. Loons and eiders are long-lived, with deferred reproductive maturity and low annual productivity of fledglings (see Table 3).

Three restoration options were evaluated to offset losses of loons resulting from the 'North Cape' oil spill: habitat protection, nest-site enhancement, and public outreach/education. The first 2 options increase loon populations through enhancement of fledgling production at nest sites, whereas public outreach/education seeks to mitigate loss of birds through prevention of human-related mortality. Specifically, habitat protection through the purchase of land or development rights in areas of bird nesting is expected to restore bird populations by preventing future decline in fledgling production resulting from land development and habitat degradation. Nest-site enhancement involves the installation of artificial nest sites (Piper et al. 2002) on lakes that have poor nesting habitat, fluctuating water levels, or histories of low reproductive output of loons. The education and public outreach option seeks to decrease adult loon deaths from human activity, such as motorboat trauma, lead sinker poisoning, or fishing line entanglement (Caron & Robinson 1994, Carney & Sydeman 1999). Public outreach also could reduce human interference with breeding loons by boaters, swimmers, and other recreators, thus increasing fledgling production per nest site.

Table 3. Values for biological, economic and project parameters used in the restoration scaling calculations for common loons *Gavia immer*, red-throated loons *G. stellata* and common eiders *Somateria mollissima*

Biological parameter	Loon restoration	Eider restoration
Productivity gain at protected area	0.5 fledglings nest site <sup>-1</sup> yr <sup>-1</sup>	0.4 fledglings nest site <sup>-1</sup> yr <sup>-1</sup>
Productivity of offspring	0.54 fledglings territorial pair <sup>-1</sup> yr <sup>-1</sup>	0.4 fledglings eider pair <sup>-1</sup> yr <sup>-1</sup>
1st year (Fledgling) survival rate	0.76	0.20
Adult survival rate	0.88	0.68
Average life expectancy of a newly hatched bird (discounted)	4.95 yr	0.57 yr
Breeding age	5 yr	2 yr
Maximum age	24 yr	15 yr
Proportion of adult birds that maintain territories	0.80	1.0
Discount rate	0.03 yr <sup>-1</sup>	0.03 yr <sup>-1</sup>
Project life-time	100 yr	100 yr

Scaling the proposed restoration options to compensate for lost bird-years requires quantifying the degree to which bird populations are enhanced by each restoration option. Enhancement was estimated through a comprehensive review of available (both published and unpublished) data sets that (1) contrast or estimate productivity differences between developed and undeveloped breeding areas (habitat protection option), (2) evaluate fledgling production at artificial nest sites (nest-site enhancement option), and/or (3) report the number of deaths or other impacts from human-related disturbance and quantify success in past efforts to reduce such impacts (education/public outreach). Once the degree of benefit was estimated, the next step in the scaling computations involved determining the appropriate size of the restoration based on the benefit, the life expectancy of the restoration project and life-history parameters for each species of birds.

For the habitat protection option, we estimated the productivity gains for a single protected nest to determine the total number of protected nests necessary to compensate for the bird injury. Offspring hatched at each protected nest site (first-generation productivity) as well as offspring later produced by these birds (second-generation productivity) were included in the calculations of habitat protection benefits. First-generation production of each nest site (expressed in bird-years) was calculated by multiplying the productivity gain per protected nest site (the difference in fledgling production between a protected and an unprotected nest, PG) by the average life expectancy ( $L$ ) of a newly hatched bird. The productivity gain was assumed to recur each year ( $t$ ) over a 100 yr project life time (PL). Although the benefits of the project are theoretically indefinite since the land cannot be developed, application of economic discounting at a 3% annual rate (see 'Discounting' section below) means that birds produced near the end of the 100 yr lifetime contribute little to the total productivity gain. Thus, the

equation to calculate augmented production of fledglings associated with the first-generation of offspring attributed to a protected nest site is:

$$\sum_{t=1}^{PL} (PG \times L) \quad (1)$$

The first-generation offspring resulting from a protected nest site begin producing their own offspring (second-generation offspring) from their species-specific breeding age (BA) until they die at their species-specific maximum age (MA). To calculate the restoration benefit of expected bird-years achieved by these second-generation offspring, we used the equation

$$\sum_{t=BA}^{MA} (PG \times FS \times AS^{t-1} \times pA \times \frac{PLO}{2} \times L) \quad (2)$$

where FS is the fledgling survival rate, AS is the annual adult survival rate, pA is the proportion of adults that breed, PLO/2 is the annual productivity (based on average sites across the population) of bird offspring (per individual) and the other terms are the same as in Eq (1). Inclusion of the FS and AS variables to PG in Eq. (2) accounts for the expected mortality rates of the first-generation birds (i.e. the product of the first 3 terms in the equation gives the number of first-generation offspring per protected nest that could breed). Application of the pA term accounts for the fact that not all adults breed, generally because of behavioral and environmental constraints (i.e. the product of the first 4 terms in the equation gives the number of birds per protected nest that actually breed). Multiplication of the actual number of breeders by PLO/2 gives the number of second-generation offspring per protected nest produced in a single year. The PLO term is divided by 2 to account for the fact that the productivity parameter is a per-pair estimate, rather than a per-individual estimate. The number of second-generation offspring per protected nest is then multiplied by  $L$  to

estimate the number of bird-years expected from these second-generation offspring. Credit for fledglings produced beyond the second generation was not included in the restoration scaling nor was it included in the damage assessment. Given the potential role of density-independent factors that may affect populations over long time spans, extending impacts or benefits beyond the second generation was viewed as too speculative. The sum of the second-generation bird-years produced by the offspring of all of the first-generation birds is calculated as:

$$\sum_{t=1}^{PL} \text{Second-generation bird-years produced by Year } t \text{ first-generation birds} \quad (3)$$

Once the productivity gain in bird-years per protected nest site over the 100 yr project (Eq. 1 + Eq. 3) was estimated, we then determined the number of nests required to compensate for the bird injury.

In addition to enhanced production of fledglings, protection of nest sites may result in higher survivorship of adult birds through prevention of recreation/development-related mortality at nest sites. To estimate this benefit, we reviewed 10 yr (1989 to 1998) of monitoring data collected by the Loon Preservation Committee for New Hampshire lakes. The data set documents mortality of loons by region within the state and includes cause of death determinations made by veterinarians at Tufts University. The data set was examined by region to determine the differences between developed and undeveloped areas. To calculate the adult survival credit for habitat protection, the numbers of loon deaths due to boat trauma, fishing gear, plastics, and lead sinkers were determined for developed and undeveloped areas. The total number of deaths due to these human-induced traumas was then divided by the regional bird population estimate to determine the proportion of birds likely to be killed. The proportion for undeveloped lakes was then subtracted from that for developed lakes to calculate the survival credit for protecting adults. To determine the number of adults that are 'saved' through reducing human-induced mortality, the estimated bird population in the protected area (the area purchased as part of the restoration project) was multiplied by the survival credit. The resulting number of birds saved was then substituted for PG in Eq. (1) to determine the number of bird-years credited to this component of the restoration option.

**Discounting.** To account for the time-lag between the injury and the start of restoration as well as the time required (several decades) for the restoration project to balance the original injury, damages and restoration credits were adjusted by an annual discounting rate of 3%. This rate, commonly used in

natural resource damage assessments (NOAA 1999), approximates the additional amount of a good or service required by society as compensation for delaying provision of the good or service by an additional year. In our computation, the injury was expressed in 1996 bird-years (the year of the oil spill) and the total compensatory restoration goal (injury adjusted by 3% annually) and restoration scaling calculations were expressed in 2000 bird-years (the start of the restoration project). In calculating the injury, the annual survival rate (both fledgling and adult rates) was discounted by 3% to estimate the 1996 value of bird-years lost in the future. For example, annual survival rate for post-fledgling (adult) scoters is 0.75 (Table 1). After 1 yr (i.e. 1997) this value decreases to 0.73 ( $0.75/1.03^1$ ) and after 2 yr the value decreases to 0.71 ( $0.75/1.03^2$ ). In calculating the restoration credit, the annual production credit for each nest site (Eq. 1) was discounted to the year that the restoration project starts. Specifically, Eq. (1) is multiplied by the term  $(1 + DR)^{-t}$ , where  $t$  is equal to the year after the start of the restoration project (1 to 100) and DR is the annual discount rate (0.03). Because fledglings hatched in that year will live for multiple years (predicted by their average life expectancy), the future years of fledgling production are also discounted (the DL term in Eq. 4). This latter discounting is achieved through discounting the annual survival rate of fledglings produced during that year (as in the injury calculations). Applying the above discounting to Eq. (1), the equation calculating the restoration benefit associated with the first-generation of offspring attributable to a protected nest site (measured in Year 2000 bird-years) is:

$$\sum_{t=1}^{PL} (PG \times DL) \times (1 + DR)^{-t} \quad (4)$$

where DL is the life expectancy calculated using the discounted survival rates and all other parameters are the same as defined under Eq. (1).

The production of fledglings by birds hatched at a protected nest site (second-generation birds) is discounted back to the year that their parents were hatched ( $t - BA$ ). Because these second-generation fledglings live beyond the year when they are hatched, their future production is adjusted through discounting their future annual survival rates (as in the injury calculations). Applying the above discounting to Eq. (2), the equation calculating the restoration benefit associated with the fledglings produced by the first-generation birds is:

$$\sum_{t=BA}^{MA} \left[ PG \times FS \times AS^{t-1} \times pA \times \frac{PLO}{2} \times DL \times (1 + DR)^{-(t-BA)} \right] \quad (5)$$

Finally, Eq. (3), which sums bird-years produced by the offspring of all of the first-generation birds, is expressed in terms of Year 2000 bird-years by application of a discounting term:

$$\sum_{t=1}^{PL} \text{Second-generation bird-years produced by Year } t \text{ first-generation birds} \times (1+DR)^{-t} \quad (6)$$

## RESULTS

### Injury quantification

During and after the 'North Cape' oil spill, 405 oiled birds (of which 392 eventually died) were recovered. After application of the multiplier to account for dead but unrecovered water birds, total direct mortality of birds was estimated to be 2292 individuals. Marine birds (sea ducks, loons, grebes, alcids, gannets, gulls and cormorants) comprised the majority (2082), with salt pond birds (ducks, geese, swans and herons) and non-water birds (owls and doves) contributing much less (Table 2). For marine birds, gulls (444) were killed in greatest numbers, followed by common loons (402), eiders (354), grebes (228), mergansers (204), and goldeneyes (192).

Available data on productivity, age-specific survivorship, and population abundances indicate that non-water birds, salt pond birds, alcids (murre, doves, razorbills) and gannets likely were restored through natural recovery during the first breeding season following the spill. Relatively few individuals of each of these species (<40) were estimated to have been killed, and natural compensatory mechanisms were expected to quickly restore these bird populations to baseline levels. Natural compensatory mechanisms (i.e. decreased competition for resources, increased availability of nest sites) also were expected to allow rapid natural restoration of gulls and cormorants to baseline levels. Although these taxa were killed in larger numbers (444 gulls and 96 cormorants), their populations are known to be increasing in size in this region. In contrast, recovery times for sea ducks (mergansers, goldeneye, bufflehead, scoters and eiders), loons (common and red-throated) and grebes (Table 2) were determined to require more than 1 breeding season. Although the regional breeding populations of these species may be adequate to allow natural recovery, the relatively late age of first breeding and low reproductive success (Table 1) coupled with the large numbers of these birds killed by the spill contributed to a judgement that natural recovery would extend beyond 1 breeding season.

The total interim loss of bird production resulting from the 'North Cape' oil spill (Table 2) was estimated as 6275 bird-years. Marine birds whose recovery was

estimated to extend beyond 1 breeding season accounted for 87% of this total (5459 bird-years) with marine birds whose recovery was complete during the first post-spill breeding season accounting for 10% (606 bird-years) and pond and non-water birds accounting for 3% (198 bird-years). Loss of the first generation of fledglings accounted for 26% (1434 bird-years) of the total injury to marine birds with recovery periods extending beyond 1 breeding season (5459 bird-years). Losses were greatest for loons (2835 bird-years) and eiders (853 bird-years).

### Restoration scaling

Limited information was available to quantify the expected production gain for loons for the 3 restoration options. Based on data collected by the Loon Preservation Committee from 1993 to 1998 from developed and undeveloped areas, protected nest sites produced 0.4 more fledglings per nest than nest sites in developed areas. However, for our calculations, the magnitude of improved productivity between undeveloped lakes and developed lakes without management was estimated to be 0.5 more fledglings per nest because the Loon Preservation Committee's data were based on a contrast between developed lakes that had management and educational programs and undeveloped lakes. Unfortunately, similar data to assess the productivity gains for the nest site creation and education/public-outreach options were not available. The lack of data to quantitatively evaluate these options led to the rejection of these 2 restoration choices. Furthermore, many areas that provided the best opportunities for nest site enhancement were already being managed for nesting enhancement; consequently, further potential productivity gains were viewed as marginal at best. However, some qualitative assessment of the nest site creation and education/public outreach options can be made based on the scaling calculations for the habitat protection option.

Based on our estimates of the relevant biological parameters (Table 3), each protected breeding pair of loons and associated nest site will generate approximately 128 additional loon-years (measured in Year 2000 loon-years) over a 100 yr project lifetime. Assuming implementation of the restoration project in 2000, the total loon injury (common and red-throated loons) to be restored is 3286 loon-years, the damage calculation for 1996 (2920 loon-years) expressed in 2000 bird-years ( $2920 \times [1.03]^4$ ). Therefore, approximately 25.5 nests would be required to meet the restoration goal of 3286 loon-years.

Preventing development of currently undeveloped loon breeding habitat would also be expected to result in higher adult survivorship through prevention of

recreation-/development-related mortality. Based on the data set collected by the Loon Preservation Committee, the habitat protection project designed to enhance fledgling production would 'save' 2.54% of the adult loon population each year by reducing mortality resulting from the use of lead sinkers. An additional 0.43% of the population would be saved each year through decreases in loon mortality resulting from boat trauma, fishing gear and plastics. The adult credit for prevention of boat trauma, fishing gear and plastic was calculated for the 100 yr project lifetime using appropriate discounting. The credit for the prevention of mortality related to the use of lead sinkers was calculated for only the first 10 yr of the project life. The adoption of legislation restricting the use or sale of lead sinkers by Maine and New Hampshire (the likely location for habitat protection) and the likely adoption by neighboring states was presumed to result in reduced mortality rates on developed lakes over the next 10 yr. Thus the annual benefit is 1.5 adult loons per year for each of the first 10 yr based on the 2.97% credit and a population size of 50 protected loons (i.e. 25 protected nest site  $\times$  2 loons at each site  $\times$  0.0297). For the remaining 90 yr of the project, the annual benefit is 0.2 loons  $\text{yr}^{-1}$  (50 loons  $\times$  0.0043). Consistent with the other injury and restoration calculations, the expected number of loon-years 'saved' by protecting an averaged-age adult is 5.4. Discounting the annual benefits by 3% annually and summing over a project lifetime of 100 yr results in a credit of 93 loon-years. This credit reduces the number of loon-years needed for restoration through production of fledglings from 3286 to 3193 loon-years and reduces the nest requirements from 25.5 to 25.

The remainder of the marine bird injury was 2933 bird-years, measured in Year 2000 bird-years. Experiences with human-induced disturbance on islands suggested that development would likely eliminate nesting opportunities for eiders on most islands. Consequently, protection and management of eider nesting islands in Maine could potentially result in improved production to 0.4 fledglings eider pair $^{-1}$  yr $^{-1}$  (B. Allen pers. comm.). Using this information for eiders and using eiders as the target group for restoring the remainder of the marine bird injury, each protected nest for eiders would be expected to produce an additional 9.3 bird-years (measured in Year 2000 eider-years). Thus, 315 nest sites would need to be protected to restore the remainder of the marine bird injury.

## DISCUSSION

The accuracy of our analyses depends on the assumptions used in both the injury quantification and

the restoration scaling. Assumptions are often needed because of the lack of area-specific data, large uncertainty in relevant biological parameters and/or the lack of clear consensus in the literature on key issues (Peterson et al. 2003a). Injury estimates and restoration scaling are highly sensitive to life history data for individual species. Therefore we encourage future users of this method to rely upon the most recent literature to help minimize uncertainty.

The calculated injury does not include longer-term, chronic effects of the spill because our calculations of bird injury resulting from the 'North Cape' oil spill were derived from estimates of acute mortality. Therefore, our calculation represents a conservative estimate of the injury. Decreases in adult or fledgling fitness resulting from direct (exposure to residual hydrocarbon) and indirect effects (oil spill impacts on prey populations) have the potential to adversely impact birds for years after an oil spill (Burger & Gochfeld 2001, Peterson 2001, Golet et al. 2002). Unfortunately, few empirical data are available to quantify this effect. The most important assumptions regarding restoration are ones that involve identification of the factor(s) that currently limit the target population(s). Once the population bottleneck is identified, restoring the injury involves identifying and scaling the most effective mechanism to overcome this limitation. In our restoration strategy, the primary assumption was that nest-site availability and/or quality limits production of new individuals: an assumption that is supported by regional data sets and is consistent with a larger body of literature. Clutch size and fledgling success have been shown to increase with increasing habitat quality for both common loon and common eider (e.g. Kilpi & Lindstrom 1997, Gingras & Paszkowski 1999).

The most reliable mechanism to restore injured loon and eider populations, the target groups for our restoration projects, was judged to be the prevention of future losses in fledgling production of wild populations resulting from expected decreases in the quantity and quality of nesting sites due to development. For loons, purchasing sufficient land and/or land development rights to protect 25 nest sites along shorelines of freshwater lakes with existing loon populations would be expected to compensate for the lost loon productivity resulting from the 'North Cape' oil spill. Similarly, the purchase of sufficient land to protect 315 eider nesting sites would be expected to compensate for the loss of eiders plus all other injured marine birds whose recovery period following the 'North Cape' oil spill was likely to exceed 1 breeding season.

In order for the restoration strategy adopted to be successful, the development pressure must be real: purchase of non-threatened sites would have no impact on productivity of the target species. Caron &



Robinson (1994) found that modest levels of human activity (increased recreational use of largely undeveloped lakes in Canada) did not result in decreased fledgling production but suggested that higher levels of human activity or shoreline development could. The closest breeding grounds for loons injured in the 'North Cape' oil spill, which occurred in Rhode Island, are in New Hampshire and Maine where many of these areas are indeed under growing development pressure. Concerns about the stability of loon populations in the northeastern US reflect the large number of specific threats to breeding and wintering populations. Currently, Vermont lists the common loon as an endangered species. In New Hampshire loons are listed as threatened, and in Massachusetts, Connecticut and New York they are listed as species of special concern. Shoreline development on loon breeding lakes is a conservation issue because it eliminates use of historically productive territories and increases human disturbance at nest sites. Similarly, increased development on privately owned islands in Maine, which support substantial numbers of breeding eiders, may dramatically reduce fledgling production of eiders. Purchase and protection of a subset of these islands could meet the requirements necessary for eider restoration by decreasing the adverse effects associated with development on many of them.

The 2 options that were not chosen for the restoration project, nest-site creation and education/public outreach, were judged too uncertain in the degree to which they could produce the large quantity of bird-years required by the restoration plan. This uncertainty was primarily a function of the lack of applicable data sets, particularly for the education/outreach component, and a lack of remaining opportunities (nest-site enhancement) for the expected number of sites needed. The underlying mechanism by which nest-site creation results in additional loon productivity is similar to that of habitat protection, increasing nest-site availability/quality. The specific number of nest site platforms required will depend on the productivity benefit attributable to each platform, as well as platform duration. At the time when the restoration project was planned, there were few empirical data available to quantify the productivity gains of artificial nest sites. However, a recent study by Piper et al. (2002) conducted in several small Wisconsin lakes concluded that floating platforms could increase reproductive success of common loons. When compared to natural nest sites, platforms increased both hatching success (+69%) and early fledgling survival (+32%). The increased success was attributed to decreased levels of mammalian predation (primarily raccoons). Compared with reference lakes that had a fledgling rate of 0.56 chicks pair<sup>-1</sup> season<sup>-1</sup>, similar lakes with platforms had fledgling

rates of 0.74 pair<sup>-1</sup>. The low durability of the platforms over multiple seasons was considered a serious limitation for the restoration potential of floating platforms. The preferred loon habitat protection project requires protection of 25 nests. The associated productivity benefit (0.5 fledglings per nest) and protection duration (+100 yr) is greater than could be achieved by nesting platforms (assuming Piper et al. 2002 results apply to New Hampshire lakes). As a result, the number of platforms needed to meet the restoration goal for loons would be 3 to 4 times the number of nests that must be protected under the habitat protection project. In addition, a long-term management and maintenance plan (Piper et al. 2002) would need to be adopted to insure the necessary project lifetime of the floating platforms. Such considerations will generally apply to restoration options that involve engineered structures instead of allowing natural processes to proceed to enhance populations.

Productivity benefits associated with the education/public outreach option were judged too uncertain for choice as the restoration option. Although undoubtedly beneficial (e.g. McIntyre 1988, Burger 2003), it is extremely difficult to quantify the benefits of existing programs in the absence of long-term studies. Further complicating this analysis would be quantifying the marginal benefits generated by additional spending on education and outreach above the programs already in place. In areas that do not have existing education/public-outreach programs or where human activity is known to be a significant source of disturbance (e.g. personal water craft, Burger 2003), closer examination of this restoration option is necessary. For our analysis, any benefit gain would at most be similar to those calculated for the adult credit of breeding ground protection: the expected number of loon-years 'saved' by protecting an averaged-age adult is 5.4 yr<sup>-1</sup> assuming an adult population of 50 in the area. Discounting the annual benefits by 3% annually and summing over a project lifetime of 100 yr results in a credit of 93 loon-years. This benefit is substantially smaller than the increases in fledgling production achieved through nest-site protection. Expanding the education/public outreach to a larger area could increase the number of loon-years saved through this restoration option; however, the cost of such a long-term program would probably be higher than the purchase and protection of nest sites.

Offsetting injury to marine birds by prevention of future losses through habitat protection has advantages over any alternative that might involve artificial propagation of replacement birds over a short time period. The injection of a short-term pulse of relatively large numbers of replacement birds could result in compensatory mortality or reproduction processes that

render such restoration ineffective or even counter-productive. Particularly in cases where breeding habitat is ultimately limiting, habitat protection would often seem the wisest choice for restoration. In addition, there are unforeseen but possible ecosystem changes that could result from the rapid addition of large quantities of predators. By preventing future declines in bird populations, the effect on their prey communities remains relatively unchanged. Many of these marine birds can exert a high level of control on prey communities (Hamilton 2000). Rapidly increasing current levels of predation through artificial breeding programs could inadvertently injure other consumers that feed on similar prey. For example, many fish and crab species prey on the same benthic invertebrates that loons and eiders prey upon (Hamilton 2000).

The decision to compensate for losses to a wide suite of marine birds by developing and implementing a restoration project for a single species, the common eider, raises several issues. First, such a choice has implications to the ecosystem in which these birds are a part. The injury clearly affected a diversity of species, which restoration will not necessarily enhance. The importance of biodiversity to the stability and resilience of communities has been demonstrated in several studies (Naeem et al. 1994, Tilman & Downing 1994). Furthermore, preserving biodiversity is a major focus of conservation biology for multiple reasons, including ethics, aesthetics, and sustainability of ecosystem function (Wilson 1992). Consequently, one could challenge the decision to restore many with one. Such a choice is motivated in large measure by efficiency: development and implementation of many small restoration projects would multiply costs several fold and result in fewer birds produced per unit expense. Nevertheless, the question remains of whether the public trust resource is truly restored by ecologically unbalanced restoration and whether using lower costs to justify that action is defensible for agencies charged with protecting the public trust resources. Fortunately, in the case of selecting a habitat preservation option, it is clear that numerous species besides the targeted one will benefit.

Habitat protection, particularly of breeding and spawning grounds, represents an effective and ecologically responsible mechanism to restore natural population of marine species. For marine fishes and invertebrates, establishment of marine reserves as well as the protection and/or restoration of essential fish habitat can be viewed as adopting a similar philosophy. Recent studies have demonstrated the effectiveness of both strategies in restoring marine fish populations (Roberts et al. 2002, Peterson et al. 2003b, in this Theme Section). Our analyses here use a combination of syntheses of regional empirical studies and

broader conceptual theory to make quantitative predictions of the net benefits of habitat protection/restoration for 2 marine birds: loons and eiders. Such calculations can be viewed as explicit hypotheses for future studies and could be evaluated through rigorous 'follow-up' monitoring of restoration projects.

*Acknowledgements.* Funding for the preparation of this manuscript was provided by the National Oceanic and Atmospheric Administration (NOAA), Damage Assessment Center and the US Fish and Wildlife Service. The comments of C. H. Peterson, J. Burger, D. Esler, K. Carr and B. Allen improved this manuscript. D. Evers, C. Hebert and D. Kane guided and assisted the process.

#### LITERATURE CITED

- Agler BA, Kendall SJ, Irons DB, Klosiewski SP (1999) Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. *Waterbirds* 22:98–103
- Belant JL, Anderson RK (1991) Common loon, *Gavia immer*, productivity on a northern Wisconsin impoundment. *Can Field Nat* 105:29–33
- Bellrose FC (1976) Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA
- Blumton AK, Owen RB Jr, Krohn WB (1988) Habitat suitability index models: American eider (breeding). US Fish and Wildlife Service Biological Report 82(10.149), Washington, DC
- Boersma PD, Clark JA, Hillgarth N (2001) Seabird conservation. In: Schreiber EA, Burger J (eds) *Biology of marine birds*. CRC Press, Boca Raton, FL, p 559–580
- Bordage D, Savard JL (1995) Black scoter (*Melanitta nigra*). In: Poole A, Gill F (eds) *The birds of North America*. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, DC, No. 177, p 1–20
- Burger AE (1993) Mortality of seabirds assessed from beached-bird surveys in southern British Columbia. *Can Field Nat* 107:164–176
- Burger J (1997) *Oil spills*. Rutgers University Press, New Brunswick, NJ
- Burger J (2003) Personal watercraft and boats: coastal conflicts with common terns. *Lake Reserv Res Manag* 19: 26–34
- Burger J, Gochfeld M (2001) Effects of chemicals and pollution on seabirds. In: Schreiber EA, Burger J (eds) *Biology of marine birds*. CRC Press, Boca Raton, FL, p 495–526
- Carney KM, Sydeman WJ (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22:68–79
- Caron JA, Robinson WL (1994) Responses of breeding common loons to human activity in upper Michigan. *Hydrobiol* 280:431–438
- Clapp RB, Banks RC, Morgan-Jacobs D, Hoffman WA (1982) Marine birds of the southeastern United States and Gulf of Mexico. Part I. Gaviiformes through Pelecaniformes. Report FWS/OBS-82/01, US Fish and Wildlife Service, Washington, DC
- Coon N, Dieter MP (1981) Responses of adult mallard ducks to ingested south Louisiana crude oil. *Environ Res* 24: 309–314
- Croskery PR (1991) Common loon, *Gavia immer*, nesting suc-

- cess and young survival in northwestern Ontario. *Can Field Nat* 105:45–58
- Eadie JM, Mallory ML, Lumsdem HG (1995) Common goldeneye (*Bucephala clangula*). In: Poole A, Gill F (eds) *The birds of North America*. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, DC, No. 170, p 1–32
- Esler D, Schwartz JA, Jarvis RL, Mulchay DM (2000) Winter survival of adult female harlequin ducks in relation to history of contamination by the 'Exxon Valdez' oil spill. *J Wildl Manag* 64:839–847
- Evers DC (1993) Northern Great Lakes common loon monitoring program: 1993 Field Season Final Report. Whitefish Point Bird Observatory, Paradise, MI
- Evers DC (2001) Common Loon population studies: continental mercury patterns and breeding territory philopatry. PhD dissertation, University of Minnesota, St. Paul
- Fjeldsa J (1973) Territory and the regulation of population density and recruitment in the horned grebe *Podiceps auritus arcticus* Boje, 1822. *Vidensk Medd Dan Nat.hist Foren* 136:117–189
- French DP, Reed M, Jayko K, Feng S and 16 others (1996) The CERCLA Type A Natural Resource Damage Assessment Model for Coastal and Marine Environments (SIMAP). Technical Documentation, Vol. I—Model Description. US Dept of Interior, Washington, DC
- Fry DM, Swenson J, Addiego LA, Grau CR, Kang A (1986) Reduced reproduction in wedge-tailed shearwaters exposed to weathered Santa Barbara crude oil. *Arch Environ Contam Toxicol* 15:453–463
- Gauthier G (1993) Bufflehead (*Bucephala albeola*). In: Poole A, Gill F (eds) *The birds of North America*. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, DC, No. 67, p 1–32
- Gingras BA, Paszkowski CA (1999) Breeding patterns of common loons on lakes with three different fish assemblages in north-central Alberta. *Can J Zool* 77:600–609
- Golet GH, Seiser PE, McGuire AD, Roby DD and 6 others (2002) Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on pigeon guillemots in Prince William Sound, Alaska. *Mar Ecol Prog Ser* 241:287–304
- Goudie RI, Robertson GJ, Reed A (2000) Common eider (*Somateria mollissima*). In: Poole A, Gill F (eds) *The Birds of North America*. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, DC, No. 546, p 1–32
- Grau CR, Roudybush T, Dobbs J, Wathern J (1977) Altered yolk structure and reduced hatchability of eggs from birds fed single doses of petroleum oils. *Science* 195:779–781
- Hamilton DJ (2000) Direct and indirect effects of predation by common eiders and abiotic disturbance in an intertidal community. *Ecol Monogr* 70:21–43
- Hlady DA, Burger AE (1993) Drift-block experiments to analyze the mortality of oiled seabirds off Vancouver Island, British Columbia. *Mar Pollut Bull* 26:495–501
- Hoffman DJ (1990) Embryotoxicity and teratogenicity of environmental contaminants to bird eggs. *Rev Environ Contam Toxicol* 115:40–89
- Irons DB, Kendall SJ, Erickson WP, McDonald LL, Lance BK (2000) Nine years after the 'Exxon Valdez' oil spill: effects on marine bird populations in Prince William Sound, Alaska. *Condor* 104:723–737
- Johnsgard PA (1975) *Waterfowl of North America*. Indiana University Press, Bloomington
- Johnsgard PA (1987) *Diving birds of North America*. University of Nebraska Press, Lincoln
- Kilpi M, Lindstrom K (1997) Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. *Oecologia* 111:297–301
- McIntyre JW (1988) *The common loon: spirit of Northern Lakes*. University of Minnesota Press, Minneapolis
- McIntyre JW, Barr JF (1997) *Common loon (Gavia immer)*. In: Poole A, Gill F (eds) *The birds of North America*. The Academy of Natural Sciences, Philadelphia and The American Ornithologist's Union, Washington, DC, No. 313, p 1–32
- Montevocchi WA (2001) Interaction between fisheries and seabirds. In: Schreiber EA, Burger J (eds) *Biology of marine birds*. CRC Press, Boca Raton, FL, p 527–558
- Naeem S, Thompson LJ, Lawlor SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–737
- NOAA (1999) Discounting and the treatment of uncertainty in natural resource damage assessment. Tech Paper 99-1, NOAA, Silver Spring, MD
- Owen M, Black JM (1989) Barnacle goose. In: Newton I (ed) *Lifetime reproduction in birds*. Academic Press, San Diego, CA, p 349–362
- Peterson CH (2001) The 'Exxon Valdez' oil spill in Alaska: acute, indirect and chronic effects on the ecosystem. *Adv Mar Biol* 39:1–103
- Peterson CH, Kneib RT, Manen C-A (2003a) 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)
- Peterson CH, Grabowski JH, Powers SP (2003b) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar Ecol Prog Ser* 264:249–264 (in this Theme Section)
- Piatt JF, Lensink CJ (1989) 'Exxon Valdez' bird toll. *Nature* 342:865–866
- Piper WH, Tischler KB, Klich M (2000) Territory acquisition in loons: the importance of the take-over. *Anim Behav* 59:385–395
- Piper WH, Meyer MW, Klich M, Tischler KB, Dolsen A (2002) Floating platforms increase reproductive success of common loons. *Biol Conserv* 104:199–203
- Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2002) Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923
- Taylor K, Vogel H (1998) Summary of loon restoration preservation committee research and management activities for the 1997 field season. Loon Preservation Committee, Holderness, NH
- Taylor K, Vogel H (2000) New Hampshire Report. In: McIntyre JW, Evers DC (eds) *Loons: old history and new findings*. Symp Proc 1997 meeting, American Ornithologists' Union, N Am Loon Fund, Holderness, NH, p 110–113
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367:363–365
- Trivelpiece WR, Butler RG, Miller DS, Peakall DB (1984) Reduced survival of chicks of oil-dosed Leach's storm petrels. *Condor* 86:81–82
- Wilson EO (1992) *Diversity of life*. Harvard University Press, Cambridge, MA
- Wooller RD, Bradley JS, Skira IJ, Serventy DL (1989) Short-tailed shearwater. In: Newton I (ed) *Lifetime reproduction in birds*. Academic Press, San Diego, CA, p 405–418

# Habitat restoration as mitigation for lost production at multiple trophic levels

Deborah P. French McCay\*, Jill J. Rowe

Applied Science Associates, 70 Dean Knauss Drive, Narragansett, Rhode Island 02882, USA

**ABSTRACT:** Seagrass beds and salt marshes are important in the life histories of many fish, invertebrates, and aquatic birds, such that population size and production of these organisms can be limited by the loss of these habitats. Therefore, restoring seagrass or salt marsh would be expected to benefit species dependent on these resources. Following the 'North Cape' oil spill of January 1996 in Rhode Island (northeastern USA), habitat restoration was used to compensate for losses of fish, invertebrates, and aquatic birds. A habitat restoration model based on food-chain transfers was used to estimate equivalent production at the same trophic level as the losses, a novel approach that uses energetic efficiencies to scale across trophic levels. Benefits of habitat to each trophic level were estimated by assuming that the production of consumers is proportional to prey production gained by the restoration of habitat. The habitat restoration model balanced the losses with trophically equivalent production, discounting future gains in compensatory production relative to present losses such that interest is paid, analogous to economic discounting. Results showed that restoration of seagrass beds would be more productive than salt marsh restoration in southern New England and, likely, other temperate zone locations. Moreover, benthic faunal production in salt marshes could be accounted for by *in situ* primary production of angiosperms and benthic microalgae, whereas in seagrass beds, benthic faunal production exceeded that expected from in-bed primary production. The trophic model provides a methodology to estimate the scale of a restoration project that will provide production (ecological services) equivalent to losses of organisms at multiple trophic levels, applicable to natural resource damage assessments and other environmental assessments.

**KEY WORDS:** Restoration · Habitat · 'North Cape' oil spill · Natural resource damage assessment · Trophic transfer · Food web modeling

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

In response to pervasive degradation of coastal marine ecosystems, especially including vegetated and other structured habitats, such as seagrass and wetlands of great importance as larval settlement areas, nurseries, refugia from predation, and foraging habitats (Heck & Orth 1980, Kneib 1997, Beck et al. 2001, Heck et al. 2003, Minello et al. 2003), considerable interest has developed in their protection and restoration (Thayer 1992, Matthews & Minello 1994, Fonseca et al. 1998, Beck et al. 2003). In the USA, when natural resources are impacted by environmental incidents, such as oil and chemical spills, pollutant relea-

ses, or physical destruction of habitat, federal and state agents are legally mandated to obtain funds from responsible parties to restore equivalent ecological and human services (NOAA 2002). Because restoration of highly productive structural habitats such as seagrass and salt marsh would benefit dependent fish, invertebrates, birds, and other wildlife, and these habitats have suffered great losses from eutrophication and other perturbations (e.g. Orth & Moore 1983), salt marsh or seagrass restoration is often the preferred choice for compensation of injuries to natural resources in coastal marine ecosystems.

Estimation of the benefits of habitat restoration is rarely performed to render the scale of the restoration

\*Email: dfrench@appsoci.com



project compensatory (equivalent in value to the loss). Here we develop a method for estimating the appropriate scale of restoration, and demonstrate the approach by application to the 'North Cape' oil spill, which occurred in January 1996 on the Rhode Island coast (northeastern USA). The habitat restoration model builds upon food chain energetics (e.g. Slobodkin 1960, Ryther 1969, Odum 1971, Steele 1974, Odum & Heald 1975) and habitat equivalency analysis (HEA: NOAA 1997, 1999, Julius 1999). Our model converts losses of production of multiple species to an energetically equivalent single trophic level so that the scale of necessary compensatory restoration can be computed. Data required for the model include the net gain in primary production expected from restoration of the structured habitat, the food web structure, and energetic transfer efficiencies. Assuming that augmentation of production of consumers is proportional to net gains in production of their prey (i.e. the consumers' production is food-limited), we estimate the production benefits to each higher trophic level. HEA is a modeling approach that translates lost or gained ecological and human services to present-day value by applying the economic concept of discounting, to account for the delay in benefits between the time of loss and the gain in production (Julius 1999, NOAA 1999).

We structure this paper as follows: First, we summarize the injury estimation methods and results for the 'North Cape' oil spill. Next, we review restoration options and develop the habitat restoration model approach, including specific methods for estimating the scale of restoration required to compensate an injury comprised of species of multiple trophic levels. The results of application of the restoration model to the 'North Cape' oil spill are described, along with more general implications of comparing salt marsh and eelgrass bed food webs. Finally, we characterize sensitivity of model results to its assumptions and the implications for effectively restoring losses resulting from environmental impacts.

## INJURY ESTIMATION

The 'North Cape' oil spill was a release of 2682 metric tons (828 000 gallons; 3130 m<sup>3</sup>) of home heating (No. 2 fuel) oil into heavy surf, resulting in high concentrations of polynuclear aromatic hydrocarbons (PAHs) in shallow water that caused severe acute mortality by narcosis (French McCay 2002, 2003). The majority of the impact (measured as biomass lost) was to near-shore benthic marine invertebrates (American lobster *Homarus americanus*; rock crabs *Cancer* spp.; blue mussel *Mytilus edulis*; sea stars; surf clam *Spisula solidissima*; and benthic amphipods) and fishes associ-

ated with rocky reefs (tautog *Tautoga onitis*; and cunner *Tautoglabrus adspersus*) along the exposed southern coast of Rhode Island (French McCay 2003). PAHs from the oil also entered coastal lagoons ('salt ponds') behind the impacted barrier beaches, killing soft-shell clams *Mya arenaria*, American oysters *Crassostrea virginica*, bay scallops *Argopecten irradians*, other invertebrates and fish (French & Rines 1998). Four hundred oiled birds were collected after the spill, indicating several thousand killed by direct oiling, based on recovery rates of beached birds (NOAA et al. 1999) and modeling of the area swept by oil multiplied by species density (French McCay 2003). Because the oil was quickly and effectively dispersed by high turbulence and waves, impacts were primarily from acute exposure to dispersed and dissolved oil concentrations (fish and invertebrates) and oil sheens (birds), rather than chronic contamination. Wetlands and seagrass beds were not significantly impacted by the spill.

Modeling of oil fates and biological effects was used (French McCay 2003) to estimate mortalities of marine organisms. A physical-fates model predicted water column PAH concentrations, which were validated with field sampling results. A linked biological effects model estimated acute exposure (concentrations and duration) to oil PAHs and resulting mortality. The modeled estimate of lobster mortality (8.3 million: French McCay 2003) was similar to estimated numbers of lobsters killed based on field sampling (9.0 million: Cobb et al. 1999), validating the biological effects model (French McCay 2003). The model was used to calculate injury (as biomass lost) to other marine organisms, based on estimates of biomass density, size structure, growth rate and mortality rates (French et al. 1996a, French McCay 2003, French McCay et al. 2003b, in this Theme Section).

PAH concentrations in each of the salt ponds over time were estimated by Hinga (1997) by fitting exponential decay curves to measured concentrations to account for volatilization and degradation (Hinga 1988), using source contamination estimated by the marine modeling (French McCay 2003). Exposure and mortality of biota were estimated using the biological effects model (French McCay 2002, 2003) and pre-spill abundance in each pond (French & Rines 1998).

Injuries (kg wet weight) to fish and invertebrates in the marine environment and the salt ponds are summarized in Tables 1 & 2, calculated as the sum of the biomass killed, which represents net production realized previous to the spill, and lost future production that the killed organisms are expected to have provided had they not been killed (production foregone). Production foregone was estimated using a demographic population model (French McCay et al. 2003b), where somatic growth was summed over age classes (indexed



Table 1. Injuries (kg wet weight, without shells) in the marine environment (Block Island Sound) resulting from the 'North Cape' oil spill, estimated by field data collections (lobsters: Cobb et al. 1999) or ecotoxicological modeling of oil fates and effects (other species: French McCay 2003). Production foregone is estimated by summing somatic growth over the remaining lifespan of the killed individuals by annual age class. -: not estimated

Species category	Number killed ( $\times 10^3$ )	Biomass killed (kg)	Production foregone (kg)	Total injury (kg)
Alewife <i>Alosa pseudoharengus</i>	0.01	3	3	6
Herring (sea) <i>Clupea harengus harengus</i>	392	3040	4190	7240
Hakes (red and white) <i>Urophycis</i> spp.	1.7	125	824	949
Cod <i>Gadus morhus</i>	3.6	350	1250	1600
Spiny dogfish <i>Squalus acanthias</i>	0.46	1	194	195
Haddock <i>Melanogrammus aeglefinus</i>	0.005	4	3	7
Atlantic pollock <i>Pollachius virens</i>	0.24	2	3	4
Northern searobin <i>Prionotus carolinus</i>	12.2	94	130	225
Silver hake <i>Merluccius bilinearis</i>	5.0	39	53	92
Ocean pout <i>Macrozoarces americanus</i>	45	351	484	835
Flounders (Pleuronectidae)	0.55	480	398	879
Sculpin <i>Myoxocephalus octodecimspinos</i>	28.6	222	306	529
Skates <i>Raja</i> spp.	1950	15130	20800	35980
Tautog <i>Tautoga onitis</i>	16.5	459	544	1000
Cunner <i>Tautoglabrus adspersus</i>	1740	9758	51300	61000
Crabs (rock) <i>Cancer</i> spp.	3890	41730	49300	91010
Crabs (hermit) <i>Pagurus</i> spp.	3730	3732	2430	6160
American lobster <i>Homarus americanus</i>	9040	312400	-	312400
Northern quahog larvae <i>Mercenaria mercenaria</i>	37.5	7	798	805
Atlantic surf clam <i>Spisula solidissima</i>	150600	192500	172000	364000
Blue mussel <i>Mytilus edulis</i>	20250	879	1200	2080
Sea stars <i>Asterias forbesi</i> and <i>Henricia sanguinolenta</i>	2460	24580	6880	31460
Benthic macrofauna	4890000	489000	310500	799500
Total	5084000	1095000	623000	1718000

Table 2. Injuries (kg wet weight, without shells) in the salt ponds resulting from the 'North Cape' oil spill (French & Rines 1998). Production foregone is estimated by summing somatic growth over the remaining lifespan of the killed individuals by annual age class. -: not estimated

Species category	Number killed ( $\times 10^3$ )	Biomass killed (kg)	Production foregone (kg)	Total injury (kg)
Winter flounder <i>Pseudopleuronectes americanus</i>	1.59	1377	1142	2519
Forage fish (Cyprinodontidae) <i>Menidia</i> spp.	533	2667	2370	5037
Northern quahog <i>Mercenaria mercenaria</i>	-	-	-	-
Soft shell clam <i>Mya arenaria</i>	499	5712	3888	9600
Eastern oyster <i>Crassostrea virginica</i>	149	1857	905	2762
Bay scallop <i>Argopecten irradians</i>	0.16	5	0	5
Crabs <i>Cancer</i> spp.	318	3181	3756	6937
Grass shrimp <i>Palaemonetes</i> spp.	324	81	88	169
Zooplankton	5397	229	-	229
Benthic macrofauna	6591800	65920	98110	164030
Total	6599000	81030	110260	191290

at the midpoint of each year of life, i.e. in winter), accounting for survival and discounting of future losses. For lobsters and bivalves, abundance data and parameters for the demographic model are described in French McCay (2003) and French McCay et al. (2003a,b, in this Theme Section). The demographic model parameters of

the other fish and invertebrate species were from French et al. (1996a), with abundances in the marine environment as described in French McCay (2003). Abundance of non-bivalve species in the salt ponds was based on previous studies in the specific ponds affected (French & Rines 1998).

## ALTERNATIVES FOR RESTORATION

### Restoration approaches to compensate for injuries

Following the 'North Cape' oil spill, lobsters and bivalves were restored by species-specific restocking programs, described in French McCay et al. (2003a,b). Sea stars were assumed restored by restoration of their prey, the bivalves. For species other than lobsters, bivalves and sea stars, the trustees responsible for restoration of resources injured during the 'North Cape' spill determined that injuries were not large enough, or that restocking methods were not sufficiently developed (e.g. benthic amphipods, skates, and cunner), to warrant species-specific restoration projects (NOAA et al. 1999). Because many of these species would benefit from the production, refuge and nursery services of structured habitats, habitat restoration projects were considered, specifically for salt marsh (dominated by *Spartina alterniflora* and *S. patens*) and seagrass beds (eelgrass *Zostera marina*), the most important structured habitats in southern New England marine and estuarine waters.

Of the 2000 to 3000 aquatic birds killed by the 'North Cape' oil spill, ca. 200 were of species that normally forage in the salt ponds, wetlands and seagrass beds (Table 3). These species were restored by habitat restoration, along with the fish and invertebrates not included in species-specific restorations. Expressed as wet weight production lost, the total 'pond' bird injury was 476 kg, with estimates of average weight per bird from French et al. (1996a). It is assumed that these birds were fully grown, so there is no additional production (foregone) from weight gain expected over their remaining lifetime. Additional losses of birds were compensated by restoration targeted at increasing fledgling production of eiders, loons, and piping plovers (NOAA et al. 1999).

Table 3. Estimated bird injury for species that use the salt ponds, wetlands and seagrass beds for foraging, expressed as numbers and kg (wet weight) of injury. Average wet weight per bird is from French et al. (1996a)

Species	Number killed	Mean weight ind. <sup>-1</sup> (kg)	Injury (kg)
Black duck <i>Anas rubripes</i>	30	0.8	24
Coot <i>Fulica americana</i>	6	0.8	5
Mallard <i>Anas platyrhynchos</i>	18	0.8	14
Pintail <i>Anas acuta</i>	12	0.8	10
Ruddy duck <i>Oxyura jamaicensis</i>	12	0.8	10
Canadian geese <i>Branta canadensis</i>	36	5	180
Swans (Anatidae: Cygninae)	24	6.7	161
Scaups <i>Aythya</i> spp.	24	1.1	26
Hérons (Ardeidae)	36	1.3	47
Total	198		476

### Development of function in created marshes and seagrass beds

The degree to which ecological functions of created salt marshes match natural habitat depends on how well geomorphology and hydrology mimic natural systems (Seneca & Broome 1992, Zedler 1992, Minello & Webb 1997, Williams & Zedler 1999). Assuming that appropriate geomorphology and hydrology are recreated, the time for recovery of function depends on the parameters measured: vegetation develops rapidly and fish populate new salt marsh habitat at natural levels in as little as 2 to 5 yr, but invertebrates, sediment chemistry and nutrient cycling take longer to become equivalent to natural systems (Moy & Levin 1991, Minello & Zimmerman 1992, Zedler 1992, Williams & Zedler 1999). Restoring tidal flows in systems degraded by tidal restrictions and impoundments will bring back fully functioning tidal salt marshes in 1 to 2 decades (Warren et al. 2002). In the 'North Cape' restoration planning, it was assumed that salt marsh restoration would produce habitat with appropriate geomorphology, hydrology, and biology (dominated by *Spartina alterniflora*), and that after 15 yr ecological functions would reach 99% of full function. This recovery period is based on studies of salt marsh functional recovery rates in California, North Carolina and France (PERL 1990, Seneca & Broome 1992, Zedler 1992, French et al. 1996b).

Successful seagrass bed restoration is contingent on good water quality, as well as appropriate site selection, planting techniques, monitoring and corrective actions as needed (Fonseca et al. 1998). Fonseca et al. (1990) found fish and shrimp abundance in restored eelgrass beds indistinguishable from natural beds 6 mo after seeding or 2 yr after transplanting eelgrass. Abundance in the eelgrass was higher than over unvegetated bottom. For the 'North Cape' restoration planning calculations, created seagrass beds were assumed to be transplanted into appropriate sites and to require 3 yr to develop full (99%) function, based on the recent restoration projects reviewed by Fonseca et al. (1998).

### Creation versus preservation

Although planting seagrass is not technically complex and seagrass beds can be created under appropriate conditions, preservation (prevention of loss) is the most effective and reliable process to sustain seagrass habitat and associated resources (Fonseca et al.

1998). Restoration of salt marsh grasses is also feasible, but full function of created marshes takes many years or may never be achieved (Seneca & Broome 1992, Zedler 1992), rendering preservation preferable to mitigation of (purposeful) marsh loss. However, preservation can only be used as compensatory mitigation for an environmental incident where imminent loss of habitat would otherwise occur. If not, there would be no net gain in ecosystem services to match the losses.

Such an opportunity for prevention of imminent loss of seagrass habitat was available in southern Rhode Island near the 'North Cape' oil spill site. Seagrass habitat has declined generally throughout the estuaries of the Atlantic coast of North America, largely in response to eutrophication (Orth & Moore 1983, Short & Burdick 1996, Short et al. 1996). Using an approach developed for a Massachusetts estuary (Short & Burdick 1996), Short et al. (1996) evaluated whether the condition and status of eelgrass *Zostera marina* habitat changed as a function of increasing housing development in the watershed of a shallow coastal lagoon, Ninigret Pond, in Rhode Island over a 32 yr period. In that time, housing quadrupled and eelgrass beds declined by 41%. Short et al. (1996) linked nutrient flow from home septic systems to the decline in eelgrass, suggesting that eutrophication caused an inverse relationship between seagrass area and housing, and concluding that further development is likely to cause more losses of eelgrass. This relationship is supported by nutrient enrichment studies in mesocosms, where eelgrass growth decreased with nitrate enrichment (Burkholder et al. 1992, Short et al. 1995). Thus, instead of constructing new eelgrass beds, compensation for injuries could be achieved by avoiding future losses (preservation) through land acquisition and protection from development.

## METHODS FOR SCALING HABITAT RESTORATION ALTERNATIVES

### Scaling restoration based on equivalent production

The approach used in the 'North Cape' case was that the restoration project (of sufficient scale to compensate the injury to fish, invertebrates other than lobsters and bivalves, and 'pond' birds) would be implemented in one or more of the salt ponds affected and/or adjacent to the area of the marine injuries. The ecological and human services provided by the injured organisms were measured by production, biomass directly lost plus that not produced. Many ecosystem and human services increase in proportion to biological productivity. Particularly in aquatic ecosystems, the rate of turn-

over (production) is a better measure of ecological services than density or biomass (Odum 1971, Beck et al. 2003). Thus, the sum of the standing-stock killed (production previous to the spill) plus loss of expected future production is an appropriate metric for computing lost ecological services. Using production as the scaling metric also allows for differences in body size and growth rate between the individuals killed and the ones added by restoration while still achieving equivalence and thus compensatory replacement.

Our trophic model for quantifying benefits of habitat restoration (or preservation) is designed to account for the different ecological values of the production as a function of trophic level. The production losses for each of the injured species are translated to a common lower trophic level (primary or secondary) via simple energetics and a food web model so that production of that lower trophic level can represent the metric used to scale the size of the habitat restoration project. This approach is based on the assumption that the entire food web benefits from the additional primary or secondary production contributed by the restored habitat, i.e. that consumers at each trophic level are food-limited. Compensation is needed for lost production of each species injured, and those losses are additive. Restoration for a prey species killed will compensate for that prey killed and all the services that prey would have provided in the future to its predators and other resources. The predators that would eat that prey but were directly killed were produced before the spill by eating different prey individuals as food. Thus, compensation must include both the predator's production loss and that of the prey animals directly killed. This can be accomplished by providing additional prey production to compensate for the direct predator loss and resulting production foregone.

Correction for the delay between the injury occurrence and its restoration was achieved through discounting at a 3% (NOAA 1997) annual rate. The restoration project should be of a scale to provide production, in present day value (i.e. in the year of the spill), equivalent to the present day value of the direct kill plus production foregone. Two types of time lags are compensated: (1) the time from the spill to commencement of restoration, and (2) the time for the restored habitat to develop full function (with partial credit while it develops).

### Habitat restoration model

Primary production is used to measure the benefits of the restoration project, such that in the habitat restoration model the total injuries in kg of lost production are translated into equivalent plant production.

The majority of the primary production is by angiosperms *Spartina alterniflora* and *S. patens* in salt marshes and *Zostera marina* in eelgrass beds of the northeastern USA (Teal 1962, Howes et al. 1985, Adam 1993, Fonseca et al. 1998). However, in both salt marshes and seagrass beds, benthic and epiphytic microalgae provide an important, more readily assimilated form of primary production (Thayer et al. 1984, Currin et al. 1995, Sullivan & Currin 2000). The model assumes that net primary production of phytoplankton and macroalgae are not significantly different in the restored and previously existing habitat, such that the restoration does not change those energy sources to the food web.

Angiosperm biomass passes up the marine food web primarily via detritivores consuming the plant material and (more importantly) the attached microbial communities (Teal 1962, Odum & de la Cruz 1967, Thayer et al. 1984, Howes et al. 1985, Newell & Porter 2000). The detritivores are then prey for larger animals (e.g. in marshes: decapods, such as grass shrimp *Palaemonetes pugio*, and small fish, such as the mummichog *Fundulus heteroclitus*, and other killifishes) and ultimately support production of recreationally and commercially important finfish, shellfish, waterfowl and wading birds (Teal 1962). The ecological efficiency (consumer production per unit producer production) is low because a high percentage of biomass produced by the plant is broken down by microorganisms (primarily fungi: Newell & Porter 2000) before it can be assimilated. Benthic meiofauna and macrofauna also directly consume benthic and epiphytic microalgae directly and thus with higher transfer efficiency.

We also employed an alternative trophic level to scale the habitat restoration, field-based estimates of benthic meiofauna plus macrofauna production instead of primary production. Scaling to primary production assumes that all the benefits to animals in the restored habitat are generated by the additional plant production as food. However, the habitat provides other ecological services to animals, such as supplying shelter, nursery areas, and refuge from predators that increase survival and growth (Boesch & Turner 1984, Heck et al. 2003). For example, while the phytoplankton production in the overlying water is likely the same over eelgrass beds and unvegetated areas, one economically important species, the bay scallop, is found exclusively in seagrass meadows despite its dependence upon phytoplankton for food (Peirson 1983). Thus, bay scallop production would be enhanced by habitat restoration, but not because of enhanced primary production. Benthic animal production in structured habitats is often larger than that which can be accounted for by observed primary production (e.g. Nixon & Oviatt 1973, Heck et al. 1995). Using benthic

faunal production for scaling therefore would implicitly include these habitat services gained. Thus, we used benthic production as an alternative trophic level for scaling restoration.

In the habitat restoration model, each species group injured was assigned a trophic level relative to that of the benthic fauna (implying the herbivore or detritivore trophic level). For species at the same trophic level (e.g. zooplankton), their production was assumed to be equivalent in ecological value. The production loss of small nekton that prey on benthic fauna (e.g. decapods and killifish) was translated to equivalent benthic faunal production loss by dividing by the ecological efficiency of trophic transfer from the prey to the predator. For each step higher in the chain, the trophic transfer efficiency was applied to estimate the production yield (i.e. production loss divided by ecological efficiency for each step in the food web) at that upper trophic level.

Values for production of predator per unit production of prey (i.e. ecological efficiency) for invertebrate and fish consumers of animal prey have been estimated to be 10 to 30% in both freshwater and marine environments by a number of authors (e.g. Slobodkin 1960, Odum 1971, Steele 1974, Cohen et al. 1982, Jennings et al. 2002). While some have argued that 10% is the appropriate average value for all marine animals (Pauly & Christensen 1995), Pimm (1982) indicated that ecological efficiency is 10% for fish and 21 to 36% for non-insect invertebrates. Jennings et al. (2002) estimated transfer efficiencies of 3.7 to 12.4% based on measured standing stock biomass in the North Sea for fishery species of a broad range of sizes. However, if species greater than 512 g (many of which are intensely fished) are excluded, the efficiency was estimated as 12.4%. Excluding species greater than 256 g results in a calculated efficiency based on the North Sea sampling data of 27.1%. Thus, the evidence suggests that smaller species, and particularly invertebrates, are more efficient than large fish. In our habitat restoration model, the transfer efficiency of fish and invertebrates <200 g was assumed to be 20%, that for 200 to 1000 g fish to be 10%, and 4% for fish >1000 g.

For birds and mammals (which as homeotherms are less efficient), ecological efficiency is much lower, with estimates ranging from 1 to 5% (McNeill & Lawton 1970, Steele 1974, Grodzinski & Wunder 1975, Whitaker 1975, Pimm 1982). In our habitat restoration model, the ecological efficiency of birds and mammals feeding on fish or invertebrate prey was assumed to be 2%.

Equivalent compensatory benthic faunal production produced by the restored habitat was computed as kg of production lost divided by ecological efficiency for each step in the food web above benthic fauna (termed

the production yield). Table 4 summarizes the injury (as dry weight) for the 'North Cape' oil spill and the estimated production yield of each trophic level as a percentage of benthic faunal production. The dry weight (DW) equivalent of the injury was assumed to represent 22% of wet weight (Nixon & Oviatt 1973). In benthic faunal production equivalents, the majority of the injury was to benthic macrofauna, bivalves, sea stars, crabs, and small fish (cunner). In Table 4 and subsequent tables, lobsters are not included, but bivalves and sea stars are carried forward in the calculations for illustrative purposes and because habitat restoration was considered for these species even though the alternative that was selected involved restocking (French McCay et al. 2003b).

Equivalent compensatory primary production of the restored habitat is the equivalent compensatory benthic production divided by a factor representing the integrated production yield from primary producers to benthic fauna, which is the weighted sum (by fraction of total primary production derived from angiosperms vs benthic microalgae) of the product of the ecological efficiency of transfer from angiosperm to invertebrate detritivore and that from benthic microalgae to benthic herbivore.

In salt marsh stands of *Spartina alterniflora*, >95% of the below-ground primary production is remineralized to CO<sub>2</sub> in the sediments, with <5% exported as dissolved organic carbon (Howes et al. 1985). Thus, essentially none is transferred to benthic fauna. Assuming that 10% of the above-ground *Spartina* production is consumed by terrestrial insects (Kreeger & Newell 2000), 90% of the above-ground production enters the marsh food web. Newell & Porter (2000) estimated that 50 to 60% of *Spartina* shoot production is transferred to fungal production. The fungi are consumed by the gammaridean amphipod *Uholorchestia spartinophilia* to produce an estimated 0.92 g DW m<sup>-2</sup> yr<sup>-1</sup> in Georgia marshes (Covi & Kneib 1995), with most of the remainder of the fungal production passing through additional microbial degraders before being consumed

by benthic meiofauna and macrofauna. Assuming an above-ground *Spartina* production in Georgia marshes of 1000 g DW m<sup>-2</sup> yr<sup>-1</sup> (Kneib 2003, in this Theme Section), 55% transfer efficiency to fungi, and 20% transfer efficiency to *U. spartinophilia* (i.e. joint production yield = 11%), 1% of the above-ground *Spartina* production is transferred to the amphipod via directly from fungi (900 g DW m<sup>-2</sup> yr<sup>-1</sup> × 0.55 × 0.20 × 0.01 = 1 g DW m<sup>-2</sup> yr<sup>-1</sup>). Summarizing multiple stable isotope analyses, Sullivan & Currin (2000) concluded that benthic microalgae are responsible for 50% or more of the carbon assimilated by consumer organisms. The production yield from benthic microalgae to benthic fauna is assumed to be 10% (based on the above review of trophic transfer efficiencies and the likelihood that transfer efficiency from algae to invertebrate would be less than from animal prey). The remaining carbon assimilated by benthic fauna derives from *Spartina* production that has passed through the microheterotrophic community. The production yield of this pathway is at a maximum 2.2% (0.55 to fungi × 0.20 to microheterotrophs × 0.20 to benthic fauna), but would be lower if more steps are involved in the microbial web. The combined production yield from above-ground *Spartina* production to benthic meio- and macrofauna based on these assumptions is 2.1%. Adding an additional step to the microbial pathway gives a production yield of 0.5%.

Direct grazing on eelgrass leaves is considered relatively unimportant as a trophic pathway in temperate seagrass beds, with the majority (assumed 100% in our restoration model) of the organic matter produced by eelgrass decomposing and entering the food chain through the detrital pathway (Thayer et al. 1984). We assume that similar transfer efficiencies from angiosperm and epiphytic/benthic microalgal production to benthic faunal production apply in eelgrass beds as for salt marshes. The production yield from benthic and epiphytic microalgae to benthic fauna is assumed to be 10%. Assuming 55% transfer to fungi and depending on number of consumer steps following that transfer,

Table 4. Summary of injuries by trophic group and production yield from benthic faunal production to the trophic group, based on assumed ecological efficiencies for the trophic steps involved. DW: dry weight

Species in trophic group	Total injury (×10 <sup>3</sup> kg DW)	Feeding method or community	Production yield (%)	Compensatory benthic production (×10 <sup>3</sup> kg)
Large fish	10	Bottom feeders	10	99
Bivalves	83	Filter feeders	20	417
Sea stars	7	Bivalve predators	4	173
Crabs, shrimp, small fish	39	Bottom feeders	20	195
Benthic macrofauna	160	Benthic fauna	100	160
Pond birds	0.1	Bottom feeders	2	5
Total all species	300			1050
Total without bivalves and sea stars	209			459



the production yield from eelgrass to benthic faunal production is 2.2 to 11% (6.6% if half the fungal production is consumed by benthic fauna without an additional microheterotroph step).

The equivalent compensatory production ( $P_c$ ) is translated to area of restored habitat ( $H_R$ ) by dividing by expected net gain in annual productivity per area in the restored habitat ( $P_R$ ) times a discounting factor ( $D$ ) accounting for the project life (the number of years the restored habitat will exist:  $\lambda$ ), and the delay before realizing the benefits. Thus:

$$H_R = P_c / (P_R \times D)$$

$$D = (1 + d)^\rho \sum_{n=0}^{\lambda} F_n (1 + d)^{-n}$$

where  $d$  is the annual discount rate (0.03),  $\rho$  is the number of years after the spill when the restoration project begins, and  $F_n$  is the functional value of the restored habitat  $n$  years after planting as a fraction of full function. The discount factors,  $(1 + d)^\rho$  and  $(1 + d)^{-n}$ , decrease the value of the production by 3% for each year that passes before that production is realized. This follows economic discounting, in that losses and gains in the future are less valued than present production. Including identical discounting on both the injury and restoration sides of the equation allows time lags in both losses and benefits to be appropriately treated in order to measure values lost and gained fixed to a common year.

If the habitat is fully functional from the start of the restoration project (i.e. in the case of preservation),  $F_n = 1$  for all values of  $n$ , while the value of  $\rho$  is the years after the spill the habitat would be lost if it were not preserved. For an expected project life greater than 50 yr, the value of  $\sum (1 + d)^{-n}$  approaches 31.6. However, if new habitat was created, there would be a period of 'recovery' while it developed to full function. The recovery curve is assumed sigmoid in shape and to fit to a logistic equation (French et al. 1996a). The sigmoid curve is based on the notion that habitats would develop function slowly at first and then more rapidly, but that the increase in function would level off as an asymptotic full-function level is approached. Alternative functions could also be used, such as a linear increase or one where full-function is never reached. The fraction of full production rate attained by year  $n$  after planting,  $F_n$ , is calculated from  $y_r =$  years to 99% of full function, using the following rearrangement of the standard logistic equation:

$$F_n = 1/(1 + 99e^{-rn})$$

where  $r = 9.19024/y_r$ .

Because restoration involves the replacement of one habitat with another, the production gain ( $P_R$ ) is the dif-

ference between production in the new and in the replaced habitat. Production gains for transforming subtidal areas into seagrass beds were calculated as the difference between production in shallow subtidal unvegetated habitats and in vegetated habitat. For salt marshes, we assumed that the created marsh would be on land or shoreline (e.g. filled areas) that otherwise provide no net production to the estuarine and marine system, and no accounting was made of any terrestrial system losses that might be of concern in certain locations. However, if, for example, a mud flat were planted to become a marsh, the benthic microalgal production rate for the flat would need to be subtracted from the similar production rate in the resulting marsh. Assuming that mud flats and vegetated portions of marshes have similar benthic microalgal production rates (Sullivan & Currin 2000), the only net gain in primary production would then derive from the angiosperms.

#### Credit for increased scavenger production

The total biomass directly killed during the oil spill remained in the marine and salt pond ecosystems in the form of food for scavengers. We assumed that the killed biomass was consumed by the benthic meiofauna and macrofauna, and so enhanced production of benthos occurred, with the ecological efficiency for this trophic transfer (20%, defended above) determining the production yield. The resultant scavenger production ( $235 \times 10^3$  kg) was credited against the production foregone of the benthic fauna, such that the net injury of benthic fauna to be compensated was  $729 \times 10^3$  kg. While it may be argued that some of the killed organisms would have eventually provided food for these or other scavengers (e.g. crabs), or may have been subject to microbial degradation, the spill provided an earlier and presumably much larger biomass to scavengers than would have occurred in its absence. Despite failure to correct for the fraction of killed biomass that would have eventually provided food for the scavengers, the amount of credit associated with feeding scavengers was relatively small compared to the total injury. Similarly, no correction was made for the percentages of dead fauna consumed at lower or higher trophic levels than the benthic fauna, which would affect its value when converted to production at the benthic faunal trophic level.

#### Restoration scale compensatory for the 'North Cape' injuries

Salt marsh and eelgrass beds were assumed to take 15 and 3 yr, respectively, to reach 99% of full function,

based on the studies reviewed above. The project lifetime was assumed to be 100 yr (essentially in perpetuity) for both habitats, although an alternative of a 10 yr project life for eelgrass beds was also computed because some areas considered for seagrass restoration would not be protected from degradation of water quality for longer than that time frame. The results were quite sensitive to these assumptions, as illustrated below.

Estimates of above-ground production of *Spartina alterniflora* are available for several sites in New England. In a Rhode Island marsh, 72% of the marsh was short *S. alterniflora* with an estimated annual production of 432 g DW m<sup>-2</sup> yr<sup>-1</sup>, while production in tall *S. alterniflora* areas (7% of the marsh) and mixed stands of *Spartina patens* and *Distichlis spicata* (19% of the marsh) were 840 and 680 g DW m<sup>-2</sup> yr<sup>-1</sup>, respectively (Nixon & Oviatt 1973). Roman et al. (1990) estimated similar above-ground production rates in low and high marsh areas ranging from 445 to 732 g DW m<sup>-2</sup> yr<sup>-1</sup>. Valiela et al. (1976) estimated above-ground production of 420 g DW m<sup>-2</sup> yr<sup>-1</sup> in low marsh and 630 g DW m<sup>-2</sup> yr<sup>-1</sup> in high marsh of the Great Sippewisset salt marsh, Massachusetts. Thus, southern New England salt marsh angiosperm above-ground production averaged over a typical marsh (i.e. as studied by Nixon & Oviatt 1973) is 500 g DW m<sup>-2</sup> yr<sup>-1</sup>.

Benthic microalgal production in the vegetated low marsh area of the Great Sippewisset salt marsh was estimated as 105.5 g DW m<sup>-2</sup> yr<sup>-1</sup>, ca. 25% of above-ground angiosperm production (Van Raalte et al. 1976), and within the range described by Sullivan & Currin (2000) for USA east coast marshes generally. Benthic microalgal production in unvegetated areas of Delaware marshes was estimated as 84 g DW m<sup>-2</sup> yr<sup>-1</sup> on a creek bank and 202 g DW m<sup>-2</sup> yr<sup>-1</sup> in a salt panne (Sullivan & Currin 2000, assuming 45% carbon). Thus, averaging over vegetated and unvegetated areas would likely yield a value close to the 106 g DW m<sup>-2</sup> yr<sup>-1</sup>, which was used in the model calculations. Note that there would only be a net gain in benthic microalgal production if the area where marsh is created had not previously been mud flat and/or other habitat producing similar algal production.

Total benthic meiofauna and macrofauna production rates for salt marshes in southern New England were obtained from several sources. Production of macrofauna in unvegetated areas (tidal creeks and channels) of the Great Sippewisset salt marsh averaged 26.9 g DW m<sup>-2</sup> yr<sup>-1</sup> (weighted by the areas of different sediment types measured), with production to biomass ratios (P:B) averaging 4.0 (Sarda et al. 1995). Using measured meio- and macroinfaunal biomass from Nixon & Oviatt (1973) and a P:B ratio of 4, production in vegetated areas of a Rhode Island marsh would be

7 g DW m<sup>-2</sup> yr<sup>-1</sup>. Based on the estimate of 0.9 g DW m<sup>-2</sup> yr<sup>-1</sup> for the gammaridean amphipod from Covi & Kneib (1995) and molluscan production in *Spartina* beds in Nova Scotia (eastern Canada) of 6.5 g DW m<sup>-2</sup> yr<sup>-1</sup> from Burke & Mann (1974), epifaunal production rate in vegetated areas of southern New England marshes was estimated at 18.7 g DW m<sup>-2</sup> yr<sup>-1</sup>.

Based on the angiosperm and benthic microalgal production rates entering the marine food web (450 and 106 g DW m<sup>-2</sup> yr<sup>-1</sup>, respectively) and the estimated production yield from each to benthic fauna (2.1 and 10%, respectively), expected benthic faunal production is 20.8 g DW m<sup>-2</sup> yr<sup>-1</sup>, very close to the estimate based on field sampling. If the production efficiency from benthic microalgae to benthic fauna is actually 20% (as for invertebrates consuming animal food), the expected benthic faunal production is 31.4 g DW m<sup>-2</sup> yr<sup>-1</sup>. This may be a more reasonable estimate given that the benthic macroinfaunal production values for unvegetated areas taken from Sarda et al. (1995) did not include meiofaunal or epibenthic faunal production.

Using 20% transfer efficiency to small nekton (killifish and shrimp), these benthic production estimates of 18.7, 20.8, and 31.4 g DW m<sup>-2</sup> yr<sup>-1</sup> imply small nekton production of 3.8, 4.2, and 6.3 g DW m<sup>-2</sup> yr<sup>-1</sup>, respectively. Based on Kneib's (2003) review of small nekton production in east coast USA marshes (averaged over the entire marsh), fish production is ca. 1 to 2 g DW m<sup>-2</sup> yr<sup>-1</sup> and shrimp production is similar or somewhat higher. Thus, small nekton production is ca. 2 to 4 g DW m<sup>-2</sup> yr<sup>-1</sup>. Production of transient species that also consume benthic fauna is not included in this computation, but would be less than that of the resident species (Kneib 2003). Assuming 20% transfer efficiency and one trophic step to the small nekton, the benthic production estimates imply nekton production of 3.8 g DW m<sup>-2</sup> yr<sup>-1</sup> (based on field estimates of benthic biomass and P:B ratios), 4.2 g DW m<sup>-2</sup> yr<sup>-1</sup> (based on 2.1 and 10% production yield from angiosperm and benthic microalgal production), or 6.2 g DW m<sup>-2</sup> yr<sup>-1</sup> (based on 2.1 and 20% production yield from angiosperm and benthic microalgal production). In the example calculations below, scaling of salt marsh restoration from primary production was based on 2.1 and 10% production yield from angiosperm and benthic microalgal production, respectively.

By using stable isotope analyses, Sullivan & Currin (2000) showed that benthic microalgae are responsible for 50% or more of the carbon assimilated by consumer organisms on the salt marsh. Using the angiosperm (450 g DW m<sup>-2</sup> yr<sup>-1</sup>) and benthic microalgal (106 g DW m<sup>-2</sup> yr<sup>-1</sup>) production rates and the estimated production yield from each to benthic fauna (2.1 and 10%, respectively), our food web model indicates that 51%

of benthic faunal production results from consumption of benthic microalgae. If the production yield from benthic microalgae to benthic fauna were 20%, the percentage of faunal production resulting from microalgae would become 67%.

Annual primary production rates of eelgrass were assumed to be  $1423 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , based on data for Ninigret Pond, Rhode Island, one of the salt ponds affected by the spill (Thorne-Miller & Harlin 1984). Benthic microalgal production in shallow unvegetated subtidal areas of southern New England lagoons were assumed to be similar to those <1 m deep in South Carolina marshes, i.e.  $124 \text{ g DW m}^{-2} \text{ yr}^{-1}$  (Sullivan & Currin 2000, assuming 45% carbon). In lower Chesapeake Bay, sediment and epiphytic microalgal production rates in *Zostera marina* beds were 117.9 and  $62.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ , respectively (Buzzelli et al. 1998), totaling  $180.1 \text{ g C m}^{-2} \text{ yr}^{-1}$  ( $400 \text{ g DW m}^{-2} \text{ yr}^{-1}$ ). Thus, the net gain of benthic microalgal production in unvegetated shallow waters where eelgrass might be planted is expected to be  $276 \text{ g DW m}^{-2} \text{ yr}^{-1}$ .

A review of available benthic macrofaunal production rates in shallow subtidal habitats of similar climate zones as in southern New England suggests benthic faunal production in eelgrass beds of 100 to  $300 \text{ g DW m}^{-2} \text{ yr}^{-1}$  and in shallow unvegetated habitats of <50  $\text{g DW m}^{-2} \text{ yr}^{-1}$  (Heck et al. 1995). Benthic macrofaunal production in a southeastern Massachusetts eelgrass bed was 79 to  $175 \text{ g DW m}^{-2} \text{ yr}^{-1}$  (Heck et al. 1995, assuming  $0.8 \text{ g ash free DW g}^{-1}$  of dry weight from Nixon & Oviatt 1973). Fredette et al. (1990) estimated benthic faunal production in eelgrass beds in lower Chesapeake Bay at  $200 \text{ g DW m}^{-2} \text{ yr}^{-1}$  based on estimated production of  $42 \text{ g DW m}^{-2} \text{ yr}^{-1}$  for 20% of the species by density. Based on the judgment of these authors that their macrofaunal production estimates were underestimates, and using the mid-points of the ranges in the broader literature, we estimated the net gain in an eelgrass bed in Rhode Island to be  $200 - 25 = 175 \text{ g DW m}^{-2} \text{ yr}^{-1}$ .

Using production rates for eelgrass and microalgae of 1423 and  $276 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , respectively and the estimated production yields of 2.2 to 11% from eelgrass and 10% from microalgae to benthic fauna, expected benthic faunal production is 59 to  $184 \text{ g DW m}^{-2} \text{ yr}^{-1}$ . This calculation assumes that none of the eelgrass production is exported from the bed. If the production yield from benthic microalgae to benthic fauna were actually 20%, the expected benthic faunal production would become 87 to  $212 \text{ g DW m}^{-2} \text{ yr}^{-1}$ . The expected benthic faunal production rates decrease to 43– $106 \text{ g DW m}^{-2} \text{ yr}^{-1}$  if 50% of the eelgrass blade production is not consumed by the benthos within the eelgrass bed (and transfer efficiency of microalgae to benthic fauna is 10%). Comparison of the expected

benthic faunal production estimates to  $175 \text{ g DW m}^{-2} \text{ yr}^{-1}$  (since the unvegetated area benthic faunal production,  $25 \text{ g DW m}^{-2} \text{ yr}^{-1}$ , would be that resulting from phytoplankton production) suggests that eelgrass bed benthic faunal production is greater than that projected by trophic transfer from primary production within the bed, given that a substantial fraction of the eelgrass blade production would likely be exported from the bed by currents. In estimating the net gain from restoration of eelgrass, we recognize that the fraction of eelgrass production exported from the bed will still nourish fauna in the broader area and accomplish the objective of restoring the injury. Thus, 100% of the production yields from eelgrass (6.6%, assuming that half the fungal production is consumed by benthic fauna without an additional microheterotroph step) and microalgae (10%) to benthic fauna were used as the net gain in the application of the habitat restoration model.

The areas (created or preserved) of salt marsh or eelgrass required for compensation of the injured species were computed based on primary production (Table 5) and on benthic faunal production (Table 6). Planting was assumed to begin 3 yr after the spill and the project life was 100 yr (i.e. the project would be protected and maintained in perpetuity). Although the scale of habitat restoration required for bivalves and sea stars was calculated, these injuries were ultimately restored by direct stocking of bivalves (French McCay et al. 2003b), so the project sizes actually considered were totals without these species. Table 5 is based on the assumption that gains in primary production will result in proportionate gains in secondary production of benthic fauna (18 and  $24 \text{ kg DW m}^{-2} \text{ yr}^{-1}$  for salt marsh and eelgrass, respectively) as the result of additional food resources produced within the restored habitat. The alternative computations for salt marsh based on gains in benthic faunal production ( $19 \text{ kg DW m}^{-2} \text{ yr}^{-1}$ ; Table 6) match those based on primary production, which suggests that salt marsh benthic production is food-limited and that little of that production is based on allochthonous sources. In contrast, the alternative computation for eelgrass based on benthic faunal production ( $175 \text{ kg DW m}^{-2} \text{ yr}^{-1}$ ) is much higher than that starting with primary production in the bed ( $24 \text{ kg DW m}^{-2} \text{ yr}^{-1}$ ), implying that allochthonous sources contribute substantially and that production enhancement in eelgrass is provided by habitat structure as well as by *in situ* primary production. Thus, the scaling for eelgrass based on benthic production (Table 6) includes an additional ecosystem service beyond merely augmentation of primary production, which results in lower, but more appropriate, compensatory area requirements. In addition, the much higher benthic productivity in eelgrass beds combined with the similar

Table 5. Size of a compensatory restoration project using primary production as the scaling metric. Times for development of full function in salt marsh and eelgrass beds were assumed to be 15 and 3 yr, respectively. Planting was assumed to begin 3 yr after the spill. Project life was assumed to be 100 yr in all options, i.e. the project is protected and maintained in perpetuity. The land acquisition is for prevention of building on the indicated number of house lots to prevent associated degradation of water quality and resulting loss of eelgrass (see 'Creation versus preservation' for explanation)

Species category	Preserved salt-marsh area (ha)	Preserved eelgrass area (ha)	Land acquisition (no. of house lots)	Created salt-marsh area (ha)	Created eelgrass area (ha)
Large fish	16.4	2.8	22	20.3	2.9
Bivalves	69.2	11.9	91	85.9	12.3
Sea stars	28.7	4.9	38	35.6	5.1
Crabs, shrimp, small fish	32.4	5.6	43	40.2	5.7
Benthic macrofauna	26.6	4.6	35	33.0	4.7
Pond birds	0.9	0.1	1	1.1	0.2
Total all species	174.1	29.9	230	216.2	30.8
Total without bivalves and sea stars	76.2	13.1	101	94.6	13.5

Table 6. Size of a compensatory restoration project using benthic faunal production as the scaling metric. Times for development of full function in salt marsh and eelgrass beds were assumed to be 15 and 3 yr, respectively. Planting was assumed to begin 3 yr after the spill. Project life was assumed to be 100 yr in all options, i.e. the project is protected and maintained in perpetuity. Land acquisition is for prevention of building on the indicated number of house lots to prevent associated degradation of water quality and resulting loss of eelgrass (see 'Creation versus preservation' for explanation)

Species category	Preserved salt-marsh area (ha)	Preserved eelgrass area (ha)	Land acquisition (no. of house lots)	Created salt-marsh area (ha)	Created eelgrass area (ha)
Large fish	18.2	1.9	15	22.6	2.0
Bivalves	77.1	8.2	63	95.8	8.5
Sea stars	32.0	3.4	26	39.7	3.5
Crabs, shrimp, small fish	36.1	3.9	30	44.9	4.0
Benthic macrofauna	29.6	3.2	24	36.8	3.3
Pond birds	1.0	0.1	1	1.2	0.1
Total all species	194.1	20.7	160	241.0	21.4
Total without bivalves and sea stars	85.0	9.1	70	105.5	9.4

cost per acre for implementing restoration (French et al. 1996a) suggest that eelgrass restoration is more cost-effective than salt marsh restoration, particularly if land purchase costs need to be included in a salt marsh project.

If eelgrass beds were to be created in the salt ponds affected by the spill, the water quality would need to be sufficient to allow eelgrass beds to develop and remain healthy. However, in Ninigret Pond, for example, eelgrass has declined in recent years because of eutrophication (Short et al. 1996). Thus, water quality improvements would be a prerequisite for any restoration plan involving eelgrass bed creation in Ninigret Pond (as well as many other coastal areas). Pervasive decline in water quality in coastal waters, as well as the need for long-term maintenance of restored habitats, suggests that an assumed project life of 100 yr, as used in the calculations presented in Tables 5 & 6, is optimistic. The impacts of alternative assumptions about the duration of the project were examined (summarized in Table 7). Because of discounting future contributions, benefits in the first few years after restoration

are more valuable and varying project life span does not affect benefits proportionately. Nevertheless, restoration requirements increase dramatically if the project is not expected to be sustained for more than a decade, particularly if the restored habitat requires several years to achieve full functionality (e.g. salt-marsh where results were calculated for 10, 15 and 20 yr development times). The sensitivities to the assumed project life and the development time of the restored habitat demonstrate the importance of long-term adaptive management based on monitoring to realize maximum benefits of restoration.

Preservation of eelgrass habitat was the selected restoration alternative for the 'North Cape' oil spill, in part because maintenance of water quality issues and prevention of eelgrass loss in the coastal ponds had been long-term objectives of local managers. The scaling (Tables 5 & 6) employed Short et al.'s (1996) empirical relationship (linear regression) between numbers of houses in the watershed and loss of area of eelgrass habitat in Ninigret Pond: 1300 m<sup>2</sup> of eelgrass habitat lost per house. Computation of the acreage of

Table 7. Area (ha) of salt marsh or eelgrass restoration required for compensation of all species in Table 4 under varying assumptions: PP, based on primary production gained; BP, based on benthic faunal production gained; years for development of full function in the habitat; and project life for the restoration (years the habitat will be protected or maintained). Planting was assumed to begin 3 yr after the spill in all cases

Action	Project life (yr)	Marsh PP (15 yr)	Marsh BP (15 yr)	Marsh PP (10 yr)	Marsh PP (20 yr)	Eelgrass PP (3 yr)	Eelgrass BP (3 yr)
Created	10	2160	2407	1246	3992	125	87
Created	20	630	703	511	801	68	47
Created	30	409	456	355	475	51	35
Created	40	324	362	290	364	43	30
Created	50	281	313	255	311	38	26
Created	100	216	241	200	233	31	21
Preserved	100	174	194	174	174	30	21

land required for compensation included only land zoned for and suitable for development because otherwise purchase would not afford additional protection of water quality.

## DISCUSSION

Minello et al. (2003) showed that seagrass beds had higher nursery value, as measured by fish and crustacean growth and survival, than saltmarsh habitat, and both were more valuable than open water. Our estimates of gains in benthic faunal production in eelgrass and salt marsh restorations in southern New England are consistent with their findings. In addition, our trophic energetics model suggests that the percentage of benthic secondary production resulting from benthic microalgae is 50% or more in salt marshes, in agreement with the conclusions of Sullivan & Currin (2000). For eelgrass beds, the percentage of benthic faunal production generated by benthic and epiphytic microalgae is dependent on the fraction of eelgrass production consumed within the bed. If 100% of the eelgrass were consumed locally, the percentage of carbon assimilated via the microalgal pathway would be 15 to 47%. However, if 50% of the eelgrass were exported from the bed, microalgae would account for 26 to 64% of benthic secondary production. Clearly, additional research is needed to determine the carbon and energy budgets of eelgrass beds. The proportion of eelgrass blades retained within a bed almost certainly will be shown to vary with physical transport regime and bed size.

The critical importance of salt marshes, seagrass beds, and other structured habitats to many estuarine and marine species for reproduction, foraging and shelter, combined with the pervasive decline in these habitats due to pollution and other environmental impacts, makes them likely and appropriate targets of restoration for mitigation. Considerable research has identi-

fied the requirements for successful restoration of salt marshes and eelgrass beds (Seneca & Broome 1992, Matthews & Minello 1994, Fonseca et al. 1998). The trophic energetics model developed here provides a novel approach for estimating the appropriate scale of the restoration to be compensatory, based on food-web structure, transfer efficiencies, and economic discounting. The estimation of biological losses involves demographic modeling to include not only the biomass of organisms that are killed directly, but also the production foregone. Restoration employs food-web modeling to replace losses in biotic production with enhancements at the same or energetically equivalent trophic levels. Finally, the habitat restoration model uses the same scaling metric on both the injury and the restoration side of the equation (i.e. production by trophic level), which is essential for the restoration to be compensatory.

There is substantial uncertainty associated with estimating the benefits of habitat restoration to the injured biota. The quantitative scaling methods developed here are based solely on production, justified by arguing that production serves as a proxy for most important ecosystem functions, including provision of food, and nutrient cycling. One limitation to this approach is a failure to include organism size in the accounting. A way to address this limitation would be to partition the trophic-level analysis not only by species but also by size class. In addition, the food web could be more accurately depicted by using weighted average trophic steps (such as in Odum & Heald 1975). Finally, benefits of restoration could be assessed using other measures of habitat function as future research more clearly identifies and quantifies ecosystem services.

Compensatory restoration on a species-by-species basis could be carried out in a fashion designed to replace ecosystem and human services provided by all injured species. However, because of the operation of complex webs of interactions among species within the ecosystem, projects that benefit one species may adversely impact others. For example, protection of a



prey species from predators would presumably reduce production of the predators. The use of habitat restoration to restore many species simultaneously is more likely to achieve the intended net benefits to the ecosystem as a whole and help maintain biodiversity, important goals of environmental conservation (Wilson & Peters 1988).

Habitat restoration also involves a substantial degree of uncertainty. Creating one desired habitat involves destroying an equal area of another. Careful consideration needs to be given to the loss of the original habitat and the direct and interactive role that this habitat plays in the marine ecosystem. In response to uncertainty in estimating the necessary scale of restoration needed for compensation, and in performance of the restoration project, quantitative monitoring metrics (such as achieving certain levels of productivity at defined times) should be included in restoration planning (Fonseca et al. 1998, Julius 1999). The degree of success in restoring ecosystem functions and services depends on the ability to adaptively manage the restoration efforts based on results of a thorough monitoring plan (Fonseca et al. 1998). In mitigating for environmental injuries, uncertainty is often handled by requiring the scale of mitigation to exceed what is necessary to replace the loss by some mitigation ratio that increases with uncertainty. For example, ratios of 2 to 3 acres of restoration for each acre of salt marsh lost are commonly used (Thayer 1992). The trophic scaling model developed here may help reduce the uncertainty in habitat restoration by using growing scientific understanding of habitat function to quantify benefits to the ecosystem.

*Acknowledgements.* Support for this work was provided by NOAA (the National Oceanographic and Atmospheric Administration). We thank Carol-Ann Manen and John Catena for their guidance and all the 'North Cape' oil spill trustees for thoughtful contributions. Mike Donlan provided administrative assistance and critical review. Comments and editorial suggestions by C. H. Peterson and anonymous reviewers are gratefully acknowledged.

#### LITERATURE CITED

- Adam P (1993) Saltmarsh ecology. Cambridge University Press, Cambridge
- Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641
- Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2003) The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* No. 11. Ecological Society of America, Washington, DC (available at [www.esa.org/sbi/sbi\\_issues/](http://www.esa.org/sbi/sbi_issues/))
- Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7: 460–468
- Burke MV, Mann KH (1974) Productivity and production: biomass ratios of bivalve and gastropod populations in an eastern Canadian estuary. *J Fish Res Board Can* 31: 167–177
- Burkholder JM, Mason KM, Glasgow HB Jr (1992) Water-column nitrate enrichment promotes decline of eelgrass *Zostera marina*: evidence from seasonal mesocosm experiments. *Mar Ecol Prog Ser* 81:163–178
- Buzzelli CP, Wetzel RL, Meyers MB (1998) Dynamic simulation of littoral zone habitats in lower Chesapeake Bay. 2. Seagrass habitat primary production and water quality relationships. *Estuaries* 21:673–689
- Cobb JS, Clancy M, Wahle RA (1999) Habitat-based assessment of lobster abundance: a case study of an oil spill. *Am Fish Soc Symp* 22:285–298
- Cohen EB, Grosslein MD, Sissenwine MP, Steimle F, Wright WR (1982) Energy budget of Georges Bank. In: Mercer MC (ed) *Multispecies approaches to fisheries management advice*. *Can Spec Publ Fish Aquat Sci* 59:95–107
- Covi MP, Kneib RT (1995) Intertidal distribution, production dynamics and production of the amphipod *Uthlorchestia spartinophilia* in a Georgia, USA, salt marsh. *Mar Biol* 121: 447–455
- Curran CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Mar Ecol Prog Ser* 121:99–116
- Fonseca MS, Kenworthy WJ, Colby DR, Rittmaster KA, Thayer GW (1990) Comparison of fauna among natural and transplanted eelgrass *Zostera marina* meadows: criteria for mitigation. *Mar Ecol Prog Ser* 65:251–264
- Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. NOAA Coastal Ocean Program Decision Analysis Series No 12, NOAA Coastal Ocean Office, Silver Spring, MD
- Fredette TJ, Diaz RJ, van Montfrans J, Orth RJ (1990) Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in lower Chesapeake Bay. *Estuaries* 13:431–440
- French DP, Rines H (1998) Estimation of losses in the salt ponds resulting from water column and sediment acute toxicity from the North Cape oil spill. NOAA Damage Assessment Center, Silver Spring, MD (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- French DP, Reed M, Jayko K, Feng S and 16 others (1996a) The CERCLA type A natural resource damage assessment model for coastal and marine environments (NRDAM/CME), technical documentation, Vol I–V. Final Report, Contract No. 14-0001-91-C-11, Office of Environmental Policy and Compliance, US Department of the Interior, Washington, DC
- French DP, Rines H, Gifford D, Keller A and 7 others (1996b) Primary restoration: guidance document for natural resource damage assessment under the Oil Pollution Act of 1990. NOAA Damage Assessment and Restoration Program, Silver Spring, MD
- French McCay DP (2002) Development and application of an oil toxicity and exposure model, OilToxEx. *Environ Toxicol Chem* 21:2080–2094
- French McCay DP (2003) Development and application of damage assessment modeling: example assessment for the North Cape oil spill. *Mar Pollut Bull* 47:341–359
- French McCay DP, 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 DP, 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)
- Grodzinski W, Wunder BA (1975) Ecological energetics of small mammals. In: Golley FB, Petrusewicz K, Ryszkowski L (eds) *Small mammals: their productivity and population dynamics*. Cambridge University Press, Cambridge, p 173–204
- Heck KL Jr, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy VS (ed) *Estuarine perspectives*. Academic Press, New York, p 449–464
- Heck KL Jr, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macrofauna in a New England estuary: comparisons among eelgrass meadows and other nursery habitats. *Estuaries* 18:379–389
- Heck KL Jr, Hays C, Orth RJ (2003) A critical evaluation of the nursery role hypothesis for seagrass meadows. *Mar Ecol Prog Ser* 253:123–136
- Hinga KR (1988) Seasonal predictions for pollutant scavenging in two coastal environments using a model calibration based on Thorium scavenging. *Mar Environ Res* 26:97–112
- Hinga KR (1997) Concentrations over time of North Cape oil in water and sediments in Rhode Island's south shore ponds. Report by University of Rhode Island, Narragansett, to NOAA Damage Assessment Center, Silver Spring, MD (part of case administrative record, available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- Howes BL, Dacey JWH, Teal JM (1985) Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology* 66:595–605
- Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Mar Ecol Prog Ser* 240:11–20
- Julius B (1999) Discounting and the treatment of uncertainty in natural resource damage assessment. Technical Paper 99-1, NOAA Damage Assessment and Restoration Program, Silver Spring, MD
- Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr Mar Biol Annu Rev* 35:163–220
- 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)
- Kreeger DA, Newell RIE (2000) Trophic complexity between producers and invertebrate consumers in salt marshes. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 187–220
- Matthews GA, Minello TJ (1994) Technology and success in restoration creation, and enhancement of *Spartina alterniflora* marshes in the United States, Vol 2. Inventory and Human Resources Directory. NOAA Coastal Ocean Program Decision Analysis Series No 2. NOAA Coastal Ocean Office, Silver Spring, MD
- McNeill S, Lawton JH (1970) Annual production and respiration in animal populations. *Nature* 225:472–474
- Minello TJ, Webb JW (1997) Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Mar Ecol Prog Ser* 151:165–179
- Minello TJ, Zimmerman RJ (1992) Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. *Mar Ecol Prog Ser* 90:273–285
- Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Mar Ecol Prog Ser* 246:39–59
- Moy LD, Levin LA (1991) Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. *Estuaries* 14:1–16
- Newell SY, Porter D (2000) Microbial secondary production from salt marsh-grass shoots, and its known and potential fates. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 159–185
- Nixon SW, Oviatt CA (1973) Ecology of a New England salt marsh. *Ecol Monogr* 43:463–498
- NOAA (National Oceanic and Atmospheric Administration) (1997) Natural resource damage assessment guidance document: scaling compensatory restoration actions (Oil Pollution Act of 1990). NOAA Damage Assessment Center, Silver Spring, MD
- NOAA (National Oceanic and Atmospheric Administration) (1999) Habitat equivalency analysis: an overview. NOAA Damage Assessment Center, Silver Spring, MD
- NOAA (National Oceanic and Atmospheric Administration) (2002) Natural resource damage assessments, final rule. *US Federal Register* 67(190):61483–61493 (available at <http://wais.access.gpo.gov> [DOCID:fr01oc02–8])
- NOAA (National Oceanic and Atmospheric Administration), Rhode Island Department of Environmental Management, US Department of the Interior, and US Fish and Wildlife Service (1999) Restoration plan and environmental assessment for the January 19, 1996 North Cape oil spill. Revised Draft for Public Comment, NOAA, Silver Spring, MD (available at [www.darp.noaa.gov/neregion/ncape.htm](http://www.darp.noaa.gov/neregion/ncape.htm))
- Odum EP (1971) *Fundamentals of ecology*. WB Saunders, Philadelphia
- Odum E, de la Cruz A (1967) Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. In: Lauff G (ed) *Estuaries*. American Association for the Advancement of Science Publication No. 83, Washington, DC, p 383–388
- Odum WE, Heald EJ (1975) The detritus based food webs of an estuarine mangrove. In: Cronin LE (ed) *Estuarine research, Vol I. Chemistry, biology and the estuarine system*. Academic Press, New York, p 265–286
- Orth RJ, Moore KA (1983) Chesapeake Bay—an unprecedented decline in submerged aquatic vegetation. *Science* 222:51–53
- Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374:255–257
- Peirson WM (1983) Utilization of eight algal species by the bay scallop, *Argopecten irradians concentricus* (Say). *J Exp Mar Biol Ecol* 68:1–11
- PERL (Pacific Estuarine Research Laboratory) (1990) A manual for assessing restored and natural coastal wetlands with examples from southern California. California Sea Grant Report No. T-CSGCP-021, La Jolla, CA
- Pimm SL (1982) Food webs. Chapman & Hall, New York
- Roman CT, Able KW, Lazzari MA, Heck KL (1990) Primary productivity of angiosperm and macroalgae dominated habitats in a New England salt marsh: a comparative analysis. *Estuar Coast Shelf Sci* 30:35–45
- Ryther JH (1969) Photosynthesis and fish production in the sea. *Science* 166:72–76
- Sarda R, Foreman K, Valiela I (1995) Macroinfauna of a

- southern New England salt marsh: seasonal dynamics and production. *Mar Biol* 121:431–445
- Seneca ED, Broome SW (1992) Restoring tidal marshes in North Carolina and France. In: Thayer GW (ed) Restoring the nation's marine environment. Maryland Sea Grant College Program, College Park, MD, p 53–78
- Short FT, Burdick DM (1996) Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19:730–739
- Short FT, Burdick DM, Kaldy JE (1995) Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnol Oceanogr* 40:740–749
- Short FT, Burdick DM, Granger S, Nixon SW (1996) Long-term decline in eelgrass, *Zostera marina* L., linked to increased housing development. In: Kuo J, Phillips RC, Walker DI, Kirkman H (eds) Seagrass biology. Proc Int Workshop, Rottneest Island, Western Australia, 25–29 January 1996. University of Western Australia, Nedlands, WA, p 291–298
- Slobodkin LB (1960) Ecological energy relationships at the population level. *Am Nat* 95:213–236
- Steele JH (1974) The structure of marine ecosystems. Harvard University Press, Cambridge, MA
- Sullivan MJ, Currin CA (2000) Community structure and functional dynamics of benthic microalgae in salt marshes. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, p 81–106
- Teal JM (1962) Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624
- Thayer GW (ed) (1992) Restoring the nation's marine environment. Maryland Sea Grant College Program, College Park, MD
- Thayer GW, Kenworthy WJ, Fonseca MS (1984) The ecology of eelgrass meadows of the Atlantic coast: a community profile. Report No. FWS/OBS-84/02, US Fish and Wildlife Service, Washington, DC
- Thorne-Miller B, Harlin MM (1984) The production of *Zostera marina* L. and other submerged macrophytes in a coastal lagoon in Rhode Island, USA. *Bot Mar* 27:539–546
- Valiela I, Teal JM, Persson NY (1976) Production and dynamics of experimentally enriched salt marsh vegetation: below ground biomass. *Limnol Oceanogr* 21:245–252
- Van Raalte CD, Valiela I, Teal JM (1976) Production of epibenthic salt marsh algae: light and nutrient limitation. *Limnol Oceanogr* 21:862–872
- Warren RS, Fell PE, Rozsa R, Brawley AH, Orsted AC, Olson ET, Swamy V, Niering WA (2002) Salt marsh restoration in Connecticut: 20 years of science and management. *Restor Ecol* 10:497–513
- Whittaker RH (1975) Communities and ecosystems, 2nd edn. MacMillan Publishing, New York
- Williams GD, Zedler JB (1999) Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: relative influence of channel morphology and restoration history. *Estuaries* 22:702–716
- Wilson EO, Peters FM (eds) (1988) Biodiversity. National Academy Press, Washington, DC
- Zedler JB (1992) Restoring cordgrass marshes in southern California. In: Thayer GW (ed) Restoring the nation's marine environment. Maryland Sea Grant College Program, College Park, MD, p 7–51

*Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA*

*Submitted: August 4, 2003; Accepted: November 24, 2003  
Proofs received from author(s): December 9, 2003*



# Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation

Charles H. Peterson<sup>1,\*</sup>, Jonathan H. Grabowski<sup>1</sup>, Sean P. Powers<sup>2</sup>

<sup>1</sup>Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA

<sup>2</sup>Department of Marine Sciences, University of South Alabama and Dauphin Island Sea Lab, Dauphin Island, Alabama 36528, USA

**ABSTRACT:** We reviewed studies providing quantitative measurements of abundance of fishes and large mobile crustaceans on oyster reefs and on nearby sedimentary habitat in the southeast United States. For each species, we compared density by size (age) class on oyster reefs and sedimentary bottom as a means of estimating the degree to which restoration of oyster reef on sedimentary bottom could augment abundances. By applying published information on growth rates of each species and a combination of empirical data and published information on age-specific survivorship, we calculated the per-unit-area enhancement of production of fishes and large mobile crustaceans expected from the addition of oyster reef habitat. For this calculation, we gave the reef habitat full credit for the expected lifetime production of species whose recruitment was judged to be limited by the area of oyster reefs based on nearly exclusive association of recruits to reefs. For species that were only modestly enhanced in abundance by oyster reefs, we gave the reef credit for the fraction of production that is derived from consumption of reef-associated prey, using a combination of gut content data and natural history information. This combination of analyses and calculations revealed that 10 m<sup>2</sup> of restored oyster reef in the southeast United States is expected to yield an additional 2.6 kg yr<sup>-1</sup> of production of fish and large mobile crustaceans for the functional lifetime of the reef. Because the reef is biogenic and self-sustaining, the lifetime of a reef protected from bottom-disturbing fishing gear is limited by intense storms or sedimentation. A reef lasting 20 to 30 yr would be expected to augment fish and large mobile crustacean production by a cumulative amount of 38 to 50 kg 10 m<sup>-2</sup>, discounted to present-day value. This set of calculations assumes that oyster reef habitat now limits production of reef-associated fish and crustaceans in the southeast United States. This assumption seems reasonable based on the tight associations of so many fishes with reef-dependent prey, and the depletion of reef habitat over the past century.

**KEY WORDS:** Habitat restoration · Oyster reef · Fish production · Mitigation · Restoration scaling · Essential fish habitat

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

The application of ecology to achieve explicit goals in conservation and restoration represents a challenge to the discipline, and typically demands novel syntheses of relevant data and conceptual theory (Carpenter & Kitchell 1993, Peterson 1993, Lawton 1996). Because of societal demands to compensate for growing degradation of natural resources on land (Vitousek et al.

1997) and in the sea (Botsford et al. 1997), recent growth in the practice of restoration has been so dramatic that restoration ecology is anticipated to become a dominant focus of environmental science of the new century (Wilson 1992, Hobbs & Harris 2001). Ecological restorations have generally proceeded faster than the development of the theoretical and conceptual bases which support them (Allen et al. 1997, Palmer et al. 1997, van Diggelen et al. 2001). While the history of



restoration of wetlands, terrestrial plant systems, salt marshes, and seagrass beds is relatively long (Jordan et al. 1987, Thayer 1992), restoration of marine biogenic habitats created by animals, such as corals, oysters, mussels, polychaetes, and vermetid gastropods, is a new development (Coen & Luckenbach 2000). For oyster reefs, even their wide recognition as an important biogenic habitat rather than merely a commodity to exploit is very recent (Lenihan & Peterson 1998).

Oyster reef habitat provides numerous important ecosystem services, which have only recently been documented and quantified. Oyster reefs serve as important biogenic habitat for benthic invertebrates (Wells 1961, Zimmerman et al. 1989) as well as fishes and mobile crustaceans (Bahr & Lanier 1981, Breitbart 1999, Coen et al. 1999, Lenihan et al. 2001). Through their filtration activities, oysters and other suspension-feeding bivalves also help counteract impacts of estuarine eutrophication (Jackson et al. 2001). Feeding oysters remove suspended inorganics, phytoplankton, and detrital particles, thereby reducing turbidity and improving water quality (Dame 1996). Biodeposits from feces and pseudofeces of oysters accumulate around reefs and induce denitrification (Newell et al. 2002). Oyster reefs sequester carbon in the form of calcium carbonate of the accumulating shell matrix (Hargis & Haven 1999), and thus contribute to global carbon budgets. Through their removal of organic particles in the water column, oysters divert energy to benthic food chains and depress pelagic energy flows that may otherwise lead to noxious sea nettles (Newell 1988). Furthermore, the physical structure of a fringing oyster reef can serve to protect salt marsh habitat by dissipating erosive wave energy (Meyer et al. 1996). Oysters and the reefs that they build have been depleted dramatically in many estuaries of the southeast USA and the world (Rothschild et al. 1994, Lenihan & Peterson 1998), motivating restoration efforts.

In part because of the short history of recognition of oyster reefs as important fish habitat, no estimates have been generated of how much additional fish production might be reasonably expected from restoring an oyster reef. Such an understanding is important in designing restoration projects to compensate for losses in fish production from chemical spills or some other environmental incident. In the USA, the National Oceanographic and Atmospheric Administration (NOAA) and other natural resource trustees use 'habitat equivalency analysis' to determine how to scale a restoration project to match, and therefore compensate for, the quantified injury to natural resources (e.g. NOAA 1997, Fonseca et al. 2000). This process seeks to replace lost ecosystem services, which are commonly based upon the lost production of higher trophic levels, such as fish and large mobile crustaceans. Losses

include not only the biomass killed but also the interim losses associated with production foregone that would have been expected had those individuals been able to live their full natural life spans (French 1999).

Quantifying the expected enhancement of production by fish and large mobile crustaceans from creation of an oyster reef requires consideration of some of the most fundamental questions in fisheries ecology. First, one must address whether the recruitment of any species of fish is limited by the extent of available reef habitat. If addition of reef habitat serves to overcome a survival bottleneck in the early life history of any species, then installation of additional reefs would promote a numerical response of enhanced recruitment in those species. Because oyster reef habitat has declined dramatically by 2 orders of magnitude in many estuaries of the southeastern USA (Rothschild et al. 1994, Lenihan & Peterson 1998), we assume that any species exhibiting greatly enhanced abundance of recruits on reefs, relative to nearby unstructured sedimentary habitats, is limited in recruitment by oyster reef area. By recruitment, we adopt the marine ecologists' usage referring to individuals surviving early post-settlement mortality to a size that can be reliably censused (Doherty & Williams 1988). Second, new reefs may enhance fish production by providing spatial refuges from predation and alleviating food limitation through producing reef-associated prey resources. This response then enhances fish production, not by adding new fish to the system, but rather by enhancing survival and subsidizing growth of individuals already present in the regional population and thereby producing gains in fish production. The enhanced survival that may result from provision of structural refuges from predation (Hixon 1998) is incorporated into both of these measures of reef impact on fish production, because enhanced densities of both recruits and older fishes on reefs reflect effects of the reef on survival.

Here we utilize these concepts of habitat and food limitation on fish production on oyster reefs to estimate the augmented production of fish and large mobile crustaceans expected per unit area of created oyster reef. We focus our analysis on southwest Florida to develop information that would allow compensation for losses of fish production arising from an acidic process water spill in a Tampa Bay tributary. Losses of production by fish, shrimp, and crabs from that spill had been determined by sampling the numbers of dead organisms of each species by age class to estimate the immediate loss of biomass, and then using published survival and age-specific growth curves to calculate the future production foregone by their untimely loss (French 1999). We follow this same approach of calculating the ecosystem service of fish production provided by installation of oyster reefs so as

to allow losses to be matched to gains from restoration in an identical currency (a habitat equivalency analysis: Fonseca et al. 2000). To develop our estimates, we draw upon data from available published and gray literature from the southeast USA, thereby rendering the calculations applicable to a broad biogeographic region. This approach should be transferable to quantifying oyster reef services elsewhere.

### MATERIALS AND METHODS

**Overview.** To quantify the enhancement in fish and mobile crustacean production expected per unit area of added oyster reef habitat, we adopted the following procedure (Fig. 1) to estimate the contributions by (1) species limited in recruitment by habitat area (termed recruitment-enhanced), and (2) species limited in production by reef refuges from predation and available food (growth-enhanced). We synthesized results of available empirical, quantitative studies from the southeast USA to estimate the magnitude of density enhancement for each species of fish and mobile crustacean on oyster reefs relative to unstructured

sedimentary habitat. First, species showing no numerical association with reefs made no contribution to our estimate of enhancement of fish production by reefs. Second, we identified species whose recruitment was habitat-limited based on nearly exclusive association of recruits with oyster reefs instead of mud/sand habitat, and on life-history information indicating obligate association with structural features of benthic habitat. The remaining species formed a third class that was not limited in recruitment by reef habitat but whose growth and survival was limited by reef-associated resources, as judged by significant augmentation of abundance on oyster reefs as opposed to mud/sand habitats. We then calculated the average augmentation of abundance per unit reef area by species and by age class within species. Published species-specific growth and survivorship parameters were then used to convert the augmented abundance by age class into expected enhancement of lifetime production for each species. For each species judged not to be limited in recruitment by reef area, but instead limited in production, we used dietary information to calculate an index of reef exclusivity in feeding so as to credit the oyster reef for only that fraction of growth derived from

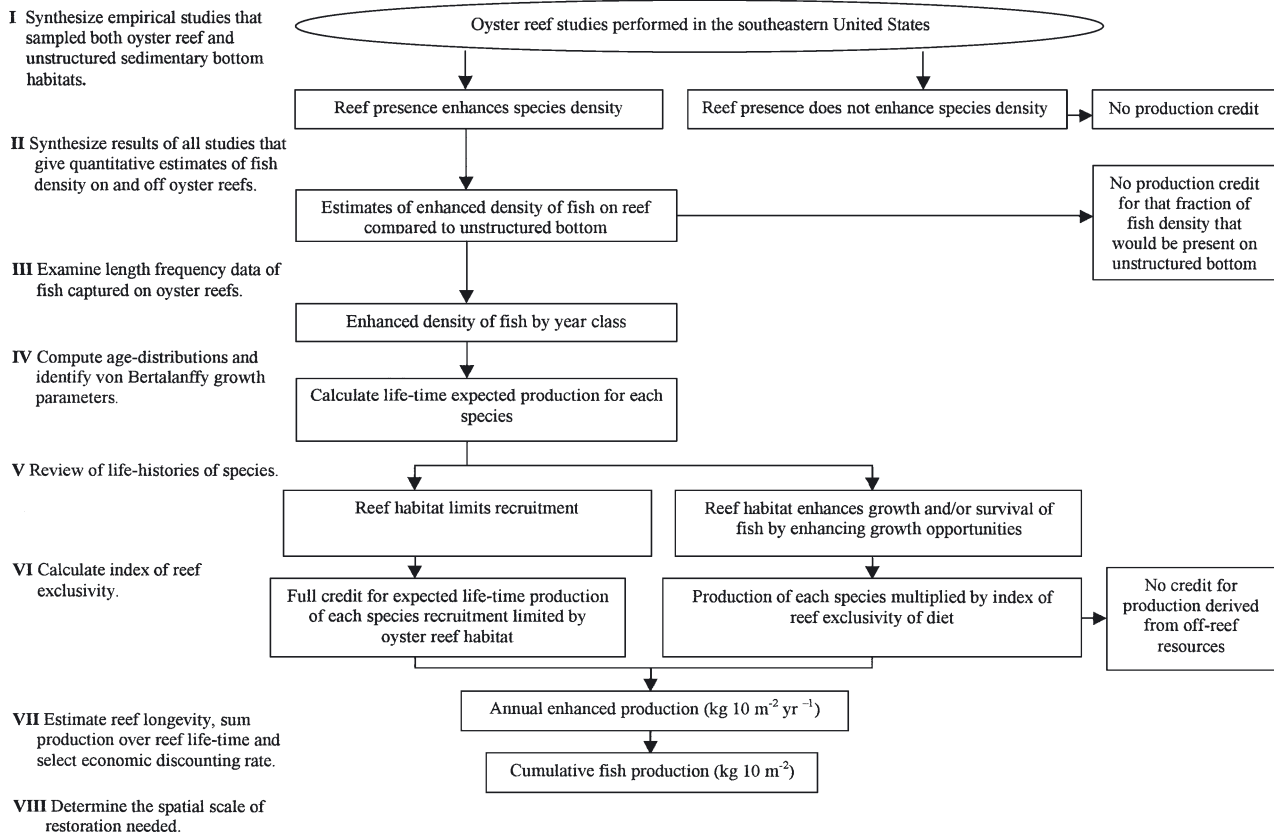


Fig. 1. Flow diagram illustrating our approach to calculating expected enhancement of fish and mobile crustacean production resulting from the restoration of oyster reefs in the southeastern USA

reef-associated prey. Partitioning growth by prey source helps address the long-standing question of whether reefs simply aggregate fish or increase their production by providing reef-associated prey resources (Bohnsack 1989). We then summed these reef-dependent enhancement estimates across all species to produce the total expected enhancement of fish and crustacean production per unit reef area. Finally, economic discounting was applied to amend these calculations to account for the time value of resources and services in matching resource loss to resource gain through creation of oyster reefs.

**Synopsis of studies.** Six studies conducted in the southeastern USA (Fig. 2) formed the basis of our synthesis (Table 1). Zimmerman et al. (1989) used 2.6 m<sup>2</sup> circular drop samplers to quantify animals that use shallow, subtidal oyster reefs and adjacent sand/mud habitats in the West Bay region of Galveston Bay, Texas. Wenner et al. (1996) quantified fish and mobile crustaceans on both restored and natural oyster reefs near Charleston Harbor, South Carolina. Their study used 3.2 mm-mesh lift nets, which were folded and buried along the perimeter of oyster reef and then raised on a falling tide to enclose the entire area (24 m<sup>2</sup>). Meyer et al. (1996) used block and fyke nets to quantify fish and mobile crustaceans in 3 *Spartina* marsh-edge habitats (bordered by restored oyster reef, natural oyster reef or unstructured bottom) at each of 3 sites in North Carolina. Two block nets (19.3 m long × 1.3 m high with 3.2 mm mesh) were positioned perpendicular to the shoreline, and a 1.3 m high fyke net

with 3 m wings was placed along the 5 m long, low-tide mark. Nets were set on a falling tide and animals collected at low tide. Grabowski (2002) used a variety of sampling gear (gill nets, crab traps, fish traps, minnow traps, and 1 m<sup>2</sup> colonization trays filled with oyster shell) to sample fish and mobile crustaceans on restored intertidal oyster reef and nearby unstructured bottom in Back Sound, North Carolina. Lenihan et al. (1998, 2001) used the same gear as Grabowski (2002), along with visual observations, to sample restored and natural oyster reefs and nearby sand/mud bottom in subtidal areas of the Neuse River estuary and West Bay, Pamlico Sound, North Carolina. Finally, investigators at the Virginia Institute of Marine Sciences (VIMS: Mann & Harding 1997, 1998, Harding & Mann 1999, O'Beirn et al. 1999) sampled fish and mobile crustaceans by otter trawl and gill nets at a large (210 × 30 m) restored oyster reef and 2 mud/sand flats in the Piankatank River, Virginia, and at several smaller restored reefs and unstructured bottom areas near Fisherman Island at the mouth of Chesapeake Bay.

**Relative enhancement estimates.** To evaluate the questions of whether and to what degree a species abundance was enhanced by the presence of oyster reef, we used only those 5 studies that sampled fish and mobile crustaceans both on oyster reef and on adjacent unstructured habitat (Zimmerman et al. 1989, Meyer et al. 1996, Lenihan et al. 1998, 2001, the VIMS studies [see above], and Grabowski 2002). We compiled data on comparisons of fish and mobile crustacean catches on oyster reefs to nearby unstructured

bottom. The results from each of the 5 studies were then summarized into 1 database that computed the ratio of catch on-reef to catch off-reef for each sampling period by gear type (see Table 5). When a ratio could not be calculated because a species occurred in a single habitat, that fish or mobile crustacean was designated as 'all reef' or 'all mudflat'. A species was judged to be enhanced in abundance by the presence of an oyster reef if a majority of studies either had index values above 1 or indicated 'all reef' (see Table 5). In cases where only 1 study reported data for a given species, we used the more conservative threshold of >2 to declare a species enhanced by reef presence.

We next assigned each species of fish and crustacean judged to be enhanced by the presence of oyster reef to 1 of our 2 conceptual groupings: (1) recruitment-enhanced and (2) growth-enhanced

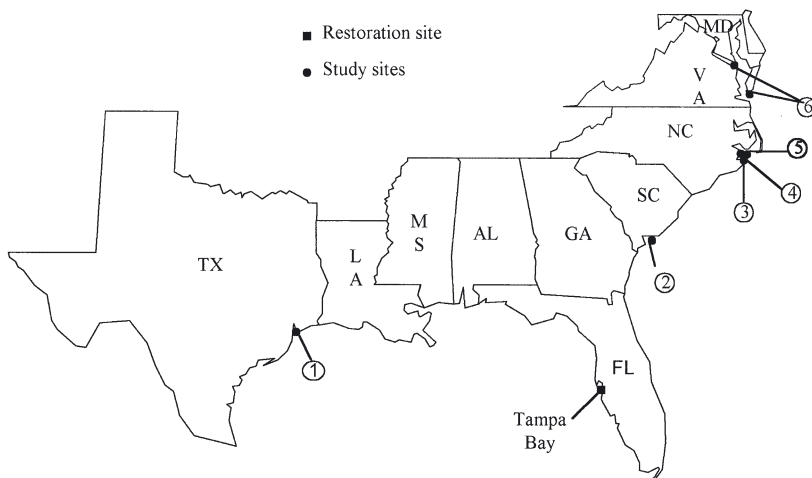


Fig. 2. Southeastern USA, with the sites of empirical studies used in our synthesis noted by filled circles and the targeted restoration site, Tampa Bay, FL, noted by the filled square. Numbers identify the location and sources of data: (1) Galveston Bay, TX, Minello & Zimmerman (1989); (2) Charleston Harbor, SC, Wenner et al. (1996); (3) Back Sound, NC, Grabowski (2002); (4) Back Sound, White Oak River and New River, NC, Meyer et al. (1996); (5) Neuse River and Pamlico Sound, Lenihan et al. (1998, 2001); and (6) Chesapeake Bay, VA, Mann & Harding (1997, 1998), Harding & Mann (1999), O'Beirn et al. (1999)

Table 1. Summary of some key features of the 6 studies used in our data synthesis. For number of reefs restored, date of reef construction is included in parentheses; sampling method lists only sampling methods that were used to determine whether reefs enhance fish abundance and/or to estimate fish density

Location	Depth	Off-reef control (n)	Natural-reef reference (n)	No. of restored reefs	Sampling method	Sampling date(s)	Source
Galveston Bay, TX	0.5 m	Yes (3)	Yes (3)	None	2.6 m <sup>2</sup> drop-sampler	Summer and Fall 1988	Zimmerman et al. (1989)
Inlet Creek, SC	Intertidal	None	Yes (3)	3 (Oct 1994)	24 m <sup>2</sup> lift net	Spring, Summer and Fall 1995	Wenner et al. (1996)
Toler's Cove, SC	Intertidal	None	Yes (3)	3 (Oct 1994)	Block & fyke nets, 1/4 m <sup>2</sup> excavations	Nets: Spring, Summer and Fall 1993, 1994 at all sites	Meyer et al. (1996)
New River, NC	Intertidal	Yes (6)	Yes (6)	6 (Aug 1992)		Excavations: Fall 1992, Spring and Summer 1993 and 1994 at all sites	
White Oak River, NC	Intertidal	Yes (6)	Yes (6)	6 (Aug 1992)			
Back Sound, NC	Intertidal	Yes (6)	Yes (6)	6 (Aug 1992)			
Middle Marsh, NC	Intertidal	Yes (12)	None	12 (Jul 1997)	Gill nets, colonization trays, fish, minnow and crab traps	Monthly Summer and Fall 1997 Spring to Fall 1998, 1999	Grabowski (2002)
Neuse River, NC	3, 4, 6 m	Yes (4)	None	4 (Jun 1993)	Gill nets, fish traps and diver census	Monthly Summer and Fall 1996	Lenihan et al. (1998, 2001)
West Bay, NC	3 m	Yes (8)	None	8 (Jul 1996)		Spring and Summer 1997	
Plankatank River, VA	Intertidal	Yes (2)	None	1 (Jul 1993)	Gill nets, otter trawls above reef and reef perimeter	Semimonthly Spring and Summer 1996, 1997	Mann & Harding (1997, 1998), Harding & Mann (1999)
Fisherman Island, VA	Intertidal	Yes (multiple)	None	13 (2 in 1995, 11 in 1996)	Gill nets, otter trawls above reef and reef perimeter	~ Monthly Summer 1998 to Spring 1999	O'Beirn et al. (1999)

species. Our distinction between these 2 classes was based on the magnitude of enhancement as well as a careful review of life-history information. Our practice was to assign demersal species that had nearly exclusive occupation of oyster reefs as recruits (demonstrated by a majority of studies characterizing that species as 'all reef') to the first group, and those demersal species that showed more moderate enhancement plus pelagic species showing all levels of enhancement to the second group.

Because comparisons of catches occurred between 2 different habitats, we must consider potential differential biases in sampling efficiency between habitats (*sensu* Peterson & Black 1994). Crab pots, fish-traps, minnow pots, and colonization trays constitute structural elements: fish may be attracted to such structures in greater numbers in an unstructured environment than in a highly structured one (Sheaves 1992). Any bias of this nature would result in a more conservative estimate of our enhancement ratio. Similarly, any biases in trawling would tend to produce artificially low catches of animals on reefs because of the difficulty of towing trawls over highly structured reef areas.

**Density estimates.** After we had determined that a particular species was enhanced in abundance by the presence of oyster reef habitat, we then assessed whether that species or a close ecological counterpart occurred at the targeted restoration site, Tampa Bay, Florida (using faunal listings in Livingston 1984, 2001, Lewis & Estevez 1988). Next, we addressed the issue of sampling efficiency for each gear type used in the 6 studies. Of these studies, only Zimmerman et al. (1986, 1989) and Wenner et al. (1996) tested gear efficiency against a known standard number of fish and invertebrates. Zimmerman et al. (1986) found that recovery efficiency of their 2.6 m<sup>2</sup> drop samplers was 96% for small invertebrates. Efficiency of lift nets in Wenner et al. (1996) ranged from 54 to 68.5% for a small benthic fish (*mummichog*) and 43 to 54% for a benthic invertebrate (*grass shrimp*). Testing a similar lift net, Rozas (1992) had previously shown catch efficiencies of 32 to 93%. Because these methods demonstrated relatively high sampling efficiencies and wide ranges among and within species, we did

not use any correction factor for densities measured with drop samplers or lift nets.

One of 2 alternative procedures was employed to estimate the quantitative enhancement on a per-unit-area basis for each species whose abundance was judged to be enhanced by oyster reefs. For those species collected by Zimmerman et al. (1989) and/or Meyer et al. (1996) that sampled a defined area, we used their estimates (averaged across studies for any species that appeared in both studies) of absolute density on and off reefs. For reef-enhanced species that were not collected in Zimmerman et al. (1989) or Meyer et al. (1996), estimates were derived from trap catches in Lenihan et al. (2001) and Grabowski (2002) and converted to densities. The 'habitat traps' or 'M-traps' used by Lenihan et al. (2001) and Grabowski (2002) lacked standardization to the area sampled. Thus, to convert their data on differences between average catches on reefs and sand/mud flats to density enhancement per unit area, we standardized abundances of fish caught on reefs in traps by the observed densities on reefs in lift nets taken from Wenner et al. (1996) for gray snapper and pigfish (pooled), species common to all 3 studies. The resulting conversion factor was applied to transform catches in traps to densities. For example, if the average density (from Wenner et al. 1996) of gray snapper plus pigfish on reefs is  $x$ , and the average numbers per habitat trap on reefs is  $y$ , then the conversion factor would be  $x/y$ . The VIMS studies were not used for density calculations because, for all species judged to be enhanced by oyster reefs, quantitative data existed in the other studies at sites geographically closer and environmentally more similar to the Tampa Bay restoration area.

To determine the expected enhancement of density for each species by oyster reef presence, we subtracted our off-reef average density from our on-reef density estimate. The rationale was that the off-reef density represents fish that would be present in the absence of reef habitat, and that the reef should be credited only for the enhancement of fish. With the exception of blennies, gobies and silversides, which consist of multiple species within each group, we calculated density enhancement by species. Because of similarity in life history, mortality rate, and functional niche, and differences in biogeographic ranges of sibling species, we grouped blennies, gobies, and silversides into 3 taxa. In estimating density enhancements, we chose to use data from the date of peak density for each species, which consistently occurred in summer or early fall. We averaged these seasonal maxima across studies (except for 3 species that occurred in only a single study) to provide density estimates reflective of the time of peak recruitment and utilization of the estuarine habitats.

**Age distributions of fish on reefs.** Once the estimate of enhanced density ( $N$ ) was calculated for a given species, we determined how various age classes ( $i$ ) contributed to that density (Table 2). Using published estimates of annual growth for each species (Table 3), we partitioned available length-frequency data of fish on reefs by age class ( $N_i$ ). This process sufficed for 3 taxa of small fishes that are readily caught and whose densities through all age classes are well estimated by lift nets (Table 2). For taxa (7 of the 11 total species that are not annuals) in which our quantitative sampling only provided reliable density estimates of 0 yr class individuals, we calculated expected abundances of older age classes based on (1) the known numbers of 0 yr-old recruits measured in the empirical studies, and (2) published estimates of their annual mortality rate (Table 3). We assumed that the distribution of age classes follows a stable age distribution, if annual mortality rate remains constant, using the formula:

$$S_i = S_0 \times e^{(-M \times i)} \quad (1)$$

where  $S_i$  is the proportion of individuals in age class ( $i - 1$ ) surviving to age class  $i$ , and  $M$  is the natural mortality rate for age class  $i$ . For species that are fished, mortality rate does not remain constant with age, but increases by the rate of fishing mortality ( $F$ ) added at the age of first harvest ( $r$ ). Thus, for harvested species,  $S_i$  was computed using Eq. (1) until  $i > r$ , when:

$$S_i = S_r \times e^{[-(M_i + F)(i - r)]} \quad (2)$$

The density of fish in age class  $i$  ( $N_i$ ) was then determined by multiplying  $N_{(i-1)}$  by the survival rate ( $Sx_i$ ) for  $i$ , calculated by using  $S_i$  and  $S_{(i-1)}$  from either Eq. (1) or (2), by

$$Sx_i = S_i / S_{(i-1)} \quad (3)$$

Table 2. Age classes observed in density estimates from field sampling for those species or species groups determined to be enhanced by oyster reef. Blenny and goby species are treated as annuals; consequently, only 1 age class was present in the population. The 0 yr class includes fish from the time they recruit to their first birthday

Species or species group	Age (yr) class(es) included in density estimate
Sheepshead	0
Stone crab	0
Gray snapper	0
Gag grouper	0
Black sea bass	0
Spottail pinfish	0
Pigfish	0
Toadfish	0, 1, 2
Sheepshead minnow	All
Bay anchovy	All
Silversides	All



Table 3. Values of survival rate, age-length and length-weight parameters used in production calculations. See 'Materials and methods' for definitions of parameters and computation formulae

Species or species group	Survival rates		Age-length and length-weight relationships			Source			
	$M$	$F$	$r$	$L_{\infty}$	$K$		$t_0$	$a$	$b$
Sheepshead minnow	2.00	0.00		19.4	0.130	-0.940	0.0087	3.27	Abraham (1985)
Bay anchovy	1.50	1.00	1	12.0	0.280	-1.100	0.0111	2.81	French et al. (1997)
Silversides	2.00	0.00		10.0	0.460	0.000	0.0138	2.96	Middaugh & Hemmer (1992)
Gobies									Annual species
Blennies									Annual species
Sheepshead	0.20	0.40	3	45.1	0.205	-1.540	0.0283	2.96	French 1999
Stone crab	0.70	0.30	3	14.0	0.173	-0.397	0.1170	3.30	Savage & Sullivan (1978), Sullivan (1979), Lindberg & Marshall (1984), Millikin & Williams (1984)
Gray snapper	0.20	0.53	2	50.1	0.130	-1.490	0.0156	2.93	Manooch & Mason (1984), Goodyear (1988), Brown et al. (1990), Goodyear & Schirripa (1991)
Toadfish	0.60	0.00		30.0	0.193	-0.180	0.0170	4.98	Wilson et al. (1982), Seraty et al. (1997)
Gag grouper	0.20	0.53	2	119.0	0.166	-0.740	0.0140	2.99	Manooch & Haimovici (1978), Goodyear (1988), Brown et al. (1990), Goodyear & Schirripa (1991), Hood & Schlieder (1992)
Black sea bass	0.30	0.30	3	35.0	0.222	0.186	0.0280	3.02	South Atlantic Fishery Management Council (1983)
Spottail pinfish	0.60	0.40	1	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)
Pigfish	0.60	0.40	1	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)

Using this calculation procedure, we compensate for the underestimation of density of larger, older fish by assuming that the expected numbers of older age classes are indeed present. This addition of ghost fish to our estimate of enhanced density makes the assumption that the older fish continue to utilize reef habitat, which was confirmed by both visual observations and gill net samples. For one species (toadfish), the quantitative sampling by traps and lift nets provided reliable estimates of densities of the first 3 age classes, but no fish in the remaining 5 age classes (Table 2). To estimate densities of these rarer, older age classes, we first applied the age-specific mortality rates to the sum of abundances of the 3 early age classes to compute the expected distribution of abundances among those 3 age classes. This computation allowed us to depreciate the numbers in the oldest (third) age class by applying the age-specific mortality schedule to estimate numbers of fish beyond age class 3. The sum of numbers of fish in the 3 early age classes remained constant, but the total numbers were augmented by ca. 14 % when older ghost fish were added.

**Production calculations.** We chose an area of 10 m<sup>2</sup> over which to calculate our estimated enhancement of annual production of fishes and large mobile crustaceans by oyster reefs. Using our estimate of enhanced density in each age class, we quantified how much annual production each age class would be expected to achieve, and summed these production estimates over all ages to estimate total annual enhanced production for each species. Our computation assumed that the 0 yr-class recruits, assessed in most studies at an age of approximately 1/2 yr, would all survive to their first birthday. This overestimate of annual production by fish surviving from their half birthday to their first birthday is assumed to compensate for the failure to include estimates of production of those other fish in that same age cohort that had recruited to the reefs and grew to some size but died before sampling occurred on the half birthday. For annual species (gobies and blennies), we calculated annual production by multiplying average fish weight by the estimate of density enhancement. For all other species, we first calculated the average length at age  $i$  ( $L_i$ ) using the von Bertalanffy growth equation:

$$L_i = L_{\infty} \times \{1 - e^{-K \times (i - t_0)}\} \tag{4}$$

where  $L_{\infty}$  (the asymptotic maximum length),  $K$  (the Brody growth coefficient), and  $t_0$  (a constant representing the age at zero length) are derived from literature values for each species (Table 3). To convert  $L_i$  to an average weight at age  $i$  ( $W_i$ ), we used the length-weight relationship:

$$W_i = a \times L_i^b \tag{5}$$

where  $a$  and  $b$  are species-specific constants available from the literature (Table 3). The change in weight between successive age classes is equal to the annual production of an individual surviving through age class  $i$  ( $P_i$ ):

$$P_i = W_i - W_{(i-1)} \quad (6)$$

We treated the 2 groups of fishes deemed 'enhanced by reef presence' differently, in calculating the enhanced annual production credited to the construction of 10 m<sup>2</sup> of oyster reef. For recruitment-enhanced species, we credited their complete expected lifetime production to the reef, independent of whether they fed on reef-associated resources or even remained on the reef after recruitment. Our rationale is that these additional individuals that recruit to the reef would not be present in the population in the absence of the reef. Two of the augmented species, gag grouper and gray snapper, recruit to oyster reefs before migrating to offshore reefs to complete their adult lives. On the basis of the depletion of fish within the snapper-grouper complex on offshore reefs, we assume that adding to their populations by constructing oyster reefs and enhancing snapper-grouper recruitment does not lead to compensatory reductions in growth from food competition offshore. To account for the future production expected from the cohort of recruits sampled on the reef, we computed expected lifetime production using the method described above, adjusting each future year's contribution by a standardly applied 3% annual discount rate ( $d$ ) (NOAA 1997):

$$P_i \times 1/(1+d)^i \quad (7)$$

Consequently, for gag grouper and gray snapper the annual production estimate for any year is the sum of the production of the 0 age class, plus its discounted future expected production.

For growth-enhanced species, we developed and applied an index of reef exclusivity (IRE) to weight the expected production of each of these species by the degree to which its growth is attributed to resources produced on the reef. If, for example, a species of fish merely aggregates behaviorally around the reef structure yet feeds entirely on prey from other habitats (e.g. sand bottom, water column), then it may be inappropriate to credit all its observed growth to the presence of the reef. Alternatively, if a species whose abundance is enhanced by reef presence forages exclusively on benthic or demersal resources that are produced on reefs, then its entire production should be credited to the new reef. Accordingly, we weighted the production credit for this category of fish species limited by reef resources by IREs ranging from 0.10 to 1.0 (Table 4). We used 0.10 as a minimum value to account for the likelihood that some fishes gain survival bene-

fits from association with reef structure, despite foraging on soft-sediment or water-column resources (e.g. Lindquist et al. 1994). The index was constructed for each species from available gut content information (Mann & Harding 1997, 1998, Grabowski 2002). For species lacking quantitative information on gut contents at a level of taxonomic discrimination that allowed reef-exclusive prey to be identified, we used life-history profiles and observed feeding behaviors to set the value of the index. The index primarily reflected a distinction between fishes feeding on benthic or demersal prey versus those feeding on planktonic prey, but it is further modified by the knowledge of whether the benthic prey themselves grow on reefs or on other substrata, such as sand and mud (Table 4).

Applying the IRE, total enhanced annual production for year  $y$  ( $P_y$ ), attributable to the presence of 10 m<sup>2</sup> of oyster reef for a particular species, was calculated by:

$$P_y = \text{IRE} \times \sum(P_i \times N_i) \quad (8)$$

For recruitment-enhanced species, the IRE was set to 1.0. For growth-enhanced species, the IRE ranged from 0.1 to 0.75 (Table 4). Finally, total annual enhancement of reef fish and large mobile crustacean production per 10 m<sup>2</sup> of reef was expressed as the sum of  $P_y$  across all 13 species or species groups. We provide an example of the full set of calculations estimating expected enhancement of production for 1 species, sheepshead, to illustrate the sequence of operations (Appendix 1).

**Discounting and scaling factors.** The factor of time enters into valuation of ecosystem services from habitat or species restoration actions that are intended to compensate for natural resource losses. First, although replacement of lost resources by restoration of like or similar resources does not involve translation into dollar values, the time cost of lost resources enters into the process of establishing equivalency. By US federal guidance, a standard annual discount rate of 3% is applied to account for time delays between loss of resources or resource services and their restoration (NOAA 1997). Accordingly, we applied this discount rate to convert any future expected gain in fish production from reef restoration into present-day value.

Time also enters into the process of assessing the rate of establishment of ecosystem services following initiation of the restoration action. To address this issue, we examined the change in abundance of fish and large mobile crustaceans over time on restored oyster reefs (Wenner et al. 1996, Lenihan et al. 1998, Grabowski 2002). We also compared catches of mobile species on restored and naturally occurring reefs in those studies that included this contrast (Meyer et al. 1996, Wenner et al. 1996, Lenihan et al. 2001). Additionally, we evaluated changes in densities and composition of benthic prey (primarily small crustaceans)

Table 4. Estimated enhanced density and production for the 13 species or species groups (2 goby, 2 blenny, and 3 silverside species are grouped because the species within each group exhibit similar life histories) that were more densely populated on oyster reef habitat than on unstructured sedimentary habitat. For sheepshead minnow, bay anchovy, and silversides, density augmentation estimates include all age classes. The density estimate for toadfish includes age classes 1 to 3. Gobies and blennies <1 yr. All other species include estimates of young of year (YOY) only. Index of reef exclusivity (IRE) is an estimate of species utilization of food resources associated with oyster reef compared to resources from adjacent non-reef habitat; this is derived from comparison of the density of the species on and off the reef, gut content analyses where available, and life history profiles. (IRE is not calculated for species in the RE group because all production is attributed to the reef; for calculation purposes the IRE is set to 1.0) Grouping is assigned for augmented production estimates: RE = species that recruited exclusively to reefs (compared to unstructured mud/sand bottom) and were intimately associated with the reef structure — all production is attributed to the reef; G = these species showed aggregation around the reef but diet analyses and life history information did not indicate that these species were limited by reef habitat; however, these individuals probably have some augmented growth because of the presence of the reef structure/resources

Species or species group	Average increase of density (ind. 10 m <sup>-2</sup> )	IRE	Grouping	Annual increase in secondary production (kg 10 m <sup>-2</sup> yr <sup>-1</sup> )
Gobies (2 spp.)	128.85	–	RE	0.644
Blennies (2 spp.)	5.00	–	RE	0.050
Sheepshead	1.04	–	RE	0.586
Stone crab	25.77	–	RE	0.653
Gray snapper	0.96	–	RE	0.114
Toadfish	0.96	–	RE	0.022
Gag grouper <sup>a</sup>	0.16	–	RE	0.293
Black sea bass	0.39	0.75	G	0.046
Spot tail pinfish	0.08	0.75	G	0.005
Pigfish	4.22	0.75	G	0.135
Sheepshead minnow	2.59	0.10	G	0.000
Bay anchovy	158.80	0.10	G	0.019
Silversides (3 spp.)	15.38	0.10	G	0.002
Total annual increase in fish production:				2.570
<sup>a</sup> Although gag use oyster reefs only during their first year of life, the gag-grouper biomass-augmentation estimate is for the life span of the fish				

over time in restored oyster reefs, and drew comparisons between natural and restored reefs. From this synthesis, we estimated the time to develop complete functional equivalence in fish and mobile crustacean production on a restored oyster reef as input to the valuation calculation.

Once the expected annual enhancement of fish and mobile crustacean production per unit area of restored oyster reef (kg 10 m<sup>-2</sup>) has been calculated, including appropriate discounting to convert both losses and gains of production to present-day values, then scaling the size of the restoration project to a quantified production loss requires determination of the expected functional lifetime of the restoration. The longer the restoration successfully provides ecosystem services, such as living resource production, the smaller the spatial scale of the restoration that is required to achieve compensation. Given the uncertainty regarding the effects of storms (Livingston et al. 1999), adequacy of spawning stock biomass (Rothschild et al. 1994), water quality (Lenihan & Peterson 1998, Lenihan et al. 2001), oyster diseases (Krantz & Jordan 1996, Lenihan et al. 1999), and degradation of reef materials on oyster reef longevity, we calculated expected enhanced production values for several alternative project lifetimes. Our

single best estimate of expected project lifetime was developed through consultation with other investigators in the southeastern USA, as well as our professional judgement. Once a project life span has been determined, the expected enhanced production attributable over the lifetime of a given area of restored habitat can be calculated, and the area of reef required to replace the total injury determined.

## RESULTS

### Enhancement estimates

Abundances of 19 species of fish and large mobile crustaceans were judged enhanced in abundance by the presence of oyster reef habitat. Based on the degree of observed density enhancement and life history, 10 were placed within the recruitment-enhanced group (Table 5). Included in this group were stone crabs, gag grouper, sheepshead, gray snapper, toadfish, tautog, feather blenny, striped blenny, and 2 species of gobies (skilletfish and naked goby). The remaining 9 species were classified as growth-enhanced. This second group included black seabass,

pigfish, southern flounder, spotail pinfish, sheepshead minnow, bay anchovy, and 3 species of silversides (rough, inland, and Atlantic).

The presence of oyster reef habitat probably enhanced the densities of 9 additional species; however, there were insufficient data either to provide compelling support for this conclusion or to resolve inconsistencies between studies. Five of these species (striped bass, white perch, weakfish, Atlantic spadefish, and butterfly) were collected in only a single study (striped bass and white perch in the VIMS studies; and weakfish, spadefish, and butterfly in Lenihan et al. 1998, 2001). Although catches were either higher on, or exclusive to, oyster reefs, low total numbers of these fishes failed to provide conclusive evidence of enhancement. White mullet was caught by Meyer et al. (1996) in high densities; however, the enhancement index value (1.8) did not exceed 2, our criterion for enhancement in a single study. Two species, red drum and spotted seatrout, exhibited conflicting evidence. Red drum were caught in both the VIMS and Grabowski (2002) studies: Grabowski's data indicated enhancement, whereas the VIMS studies caught red drum only away from reef sites. Spotted seatrout were collected in 2 studies: exclusively on oyster reefs in Grabowski (2002), but only on the sand/mud bottom in Zimmerman et al. (1989). This contradiction between studies may be explained by size-dependent changes in behavior. Zimmerman et al. (1989) collected small juveniles with drop samplers, whereas Grabowski (2002) caught larger adults with gill nets. Unfortunately, there were too few fish caught in either study to resolve the question. Size differences may also explain inconsistencies in blue crab data. In several studies with intense sampling effort, adult blue crabs caught in crab pots failed to show elevated densities on oyster reefs. However, in the VIMS studies, the only one reporting juvenile blue crabs separately from adults, blue crabs appeared to be enhanced by oyster reefs.

### Density estimates

Of the 19 species judged to be enhanced by oyster reefs, 2 (tautog and summer flounder) are not reported in Tampa Bay, and have no obvious ecological equivalent. Numerically, pelagic bait-fish (bay anchovy, silversides, sheepshead minnow) and small demersal residents (gobies and blennies) accounted for the largest density enhancements among fishes (Table 4). Stone crabs, the only large mobile crustacean that exhibited compelling density enhancement, were also found in high densities. Longer-lived, commercially and recreationally exploited fish (sheepshead, gray snapper, black sea bass, gag grouper) were enhanced

in abundance by oyster reefs but still remained at substantially lower densities than these bait-fishes, small demersals, and stone crabs (Table 4).

### Production estimates

The 7 recruitment-enhanced species or species groups that occur in Tampa Bay account for the majority of the enhancement of production of fishes and mobile crustaceans (Table 4). Of the total enhanced production created annually by oyster reef restoration (2.57 kg 10 m<sup>-2</sup>), 92% is attributable to recruitment-enhanced species, whose recruitment is limited by reef area and whose production did not require adjustment by an IRE. Within this group, stone crabs (0.653 kg 10 m<sup>-2</sup>), gobies (0.644 kg 10 m<sup>-2</sup>), sheepshead (0.586 kg 10 m<sup>-2</sup>) and gag grouper (0.293 kg 10 m<sup>-2</sup>) account for most of the enhanced production. Those growth-enhanced species and species groups whose recruitment did not appear limited by oyster reef area, but were credited for realizing enhanced production in the presence of reefs, account for the remaining 8% (0.21 kg 10 m<sup>-2</sup>) after the IRE was applied to production estimates. Production of pigfish (0.135 kg 10 m<sup>-2</sup>) and black seabass (0.046 kg 10 m<sup>-2</sup>) represent the majority of the production from this second group. Along with spottail pinfish, these species derive the majority of their food from the reef (IRE = 0.75). For baitfish (bay anchovy, silversides, sheepshead minnow), the IRE was set at 0.10 because they have a behavior of aggregating at reefs but extract food largely from the water column. A small credit is appropriate because the reef may provide some protection against predation for this group of fishes and may interact with currents to create better feeding opportunities.

### Discounting and scaling

Our synthesis of data on how abundance of fish and large mobile crustaceans changes over time after creation of a restored oyster reef revealed that for reefs constructed in summer, development of fish and mobile crustacean abundance is virtually complete by the next spring-summer season. Densities do not increase in successive years (Grabowski 2002). The 0 age class that provides 92% of the enhancement of production by fish and mobile crustaceans exhibits densities in the summer after construction that are indistinguishable from densities in succeeding years. Furthermore, the fish community compositions and species abundances on oyster reefs restored 6 yr before sampling were largely indistinguishable from those on natural oyster reefs (Lenihan et al. 2001). Prey

Table 5. Brief synopsis, including number of studies (out of 5) in which a species was collected, number of studies showing higher density of that species on oyster reefs (enhanced), range of enhancement index values (enhancement index), and group designation (grouping) from our synthesis of common fish and mobile crustaceans found on oyster reefs in the southeastern USA. See 'Materials and methods' for definitions of terms and procedures. \*Contradictory results across studies

Species	Common name	Collected (no. of studies)	Enhanced (no. of studies)	Enhancement Index	Grouping
<b>Large mobile crustaceans</b>					
<i>Farfantepenaeus duorarum</i>	Pink shrimp	2	2	All mudflat – all reef	Not enhanced
<i>Litopenaeus setiferus</i>	White shrimp	1	1	1.89	Not enhanced
<i>Farfantepenaeus aztecus</i>	Brown shrimp	1	0	All mudflat	Not enhanced
<i>Callinectes sapidus</i>	Blue crab	5	1	0.2 – all reef	Not enhanced
<i>Menippe mercenaria</i>	Stone crab	4	3	0.8 – all reef	Recruitment enhanced
<b>Fish</b>					
<i>Anchoa hepsetus</i>	Striped anchovy	1	0	0.1	Not enhanced
<i>Anchoa mitchilli</i>	Bay anchovy	2	2	0.3 – 18	Growth enhanced
<i>Archosargus probatocephalus</i>	Sheepshead	2	2	All reef	Recruitment enhanced
<i>Bairdiella chrysoura</i>	Silver perch	3	2	All mudflat – all reef	Not enhanced
<i>Brevoortia patronus</i>	Gulf menhaden	1	0	1.0	Not enhanced
<i>Brevoortia tyrannus</i>	Atlantic menhaden	2	0	All mudflat – 0.2	Not enhanced
<i>Carcharhinus acronotus</i>	Blacknose shark	1	0	All mudflat	Not enhanced
<i>Carcharhinus limbatus</i>	Blacktip shark	1	0	All mudflat – 0.1	Not enhanced
<i>Centropristis striata</i>	Black sea bass	2	2	0.5 – all reef	Growth enhanced
<i>Chaetodipterus faber</i>	Atlantic spadefish	1	0	All sand – all reef	Not enhanced*
<i>Chasmodes bosquianus</i>	Striped blenny	4	4	All reef	Recruitment enhanced
<i>Chilomycterus schoepfi</i>	Striped burrfish	1	0	All mudflat	Not enhanced
<i>Cynoscion nebulosus</i>	Speckled seatrout	2	1	All mudflat – all reef	Not enhanced*
<i>Cynoscion regalis</i>	Weakfish	1	1	0.4 – all reef	Not enhanced*
<i>Cyprinodon variegatus</i>	Sheepshead minnow	1	1	0.5 – all reef	Growth enhanced
<i>Diplodus holbrooki</i>	Spotail pinfish	1	1	1.64 – all reef	Growth enhanced
<i>Eucinostomus argenteus</i>	Spotfin mojarra	1	0	0.33	Not enhanced
<i>Fundulus heteroclitus</i>	Mummichog	3	1	0.32 – all reef	Not enhanced
<i>Gobiesox strumosus</i>	Skilletfish	1	1	All reef	Recruitment enhanced
<i>Gobionellus boleosoma</i>	Darter goby	2	0	All mudflat – 1.5	Not enhanced
<i>Gobiosoma boscii</i>	Naked goby	4	4	33 – all reef	Recruitment enhanced
<i>Hypsoblennius hentz</i>	Feather blenny	1	1	All reef	Recruitment enhanced
<i>Lagodon rhomboides</i>	Pinfish	4	1	All mudflat – all reef	Not enhanced
<i>Leiostomus xanthurus</i>	Spot	5	1	All mudflat – all reef	Not enhanced
<i>Lucania parva</i>	Rainwater killifish	2	1	1 – all reef	Not enhanced*
<i>Lutjanus griseus</i>	Gray snapper	2	2	4 – all reef	Recruitment enhanced
<i>Membras martinica</i>	Rough silversides	1	1	23	Growth enhanced
<i>Menidia beryllina</i>	Inland silversides	1	1	4.1	Growth enhanced
<i>Menidia menidia</i>	Atlantic silversides	1	1	All reef	Growth enhanced
<i>Micropogonias undulatus</i>	Atlantic croaker	3	0	All mudflat – 1.2	Not enhanced
<i>Monacanthus hispidus</i>	Filefish	1	0	All mudflat – all reef	Not enhanced
<i>Morone americana</i>	White perch	1	1	All reef	Growth enhanced
<i>Morone saxatilis</i>	Striped bass	1	1	All reef	Not enhanced*
<i>Mugil cephalus</i>	Striped mullet	3	1	All mudflat – all reef	Not enhanced
<i>Mugil curema</i>	White mullet	1	1	1.8	Not enhanced*
<i>Mycteroperca microlepis</i>	Gag grouper	2	2	1 - all reef	Recruitment enhanced
<i>Opsanus spp.</i>	Toadfishes	4	4	0.4 – all reef	Recruitment enhanced
<i>Orthopristis chrysoptera</i>	Pigfish	4	3	All mudflat – all reef	Growth enhanced
<i>Paralichthys albigutta</i>	Gulf flounder	2	0	All mudflat – 0.3	Not enhanced
<i>Paralichthys dentatus</i>	Summer flounder	2	1	All mudflat – all reef	Not enhanced
<i>Paralichthys lethostigma</i>	Southern flounder	2	2	1 – 3.3	Growth enhanced
<i>Pepilus spp.</i>	Butterfish	1	1	All reef	Not enhanced*
<i>Pogonias cromis</i>	Black drum	1	0	0.66	Not enhanced
<i>Pomatomus saltatrix</i>	Bluefish	2	0	All mudflat – 0.5	Not enhanced
<i>Sciaenops ocellatus</i>	Red drum	2	1	All sand – all reef	Not enhanced*
<i>Scomberomorus maculatus</i>	Spanish mackerel	1	0	All sand	Not enhanced
<i>Tautoga onitis</i>	Tautog	2	2	2 – all reef	Recruitment enhanced
<i>Trinectes maculatus</i>	Hogchoker	1	0	All mudflat	Not enhanced



species abundances, both sessile benthic invertebrates on reefs and also small mobile crustaceans, also reached their natural densities on restored oyster reefs by the first spring–summer after a summer restoration (Grabowski 2002). One important prey species, the grass shrimp *Palaemonetes pugio* (in Wenner et al. 1996), exhibited higher densities on oyster reefs restored within the previous year than on nearby natural reefs. Consequently, we found no evidence that restoration of this ecosystem service requires more than a single year to be realized. Furthermore, the creation of a restored oyster reef does not enhance fishing pressure to a degree that would require adjustment of mortality rates of reef-dependent fishes, a factor that could conceivably require reduction of the estimated production credit assigned to the reef. The 0-age-class recruits that comprise most of the enhanced production on oyster reefs (Tables 2 & 4) are not exploited.

The production credit attributable to the creation of a restored oyster reef is dependent on the functional lifetime of the reef. Because of the need to discount the value of future production, the cumulative production value discounted to present does not increase linearly. As reef lifetime increases, the rate of increase in cumulative value of production slows (Fig. 3). For our estimated annual production of  $2.57 \text{ kg yr}^{-1}$ , the discounted cumulative production credit for 20 yr of reef function is  $38.2 \text{ kg } 10 \text{ m}^{-2}$  of reef. For 30 yr, this credit increases to  $50.4 \text{ kg } 10 \text{ m}^{-2}$ . By 100 yr, an asymptote of ca.  $80 \text{ kg } 10 \text{ m}^{-2}$  is approached (Fig. 3). Although highly variable as a consequence of unpredictable storm impacts, sedimentation, and appropriateness of site selection, a reasonable estimate for the functional lifetime of a restored oyster reef that is successfully protected from damage by bottom-disturbing fishing gear (Lenihan & Peterson 1998, Lenihan & Micheli 2000) ranges from 20 to 30 yr.

## DISCUSSION

Our estimation of enhanced production of fish and large mobile crustaceans, attributable to replacing an area of unstructured mud/sand estuarine bottom in the southeast USA with a restored oyster reef, illustrates a process that combines review and synthesis of relevant empirical data bases, followed by application of appropriate basic concepts about limits on production of species at higher trophic levels in the system. The process is a generic one, analogous to what has been done to the scaling of restoration of seagrass habitat in terms of ecosystem benefits that flow from that action (Fonseca et al. 2000). We acknowledge uncertainty about the magnitude of estimates at all stages in this set of calcu-

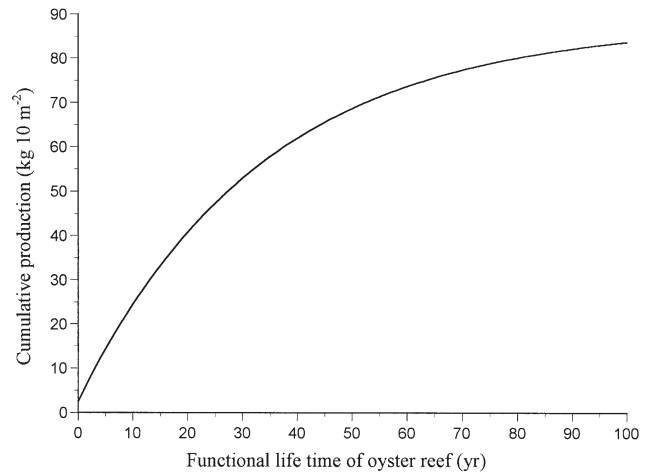


Fig. 3. Long-term projection of cumulative enhanced fish and mobile crustacean production per  $10 \text{ m}^2$  of restored oyster reef habitat, discounted to adjust for annual depreciation of resources as a function of the functional lifetime of the reef. An annual discount rate of 3% was applied

lations that lead to the fish and mobile crustacean production credit attributable to an area of restored oyster reef. However, we defend this calculation on the grounds that it makes use of extensive empirical data on restoration effectiveness and well-conceived, current conceptual understanding in fisheries ecology. Limitations in the data on rarer species that led us to exclude some species from the list of those enhanced by reef habitat contribute very little error to our estimate of total augmented production, because the rare species contribute so little to the sum. We do not include one indirect mechanism that may contribute further production benefits from oyster reef restoration. Oyster reefs tend to interfere with trawling and other bottom-disturbing fishing practices, such that if reefs are restored in areas where historic trawling operates, then their contribution to protection of benthic habitat may need to be included in the computation of production benefits.

Results of such scaling calculations are used by government resource agencies, most notably in the USA by NOAA, in legal settings to identify and provide for restoration, as the appropriate remedy for unlawful injuries to natural resources (NOAA 1997). More broadly, however, this estimate of one important ecosystem service of oyster reefs can be used by resource and coastal managers to make decisions about estuarine management and habitat restoration for a habitat that has declined over the past century by around 2 orders of magnitude in the Chesapeake Bay and Pamlico Sound (Rothschild et al. 1994, Lenihan & Peterson 1998), and has essentially disappeared from other estuaries in the northeast USA, west coast of

North America, Adriatic, and elsewhere around the world (Jackson et al. 2001). Valuation of fish production derived from oyster reefs is also central to efforts to define and then protect essential fish habitat (Coen & Luckenbach 2000).

Our estimate of the added value of restoring oyster reefs as measured by production of fish and large mobile crustaceans should be viewed as a quantitative prediction. Testing is feasible, although it would require a spatial scale appropriate to the mobility of the species to allow isolation of treatments, and controls and establishment of a well conceived *a priori* plan to couple the project with its evaluation (e.g. Lindberg & Relini 2000, Hobbs & Harris 2001). Treatment of uncertainty in restoration and mitigation projects is an important concern to provide guarantees that resources and their services are indeed replaced. Uncertainty can be incorporated in 2 fundamentally different fashions. One approach is to establish and apply a mitigation ratio such that restored habitat is made greater than the amount expected to be necessary for full replacement of lost value (e.g. Thayer 1992). This expansion of scale incorporates uncertainty of success, with ratios increasing as uncertainty increases. An alternative approach is to monitor the restoration project carefully and modify it adaptively as needed to meet the quantitative target of restoration (e.g. Ambrose & Swarbrick 1989). The adaptive management approach has the added value of providing information that can test the prediction and enhance understanding to improve future predictions and reduce uncertainty for future applications. Nevertheless, parties held responsible for restoring the lost ecosystem services typically dislike the open-ended nature of the adaptive management commitment, and prefer a fixed level of effort, as reflected in the mitigation-ratio approach.

Realized success in enhancing fish production through oyster reef restoration will depend on many variables that influence oyster reef function. Our calculations apply to a generic oyster reef in the southeastern USA, an approach dictated by the small number of data sets preventing incorporation of modifying covariates. Such covarying factors mostly involve decisions about site selection and design criteria for the reef restoration. The landscape setting in which a reef is placed dictates the ability of many higher-level consumers to utilize it. For example, intertidal oyster reefs placed adjacent to salt marshes or adjacent to subtidal seagrass beds, rather than in isolation from other structured habitats, vary in their functioning by supporting different patterns of fish and crab utilization (Meyer et al. 1996, Irlandi & Crawford 1997, Micheli & Peterson 1999, Grabowski 2002). Intertidal and subtidal oyster reefs are likely to differ in value to fish and mobile

crustaceans largely because of the need to find alternative submerged refuge at low tide. This consideration also implies that landscape setting may impact intertidal more than subtidal reef function. The choice of whether to construct a few reefs large in area or several smaller ones can affect fish utilization through modification of perimeter-to-area ratios and, thus, proportions of edges with their intrinsically higher access to mobile consumers. Networks of oyster reefs built along environmental gradients can provide refuges for fish escaping environmental degradation and thus serve to enhance fish production more than a design that isolates reefs in a single environmental regime (Lenihan et al. 2001). Because of extensive depletion of spawning stock biomass in some estuaries, siting oyster reefs where larval settlement is reliable enough to sustain oyster populations is crucial, often involving the need to understand hydrodynamic setting and locations of retention cells (Coen & Luckenbach 2000, Mann 2000). Decisions made about reef design, including height and water depth (Lenihan & Peterson 1998), shape, composition of reef material, prevailing water flow regime, and stability of underlying sediments (Luckenbach et al. 1999), all help to determine the success of achieving restoration goals.

Given that oyster reefs provide many ecosystem services beyond enhancing production of fishes and large mobile crustaceans, there are additional environmental benefits achieved by reef restoration. These include positive effects on water clarity, carbon sequestration, rate of denitrification, and oyster restocking. We do not attempt to quantify the value of these other attendant ecosystem services, largely because the currency of benefits is not comparable to the measure used in this analysis (i.e. production of fish and mobile crustaceans at high trophic levels). We chose this particular currency to match the benefit of restoration with the loss in a fundamental ecosystem service, production of fish and mobile crustaceans. The environmental incident, an acidic process water spill, which caused the loss of fish and mobile crustaceans (French 1999), clearly must have had impacts on other components of the Alafia River ecosystem. To characterize those losses fully would involve tremendous commitment of resources. For the sake of administrative simplicity and cost effectiveness, only some of the injuries to ecosystem services were estimated in this and other incidents. When compensation for those measured injuries to natural resources is achieved by habitat restoration like oyster reef creation, then one can be confident that many other ecosystem services will be simultaneously provided to help replace those that were injured, but not studied or quantified. This approach assumes that many ecosystem services scale linearly to one another. That does not seem an unreasonable assumption, yet it

also deserves rigorous testing. Independent of whether restoration of some ecosystem services is more complete than others, this approach of habitat restoration is likely to provide greater ecosystem benefits than an alternative program of species-by-species restoration at the population level. Habitat degradation is widely recognized as the greatest cause of species declines (e.g. Soule 1986), so its restoration deserves highest priority in conservation programs and in mitigation efforts.

*Acknowledgements.* We express appreciation to the investigators of the 6 studies used in this synthesis. The paper benefited from the comments of D. Breitberg, M. Carr, M. Hixon, R. Kneib, P. Levin, C. Manen, G. Stunz, R. Wolotira, and 2 referees in refining the conceptual approach used in this synthesis. D. French checked and rechecked all of our production and scaling calculations. L. Dipinto, B. Julius, and T. Penn provided guidance. The NOAA Damage Assessment Center provided funding for this synthesis and publication, with additional basic research support from Environmental Defense, and the NOAA NERRS Program.

#### LITERATURE CITED

- Abraham BJ (1985) Species profiles: life histories and environmental requirements of coastal fish and invertebrates (Mid Atlantic)—mummichog and killifish. Biological Report 82 (11.40), US Fish and Wildlife Service. US Army Corps of Engineers, TR EL-82-4, Vicksburg, MS
- Allen EB, Covington WW, Falk DA (1997) Developing a conceptual basis for restoration ecology. *Restor Ecol* 5:275
- Ambrose RF, Swarbrick SL (1989) Comparison of fish assemblages on artificial and natural reefs off the coast of southern California. *Bull Mar Sci* 44:718–733
- Bahr LM, Lanier WP (1981) The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. Report No. FWS/OBS-81/15, Office of Biological Services, US Fish and Wildlife Service, Slidell, LA
- Bohnsack JA (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bull Mar Sci* 44:631–645
- Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. *Science* 277: 509–515
- Breitburg DC (1999) Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? In: Luckenbach MW, Mann R, Wesson JA (eds) *Oyster reef habitat restoration: a synopsis and synthesis of approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, p 239–250
- Brown BE, Browder JA, Powers J, Goodyear CD (1990) Biomass, yield models, and management strategies for the Gulf of Mexico ecosystem. Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Miami, FL
- Carpenter SR, Kitchell JF (1993) *The trophic cascade in lakes*. Cambridge University Press, Cambridge
- Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecological functioning or resource exploitation? *Ecol Engineer* 15: 323–343
- Coen LD, Luckenbach MW, Breitburg DL (1999) The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: Benaka LR (ed) *Fish habitat: essential fish habitat and restoration*, Am Fish Soc Symp 22:438–454
- Dame RF (1996) *Ecology of bivalves*. CRC Press, Boca Raton, FL
- Doherty PJ, Williams DMcB (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol Annu Rev* 26: 487–551
- 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 DP (1999) Estimating injuries resulting from the December 1997 process water spill into the Alafia River. Final Report, NOAA, Damage Assessment Center, Silver Spring, MD
- French DP, Rines H, Keller A, French FW III, Gifford D, Pavignano S (1997) The CERCLA type A natural resource damage assessment model for coastal and marine environments. Technical Documentation Volume IV Biological Database Part 1, Office of Environmental Policy and Compliance, US Dept of the Interior, Washington, DC
- Goodyear CP (1988) Spawning stock biomass and yield per recruit for several reef fish species of the Gulf of Mexico. Southeast Fisheries Science Center, NOAA, Miami, FL
- Goodyear CP, Schirripa MJ (1991) A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Southeast Fisheries Science Center, NOAA, Miami, FL
- 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, Chapel Hill, NC
- Harding JM, Mann R (1999) Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bull Mar Sci* 65:289–300
- Hargis WJ Jr, Haven DS (1999) Chesapeake oyster reefs, their importance, destruction and guidelines for restoring them. In: Luckenbach MW, Mann R, Wesson JA (eds) *Oyster reef habitat restoration: a synopsis of approaches*. Virginia Inst Mar Sci Press, Gloucester Point, VA, p 329–358
- Hixon MA (1998) Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Aust J Ecol* 23:192–201
- Hobbs RJ, Harris JA (2001) Restoration ecology: repairing earth's ecosystems in the new millennium. *Restor Ecol* 9: 239–246
- Hood PB, Schlieder RE (1992) Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bull Mar Sci* 51:337–352
- Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal salt marshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and 14 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
- Krantz GE, Jordan SJ (1996) Management alternatives for protecting *Crassostrea virginica* fisheries in *Perkinsus marinus* enzootic and epizootic areas. *J Shellfish Res* 15:167–176
- Lawton JH (1996) Corncake pie and prediction in ecology. *Oikos* 76:3–4
- Lenihan HS, Micheli F (2000) Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict using ecological experimentation. *Fish Bull* 98:86–95

- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Lenihan HS, Grabowski JH, Thayer GW (1998) Recruitment to and utilization of oyster reef habitat by commercially and recreationally valuable crabs and fishes: an experiment with economic analysis. Final Report No. 1–97, National Research Council. National Marine Fisheries Service, Beaufort, NC
- Lenihan HS, Micheli F, Shelton SW, Peterson CH (1999) The influence of multiple environmental stressors on susceptibility to parasites: an experimental determination with oysters. *Limnol Oceanogr* 44:910–924
- Lenihan HS, Peterson CH, Byers JE, Grabowski JH, Thayer GW, Colby D (2001) Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol Appl* 11:746–782
- Lewis RR, Estevez ED (1988) The ecology of Tampa Bay, Florida: an estuarine profile. Biological Report 85 (7.18), US Fish and Wildlife Service, Vicksburg, MS
- Lindberg WJ, Marshall MJ (1984) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)—stone crab. Report No. FWS/OBS-82/11.21, US Fish and Wildlife Service. US Army Corps of Engineers, TR EL-82-4, Vicksburg, MS
- Lindberg WJ, Relini G (2000) Integrating evaluation into reef project planning. In: Seaman WJ Jr (ed) Artificial reef evaluation with application to natural marine habitats. CRC Press, Boca Raton, FL, p 195–235
- Lindquist DG, Cahoon LB, Clavijo IE, Posey MH, Bolden SK, Pike LA, Burk SW, Cardullo PA (1994) Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. *Bull Mar Sci* 55:308–318
- Livingston RJ (1984) The ecology of the Apalachicola Bay system: an estuarine profile. Report No. FWS/OBS 82.05, US Fish and Wildlife Service, Slidell, LA
- Livingston RJ (2001) Eutrophication processes in coastal systems: origin and succession of plankton blooms and effects on secondary production in Gulf Coast estuaries. CRC Press, New York, NY
- Livingston RJ, Howell RL, Niu X, Lewis FG, Woodsum GC (1999) Recovery of oyster reefs (*Crassostrea virginica*) in a gulf estuary following disturbance by two hurricanes. *Bull Mar Sci* 64:465–483
- Luckenbach MA, Mann R, Wesson JE (eds) (1999) Oyster reef restoration: a symposium and synthesis of approaches. Virginia Inst Marine Sci Press, Gloucester Point, VA
- Mann R (2000) Restoring oyster reef communities in the Chesapeake Bay: a commentary. *J Shellfish Res* 19: 335–340
- Mann R, Harding JM (1997) Trophic studies on constructed 'restored' oyster reefs. Grant/Contract No. CB993267-02-1, US Environmental Protection Agency, Chesapeake Bay Program Office, Annapolis, MD
- Mann R, Harding JM (1998) Continuing trophic studies on constructed 'restored' oyster reefs. Grant/Contract No. CB993267-03, US Environmental Protection Agency, Chesapeake Bay Program Office, Annapolis, MD
- Manooch CS, Haimovici M (1978) Age and growth of the gag, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the southeastern United States. *Trans Am Fish Soc* 107:234–240
- Manooch CS, Mason DL (1984) Age, growth, and mortality of lane snapper from Southern Florida. *Northeast Gulf Sci* 7: 109–115
- Meyer DL, Townsend EC, Murphy PL (1996) The evaluation of restored wetlands and enhancement methods for existing restorations. Final Report, Office of Habitat Conservation, NOAA, Silver Spring, MD
- Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conserv Biol* 13: 869–881
- Middaugh DP, Hemmer MJ (1992) Reproductive ecology of the inland silverside, *Menidia beryllina*, (Pisces: Atherinidae) from Blackwater Bay, Florida. *Copeia* 1992:53–61
- Millikin MR, Williams AB (1984) Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. NOAA Technical Report NMFS 1 FAO Fisheries Synopsis No. 138. US Dept of Commerce, NOAA, NMFS, Washington, DC
- Newell RIE (1988) Ecological changes in the Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: Lynch MP, Krome EC (eds) Understanding the estuary: advances in Chesapeake Bay research. Publication No. 129 CBP/TRS 24/88, Chesapeake Bay Research Consortium, Gloucester Point, VA, p 536–546
- Newell RIE, Cornwell JC, Owens MS (2002) Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. *Limnol Oceanogr* 47:1367–1379
- NOAA (National Oceanographic and Atmospheric Administration) (1997) Habitat equivalency analysis: an overview. Policy and Technical Paper Series, No 95-1. Damage Assessment and Restoration Program, NOAA, Silver Spring, MD
- O'Beirn FX, Luckenbach MW, Mann R, Harding J, Nestlerode J (1999) Ecological functions of constructed oyster reefs along an environmental gradient in Chesapeake Bay. *Virginia Inst Mar Sci, Gloucester Point, VA*
- Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community restoration ecology. *Restor Ecol* 5:291–300
- Peterson CH (1993) Improvement of environmental impact analysis by application of principles derived from manipulative ecology: lessons from coastal marine case histories. *Aust J Ecol* 18:21–52
- Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297
- Rothschild BJ, Ault JS, Gouletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar Ecol Prog Ser* 111:29–39
- Rozas LP (1992) Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Mar Ecol Prog Ser* 89: 287–292
- Savage T, Sullivan JR (1978) Growth and claw regeneration of the stone crab, *Menippe mercenaria*. Florida Dept of Natural Resources, St. Petersburg, FL
- Serafy JE, Hopkins TE, Walsh PJ (1997) Field studies on the ureogenic gulf toadfish in a subtropical bay. I. Patterns of abundance, size composition and growth. *J Fish Biol* 50: 1258–1270
- Sheaves MJ (1992) Patterns of distribution and abundance of fish in different habitats of a mangrove-lined tropical estuary, as determined by fish trapping. *Aust J Mar Freshw Res* 43:1461–1479
- Soule M (ed) (1986) Conservation biology. Sinauer, Sunderland, MA
- South Atlantic Fishery Management Council (1983) Fishery management plan, regulatory impact review, and final environmental impact statement for the snapper-grouper fishery of the south Atlantic region. South Atlantic Fishery Management Council, NMFS, Charleston, SC

- Sullivan JR (1979) The stone crab, *Menippe mercenaria*, in the southwest Florida fishery. Florida Marine Research Publications Number 36. Marine Research Lab, Florida Dept of Natural Resources, St. Petersburg, FL
- Thayer GW (ed) (1992) Restoring the nation's marine environment. Maryland Sea Grant College Program, College Park, MD
- van Diggelen R, Grootjans AP, Harris JA (2001) Ecological restoration: state of the art or state of the science? *Restor Ecol* 9:115–118
- Vitousek PM, Mooney HA, Lubchenco J, Mellilo J (1997) Human domination of earth's ecosystems. *Science* 277:494–499
- Wells HW (1961) The fauna of oyster reefs with special reference to the salinity factor. *Ecol Monogr* 31:239–266
- Wenner E, Beatty HR, Coen LD (1996) A method for quantitatively sampling nekton on intertidal oyster reefs. *J Shellfish Res* 15:769–775
- Wilson CA, Dean JM, Radtke R (1982) Age, growth rate and feeding habits of the oyster toadfish, *Opsanus tau* (Linnaeus) in South Carolina. *J Exp Mar Biol Ecol* 62:251–259
- Wilson EO (1992) Diversity of life. Harvard University Press, Cambridge, MA
- Zimmerman RJ, Minello TJ, Zamora G, Martinez E (1986) Measurements of estuarine shrimp densities applied to catch predictions. In: Landry AM, Kilma EF (eds) Proc Shrimp Yield Prediction Workshop. Texas A&M Sea Grant College Program, Galveston, TX, p 37–55
- Zimmerman RJ, Minello TJ, Baumer T, Castiglione M (1989) Oyster reef as habitat for estuarine macrofauna. Tech Memm NMFS-SEFC-249, NOAA, Galveston, TX

**Appendix 1.** Calculation of enhanced fish production for sheepshead. Equations and symbols can be found in the 'Materials and methods' section. All necessary parameters for the calculations (survival rates, age-length, length-weight) appear in Table 3

$i$	$S_i$	$Sx_i$	$N_i$	$L_i$	$W_i$	$P_i$	$P_i \times N_i$
0	1						
1	0.819	0.819	1.040	18.306	152.907	152.907	159.023
2	0.670	0.819	0.851	23.272	311.171	158.264	134.759
3	0.549	0.819	0.697	27.318	500.093	188.921	131.703
4	0.301	0.549	0.383	30.614	700.619	200.526	76.719
5	0.165	0.549	0.210	33.299	898.577	197.958	41.565
6	0.091	0.549	0.115	35.486	1084.776	186.199	21.456
7	0.050	0.549	0.063	37.268	1254.072	169.296	10.706
8	0.027	0.549	0.035	38.720	1404.248	150.175	5.212
9	0.015	0.549	0.019	39.902	1535.033	130.785	2.491
10	0.008	0.549	0.010	40.866	1647.348	112.315	1.174
11	0.005	0.549	0.006	41.651	1742.765	95.418	0.547
12	0.002	0.549	0.003	42.290	1823.147	80.382	0.253
13	0.001	0.549	0.002	42.811	1890.416	67.268	0.116
14	0.001	0.549	0.001	43.235	1946.415	55.999	0.053
Total			3.435				585.779

Editorial responsibility: Ronald Kneib,  
Sapelo Island, Georgia, USA

Submitted: September 18, 2001; Accepted: October 31, 2003  
Proofs received from author(s): November 27, 2003



# Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios

Sean P. Powers<sup>1,\*</sup>, Jonathan H. Grabowski<sup>2</sup>, Charles H. Peterson<sup>2</sup>, William J. Lindberg<sup>3</sup>

<sup>1</sup>Department of Marine Sciences, University of South Alabama and Dauphin Island Sea Lab, Dauphin Island, Alabama 36528, USA

<sup>2</sup>Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA

<sup>3</sup>Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, Florida 32611, USA

**ABSTRACT:** Whether artificial reefs installed in estuarine/marine waters function to produce more fish (enhancement) or simply to attract existing fish (attraction) is still under debate. Despite little resolution over this issue, artificial reefs are often considered for use as compensatory mitigation for damaged marine resources. We estimate the quantitative enhancement of fish production under 4 plausible scenarios: attraction, enhancement, enhancement with fishing, and attraction with fishing. Our intent is not to resolve the attraction-enhancement debate, but to quantify the uncertainty associated with using artificial reefs as compensatory mitigation. Pertinent parameters for production calculations (fish density by size class, length-frequency distributions, diets, behaviors, age-specific growth and mortality rates) were obtained from syntheses of findings from artificial reef studies conducted in coastal waters of the southeastern USA and from species life-history profiles. Year-round reef inhabitants were separated into 2 groups: those whose recruitment appears to be limited by available reef habitat (only 2 taxa) and those not augmented in recruitment but potentially enhanced in realized production by provision of refuges and reef-associated prey (15 taxa). Estimates of enhanced production in this latter group were discounted by an index of reef exclusivity in diet to give production credit in proportion to consumption of reef-associated prey. Estimates of annual production enhancement per 10 m<sup>2</sup> of artificial reef ranged from 0 kg under the attraction scenario to 6.45 kg wet weight under the assumption of enhancement plus protection from fishing. Application of fishing reduced the enhancement estimate by 32% to 4.44 kg 10 m<sup>-2</sup> yr<sup>-1</sup>. A 4th scenario of attraction with fishing may yield a net decline in production of a similar magnitude. In contrast to many natural structural habitats (seagrass meadows, oyster reefs, salt marshes, mangroves) that have dramatically decreased over past decades and are clearly important nursery grounds, evidence is weak that habitat provided by artificial reefs on the shallow continental shelf of the southeastern USA is currently limiting to fish production. Until convincing empirical evidence appears, high scientific uncertainty limits confidence in using artificial reefs as compensatory mitigation. Furthermore, even if augmented production were achieved, managing fishing impacts would be critical to achieving the expected production benefit.

**KEY WORDS:** Mitigation · Fish production · Southeastern USA · Restoration scaling · Artificial reefs · Fishing pressure

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Artificial reefs are structures intentionally deployed on the seafloor to influence biological or physical processes, and are widely acknowledged as habitat for fish

(Seaman 2000). Because of the association of high fish abundance with offshore artificial reefs, their construction has been used as compensatory restoration for damages to natural resources (e.g. Duffy 1985, Hueckel et al. 1989, Ambrose 1994). However, whether artificial reefs

actually enhance fish production (i.e. biomass/unit area/time interval) or simply attract fish, and thereby act mostly to facilitate exploitation rates by fishermen (Bohnsack 1989, Bohnsack et al. 1994, Grossman et al. 1997, Lindberg 1997), is still very much in debate. Further complicating resolution of the production/attraction issue is the possibility that artificial reefs function as fish habitat at temporally or spatially variable intermediate states between attraction and enhancement. If artificial reefs are installed in the marine environment with the expectation of compensating for loss of fish production, then the implications of the different answers to the attraction–enhancement question must be addressed.

Because of the high mobility of most fishes and the large spatial scale at which most fish populations are distributed, empirical tests of whether the creation of artificial reefs results in additional production of fish are problematic (Grossman et al. 1997). Peterson et al. (2003 in this Theme Section) provide the conceptual basis for computing estimates of enhancement of fish production resulting from the creation and/or restoration of marine habitats. First, one considers whether the recruitment of any species of fish is limited by the amount of a particular habitat. If addition of habitat area relaxes a survival bottleneck in the early pre-recruitment life history of a species, then the creation or restoration of additional habitat would be expected to result in a numerical enhancement of recruitment in that species. The second process described in Peterson et al. (2003), by which the addition of habitat may enhance fish production is through providing refuges from predation (e.g. Hixon 1998) and increasing the production of, or access to, additional reef-associated prey resources, which then promote more rapid growth of individual fish. This response affects fish production not by adding new fish to the system, but rather by enhancing growth of and protecting individuals already present, and thereby producing gains in fish biomass. These 2 fundamental responses are included in most models of how artificial reefs may impact populations of reef fish, often incorporated through varying the intensities of density-dependent larval settlement and post-settlement growth (Osenberg et al. 2002).

Current scientific opinion on the question of whether installation of artificial reefs on the shallow continental shelf enhances fish production can be separated into 4 plausible scenarios. Under the first scenario, high abundance associated with artificial reefs is interpreted as the sole consequence of aggregating existing fish in the system (Grossman et al. 1997). In this scenario, the production of fish does not increase as a function of additional habitat because the availability of habitat and the food resources that the habitat provides are assumed not to be limiting. Under the second scenario, the addition of reef structure (habitat area) results in increased fish production by enhancing recruitment

currently limited by habitat area, or by enhancing growth currently limited by reef refuges and associated prey resources (Peterson et al. 2003). The third scenario assumes that addition of artificial reef habitat on the shallow continental shelf enhances fish recruitment and/or realized growth, but that mortality is increased by fishermen who target their effort on the new concentrations of fish (Polovina 1991, Friedlander et al. 1994, McGlennon & Branden 1994). A 4th scenario combines this elevation of fishing mortality with the assumption that fish are merely attracted to artificial reefs. Given the wide variation in the ecology of fishes on reefs, the response of individual species to the addition of reef habitat almost certainly varies with life history and susceptibility to fishing. Consequently, estimation of expected enhancement in fish production from constructing offshore artificial reefs should assess the implications of all scenarios at the level of species.

Because of the lack of consensus on how the addition of artificial reef habitat influences key population processes in reef fish, we develop estimates of fish production that correspond to the first 3 plausible scenarios and thereby quantify the implications of the biological uncertainties. For the 4th scenario, we assume that the quantitative reduction in net fish production is a constant independent of whether reefs enhance recruitment and growth or simply attract fish. We then evaluate the assumptions that serve as the basis for each scenario. Assessing the processes by which offshore artificial reefs may affect fish production demands not only the review of applicable theory on fish population dynamics and bioenergetics, but also synthesis of available empirical data, reorganized in ways that allow insight into population dynamics, behavior, diet, and growth. We calculate our estimates of fish productivity gains expected from offshore reef construction in the southeast USA, specifically focused on the Tampa Bay region of southwest Florida. The shallow continental shelf of the southeast USA is frequently targeted for construction of artificial reefs, so quantifying the uncertainty in their impacts on fish production may guide future fishery management and restoration efforts. This specific locale was chosen to evaluate the potential for compensatory restoration (see NOAA 1997 for the use of habitat equivalency analysis in environmental mitigation) for losses that resulted from an acidic-process water spill in the Alafia River, a tributary of Tampa Bay.

## MATERIALS AND METHODS

**Synthesis of data.** We first conducted a search of both published and gray literature on offshore artificial reefs in the southeastern USA. Several studies docu-

mented fish occupation of artificial reefs; however, because of inferior construction materials and designs or poor quantification of fish densities, only a few are of use in estimating production of reef-associated fishes. No study design was adequate to demonstrate unequivocally whether production was actually increased by artificial reefs, or alternatively whether fish were merely aggregated on them. Nevertheless, using a few reasonable assumptions (see Peterson et al. 2003), calculations can be made from available field data in the applicable studies to quantify the enhancement of production under different plausible scenarios, and thereby bracket the range of expected changes in production. We utilized 2 studies conducted on the shallow shelf offshore of Tampa Bay, Florida (Smith et al. 1979, Lindberg 1996), to identify those species likely to occur on an artificial reef constructed in this area. Smith et al. (1979) performed diver surveys and collections with rotenone to document fish abundance on both natural (Dunedin Reef) and artificial (Clearwater Artificial Reefs) reefs from 1975 to 1976. Study reefs were located at 7 to 9 m depth, approximately 7 km offshore along the west coast of central Florida. Lindberg (1996) conducted a 5 yr study (1990 to 1995) examining fish utilization of multiple reefs in the Suwannee Regional Reef System, Florida. This system consists of 22 reefs, each spaced 2 km apart along the 13 m depth-contour and located 24 to 29 km offshore from the mouth of the Suwannee River. This study, designed to examine how physical attributes of reefs (i.e. reef patch size and spacing) relate to fish utilization and development of prey resources, represents the most detailed study of artificial reefs in the region.

We used 4 other studies to fulfill specific data needs for estimating production enhancement of fish resulting from installation of an offshore artificial reef. Bohnsack & Harper (1988) provide length-frequency distributions, as well as parameters for length-weight conversions for reef fish in southern Florida waters. Bohnsack et al. (1994) compare fish occupation of a south Florida offshore area before and after construction of an artificial reef. The results allow us to address important assumptions related to estimation of density enhancement by artificial reefs, and provide necessary information on life history characteristics for several of the fish species. Lindquist et al. (1985) reported information on the gut contents of fishes from offshore reefs of North Carolina. In the absence of complete information on feeding habits of reef fish from southwest Florida, we use feeding behavior data from Lindquist et al. (1985) to assign the reef fish of southwest Florida into 5 broad categories of relative reliance on reef-associated prey. This approach assumes that feeding behaviors documented in North Carolina reefs apply also to those of southwest Florida, an assumption sup-

ported by Bohnsack et al.'s (1994) assignments of Florida reef fish to various trophic guilds. Finally, Lindberg & Loftin's (1998) study examines the effects of habitat and fishing mortality on residency, growth and movement of gag grouper. This data set was central to our ability to estimate production gains under scenarios that include effects of elevated fishing pressure.

**Density estimates.** The first step in estimating enhancement of fish production by construction or restoration of a habitat is to gather data on fish abundance in that habitat. We used the work of Lindberg (1996) to derive estimates of density per unit reef area for each of 25 abundant species or species groups (listed in Table 1). We restricted our analyses to these 25 taxa because they account for the vast majority (>95%) of fish abundance and biomass on offshore reefs in this geographic region. As an estimate of the steady-state fish community, we computed an average density of each taxon calculated over the 3rd, 4th, and 5th yr after installation of the reefs, because total fish biomass stabilized by Year 3. We used the area of the seabed occupied by the reef structure, and over which fish were tallied, to convert visual abundance to density per unit bottom area. Although vertical relief and overall volume of the reef structure can be important determinants of fish utilization, we assume that artificial reefs would be designed to provide sufficient vertical relief (see Sheng 2000). Although the structural attributes, including materials and shapes, doubtless influence fish utilization of artificial reefs, we do not attempt to use these variables to explain variation among reefs, but instead base our fish density estimates upon artificial reefs made of concrete modules of varying sizes (Lindberg 1996). This construction method is the one most widely used currently to construct offshore artificial reefs. Lindberg (1996) used diver surveys to document abundance of fishes on or in close proximity to artificial reefs that were closed to fishing. In clear waters, visual censuses provide relatively reliable estimates of total numbers of reef-associated fishes (see Bohnsack et al. 1994) that can then be related to the area occupied by reef structure. While this technique samples resident fishes with accuracy, densities of the highly mobile and transient pelagic species like king mackerel and albacore may be underestimated. In principle, enhancement of fish density from construction of a reef is estimated by comparing average densities on reefs to corresponding densities over the unstructured and unmodified sea floor (Peterson et al. 2003). In the case of nearshore shelf habitat, fish density on the unstructured bottom is so low (<1% of that on artificial reefs: Bohnsack et al. 1994) that computing enhancement on artificial reefs does not require adjustment for the small fraction of fish that would be present in the absence of the reef.

Table 1. Synthesis of life history, trophic and abundance information for fish commonly associated with artificial reefs installed on the southeastern USA nearshore shelf. Information on fish reef association, trophic level and life stages utilizing reefs was derived from Smith et al. (1979), Bohnsack & Harper (1988), Bohnsack et al. (1994), and Lindberg (1996). R: recruit; J: juvenile; A: adult; ha: highly abundant ( $>1 \text{ m}^{-2}$ ); a: abundant (0.9 to  $0.02 \text{ m}^{-2}$ ); rare species ( $<0.01 \text{ m}^{-2}$ ) were not included in our analyses. Density information was derived from Lindberg (1996)

Scientific name	Common name	Reef association	Trophic level	Life stage found on reef	Relative abundance
<i>Archosargus probatocephalus</i>	Sheepshead	Reef resident	Macroinvertevore, piscivore	A	a
<i>Ballistes capriscus</i>	Gray triggerfish	Reef resident	Macroinvertevore	A	a
<i>Caranx crysos</i>	Blue runner	Brief visitor	Piscivore	A	a
<i>Centropristis striata</i>	Black seabass	Reef resident	Macroinvertevore	A	a
<i>Chaetodipterus faber</i>	Atlantic spadefish	Reef resident	Macroinvertevore	A	a
Clupeidae spp.	Herrings	Reef resident—transient occupant	Planktivore	R, J, A	ha
<i>Decapterus punctatus</i>	Round scad	Transient occupant	Planktivore	J, A	ha
<i>Diplletrum formosum</i>	Sand perch	Reef resident	Microinvertevore, piscivore	J, A	a
<i>Diplodus holbrooki</i>	Spottail pinfish	Reef resident	Herbivore, microinvertevore		a
<i>Equetus umbrosus</i>	Cubbyu	Reef resident	Microinvertevore	J, A	ha
<i>Haemulon aurolineatum</i>	Tomtate	Reef resident	Planktivore, microinvertevore	J, A	ha
<i>Haemulon plumieri</i>	White grunt	Reef resident	Planktivore, microinvertevore, macroinvertevore	J, A	ha
<i>Halihoeres bivittatus</i>	Slippery dick	Reef resident	Microinvertevore, macroinvertevore	J, A	a
<i>Hyleurochilus geminatus</i>	Crested blenny	Reef resident	Microinvertevore	R, J, A	a
<i>Lutjanus griseus</i>	Gray snapper	Reef resident	Macroinvertevore, piscivore	J, A	a
<i>Mycteroperca microlepis</i>	Gag grouper	Reef resident	Macroinvertevore, piscivore	A	a
<i>Odontoscion dentex</i>	Reef croaker	Brief visitor	Macroinvertevore, piscivore	J, A	a
<i>Opsanus pardus</i>	Leopard toadfish	Reef resident	Macroinvertevore	R, J, A	a
<i>Orthopristis chrysoptera</i>	Pigfish	Reef resident	Macroinvertevore, piscivore	A	a
<i>Parablennius marmoratus</i>	Seaweed blenny	Reef resident—transient occupant	Microinvertevore	R, J, A	a
<i>Rypticus maculatus</i>	Whitespotted soapfish	Brief visitor	Macroinvertevore	A	a
<i>Scomberomorus maculatus</i>	Spanish mackerel	Transient occupant	Piscivore	A	ha
<i>Seriola dumerili</i>	Greater amberjack	Transient occupant	Piscivore	A	a
<i>Serranus subligarius</i>	Belted sandfish	Reef resident	Microinvertevore, macroinvertevore	J, A	a
<i>Synodus intermedius</i>	Sand diver	Brief visitor	Piscivore	A	a

We next separated the 25 species or species groups into 2 categories, corresponding to: (1) species whose recruitment (ecologically defined, as in Keough & Downes 1982, Doherty & Williams 1988) appears limited by the area of reef habitat; and (2) those whose recruitment does not appear limited by reef habitat, but that experience enhanced growth from provision of additional reef-associated prey resources. Our criteria for deciding whether a species was limited in recruitment by artificial reef habitat were based upon empirical abundance data and life history profiles. Reef-limited recruitment was indicated by high occupation of the reef by 0 year-class individuals (based on interpretation of length-frequency information in Bohnsack & Harper 1988). Furthermore, to be considered as limited in recruitment by reef habitat, we required each species to possess a life history of reef habitat dependency of settlers (based on published life history profiles: Table 1). Application of these 2 criteria may result in over-estimation of the production credit for species that are judged as limited in recruitment by reef area, if a species is actually limited by abundance of larvae reaching suitable settlement habitat.

To estimate enhancement of fish abundance, we had to decide how to treat seasonal variation in abundance. Lindberg (1996) sampled fish in winter and summer for 5 yr, from which we computed seasonal means. For those species whose recruitment was judged limited by the amount of reef habitat, we chose the season with the largest average number of recruits (consistently summer) as our density estimate because that season reflects peak recruitment. For those species whose recruitment was judged not limited by reef habitat, we used the

numbers of individuals remaining on the reefs at the lower seasonal (summer vs winter) density as a conservative estimate of numbers of fish that depend on the reef for prey resources that sustain growth.

Because fish abundances in Lindberg (1996) are aggregated across multiple age classes, we partitioned the total abundance ( $N$ ) by age class  $i$  for each species. For those species whose recruitment was deemed limited by reef habitat, we generated an expected abundance curve that followed a stable age-distribution using published mortality rates (Table 2) and distributed the observed total density of fish into age classes accordingly (Table 3). Assumption of a stable age-distribution has the consequence of eliminating year-to-year variance in the subsequent estimation of production impacts. For those species whose recruitment was not judged to be limited by reef habitat, reef occupation generally began as late stage juveniles or adults, so assuming a stable age distribution starting from recruitment and continuing until death would not accurately reflect the true age distribution on the offshore reefs. To compute age distributions, and ultimately to credit the artificial reef for production of those life stages that do use the reef, we applied published age-length relationships (Table 2) to empirical fish-size distributions in Bohnsack & Harper (1988).

Because the size-frequency data come from fished reefs, and we wished to partition observed abundance by age on unfished reefs (from Lindberg 1996), we had to compute what these age distributions would be in the absence of fishing. We converted the age distributions to analogous distributions expected on reefs closed to fishing by using published estimates of age-specific fishing mortality,  $F$  (Table 2), to remove effects of fishing on each susceptible species. First, we computed modified relative age frequencies by dividing each age frequency in the fished distribution by  $e^{-F \times i}$ , where  $i$  is number of years that an age class has experienced fishing mortality ( $F$ ). This procedure assumes a species whose immigration onto the reef occurs only at a single age. For those species that immigrate over multiple year-classes (e.g. gag grouper), this procedure may overestimate the degree to which fishing has reduced abundance of older fish, because fishing mortality is assumed to have been applied for some number of years before their appearance on the reef. To determine the magnitude of error associated with this method, we used sheepshead as a model, because its immigration resulted in the highest percentages of older age-classes and recalculated the production by a more complex procedure, which actually estimated the proportions of new immigrants to survivors of previous immigrations for each age class. This complex method then allowed application of the correction for fishing mortality for only those years when the fish were present on the reef. Comparison of results of this method

and the procedure that we used for all our calculations showed a relatively trivial 1.4% overestimate for production of sheepshead, despite its high rates of ca. 40% of immigration in each older age class. Consequently, we used the simpler method to adjust age-frequency distributions for fishing effects.

Next, we took the modified relative frequency of the oldest age class observed by Bohnsack & Harper (1988) and used published estimates of natural mortality (Table 2) to compute the exponential decay in abundance over the remainder of the published life span. We then normalized these modified frequencies so that they totaled 1. This correction has the effect of extending the age distribution expected on unfished reefs to include several older age classes, while retaining total abundance at the level on unfished reefs observed by Lindberg (1996). For those 7 species (identified in Table 2) whose recruitment was not judged to be limited by reef habitat and were not reported in Bohnsack & Harper (1988), we assumed a stable age-distribution based on published (Table 2) natural mortality rates, with an age of first occupation of the reef based upon life-history profiles (Table 2).

**Production calculations.** The 25 most abundant species or species groups expected to occur on an artificial reef constructed offshore of Tampa Bay, Florida (Table 1), were reduced to 17 (Table 2) by pooling the 2 species of blennies and removing 7 species that were not present during 1 of the 2 seasons (sand diver, greater amberjack, whitespotted soapfish, reef croaker, slippery dick, Spanish mackerel, and blue runner). After we computed for each taxon the on-reef density of each age class ( $N_i$ ), we calculated expected production using the methodology in Peterson et al. (2003). Specifically, for annual species (blennies), we estimated annual production by multiplying the average weight attained by an individual that survives its full natural life span by the summer density. This computation fails to include production achieved by fish that settled but died before censusing; however, compensation for this underestimation is achieved by assuming that all individuals alive in summer grow to reach maximum size before dying.

For all other species (those that live for more than 1 yr), we determined the average weight at age  $i$  ( $W_i$ ) using the exponential weight-length relationship:

$$W_i = a \times L_i^b \quad (1)$$

in which  $a$  and  $b$  are species-specific constants (Table 2) and  $L_i$  is calculated using the von Bertalanffy growth equation:

$$L_i = L_\infty \times [1 - e^{-K \times (i - t_0)}] \quad (2)$$

The parameters  $L_\infty$  (the asymptotic maximum length),  $K$  (the Brody growth coefficient), and  $t_0$  (a constant



Table 2. Literature values for survival rate, age-length and length-weight parameters used in fish productivity calculations. *M*: annual natural mortality rate; *F*: annual mortality rate as a consequence of fishing pressure; *r*: is the age at which the fish recruits to the fishery. Age distributions of reef fish (*D*) were derived from empirical data in Bohnsack & Harper (1988) (BH), calculated stable-age distributions (S), or were not necessary because the species was an annual (A). The age-length relationship is modeled by von Bertalanffy equations.  $L_{\infty}$  (cm) is the asymptotic maximum length, *K* is a constant (the Brody growth coefficient), and  $t_0$  is a constant representing the age (in yr) at 0 length. Fish length is converted to wet weight using a length-weight exponential equation with constants *a* and *b*

Species or species group	Survival rate		Age-length and length-weight relationships					Source		
	<i>M</i>	<i>F</i>	<i>r</i>	<i>D</i>	$L_{\infty}$	<i>K</i>	$t_0$		<i>a</i>	<i>b</i>
Herring	1.50	1.00	1	S	12.0	0.280	-1.100	0.0111	2.81	French et al. (1997)
Round scad	0.30	0.30	3	S	35.0	0.222	0.186	0.0280	3.02	South Atlantic Fishery Management Council (1983)
Tomtate	0.60	0.40	1	BH	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)
Blennies				A						Annual species <sup>a</sup>
Leopard toadfish	0.60	0.00	2	S	30.0	0.193	-0.180	0.0170 <sup>b</sup>	4.98 <sup>b</sup>	Wilson et al. (1982), Serafy et al. (1997)
Sheepshead	0.20	0.40	3	BH	45.1	0.205	-1.540	0.0283	2.96	French et al. (1997)
Black seabass	0.30	0.30	3	S	35.0	0.222	0.186	0.0280	3.02	South Atlantic Fishery Management Council (1983)
Cubbyu	0.30	0.30	3	S	35.0	0.222	0.186	0.0280	3.02	South Atlantic Fishery Management Council (1983)
Gag grouper	0.20	0.53	2	BH	119.0	0.166	-0.740	0.0140	2.99	Manooch & Haimovici (1978), Goodyear (1988), Brown et al. (1990), Goodyear & Schirripa (1991), Hood & Schlieder (1992)
Gray snapper	0.20	0.53	2	BH	50.1	0.133	-1.490	0.0156	2.93	Manooch & Mason (1984), Goodyear (1988), Brown et al. (1990), Goodyear & Schirripa (1991)
Gray triggerfish	0.20	0.53	2	BH	57.0	0.133	-1.490	0.0268	2.82	Manooch & Mason (1984), Condrey et al. (1985), Wakeman & Ramsey, (1985), Goodyear (1988), Brown et al. (1990), Goodyear & Schirripa (1991)
Pigfish	0.60	0.40	1	BH	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)
Spadefish	0.60	0.40	1	BH	49.0	0.290	0.120	0.0128	3.06	South Atlantic Fishery Management Council (1983)
Spottail pinfish	0.60	0.40	1	BH	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)
White grunt	0.60	0.40	1	BH	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)
Belted sandfish	0.30	0.30	3	S	35.0	0.222	0.186	0.0280	3.02	South Atlantic Fishery Management Council (1983)
Sand perch	0.60	0.40	1	S	47.5	0.164	-1.144	0.0128	3.06	South Atlantic Fishery Management Council (1983)

<sup>a</sup>For annual species (blennies), production is calculated by multiplying fish density by average individual wet weight

<sup>b</sup>For leopard toadfish, length was converted to wet weight using the following exponential equation:  $W_l = a \times e^{b \times l^d}$ . For all other fish Eq. (1) was used (see text)

Table 3. Estimated augmented fish density and production for the 17 species or species groups (2 blenny and multiple herring species are grouped because the species within each group exhibit similar life histories) that are most densely populated on artificial reef habitat in southwest Florida. The index of reef exclusivity (IRE) is an estimate of species utilization of resources associated with artificial reef habitat compared to resources from adjacent non-reef habitat. The IRE is based on diet information when available and/or life-history profiles of each species or species group. Grouping is assigned for enhanced production estimates: R = species whose recruitment is limited by the amount of reef habitat; G = species whose recruitment is not limited by reef habitat area, but may experience enhanced growth because of the presence of reef refuges and reef-associated prey. Scenario 1 = Attraction, Scenario 2 = Enhancement, and Scenario 3 = Enhancement with intense fishing

Species or species group	Average increase of fish density (ind. 10 m <sup>-2</sup> )	IRE	Grouping	Annual increase in fish production (kg 10 m <sup>-2</sup> yr <sup>-1</sup> )		
				Scenario 1	Scenario 2	Scenario 3
Herring	1362.28	0.10	G	0.000	0.170	0.175
Round scad	1.50	0.10	G	0.000	0.010	0.024
Tomtate	29.00	0.25	G	0.000	0.505	1.284
Blennies	4.90	–	R	0.000	0.049	0.054
Leopard toadfish	0.64	–	R	0.000	0.017	0.019
Sheepshead	0.17	1.00	G	0.000	0.028	0.009
Black seabass	2.20	0.75	G	0.000	0.151	0.025
Cubbyu	8.93	0.75	G	0.000	0.433	1.844
Gag grouper	4.70	0.75	G	0.000	4.321	0.691
Gray snapper	0.07	0.75	G	0.000	0.004	0.002
Gray triggerfish	0.25	0.75	G	0.000	0.023	0.007
Pigfish	2.20	0.75	G	0.000	0.174	0.002
Spadefish	1.30	0.75	G	0.000	0.094	0.032
Spottail pinfish	1.30	0.75	G	0.000	0.071	0.034
White grunt	5.70	0.75	G	0.000	0.350	0.165
Belted sandfish	1.40	0.50	G	0.000	0.045	0.061
Sand perch	0.17	0.50	G	0.000	0.007	0.010
Total annual increase in fish production:				0.000	6.452	4.438

representing the age at 0 length) of this latter equation are derived from literature values for each particular species (Table 2). The change in weight between successive age classes is equal to the annual production ( $P$ ) of an individual surviving through age class  $i$ :

$$P_i = W_i - W_{(i-1)} \quad (3)$$

To estimate production for each age class, we multiplied the incremental weight gain of a fish surviving the entire age interval ( $P_i$ ) by the numbers of fish present in that age class ( $N_i$ ). Our  $N_i$  numbers are derived from counts made months before the end of the year, so use of  $N_i$  to compute total production of this age class fails to include contributions from fish that had been present earlier but died earlier in that year before censusing. However, use of this approximately mid-year fish density overestimates the numbers that will ultimately survive until the end of the year. In the absence of explicit information on seasonal mortality and growth rates, this approximation achieves the best possible estimate of annual production in each age class, assuming a balance between the underestimate from ignoring those that died young and the overestimate from assuming no additional deaths among those that survived to mid year. The production by species is then computed by summing  $P_i \times N_i$  over all age classes present on the reef.

Because species differ in affinity to reef habitat and use of reef resources, we weighted the production of each species or species group by the degree to which its growth is attributable to prey resources produced on the reef. Thus, we adjusted the production computation of each group by an index of reef exclusivity (IRE: Peterson et al. 2003) in diet. In some cases, this index was constructed from gut-content information. For species without quantitative information on gut contents at a level of taxonomic discrimination that allowed reef-dependent prey to be identified, we used life-history profiles and observed feeding behaviors (sources listed in Table 1) to assign a value to the index. The IRE ranged over 5 broad categories from 0.10 to 1.0 (Table 3). We used 0.10 as a minimum to reflect the assumption that survival may have been enhanced among reef-associated fishes, even if no reef-dependent prey were consumed. Values of 1.0 reflect a very strong association of the species with the reef and its resources. Applying the IRE, annual production of a species for year (AP) attributed to the presence of a standard area of 10 m<sup>2</sup> of artificial reef was calculated by:

$$AP = IRE \times \sum (P_i \times N_i) \quad (4)$$

beginning with  $i = 1$ , reflecting the convention of accounting for production at the completion of each

year of life. Finally, total annual enhancement of fish production per 10 m<sup>2</sup> of reef is the sum of AP across all 17 species or species groups. Effects of reef-associated refuges from predation are incorporated into these calculations of production, because the natural mortality rates (Table 2) that are applied come from the synthesis of data on fishes inhabiting reef habitat.

**Adjusting production for fishing and discounting over time.** We compute the quantitative estimate of enhancement of fish production reflecting each of 3 plausible alternative scenarios (attraction, enhancement, and enhancement with fishing) that may result from installation of an artificial reef. The first scenario, attraction, specifies the enhanced fish production, under the assumption that fish associated with a new artificial reef could have survived and grown as well on another artificial reef, natural hard bottom, or alternative habitat elsewhere, without any penalty from competition. The second scenario, enhancement, assumes that reef habitat and associated prey resources regulate fish survival and growth and that no fishing occurs. Under this scenario, all production estimated from Eq. (4) is credited to the reef. The third scenario, enhancement with fishing, also assumes that reef habitat regulates fish survival and growth but incorporates recent information (Lindberg & Loftin 1998) to quantify impacts of fishing on artificial reefs. Under this third scenario, the enhancement estimate for each reef

species is adjusted by multiplying by a species-specific index of fishing pressure (IFP) to account for direct effects of fishing mortality and indirect effects of reduced predation and/or competition. IFP estimates the percentage biomass change after application of fishing by comparing the actual biomass caught on fished reefs to the expected amount if these reefs were not open to fishing. The IFP was computed by dividing observed fish biomass on fished reefs by the biomass expected in the absence of fishing, based on data from Lindberg & Loftin (1998). We used the magnitude of the interaction between year and treatment (fishing for a year vs unfished) in results from Lindberg & Loftin (1998) to compute expected biomass for 5 species; for 7 species we used biomass in the year prior to fishing (Table 4). For the remaining 5 species for which species-specific changes with fishing are not provided in Lindberg & Loftin (1998), we assigned an IFP equal to the best ecological analogue (Table 4). Thus, the third scenario accounts for the very likely possibility of increased fishing pressure by appropriately adjusting the expected values under the second scenario (enhancement).

Because the fish and prey community on newly constructed artificial reefs may require several years to develop fully, we had to determine whether the estimated annual production for existing reefs required some reduction in the initial years after construction to

Table 4. Derivation of the Index of Fishing Pressure (IFP) used in the scenario of enhancement with fishing. Based on data presented in Lindberg & Loftin (1998), the IFP, the proportional change in biomass (kg) as a consequence of fishing, was calculated by dividing the biomass (kg wet wt per reef) of each fish species measured on reefs open to fishing for 1 year (1996 to 1997) by the expected biomass in the absence of fishing. The expected biomass was calculated by adjusting biomass measured in 1996 before the application of the fishing treatment by the percent gain or loss in biomass on reefs closed to fishing from 1996 to 1997 (control reefs). For those species for which density data on control (unfished) reefs in 1997 were not available (NA), the IFP was calculated by dividing the observed biomass in 1997 by the initial biomass in 1996. For the 5 species (round scad, blenny, black sea bass, spotail pinfish, and sand perch) for which taxon-specific information on the effect of fishing was not available, we chose to use the most ecologically similar species for which information was presented in Lindberg & Loftin (1998): tomtate, leopard toadfish, gag grouper, white grunt, and belted sandfish, respectively

Species	Fish biomass on reefs in 1996 that would be opened to fishing in 1997 (kg reef <sup>-1</sup> )	Expected change in biomass on reefs opened to fishing if fishing did not occur (%)	Expected biomass on open reefs in 1997 if fishing did not occur (kg reef <sup>-1</sup> )	Observed biomass on reefs opened to fishing in 1997 (kg reef <sup>-1</sup> )	IFP
Gag grouper	233.8	41	329.7	54.0	0.16
Sheepshead	4.6	-22	3.6	1.2	0.33
Gray triggerfish	5.6	53	8.7	2.6	0.30
White grunt	1.8	148	4.5	2.1	0.47
Hogfish	1.2	-56	0.5	0.0	0.01
Herring	186.7	NA	NA	192.2	1.03
Tomtate	36.6	NA	NA	93.1	2.54
Leopard toadfish	14.5	NA	NA	16.1	1.11
Cubbyu	3.0	NA	NA	12.8	4.26
Gray snapper	7.7	NA	NA	5.3	0.69
Spadefish	55.9	NA	NA	19.2	0.34
Belted sandfish	1.4	NA	NA	1.9	1.36

account for community development during succession. To address this question, we used the changing total fish biomass figures in Lindberg (1996) to adjust the production estimates in those first years of reef life. These data supported a 35% reduction from full production in Year 1 and a 25% reduction in Year 2 from the asymptote reached by Year 3. Each succeeding year achieves full production, as estimated by Eq. (4). Because a reef continues to produce enhancements in secondary production for the duration of its lifetime, calculating the quantitative compensation in fish production to mitigate for losses or to enhance fisheries requires integration of the annual contributions of the artificial reef over its full lifetime. Estimating the lifetime of an artificial reef is difficult, so we provide these calculations for a range of feasible lifetimes. Finally, to reflect the influence of time, we discount future production estimates by the standard 3% annual discount rate (NOAA 1997) to adjust for the time lags between the injury warranting restoration and when the compensating production enhancement is achieved.

## RESULTS

The 25 species or species groups included in our estimates of enhanced production (Table 1) account for over 95% of the biomass of all fishes found on artificial reefs in the offshore area of the west coast of Florida. We provide production estimates (Table 3) for 17 taxa because 7 of the original 25 were absent from reefs in either winter or summer, and 2 blennies (crested and seaweed) were pooled. Of the 17 remaining species or species groups, only 2 were judged to be limited in recruitment by reef habitat: blennies and leopard toadfish (Table 3). We inferred recruitment limitation by reef habitat from the data showing occupation of the reef by new recruits and from knowledge of the life history, suggesting saturation of available reef habitat by recruits of these 2 species. The remaining 15 taxa were expected to exhibit enhanced growth at older life stages as a result of the installation of the reef. The IRE values (Table 3) for these species ranged from 0.10 for pelagic forage fishes (herring and scad) to 1.0 for sheepshead, which feed almost exclusively on reef-dependent prey (e.g. barnacles, mussels). The planktivore tomtate is the only species that was assigned an IRE of 0.25, reflecting its feeding in the water column rather than on the reef, but also its virtually exclusive occurrence on reefs. IRE values for demersal fishes that use the reef for shelter and to a large extent for

foraging, but also consuming resources off the reef, ranged from 0.50 to 0.75 (Table 3).

Estimates corresponding to the 3 likely alternative scenarios resulting from the creation of an offshore artificial reef ranged from 0, under the attraction scenario (Scenario 1), to 6.45 kg wet wt  $10\text{ m}^{-2}\text{ yr}^{-1}$  under the conditions of enhancement and no fishing (Scenario 2). The addition of fishing pressure, typical of artificial reefs, reduced the latter estimate of enhancement by 32% to 4.44 kg  $10\text{ m}^{-2}\text{ yr}^{-1}$  (Scenario 3, Table 3). Gag grouper contributed the highest percentage of any single species (67% of the total) to the production estimates under the enhancement scenario; however, after inclusion of direct and indirect impacts of fishing, the gag contribution fell to 16% and cubbyu, at 42%, contributed most to enhanced production. Gag grouper are intensely targeted by fishermen, whereas the smaller demersal cubbyu are not. Although numerically dominant, the 2 pelagic taxa, herring and tomtate, accounted for only 10% of total production under the no-fishing Scenario 2, and 33% under Scenario 3 where fishing impacts are included (Table 3).

The large range in production estimates among the 3 scenarios is also reflected in the cumulative production over the lifetime of the artificial reef. A reef lasting 30 yr would be expected to augment fish production by a cumulative amount of 123 kg wet wt  $10\text{ m}^{-2}$  under Scenario 2, and 84 kg  $10\text{ m}^{-2}$  under Scenario 3 discounted to present-day value (Table 5). Cumulative production (Fig. 1) approaches an asymptote after 90 yr for Scenario 2 (~200 kg  $10\text{ m}^{-2}$ ) or 3 (~140 kg  $10\text{ m}^{-2}$ ) as a result of depreciating enhancement estimates by an annual discount rate of 3%. Thus, the ratio of these 2 enhanced cumulative production scenarios that vary fishing mortality approaches is 1.43.

## DISCUSSION

The 3 alternative scenarios for which we quantify expected enhancement of fish production after installation of an artificial reef offshore of southwest Florida

Table 5. Long-term projection of enhanced fish production from reefs, discounted to account for annual depreciation of resources. Total augmented fish production of offshore reefs was reduced by 35% in Year 1 and 25% in Year 2 to account for succession on reefs (Lindberg 1996). All production estimates were discounted at an annual rate of 3%

Scenario	Cumulative production (kg wet wt $10\text{ m}^{-2}$ ) for given project lifespan				
	1 yr	2 yr	10 yr	20 yr	30 yr
1. Attraction	0.00	0.00	0.00	0.00	0.00
2. Enhancement	4.07	8.66	51.32	92.28	122.75
3. Enhancement with fishing	2.80	5.94	35.30	63.47	84.43

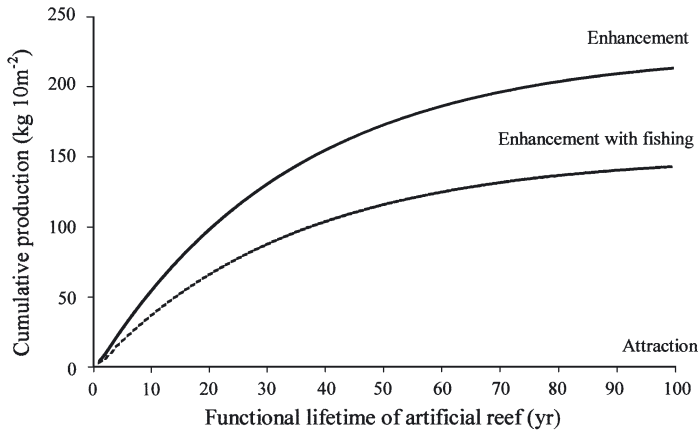


Fig. 1. Long-term projection of cumulative fish production per 10 m<sup>2</sup> of artificial reef habitat. Cumulative values were discounted at an annual discount rate of 3%. In Scenario 1 (attraction), it is assumed that sufficient habitat is already available for reef fish (i.e. zero over all years; parallel with x-axis), so that all biomass observed on the artificial reef is derived from immigrants leaving neighboring hard structures. Scenario 2 (enhancement) assumes no fishing, and that fish on the artificial reef would not have found adequate habitat if the new reef were unavailable. Scenario 3 (enhancement with fishing) also assumes that fish are dependent on artificial reef for habitat, but introduces empirically derived impacts (direct and indirect) of fishing on the 17 species or species groups

characterize the large degree of uncertainty associated with using artificial reefs as mitigation or compensatory restoration for natural resources losses (Fig. 1). Furthermore, each of these estimates is itself based upon sets of assumptions that inject further uncertainty in the quantitative estimates of enhanced fish production. Perhaps most importantly, our method of estimating enhancement of fish production for the 2 scenarios that represent enhancement assumes that prey resources and/or opportunities to exploit those prey resources through provision of refuges from predation are limited by the areal extent of reef habitat in this environment. Thus, our estimates for the enhancement scenarios are maxima because they assume that recruitment of species deemed limited by reef habitat and the full realized growth of immigrant fishes on the newly constructed reef would not have taken place in the absence of the addition of reef area. Many of these species associated with the new reef could conceivably have recruited, survived, and grown elsewhere on other artificial reefs, natural hard bottoms or on an entirely different habitat. A definitive experimental test of impacts of addition of new artificial reefs could possibly be designed to resolve this set of critical questions (Osenberg et al. 2002), but it would need to be done on a broad spatial scale appropriate to the mobility of the key species (Seaman 2000). In addition, the answer may well vary geographically. Shelf areas with

extensive natural hard-bottom habitat may not exhibit substantially enhanced fish production with addition of artificial reef habitat, whereas shelf areas with little natural hard bottom may show larger responses. Reefs that serve to anchor kelps and other large macroalgae, like those in southern California (e.g. Ambrose 1994), may differ in their effects on fish production from those that serve as substrata for suspension-feeding invertebrates (see Miller & Falace 2000).

Given the present uncertainty about the fundamental assumption of habitat limitation, and the wide range among plausible scenarios in our quantitative estimates of enhanced fish production (0 to 123 kg 10 m<sup>-2</sup> of reef over the first 30 yr of reef life), confidence in using this form of mitigation or compensation for injury to fish resources is low. The range among production estimates for the 3 scenarios that we quantify provides one means of quantifying the consequences of underlying biological uncertainty. The range in outcomes is even greater than is depicted in Fig. 1, when a 4th scenario is added that includes the combination of the attraction process with the addition of fishing mortality. This 4th scenario implies a net reduction in fish production after installation of a new artificial reef, arising from the increased ability of fishermen to catch fishes which have become aggregated on the new reef (Bohnsack 1989). A first-order estimate of the net reduction suggests a magnitude identical to the difference between Scenarios 2 and 3, or a decline in ca. 40 kg of wet wt fish production per 10 m<sup>2</sup> of reef over 30 yr. However, Bohnsack's analysis of the effects of the increasing fishing effort under the attraction scenario suggests high temporal variability, rendering the computation of cumulative declines, like those that we developed for Scenarios 1 to 3, extremely risky (Fig. 1). This temporal instability, and our concern about accurately modeling the behavior of fishermen as reef fish abundances decline, inhibit us from quantifying this 4th scenario.

Assessing which of our 4 scenarios is most likely helps resolve the uncertainty. This requires careful evaluation and synthesis of both the empirical studies as well as the conceptual literature. Our first (attraction) scenario expresses the enhanced fish production under the assumption that fish associated with a new artificial reef could recruit, survive and grow just as well on another artificial reef, natural hard bottom, or alternative habitat elsewhere, without suffering any abundance or growth penalty from competition for limited refuges or habitat-associated resources. This estimate thus assumes that reef habitat for offshore fish is not limiting, which has substantial support in the literature relative to at least the southwest Florida shelf (Bohnsack 1989, Bohnsack et al. 1994, Grossman et al. 1997). For example, Bohnsack et al. (1994) found that



fish did not colonize artificial reefs as early recruits but, instead, at larger sizes and older ages, implying that immigration from other reefs or habitats is the major mechanism by which artificial reefs become occupied by fishes. Similar processes can be inferred from the data sets in Bohnsack & Harper (1988) and Lindberg (1996). Thus, a synthesis of the best available evidence suggests that fish aggregating around a new reef first recruited elsewhere, supporting our assumption that newly installed reefs do not enhance recruitment, except for certain exceptional species. Furthermore, this synthesis shows that these recruits were growing and surviving elsewhere up to the time of migration to the new reef. That may imply that subsequent production that they achieve on the new reef would have occurred elsewhere, but whether enhanced availability of reef-associated prey resources would have increased realized growth and production is not clear. Furthermore, some demersal fishes associated with artificial reefs benefit from using the reef as a refuge from which to forage more effectively on off-reef prey buried in surrounding soft sediments (Lindquist et al. 1994).

Both the amount of reef habitat currently available in a region, as well as the possibility that many reef fish may be recruitment limited (but not by artificial reef area), offer further conceptual support for the attraction scenario that reef habitat is not limiting fish production in the coastal shelf of southwest Florida. Artificial reefs have been installed in large numbers over the past 2 decades, with over half of the artificial reefs in the USA located in Florida waters (Seaman 2000). In addition, naturally occurring hard-bottom habitats exist over large areas of the shelf in the southeastern USA, especially in southwestern Florida (Smith et al. 1979). Because overfishing has reduced populations of many marine fishes that are associated with hard-bottom and artificial reef habitats on the shelf, there is a high probability that low levels of available recruits may currently limit many of these fish populations (Sala et al. 2001). Consequently, there is little likelihood that the current cumulative area of artificial reef and hard bottom habitats limits recruitment for fishes on the shelf (Bohnsack 1989, Bohnsack et al. 1994, Grossman et al. 1997).

Under both enhancement scenarios (Scenarios 2 and 3), the increase in production is achieved largely by realizing faster individual growth rates, as a consequence of greater foraging opportunity provided by addition of artificial reef habitat. Larger sizes at age also imply better condition, greater fecundity and enhanced spawning stock biomass. Thus, for species whose recruitment is limited by low spawning-stock biomass, the enhanced growth on artificial reefs under our enhancement scenarios may have an added bene-

fit of increasing regional recruitment. We did not attempt to compute a production credit to reflect this possibility because of the absence of reliable spawner-recruit relationships for the resident fishes. However, under conditions of protection from fishing (Scenario 2), this benefit of installing artificial reefs could be significant and could contribute to a regional system of marine reserves (Roberts 1997). Without regulating fishing pressure (Scenario 3), this potential benefit would dissipate, as fishing not only reduces targeted fish populations but also selectively removes the largest, most fecund fish in the populations (Bohnsack 1992). Furthermore, the establishment of marine reserves to promote recovery of overfished stocks of recruitment-limited fishes does not require the construction of new reefs on the shallow continental shelf; rather, it requires the management of existing reefs as reserves in an effective design (Lubchenco et al. 2003).

A comparison of our second and third scenarios reveals the potential importance of management of habitats, following creation and/or restoration, if increasing fish production in the system is the ultimate goal. The possibility that any gain in production from creation of an artificial reef may be offset by intense fishing pressure, especially by recreational fishermen, has been recognized for some time (Bohnsack et al. 1997). Lindberg & Loftin (1998) provide a test of this hypothesis in their study of gag grouper and other reef fishes. They found that opening an artificial reef to fishing reduced the gag biomass by 77% in the first 8 mo, compared to simultaneous changes on analogous reefs that were not fished. Furthermore, while other intensely fished species declined after a year of fishing, some unexploited species like tomtate greatly increased, presumably from the indirect effects of removing targeted species (Table 4). Consequently, we used this information to modify the estimates of enhanced production accordingly. Thus, Scenario 3 accounts for the very likely possibility of increased fishing pressure by adjusting the expected values under Scenario 2 based on the empirical fishing mortality data of Lindberg & Loftin (1998). The decision of whether to control fishing on offshore artificial reefs, and the ability to enforce any closure, play a large role in determining levels of fish production that are realized from installation of an artificial reef in this system. More efficient fishing on more highly aggregated fish may diminish or even negate the contributions of increasing the area of even limited habitat to net production of key fish stocks. Furthermore, depending on the nature of the reef and the fishing practices in the area, management may be necessary to insure that destructive harvest practices (e.g. oyster dredging, Lenihan & Peterson 1998, Lenihan & Micheli 2000, and bottom trawling, Jennings & Kaiser 1998) do not alter the qual-

ity or lifespan of restored habitats, thereby reducing the fish production.

Substantial uncertainties exist in estimating the level of enhanced fish production from the creation or restoration of any marine habitat (Peterson et al. 2003). Such uncertainties result from the lack of empirical tests of many of the assumptions required to quantify the linkages between recruitment, survival and growth of fish and habitat availability and quality (Zedler 2000, Madon et al. 2001). A wide variety of reasons can motivate habitat creation (Hackney 2000), particularly for offshore artificial reefs (see Seaman 2000 for a full discussion). If the primary goal of habitat creation/restoration is the addition of new fish production, then the likelihood of enhancement must be carefully evaluated. For natural habitats that have dramatically decreased over recent decades and are clearly important nursery grounds for fish postlarvae (i.e. seagrass meadows, salt marshes and oyster reefs), the assumption that habitat is currently limiting is probably reasonable and agrees with the current scientific consensus (Peterson et al. 2003). However, for artificial reefs no such consensus has been reached; if there is emerging consensus, it points to a process of habitat selection, rather than release from habitat or resource limitation, as the most compelling explanation for high aggregations of fish around newly created offshore artificial reefs. Further, the probability that any enhancement in fish production resulting from artificial reefs would vary both spatially and temporally, and by species, increases the large uncertainty that the construction of artificial reefs could meet quantitative mitigation goals. Until uncertainty is resolved and actual enhancement of fish production is demonstrated, only habitats in which the current scientific consensus supports the assumption of habitat limitation represent good candidates for compensatory restoration. Our calculations of the range of outcomes in enhancement of fish production associated with the construction of a new artificial reef habitat serves to show the extreme sensitivity to the untested assumptions about key underlying biological processes.

*Acknowledgements.* The paper benefited from the comments of J. Bohnsack, M. Carr, E. Estevez, M. Hixon and P. Levin in developing the conceptual approach used in this synthesis. D. French checked and rechecked all of our production and scaling calculations. L. Dipinto, B. Julius, and T. Penn provided guidance. The NOAA Center of Damage Assessment provided funding for this synthesis.

#### LITERATURE CITED

- Ambrose RF (1994) Mitigating the effects of a coastal power plant on a kelp forest community: rationale and requirements for an artificial reef. *Bull Mar Sci* 55:694–708
- Bohnsack JA (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bull Mar Sci* 44:631–645
- Bohnsack JA (1992) Reef resource habitat protection: the forgotten factor. In: Stroud RH (ed) *Stemming the tide of coastal fish habitat loss*. *Mar Recreational Fish* 14:117–129
- Bohnsack JA, Harper DE (1988) Length-weight relationship of selected marine reef fishes from the southeastern United States and the Caribbean. *Tech Memm NMFS-SEFC-215*, NOAA, Miami, FL
- Bohnsack JA, Harper DE, McClellan DB, Hulsbeck M (1994) Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, USA. *Bull Mar Sci* 55:796–823
- Bohnsack JA, Ecklund AM, Szmant AM (1997) Artificial reef research: is there more than the attraction-production issue? *Fisheries* 22:14–16
- Brown BE, Browder JA, Powers J, Goodyear CD (1990) Biomass, yield models, and management strategies for the Gulf of Mexico ecosystem. *Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Miami, FL*
- Condrey RE, Adkins G, Wascom MW (1985) Yield-per-recruit of spotted seatrout. *Gulf Res Rep* 8:64–67
- Doherty PJ, Williams DMcB (1988) The replenishment of coral reef fish populations. *Oceanogr Mar Biol Annu Rev* 26: 487–551
- Duffy JM (1985) Artificial reefs and mitigation: a small scale case history. *Bull Mar Sci* 37:397
- French DP, Rines H, Keller A, French FW III, Gifford D, Pavignano S (1997) The CERCLA type A natural resource damage assessment model for coastal and marine environments. *Tech Doc Vol. IV, Biological Database Part 1*. Office of Environmental Policy and Compliance, US Dept of the Interior, Washington, DC
- Friedlander A, Beets J, Tobias W (1994) Effects of fish-aggregating device design and location of fishing success in the US Virgin Islands. *Bull Mar Sci* 55:592–601
- Goodyear CP (1988) Spawning stock biomass and yield per recruit for several reef fish species of the Gulf of Mexico. *Southeast Fisheries Science Center, NOAA, Miami, FL*
- Goodyear CP, Schirripa MJ (1991) A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. *Southeast Fisheries Science Center, NOAA, Miami, FL*
- Grossman GD, Jones GP, Seaman WJ Jr (1997) Do artificial reefs increase regional fish production? A review of existing data. *Fish Manag* 22:17–23
- Hackney CT (2000) Restoration of coastal habitats: expectation and reality. *Ecol Eng* 15:165–170
- Hixon MA (1998) Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Aust J Ecol* 23: 192–201
- Hood PB, Schlieder RE (1992) Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bull Mar Sci* 51:337–352
- Hueckel GJ, Buckley RM, Benson BL (1989) Mitigating rocky habitat loss through artificial reefs. *Bull Mar Sci* 44: 913–922
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Keough MJ, Downes BJ (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348–352
- Lenihan HS, Micheli F (2000) Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict by ecological experimentation. *Fish Bull* 98:86–95

- Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol Appl* 8:128–140
- Lindberg WJ (1996) Fundamental design parameters for artificial reefs: interaction of patch reef spacing and size. Final Project Report, MARFIN Grant Number C-6729. University of Florida, Gainesville, FL
- Lindberg WJ (1997) Can science resolve the attraction-production issue? *Fish Manage* 22:10–13
- Lindberg WJ, Loftin JL (1998) Effects of habitat and fishing mortality on the movements, growth and relative weights of juvenile-to-adult gag (*Mycteroperca microlepis*). Final Project Report, MARFIN Grant Number NA57FF0288. University of Florida, Gainesville, FL
- Lindquist DG, Ogburn MV, Stanley WB, Troutman HL, Pereira SM (1985) Fish utilization patterns on temperate rubble-mound jetties in North Carolina. *Bull Mar Sci* 37: 244–251
- Lindquist DG, Cahoon LB, Clavijo IE, Posey MH, Bolden SK, Pike LA, Burk SW, Cardullo PA (1994) Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. *Bull Mar Sci* 55:308–318
- 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
- Madon SP, Williams GD, West JM, Zedler JB (2001) The importance of marsh access to growth of the California killifish, *Fundulus parvipinnis*, evaluated through bioenergetic modeling. *Ecol Model* 135:149–165
- Manooch CS, Haimovici M (1978) Age and growth of the gag, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the southeastern United States. *Trans Am Fish Soc* 107:234–240
- Manooch CS, Mason DL (1984) Age, growth, and mortality of Lane Snapper from Southern Florida. *Northeast Gulf Sci* 7: 109–115
- McGlennon D, Branden KL (1994) Comparison of catch and recreational anglers fishing on artificial reefs and natural seabed in Gulf St. Vincent, South Australia. *Bull Mar Sci* 55:510–523
- Miller MW, Falace A (2000) Evaluation methods for trophic resource factors—nutrients, primary production, and associated assemblages. In: Seaman WS (ed) *Artificial reef evaluation with application to natural marine habitats*. CRC Press, Boca Raton, FL, p 95–126
- NOAA (National Oceanographic and Atmospheric Administration) (1997) *Habitat equivalency analysis: an overview*. Policy and Technical Paper Series, NO-95-1. Damage Assessment and Restoration Program, NOAA, Silver Spring, MD
- Osenberg CW, St. Mary CM, Wilson JA, Lindberg WJ (2002) A quantitative framework to evaluate the attraction-production controversy. *ICES J Mar Sci* 59:S214–S221
- Peterson CH, Grabowski JH, Powers SP (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar Ecol Prog Ser* 264:249–264 (in this Theme Section)
- Polovina JJ (1991) Fisheries applications and biological impacts of artificial habitats. In: Seaman WS, Sprague LM (eds) *Artificial habitats for marine and freshwater fisheries*. Academic Press, New York, p 154–176
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454–1457
- Sala E, Ballesteros E, Starr RM (2001) Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* 26:23–30
- Seaman WS Jr (2000) *Artificial reef evaluation with application to natural marine habitats*. CRC Press, Boca Raton, FL
- Serafy JE, Hopkins TE, Walsh PJ (1997) Field studies on the ureogenic gulf toadfish in a subtropical bay. I. Patterns of abundance, size composition and growth. *J Fish Biol* 50: 1258–1270
- Sheng YP (2000) Physical characteristics and engineering at reef sites. In: Seaman WS (ed) *Artificial reef evaluation with application to natural marine habitats*. CRC Press, Boca Raton, FL, p 51–94
- Smith GB, Hensley DA, Mathews HH (1979) Comparative efficacy of artificial and natural Gulf of Mexico reefs as fish attractants. Florida Marine Research Publications 35, Florida Department of Natural Resources, St Petersburg, FL
- South Atlantic Fishery Management Council (1983) *Fishery management plan, regulatory impact review, and final environmental impact statement for the snapper-grouper fishery of the south Atlantic region*. South Atlantic Fishery Management Council, NMFS, Charleston, SC
- Wakeman JM, Ramsey PR (1985) A survey of population characteristics for red drum and spotted seatrout in Louisiana. *Gulf Res Rept* 8:1–8
- Wilson CA, Dean JM, Radtke R (1982) Age, growth rate and feeding habits of the oyster toadfish, *Opsanus tau* (Linnaeus) in South Carolina. *J Exp Mar Biol Ecol* 62:251–259
- Zedler JB (2000) Progress in wetland restoration ecology. *Trends Ecol Evol* 15:402–407

*Editorial responsibility: Ronald Kneib, Sapelo Island, Georgia, USA*

*Submitted: June 13, 2003; Accepted: October 31, 2003  
Proofs received from author(s): November 27, 2003*



# Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes

R. T. Kneib\*

University of Georgia Marine Institute, Sapelo Island, Georgia 31327, USA

**ABSTRACT:** The connection between fishery production and vegetated intertidal habitats is often a key consideration in the rationale for protecting and restoring estuarine salt marshes. Evaluating the contribution of marsh habitats to estuarine nekton production requires an understanding of the mechanisms and constraints controlling production flows to nekton populations; this is especially important for setting and judging success criteria associated with restoration projects. This contribution considers both bioenergetic and landscape constraints on direct flows of marsh-derived production to populations of resident and migrant nekton. Nekton access to marsh resources is defined in terms of trophic (bioenergetic) and physical (landscape) constraints that determine the amount of nekton production that can be expected. Production to biomass (P:B) ratios applied to measurements of nekton standing stock from multiple marsh sites around Sapelo Island, Georgia, USA provided an example of the spatial variation in nekton production that can be expected from natural marshes. When P:B ratios of 2, 5, and 3 were applied to standing stocks of fishes, caridean shrimps and penaeid shrimps, respectively, annual net production of nekton from 12 intertidal marsh sites ranged from 0.12 to 2.88 g dry weight (dw) m<sup>-2</sup> and averaged ca. 1.50 g dw m<sup>-2</sup>; other scenarios using different sets of P:B ratios yielded production ranges of 0.11 to 2.25 and 0.17 to 4.57 g dw m<sup>-2</sup>. There was a strong sigmoid relationship between nekton production and the amount of intertidal marsh/creek edge within a 200 m radius of a site for both resident and migrant species. Production was lowest at sites with relatively little marsh/creek edge, and increased rapidly with increasing drainage density until reaching an asymptote, after which even large changes in the amount of marsh/creek edge had no effect on nekton production. The findings suggest that bioenergetic constraints determine the ultimate capacity of intertidal marsh systems to produce nekton, but nekton production may be enhanced by relatively small additions of marsh/creek edge up to a threshold level above which no additional enhancement should be expected. Site-specific bioenergetic and landscape constraints should be considered when developing realistic expectations and success criteria for marsh restoration efforts aimed at enhancing estuarine nekton production.

**KEY WORDS:** Estuaries · *Fundulus* · P:B ratio · Salt marsh · *Palaemonetes* · *Litopenaeus*

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Tidal marshes along the Atlantic and Gulf coasts of the US can produce up to 8 kg m<sup>-2</sup> yr<sup>-1</sup> of plant material, inclusive of vascular plants, benthic algae and phytoplankton (Mitsch & Gosselink 1993). The quantity of organic material annually generated in these habitats clearly suggests their potential for supporting

organisms at higher trophic levels. While most of the production from intertidal wetlands is used *in situ*, some is exported to adjacent estuarine and coastal habitats (Odum 2000, Teal & Howes 2000). There is no clear consensus regarding the magnitude of those exports or the mechanisms involved (e.g. passive movement of organic material or directional migration of animals). However, local and regional variation in

\*Email: rtkneib@uga.edu



tidal regimes, edaphic and climatic factors, together with geomorphic characteristics of the landscape (both natural and anthropogenic) may affect variation in primary production (Mendelssohn & Morris 2000) as well as material and energy fluxes between the intertidal and subtidal components of estuaries (Mitsch & Gosselink 1993).

Intertidal vegetation contributes not only to the foundation of many estuarine food webs but also to the maintenance of structural complexity at multiple spatial scales in the coastal landscape (Kneib 1994, 1997). Trophic support and refuge values have been the basis of a long-standing rationale within the scientific community for the importance of intertidal wetlands in maintaining coastal productivity (e.g. Teal 1962, Boesch & Turner 1984). Positive statistical relationships between fishery yields and either the area of vegetated intertidal habitat (e.g. Turner 1977, Zimmerman et al. 2000) or the amount of intertidal edge associated with such habitats (e.g. Teal & Howes 2000, Minello & Rozas 2002) can be found at multiple spatial scales (Webb & Kneib 2002), adding credence to the original tenet (*sensu* Teal 1962) that these habitats are net exporters of secondary production and highlighting the importance of transitional areas that promote the movements of organisms and materials among habitats (e.g. vegetated intertidal and subtidal estuary).

Recognition of the importance of intertidal wetlands in the support of estuarine and nearshore coastal secondary production has led to their designation as 'essential fish habitat' (e.g. see Benaka 1999), and promoted interest in the restoration and creation of intertidal wetlands as a management tool for enhancing ecosystem services, including fisheries production, in estuaries (e.g. Lewis 1992, Kruczynski 1999). The amount of nekton production annually attributable to a given area of vegetated intertidal habitat is a long-standing and crucial question from the perspectives of both basic science and applied management. It must encompass an understanding of what species and life stages are dependent upon the resources available in intertidal vegetated habitats, including accurate measures of densities and standing-stock biomass and how these vary in time and space. For some species, intertidal wetlands may be essential for survival, while for others their presence may simply improve survival and growth, contributing to an enhancement of production.

Marshes are only periodically available to fully aquatic organisms and the boundaries of the aquatic and terrestrial portions of the environment continuously change with the ebb and flow of the tides. Consequently, most nekton associated with intertidal vegetated environments do not permanently reside there, and exhibit a range of life-history strategies involving ontogenetic shifts in habitat use as well as

tidal, seasonal and annual migration patterns that vary across a range of spatial scales (Kneib 1994, 1997). The open nature of intertidal habitats has presented a unique challenge to researchers attempting quantitative studies of the dynamics of mobile populations, and consequently, actual estimates of production by nekton populations within tidal wetlands are uncommon.

Most estuarine species rely on the resources of many habitats during their life histories and so it is difficult to quantify the fraction of a population's total annual production that can be attributed to a specific environment (e.g. intertidal marsh, subtidal seagrass bed, etc.). Also, one must recognize that there is variation both among and within habitat types in regard to potential for contributing to production of estuarine nekton. The secondary production attributable to intertidal wetlands depends on the amount of primary production entering the base of the food web, and its accessibility to consumers. Accessibility is used here in a very general sense that encompasses *physical access* to intertidal production, which is controlled by the frequency and duration of tidal inundation as well as structural features of the landscape (e.g. tidal channels, levees, impoundments, etc.), and *trophic access*, which controls the efficiency of production transfers within the system (i.e. the number of trophic links and the amount of production lost at each link). There is substantial variation in primary production not only at the global and regional level but also within wetland ecosystems (Mitsch & Gosselink 1993, Mendelssohn & Morris 2000), and one might expect a similar degree of variation in the secondary production attributable to different intertidal wetland sites.

Here I describe constraints on nekton production from bioenergetic and structural landscape perspectives that should be considered in scaling the contributions of frequently flooded natural and restored intertidal marshes to estuarine fisheries production. The bioenergetic component focuses on availability of primary production to consumers and trophic transfer efficiency as reflected in annual production to biomass (P:B) ratios, while the landscape component considers the effect of marsh channel complexity (i.e. tidal drainage density) on habitat use, standing-stock biomass and production of nekton. The concepts are applied to data collected from Sapelo Island, Georgia, USA, to demonstrate expected levels of spatial variation (10 m to 10 km) in nekton production derived from undisturbed intertidal marshes where *Spartina alterniflora* is the characteristic emergent vegetation. This is intended to provide an empirical framework for the development of realistic targets and expectations in connection with marsh restoration projects aimed at enhancing estuarine nekton production.

### Nekton assemblages of tidal marshes

Nekton assemblages of intertidal wetlands are not easy to define because there is not a universally recognized seaward boundary for these systems. Historically, tidal marshes have been characterized by the presence of certain vegetation types found primarily at intertidal elevations between mean sea level and the highest spring-tide line (Chapman 1960). If either vegetation type or some tidal elevation above mean low water defines the boundary of the system, then subtidal waters are not—strictly-speaking—components of these habitats (e.g. Kneib 1997). From this perspective, intertidal creeks, ponds, pannes and impoundments within the vegetated matrix may be considered elements embedded within the marsh habitat, but subtidal creeks that maintain a continuous aquatic connection with the sea at low tide are transitional habitats between the marsh proper and the broader open water estuarine system.

A popular alternative perspective among estuarine fisheries researchers extends the tidal marsh to include the adjacent shallow subtidal creek system into which intertidal creeks drain (see Rountree & Able 1992 or Deegan et al. 2000). The problem with this perspective is that the boundary between the open estuary and the intertidal wetlands becomes very subjective. How far into the open estuary or coastal ocean does a tidal marsh extend? Note that this question does not refer to the influence of the intertidal vegetated habitat, but the seaward boundary of the marsh habitat. It also has important implications for the measurement of nekton secondary production from marshes. What is the relationship between distance from the intertidal habitat and the amount of estuarine secondary production supported by marshes?

Regardless of the perspective in defining the system, it is clear that as one proceeds from the open embayments and large tidal channels of the estuary into the smaller creek channels, and ultimately onto the intertidal plain of the vegetated marsh proper, the nekton assemblage becomes a smaller subset of the total estuarine nekton community. More species and higher densities of nekton usually occur at the seaward edge of intertidal vegetation than in the interior of the vegetated marsh plain (Kneib 1997, Kruczynski & Ruth 1997, Minello 1999, Rozas & Zimmerman 2000). Densities of nekton also often decline with increasing water depth and distance seaward of intertidal edge habitats (Ruiz et al. 1993, Kurz et al. 1998).

Species vary considerably in their degree of association with intertidal vegetated habitats. Some, such as the mummichog *Fundulus heteroclitus* and other killifishes, range widely throughout the habitat whenever it is tidally inundated (Kneib 2000), while others, such

as spotted seatrout *Cynoscion nebulosus* or red drum *Sciaenops ocellatus*, are found primarily at the estuarine edge of intertidal vegetated habitat (Minello 1999) and only occasionally forage across the marsh plain (see Montague & Wiegert 1990, p. 507). Detailed knowledge of how nekton species (much less their various life stages) use intertidal habitats is far from complete, but different species and size classes clearly have affinities for different portions of vegetated intertidal habitats (Hettler 1989, Montague & Wiegert 1990, Whitman & Gilmore 1993, Kneib & Wagner 1994, Minello 1999, Kneib 2000, Rozas & Zimmerman 2000). Although the estuarine nekton community comprises mostly migrant or transient species that usually spend only a portion of their life history (usually juvenile stages) in the estuary, nekton assemblages most closely associated with intertidal vegetation are dominated by resident species—those that can complete their life cycles within the shallow subtidal or even intertidal portions of the estuary (Kneib 1997). Even when maximally accessible to all estuarine nekton (e.g. at high-amplitude spring tides), interior portions of vegetated intertidal wetlands are frequented primarily by small (<10 cm) resident species (Peterson & Turner 1994, McIvor & Rozas 1996, Kneib 1997). Along the Atlantic and Gulf coasts of the southeastern US, these generally include killifishes (e.g. *Fundulus heteroclitus* on the Atlantic coast, *F. grandis* on the Gulf coast), live-bearers (e.g. *Poecilia latipinna* and *Gambusia holbrooki*) and grass shrimps (*Palaemonetes* spp.). All serve as important prey resources for juveniles of piscivorous species such as snook (Gilmore et al. 1983), red drum (Reagan 1985) and a variety of other estuarine predators (Abraham 1985) which compose the migrant or transient components of estuarine nekton assemblages.

## NEKTON ACCESS TO MARSH RESOURCES

### Trophic access

Primary production in intertidal marshes has 2 principal sources: vascular plants and benthic algae. Vascular plants are the most conspicuous and defining elements of marsh systems, but there has been considerable debate over their relative contribution to marsh food webs. Estimates of annual production from benthic algae in tidal marshes of the southeastern USA range from about 140 to 470 g dry weight (dw) m<sup>-2</sup> (converted from g C m<sup>-2</sup> yr<sup>-1</sup> given in Table 2 of Sullivan & Currin 2000—assuming 1 g C = 2 g dw), while estimates of net annual above-ground production of *Spartina alterniflora* (hereafter referred to as *Spartina*) in marshes within the same region range from 130 to

3700 g dw m<sup>-2</sup> (Table 8–7 in Mitsch & Gosselink 1993), with the lower values associated with marshes in northwestern Florida (Kruczynski et al. 1978). Algal production is generally grazed as live biomass by intertidal consumers, but relatively little (ca. 10%) of the vascular plant material produced annually in these systems is consumed live (Montague & Wiegert 1990). Instead, it enters a detritus-based food-web driven by fungi and bacteria, with a substantial loss of production to respiration of the microbial community.

In salt marshes, decomposition of *Spartina* leaves begins while the plant material is still in the standing state and fungi play a key role in the process. Recent estimates of conversion efficiency of dead *Spartina* biomass to fungi are in the range of 50 to 60% (Newell & Porter 2000). Fungi can be an important food source for a variety of invertebrate marsh consumers, including gastropods and amphipods (Kneib et al. 1997, Newell & Porter 2000). Nekton that feed on these potential prey can more efficiently capture marsh production derived from vascular plants before it enters the next phase of the decomposition process within the sediments, where bacterial communities can rapidly respire much of what remains to the atmosphere, and in the process re-mineralize nutrients that may become available to estuarine phytoplankton or benthic algal communities in adjacent habitats (e.g. unvegetated mudflat or open water column).

Diets of typical marsh resident species (e.g. killifishes) tend to include a variety of small intertidal invertebrates, such as copepods, amphipods, polychaetes, gastropods and insects (Kneib 1978, 1986). Even resident fishes with diets composed largely of algae (e.g. *Cyprinodon variegatus* or *Poecilia latipinna*) will feed opportunistically on animal prey (Harrington & Harrington 1961, 1982). Diets of common nektonic decapods (e.g. caridean and penaeid shrimps) similarly include a mixture of plant and animal food sources (e.g. Sikora 1977, Morgan 1980, Gleason & Wellington 1988, McTigue & Zimmerman 1991). Although evidence from analyses of stable isotopes (carbon, nitrogen and sulfur) in tissues of estuarine nekton has consistently demonstrated links to tidal marsh-derived organic matter (e.g. Deegan & Garritt 1997, Weinstein & Litvin 2000), the relative importance of algae and vascular plant detritus in support of estuarine nekton production is an issue that remains unresolved (Deegan et al. 2000).

Marsh systems contain an abundance of plant material in various stages of decomposition, and it is not surprising that detritus is commonly found in the gut contents of virtually all common aquatic organisms associated with these habitats, leading many investigators to identify this material as an important food source for nekton (e.g. Darnell 1967, Odum & Heald

1972, Welsh 1975). Although a few fish and shrimp species are capable of assimilating some components of plant detritus (e.g. Condrey et al. 1972, Deegan et al. 1990) and results of stable isotope studies suggest that detritus plays a role in supporting marsh food webs (e.g. Currin et al. 1995), other empirical studies have shown that plant detritus is of questionable direct nutritional value to some of the most common marsh nekton, including killifishes (Prinslow et al. 1974, D'Avanzo & Valeila 1990). In contrast, detrital diets have been shown to support not only growth, but also reproduction of smaller invertebrate prey populations such as amphipods (Kneib et al. 1997). The indirect pathway from microbial decomposers of detritus to small invertebrate prey populations and ultimately marsh nekton seems the most likely principal pathway by which detrital material contributes to nekton production.

#### Physical access to intertidal resources

Intertidal plant production, regardless of quantity or quality, cannot contribute to the production of estuarine nekton unless it is accessible. The previous section considered accessibility in terms of trophic pathways, but the physical structure of the landscape (e.g. McIvor & Rozas 1996, Kneib 1997, 2000) and the tidal regime (e.g. Rozas 1995, Kneib 2000) also define accessibility through effects on movements of nekton and food sources between the intertidal and subtidal portions of the estuarine environment. Experimental evidence for the importance of access to the intertidal marsh surface in the maintenance of estuarine nekton populations is rare. One study conducted by Weisberg & Lotrich (1982) used field enclosures to demonstrate that access to food resources available on the intertidal marsh was essential to support observed growth rates and population densities of the killifish *Fundulus heteroclitus* in Canary Creek, Delaware.

Current conceptual models of the transfer of production from intertidal to subtidal estuarine environments have been focusing on predator-prey interactions and ontogenetic shifts in the use of estuarine habitats by different species of resident and migrant nekton. Movements of production across the estuarine landscape via nekton populations have been referred to as a 'trophic relay' (Kneib 1997, 2000, Deegan et al. 2000). Vegetated intertidal habitats that are impounded or otherwise disconnected from direct communication with the open estuary obviously interfere with such transfers. This is evident in the species compositions and densities of nekton in closed and open impoundments examined in Florida wetlands (e.g. Gilmore et al. 1982, Rey et al. 1990, Vose & Bell 1994). These

studies have shown that closed impoundments, while dominated by small resident nekton, rarely contain estuarine transient species, but when these impoundments are open, usage by transient species increases while densities of residents may decline. Given that many transient species are predators, these observations imply that production accumulated in the biomass of resident species is quickly passed on to the transients when the system is physically accessible.

If there are no physical obstructions between the open estuary and intertidal wetlands, the tidal regime of a region determines the potential level of opportunity for direct use of the habitat by nekton (e.g. Rozas 1995, McIvor & Rozas 1996). The frequency and duration of tidal inundation control the amount of time that intertidal habitat is available to nekton, while tidal amplitude influences the areal extent of the habitat. Species-specific life histories, behavior and size-specific swimming ability then determine the actual level of direct use of intertidal habitats by nekton (see Kneib 1995). For example, resident nekton (e.g. killifishes such as *Fundulus* spp.) use intertidal creeks and pools as low-tide staging areas from which they have immediate access to all areas of the marsh that are tidally inundated, while some migrant species (e.g. juvenile white shrimp *Litopenaeus setiferus*) may not appear on the vegetated marsh until it has been inundated for a longer period of time (see Fig. 1 in Kneib 2000). The extent of movement by nekton across the marsh plain in response to tidal stages (i.e. flooding vs ebbing flows) varies with species and size (Kneib & Wagner 1994), and relates in part to the swimming capacity and the degree of aversion to intertidal stranding exhibited by different organisms. In general, resident species are least averse to stranding and thus tend to be the first to enter and the last to leave the marsh, thus maximizing their time directly using the resources of the tidal marsh. Transient species tend to arrive later on flood tides and leave the marsh earlier on ebbing tides than resident nekton (Kneib & Wagner 1994).

Edges defining the border between the vegetated intertidal and adjacent water bodies (embayments, tidal creeks, canals, etc.) can be described as 'critical transition zones' (Levin et al. 2001). These are areas of potentially intense biological activity and often exhibit the highest densities of nekton associated with intertidal wetlands, particularly in microtidal environments associated with marshes along the northern shoreline of the Gulf of Mexico (e.g. Minello 1999, Rozas & Zimmerman 2000). The attraction of nekton to structural edges has prompted the application of manipulative management techniques designed to enhance the amount of edge habitat as a means of increasing fish production, particularly in shallow open water habitats (e.g. Rozas & Minello 2001). A narrow (a few meters)

vegetated intertidal edge can provide a structural refuge for prey or a habitat from which predators can ambush prey organisms (Thayer et al. 1987, Whitman & Gilmore 1993), but this relatively small area of marsh habitat is unlikely to have the capacity to satisfy the nutritional requirements of the high densities of nekton often found there, unless there is additional trophic support from adjacent portions of the estuary (e.g. interior marsh, mudflat or subtidal aquatic/benthic habitats). In most estuarine marshes, tidal channels and their associated edges function to increase accessibility of intertidal resources to both resident and migrant nekton. Higher densities of nekton occur in the interior of tidal marshes associated with complex drainage networks compared to marshes drained by only a few simple tidal channels (e.g. see Fig. 6 in Kneib 1994).

## NEKTON PRODUCTION

### Bottom-up estimate of nekton production from tidal marshes

From the background information on plant production, food sources and trophic links involved in the production of nekton from intertidal habitats (previous section on *Trophic access*), together with a basic understanding of ecological energetics, one can roughly estimate the amount of net production of nekton expected from an area of *Spartina* marsh with an intermediate rate of annual plant production totaling 1250 g dw m<sup>-2</sup> (Fig. 1). For purposes of illustration, I have assumed above-ground net primary production that includes 1000 g from *Spartina alterniflora* and 250 g from benthic algae. Trophic transfer efficiencies of 10% (Pauly & Christensen 1995) were applied in all cases, except for conversion of detritus to fungi, which is more efficient and was assigned a value of 55% (Newell & Porter 2000). Neither dissolved organic carbon (DOC) nor below-ground production from *Spartina* were included here because there is currently little evidence linking these sources directly to food webs that support the production of nekton from marshes. Foliar release of DOC from *Spartina* is quickly taken up by bacteria (Hullar et al. 1996) and respired into the atmosphere, while most of the below-ground plant production—the source of which of course is aerial production—is readily translocated among living roots, rhizomes and above-ground shoots (Dai & Wiegert 1996). Thus, above-ground growth of *Spartina* in the spring depends on winter reserves stored in the below-ground rhizomes and roots. However, the current model (Fig. 1) should be viewed as an underestimate if some nekton production derives from these sources either directly or indirectly.



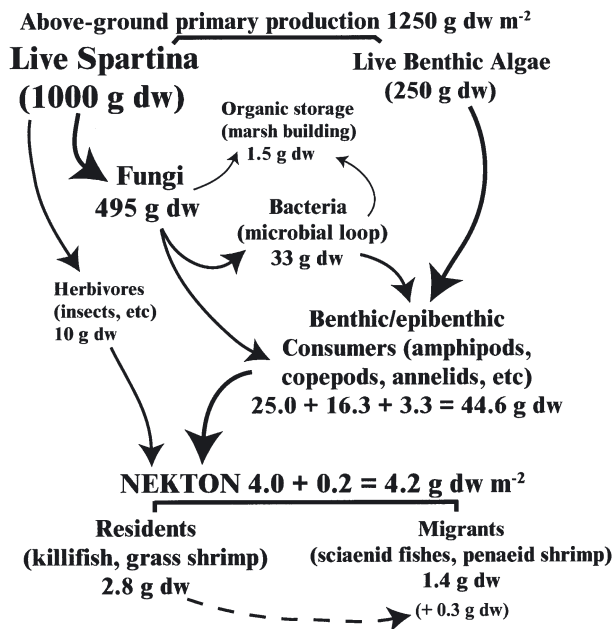


Fig. 1. Production flows to nekton populations from a hypothetical 1250 g dry weight (dw) m<sup>-2</sup> of annual primary production from an intertidal salt marsh. Size of arrows indicates relative importance of flows to nekton populations, not necessarily total magnitude of material or energy pathway. Ecological efficiencies were assumed to be 10% except for conversion of *Spartina alterniflora* to fungi, which was 55% (see section 'Bottom-up estimate of nekton production from tidal marshes' for additional constraints). It was further assumed that most of the production of herbivores (10 g dw) from live *Spartina* contributed to a terrestrial food web (i.e. spiders and birds), and only 20% was available to nekton

In the present scenario, 10% of the *Spartina* production is consumed live by insects and other herbivores (Montague & Wiegert 1990), and most of that pathway would likely contribute to a terrestrial food web (e.g. spiders and birds). Nonetheless, I presumed that 20% of that production or 2 g of insects (100 g × 0.1 × 0.2) would be available to aquatic predators and thus would yield 0.2 g of nekton (2 g × 0.1). Most of the *Spartina* production (900 g) enters a detrital pathway beginning with fungi, which yields 495 g dw m<sup>-2</sup> (900 × 0.55 efficiency of conversion to fungi) potentially available to benthic/epibenthic invertebrate consumers. Assuming further that invertebrate consumers (amphipods, annelids, insect larvae, etc.) could capture 1/3 of that material before it entered the next phase of decomposition involving bacterial communities, the available material could yield 16.3 g dw m<sup>-2</sup> (495 × 0.33 × 0.1) of invertebrate prey organisms.

The balance of detrital production which passes through the fungal component and on to bacterial communities (495 × 0.67 × 0.1 = 33 g dw) also could contribute 3.3 g dw m<sup>-2</sup> (33 × 0.1) to the invertebrate prey

assemblage through a weaker link to the microbial loop. If most of the primary production from benthic algae is readily and directly available for consumption, it would yield an additional 25.0 g dw m<sup>-2</sup> (250 × 0.1) of potential invertebrate prey, providing a potential food reservoir for nekton of 44.6 g dw m<sup>-2</sup>, not all of which would be available to aquatic predators. Some molluscs (e.g. periwinkle snails and mussels) and larger crustaceans (e.g. fiddler crabs and mud crabs) may be relatively long-lived and ultimately consumed by terrestrial predators (Carlton & Hodder 2003). However, here I have assumed that a substantial majority (90%) of invertebrate prey production is available and turns over rapidly, so could yield 4.0 g dw m<sup>-2</sup> (44.6 × 0.9 × 0.1) of nekton. Combined with the 0.2 g from the consumer pathway linked to live *Spartina* production, this yields a grand total of 4.2 g dw m<sup>-2</sup> of fishes, shrimps and crabs supported on 1250 g dw m<sup>-2</sup> of above-ground tidal marsh primary production.

If 2/3 of this total represents resident species with the balance in migrants, and the residents are an important source of prey for other estuarine migrant species (e.g. drums, flatfishes and other predatory species), a total of 1250 g dw m<sup>-2</sup> of primary production from a marsh could contribute 1.7 g dw m<sup>-2</sup> of migrant nekton to the estuary (4.2 × 0.33 = 1.4 g produced directly by the marsh and another 4.2 × 0.67 × 0.1 = 0.3 g produced as a result of migrant predators feeding on resident prey species). The estimate of 4.2 g dw m<sup>-2</sup> of total nekton production from this hypothetical marsh system provides a 'ball park' value that may not adequately account for all potential pathways by which marsh production contributes to the trophic support of adjacent estuarine and terrestrial ecosystems, including consumption by birds or other non-aquatic predators (Carlton & Hodder 2003). Neither does it account for the biomass stored in long-lived potential prey species such as marsh periwinkles *Littoraria irrorata* or ribbed mussels *Geukensia demissa*, both of which have lifespans ranging from 10 to 20 yr (Stiven & Hunter 1976, Franz 2001). However, it provides a point of reference from which to compare estimates from an alternative empirical method described in subsequent sections.

### Production:biomass ratios

Production ( $P$ ) during short time intervals can be estimated from a single measure of biomass ( $B$ ) if there is some prior knowledge of both growth ( $G$ ) and mortality ( $Z$ ) rates, as these vital rates can be related to production as follows:  $P = GB [(e^{G-Z} - 1)/(G - Z)]$ . Annual production is then calculated by summing the production over all short time intervals. Of course, this assumes that growth and mortality schedules are accu-



rately known for a sufficient number of short time intervals to define the annual pattern. Chapman (1978) pointed out that while growth rates can usually be estimated with reasonable certainty, mortality rates can be notoriously inaccurate, not to mention difficult and time-consuming to obtain. If one can assume an empirical relationship between production and biomass (i.e.  $\bar{P} = c\bar{B}$ , where  $c$  is a constant for a given species and set of conditions) on an annual basis, a reasonable estimate of one variable can be made from an accurate estimate of the other; this concept is supported by a substantial literature that has developed for some aquatic systems.

### Fishes

Production is strongly correlated with standing-stock biomass for fishes in freshwater lakes and stream systems. Several researchers (e.g. Chapman 1978, Banse & Mosher 1980, Downing & Plante 1993) have compiled lists of P:B ratios for freshwater fishes and observed that the ratio also varies consistently with species size and with regional climatic temperature regimes. Values of P:B ratios are inversely related to adult or maximum body mass (Banse & Mosher 1980), mostly because smaller species tend to exhibit more rapid growth rates and exhibit shorter generation times than large species. P:B ratios of the 11 species listed by Banse & Mosher (1980) ranged from 0.4 to 2.82 and averaged 1.78; those listed in Chapman (1978) ranged from 0.44 to 5.0 and averaged 1.69. A larger survey of 100 fish populations by Downing & Plante (1993) indicated a range of P:B values between 0.2 and 5.0, with an average value of 0.93 (Fig. 2).

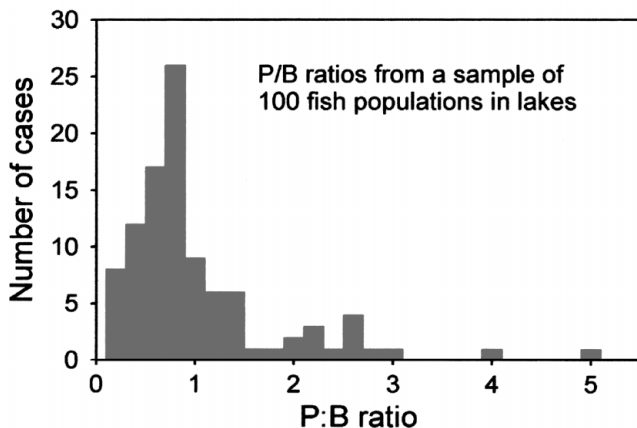


Fig. 2. Distribution of production to biomass (P:B) ratios from 100 populations of fishes. Data came from Downing & Plante (1993)

Note that there is a primary mode around a P:B ratio of 1 and another between 2 and 3. The higher P:B values are associated with smaller fish species. This is an important consideration for nekton assemblages in tidal marshes because they are characterized by species or size classes that are relatively small, averaging <10 cm in length (Kneib 1997). A survey of the few studies of fish production available from tidal marshes reveals a range of P:B ratios similar to those reported for freshwater fishes (Table 1). Mean values of P:B ratios from the few studies of marsh fishes that provided sufficient information to permit an estimate, ranged from 0.81 to 4.48, with an average value pooled across all studies of 2.41.

The P:B ratios from studies based on mark-recapture data, which should provide the most accurate estimates of population size (i.e. standing stocks) and mortality rates, yielded values around 1 (e.g. Valiela et al. 1977, Weinstein & Walters 1981). The higher values presented in some studies (e.g. Warburton 1979, Allen 1982) were based on variable intervals during which species were present in the system, and may not represent expected values on an annual basis. Consequently, a P:B ratio of 2 for marsh fishes is a reasonable compromise, given the lower values (Fig. 2) representing freshwater fishes and the paucity of information on estuarine species.

Many of the literature estimates reported for fishes from both freshwater and marine environments may not include the earliest life stages within Age 0, which often account for most of the production in a population. For example, Wang & Houde (1995) estimated production of bay anchovy in Chesapeake Bay from acoustic-calibrated data and found that young-of-the-year accounted for 92.6% of the annual production in the population; they reported a P:B ratio of 0.97 (very similar to the value for fish in lakes) when larvae and early juveniles were excluded, but when these earliest life stages were factored in, the P:B ratio jumped to 7.08 (note: incorrectly reported in the paper as 8.07). Similarly, Allen (1982) observed that the P:B ratio for young-of-the-year atherinids from the littoral zone of a California wetland system was substantially higher (7.55) than that of adults (1.27).

The high P:B values resulting from the production of the very earliest life stages in tidal wetlands are not considered further here for 2 reasons: (1) Much of the mortality in the youngest age classes of resident species has been connected to consumption by adult residents (Kneib 1987, 1993), essentially forming a closed trophic loop (i.e. early larval production is used in situ) and so is unavailable for direct export from the intertidal to the open estuary; (2) Migrant species found in tidal marshes arrive as juveniles because the early stages are generally produced elsewhere (spawned in

Table 1. Summary of annual production and production to biomass (P:B) estimates for nekton (fishes and decapod crustaceans) from tidal wetlands. Values are converted to g dry weight (g dw) m<sup>-2</sup> from units used in the original papers (conversion factors: dry wt = 0.22 × wet wt; 1 g dry wt = 4.7 kcal; 1 kcal = 4.2 kJ). YOY: young of year

Species	Location	Production (g dw m <sup>-2</sup> yr <sup>-1</sup> )	P:B	Source
<b>Fishes</b>				
<i>Fundulus heteroclitus</i>	Great Sippewissett Marsh, MA	1.6 <sup>a</sup>	0.81	Valiela et al. (1977)
<i>Fundulus heteroclitus</i>	Canary Creek, DE	8.8 (78% from YOY) for creek only		Meredith & Lotrich (1979)
<i>Fundulus parvipinnis</i>	Ojo de Liebre Lagoon, Mexico	0.32 (for lagoon only)	2.1	Pérez-España et al. (1998)
<i>Leiostomus xanthurus</i>	Creeks on Cape Fear River, NC	0.26 (creek only, YOY)	1.06	Weinstein & Walters (1981)
<i>Leiostomus xanthurus</i>	2 tidal creeks in York River, VA	4.2–4.6 in creeks only; corrected for marsh drainage area, value is 0.38		Weinstein (1983), Weinstein et al. (1984)
All fishes	Mesohaline impounded salt marsh, FL	9.6–14.0 (not inclusive of surrounding marsh drainage)		Schooley (1981)
<i>Atherinops affinis</i> : Adults	Littoral zone of tidal marsh, Upper Newport Bay, CA (not inclusive of entire intertidal);	0.13	1.27	} Allen (1982)
YOY	only species present in more than 1 mo are included here	7.96	7.55	
9 other spp.		<0.01 to 0.46 (mean: 0.16)	0.54–10.59 (mean: 3.42)	
<i>Mugil curema</i>	Caimanero Lagoon, Mexico (subtidal area only)	2.7	3.25–8.44	} Warburton (1979)
<i>Anchoa panamensis</i>		2.7	(mean: 4.48)	
<i>Galeichthys caerulescens</i>		1.8		
All other spp.		All others 2.8 (average)		
<b>Decapod crustaceans</b>				
<i>Palaemonetes pugio</i>	Killer Creek, SC	10.8 for creekbank area only, and 0.67 when adjusted for marsh drainage area	5.06	Sikora (1977)
<i>Palaemonetes pugio</i>	Bissel Cove, RI	6.8 (embayment only, not corrected for surrounding marsh drainage)	2.34	Nixon & Oviatt (1973), Welsh (1975)

<sup>a</sup>Annual production value reported in Valiela et al. (1977) was 16.0 g dw m<sup>-2</sup>, but length-weight equations used in calculations over-estimated dry mass of individuals by an order of magnitude, thus the annual production value was reduced proportionally for this table

the coastal ocean or open estuary) and so the earliest production cannot be associated directly with the marshes.

Fish production is strongly influenced by the effect of temperature on growth rates (Downing & Plante 1993) and the P:B ratios of fish populations in tropical areas are expected to be greater than in temperate areas. Chapman (1978) suggested a P:B value of 1.5 as an estimator for cold-water habitats and 1.7 to 2.0 for warmer waters for fishes in freshwater streams. However, a survey of P:B values associated with tropical fish species worldwide does not differ dramatically from those in temperate waters. For example, Lowe-McConnell (1987) reported P:B values for tropical fishes ranging from 0.68 to 3.77 and averaging 1.8. Agostinho & Penczak (1995) reported mean values of 0.79 and 0.90 for 2 small tributaries of the Paraná River in Brazil; the range for individual species at the 11 sites examined ranged from 0.51 to 1.35.

#### Decapods

P:B ratios for decapod crustaceans in tidal marshes are even less common than those for fishes. The 2 studies of grass shrimp production cited in Table 1 yield an average value of 3.70, which is substantially higher than that for fishes. Grass shrimp reach maturity at a size of 20 to 25 mm, produce multiple generations annually (Sikora 1977), and serve as important forage species for many other estuarine nekton, including marsh resident fishes. The 2 studies of grass shrimp production shown in Table 1 are from different latitudes, and thus very different climatic regimes. The higher value (5.06) reported from South Carolina compared to Rhode Island (2.34) most likely reflects latitudinal differences in mean annual temperatures and length of the growing season. The value from Sikora (1977) should be more representative of warm temperate and sub-tropical conditions in the southeastern USA.

Estimates of production from commercially harvested decapod species focus on mariculture and yields to the fishery rather than on net production from natural populations. Herke et al. (1992) reported on the net export of nekton, including penaeid shrimps, from a pair of 35 ha impoundments in a Louisiana marsh. Each impoundment enclosed ca. 26.5 ha of open water and ca. 8.7 ha of *Spartina patens* marsh (ca. 75% open water, 25% marsh); one included a fixed-crest weir across the channel connecting the impoundment to the estuary and the other had no weir. Sampling was conducted for 2 consecutive years and the average net annual export (yield) of penaeid shrimp was 4.5 g wet weight (ww) m<sup>-2</sup> (0.99 g dw) in the absence of a weir and 1.8 g ww m<sup>-2</sup> (0.4 g dw) when a weir was present, but no estimate of standing-stock biomass in the ponds was provided. Consequently, I used data from Rozas & Minello (2001) on penaeid shrimp density expressed in biomass from a reference marsh (18 g ww m<sup>-2</sup> or 4.0 g dw) and reference pond (1 g ww m<sup>-2</sup> or 0.22 g dw) in Louisiana to provide an expected value of penaeid standing stocks that reflected the vegetated condition of impoundments in Herke et al. (1992).

Data in Rozas & Minello (2001) were taken to represent conditions from spring through autumn; penaeids were assumed to be absent from these shallow marsh habitats in winter, so the values for annual standing stocks had to be adjusted (reduced to 75% of the spring to autumn average) for this seasonal effect. Thus, the annual standing stock of penaeids in the 25% of the impoundment area that was vegetated was taken to be 3.0 g dw m<sup>-2</sup> (4 × 0.75) and 0.16 g dw m<sup>-2</sup> (0.22 × 0.75) in the 75% that was open water. This gives an overall average annual standing-stock biomass estimate for the impoundments of ca. 0.9 g dw m<sup>-2</sup> (3.0 × 0.25 marsh area + 0.16 × 0.75 open water area).

If the exported biomass is considered the total net production, then the P:B ratio for penaeid shrimp in the unobstructed impoundment studied by Herke et al. (1992) would be 1.1 (0.99:0.90). However, this does not account for losses to predators such as red drum and other sciaenids, which were abundant in the impoundment. Knudsen et al. (1989) had earlier estimated mortality rates of brown shrimp in these same impoundments and, in the situation without weirs, estimated mean monthly instantaneous mortality rates of between 0.877 and 1.27. Assuming an average mortality rate of 1.07, net production would have to account for at least 2.9 times (e<sup>1.07</sup>) the standing stock to maintain a constant value for shrimp biomass in the ponds. If this rate is used as a multiplier, the estimated P:B ratio for penaeids is then 3.2 (1.1 × 2.9). Given that penaeid shrimp are larger than grass shrimp and decapods

generally exhibit growth rates greater than most fishes, a P:B value that falls between grass shrimp and fishes seems reasonable for penaeids.

## SPATIAL VARIATION IN NEKTON PRODUCTION—AN EXAMPLE

### Field collections

In order to provide an estimate of the expected spatial variation in standing-stock biomass and production of nekton from a warm-temperate/subtropical tidal marsh, samples were collected at 2 wk intervals from 6 intertidal marsh sites on Sapelo Island, Georgia (Fig. 3) using flume weirs (see Kneib 1991 for details). The flume weir was designed for the quantitative collection of nekton (>20 mm in length) from 100 m<sup>2</sup> sampling areas of tidally inundated vegetated marsh surface.

Two sampling sites were selected in each of the lower, middle and upper reaches of the Duplin River (designated LD, MD, UD, respectively) to represent relatively simple and complex (designated 1 and 2,

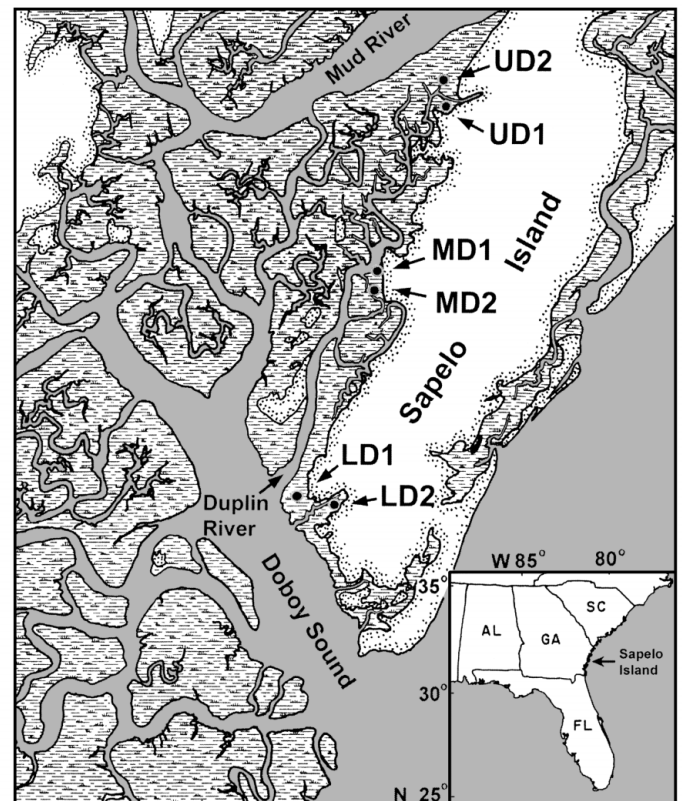


Fig. 3. Sapelo Island, Georgia, USA showing locations of the 6 principal sampling sites (lower, middle and upper reaches of the Duplin River, designated LD, MD, UD, respectively, representing relatively simple and complex tidal drainage networks, designated 1 and 2, respectively: LD1, LD2, MD1, MD2, UD1 and UD2) for nekton in marshes along the Duplin River

Table 2. Summary of physical characteristics at each of 12 sampling sites in marshes on the Duplin River, Sapelo Island, Georgia. Abbreviations represent lower, middle and upper reaches of the Duplin River, designated LD, MD, UD, respectively, representing relatively simple and complex tidal drainage networks, designated 1 and 2, respectively: LD1, LD2, MD1, MD2, UD1 and UD2. At each site, a flume weir was located at each of 2 distances (6 to 20 and 28 to 85 m) from the nearest tidal channel (designated -L and -H, respectively). +MLW: above mean low water

Physical feature	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H
Elevation (+MLW, cm)	221.2	225.4	194.2	197.1	178.2	200.8	153.9	179.4	199.9	216.3	154.7	189.2
Meters to intertidal creek	12	85	20	44	16	49	16	28	6	44	10	73
Meters to subtidal zone	178	278	89	142	97	181	168	171	276	321	149	265
Intertidal edge within 200 m radius (m)	1935	1103	2269	2472	2267	2024	5723	5660	2998	1971	5201	2781
Subtidal edge within 200 m radius (m)	326	0	805	628	436	341	164	68	0	0	132	0

respectively) tidal drainage networks. At each site, a flume weir was located at each of 2 distances (6 to 20 and 28 to 85 m) from the nearest tidal channel (designated -L and -H, respectively). For example, the sampling location designated 'LD1-L' was the flume weir nearest the creek in a relatively simple drainage system within the lower reaches of the Duplin River (Fig. 3). Nekton samples were collected from each flume weir at or very near slack high tide approximately twice monthly during 1999.

### Landscape complexity

Some physical characteristics of each of the 12 flume weir locations are given in Table 2. Included is a measure of tidal creek complexity, expressed as the linear amount of intertidal and subtidal channel edge within a 200 m radius of each flume weir location. Channel edge data were collected from digitized black & white negatives (1:16000 scale) recorded during an aerial photographic survey conducted in December 1989. A scaled circle of 200 m radius, centered on the location of each flume weir, was superimposed on the photographs (23 by 23 cm) and the combined images were enlarged to 9.5 times their original size. Outlines of the intertidal and subtidal creeks located within the circle were traced and measured using Sigma Scan Pro® (Version 4.0, SPSS) software on a Dell® Optiplex XMT 5100 desktop computer.

### Results of nekton sampling

A total of 94 827 individuals (>20 mm in total length) distributed among 33 species of nekton was collected. As is typical of estuarine nekton samples, most of the individuals were represented by only a

few species. In this case, 11 species of fishes and decapod crustaceans accounted for >99% of the individual organisms in the samples (Table 3). Three species, the caridean shrimp *Palaemonetes pugio* (49.1%), the killifish *Fundulus heteroclitus* (30.2%), and juveniles of the white shrimp *Litopenaeus setiferus* (10.8%), accounted for >80% of all the nekton. Overall, resident species composed ca. 85% of the assemblage, with the remainder (15%) considered migrants. Densities within each group were averaged across all samples to provide a mean annual density for each flume weir site (Table 4).

A substantial amount of spatial variation was evident across sites, with the maximum mean annual density of ca. 7.0 ind. m<sup>-2</sup> at the MD2-H site being >17 times greater than the minimum density of 0.4 ind. m<sup>-2</sup> at the LD1-H site. In general, densities were similar to those reported from other marshes on the east and west coasts of the USA, but were substantially lower than those reported from many sites in the Gulf of Mexico (Table 5). Resident and migrant species both were more abundant at lower intertidal elevations (Fig. 4a); slopes of regression lines relating nekton densities to elevations were significantly different from zero ( $p = 0.004$  for residents and migrants). Weaker relationships seemed to exist between nekton abundance and proximity to the marsh edge (Fig. 4b), but these regressions were not statistically significant ( $p = 0.09$  for residents and  $p = 0.116$  for migrants). Observations of decreasing nekton densities with increasing distance landward of the marsh/estuary edge are common elsewhere (Table 5).

Individual fishes and shrimps from each sample were measured (total length to the nearest mm) and biomass (mg dw) was determined from a set of empirically derived length-weight equations for each species (Table 3). The annual mean standing-stock biomass (g dw m<sup>-2</sup>) at each site (Table 4) was determined by



Table 3. Length-weight equations used to calculate dry weight (DW; mg) of individuals for each of the 11 most common species captured on the marsh surface, Sapelo Island, Georgia, USA. n = number of individuals measured and weighed; TL = total length in mm; for shrimp, TL is from the tip of the rostrum to the tip of the telson. Wet weight (WW; mg) can be estimated by applying the following: WW = DW/0.22; resident and migrant species are identified as R and M, respectively

Species	n	Equation	Regression $r^2$
<b>Fishes</b>			
<i>Fundulus heteroclitus</i> (R)	1744	DW = 0.0005616(TL) <sup>3.485</sup>	0.987
<i>Fundulus luciae</i> (R)	742	DW = 0.0007498 (TL) <sup>3.327</sup>	0.935
<i>Cyprinodon variegatus</i> (R)	351	DW = 0.0005207 (TL) <sup>3.620</sup>	0.961
<i>Poecilia latipinna</i> (R)	317	DW = 0.000740 (TL) <sup>3.428</sup>	0.973
<i>Gobionellus smaragdus</i> (R)	177	DW = 0.002117 (TL) <sup>2.854</sup>	0.984
<i>Leiostomus xanthurus</i> (M)	556	DW = 0.0005674 (TL) <sup>3.323</sup>	0.987
<i>Mugil cephalus</i> (M)	123	DW = 0.0006724 (TL) <sup>3.321</sup>	0.980
<i>Mugil curema</i> (M)	121	DW = 0.0008644 (TL) <sup>3.248</sup>	0.989
<i>Menidia menidia</i> (M)	230	DW = 0.0005886 (TL) <sup>3.218</sup>	0.991
<b>Decapod crustaceans</b>			
<i>Palaemonetes pugio</i> (R)	1385	DW = 0.0007118 (TL) <sup>3.291</sup>	0.873
<i>Litopenaeus setiferus</i> (M)	286	DW = 0.0008046 (TL) <sup>3.067</sup>	0.982

applying the length-weight relationships to the size distributions of each species, and averaging across the 24 sampling dates at each site. Standing stocks varied by more than an order of magnitude across sites, ranging from a maximum of 1.13 g dw m<sup>-2</sup> at UD1-L to a minimum of 0.05 g dw × m<sup>-2</sup> at LD1-H. In general, annual standing stocks were greater toward the upper reaches and least in the lower reaches of the Duplin River system. With respect to seasonal variation, standing stocks were greatest in the summer and autumn (July to November) and lowest during the winter (December to February).

#### Estimates of nekton production based on P:B ratios

Using the annual standing-stock biomass estimates from Table 4, and applying the appropriate set of P:B ratios, one can calculate an estimated range for ex-

pected annual secondary production of estuarine nekton from intertidal marsh sites around Sapelo Island, Georgia, USA.

Three scenarios were generated from different combinations of P:B ratios to estimate a range of production values (Table 6). Scenario 1 was the least complicated and most conservative. It applied a P:B ratio of 2 as a multiplier on the standing stocks of all species to provide an average production estimate of ca. 1.2 g dw m<sup>-2</sup> for all nekton that use intertidal marsh as habitat. In Scenario 2, production of fish was estimated by multiplying their mean annual standing-stock biomass by a P:B ratio of 2, while a multiplier of 5 was applied to grass shrimp (the most abundant of the resident nekton), and an intermediate value of 3 was used for juvenile white shrimp; this gave an annual production

estimate of ca. 1.5 g dw m<sup>-2</sup>, and is considered the most likely and defensible scenario based on current knowledge. Scenario 3 was the least conservative and applied a relatively high P:B value of 3 to fishes and 5 to all shrimp species (caridean and penaeid shrimp), resulting in a production estimate of 2.2 g dw m<sup>-2</sup>.

Much of the considerable spatial variation in production from the intertidal marsh in this example is associated with the amount of intertidal creek edge within 200 m of each sampling site (Fig. 5). The production data for both resident and migrant species were fitted to non-linear relationships using the regression wizard in SigmaPlot® Version 8 (SPSS) and both exhibited similar sigmoidal shapes, with production increasing sharply above 2000 m of edge before reaching an asymptotic limit at or above 3000 m in a radius within 200 m of the sampling sites. The fitted equations for resident and migrant species respectively were as follows:

Table 4. Summary of mean annual densities (ind. m<sup>-2</sup>) and standing-stock biomass (g dry weight m<sup>-2</sup>) of resident and migrant nekton collected by flume-weir at slack high-tide from 12 sampling sites in marshes on the Duplin River, Sapelo Island, Georgia; N = 24 collections site<sup>-1</sup> during January to December 1999. See Table 2 for site abbreviations

	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H
<b>Mean annual density</b>												
Resident species	1.00	0.39	1.96	2.89	1.46	0.88	6.28	6.30	4.69	0.94	5.12	2.00
Migrant species	0.002	0.001	0.01	0.06	1.59	0.004	0.71	0.71	0.56	0.03	1.81	0.41
Total nekton	1.00	0.39	1.97	2.95	3.05	0.88	6.99	7.01	5.25	0.97	6.93	2.41
<b>Mean annual biomass</b>												
Resident species	0.135	0.053	0.558	0.534	0.375	0.231	0.565	0.809	0.941	0.196	0.412	0.500
Migrant species	<0.001	<0.001	0.004	0.016	0.707	0.025	0.310	0.139	0.185	0.006	0.532	0.092
Total nekton	0.135	0.053	0.562	0.550	1.082	0.256	0.876	0.948	1.126	0.202	0.944	0.593



Table 5. Survey of nekton densities (ind. m<sup>-2</sup>) mostly from *Spartina alterniflora* marshes identified as natural or reference sites compared to created or restored sites

Location	Natural/reference		Restored/created		Source
	Residents	Migrants	Residents	Migrants	
Harkers Island, NC,	4.2	9.2			Meyer et al. (1996)
Swansboro, NC,	1.4	17.8			
Sneads Ferry, NC	4.0	3.0			
Newport River, NC <sup>a</sup>	1.2	0.95			Hettler (1989)
Tampa Bay, FL <sup>b</sup>	1.4	0.1	0.77	0.49	Kurz et al. (1998)
Pascagoula, MS	2.0	0.7	7.9	2.1	LaSalle (1995)
Terrebonne-Timbalier, LA (2–22 m in from marsh edge)	7.9	3.0			Rozas (1992), Rozas & Reed (1993)
Calcasieu Lake, LA <sup>c</sup> (edge)	51.9	51.8	32.2	43.3	Rozas & Minello (2001)
Pooled sites in TX and LA (>5 m in from marsh edge)	13.4	3.9			Minello (1999)
East Matagorda, TX (edge)	32.5	15.4	14.3	6.2	Minello &
Chocolate Bay, TX (edge)	136.8	34.9	29.0	21.8	Zimmerman (1992)
Stedman Island, TX (edge)	73.4	15.2	9.2	10.2	
Galveston Bay, TX (1993)					Rozas & Zimmerman (2000)
(edge, 1–2 m from water)	50.8	40.4			
(interior, 5–6 m from edge)	12.4	4.3			
East Bay, TX (1994)					Williams & Zedler (1999)
(edge, 1–2 m from water)	50.8	38.0			
(interior, 5–6 m from edge)	18.4	13.8			
San Diego, CA	1.6	0.6	2.8	1.1	

<sup>a</sup>Fish only, no decapods; <sup>b</sup>no grass shrimp included; <sup>c</sup>assumes most unspecified fish species are migrant

$$y = 1.6431 \frac{1.6431}{1 + \left( \frac{x}{2196.2} \right)^{-9.393}} \quad (1)$$

and

$$y = 0.0172 \frac{0.8026}{1 + e^{-\left( \frac{x-2911.4}{137.8} \right)}} \quad (2)$$

where  $y$  = annual production (g dw m<sup>-2</sup>) and  $x$  = the amount of intertidal creek edge (m) within a 200 m radius of the sampling location. One data point shown as an open triangle in Fig. 5 was omitted from the analysis as an outlier. It was associated with migrant species (mostly the penaeid shrimp *Litopenaeus setiferus*) at the MD1-L, which was the only frequently flooded sampling site immediately adjacent to the main channel of the Duplin River in its middle reaches where transient species that grew in the upper reaches of the system would be subject to capture during their ontogenetic migrations into the open estuary.

## DISCUSSION

Estimates of annual nekton production from the present study ranged from 0.11 to 4.57 g dw m<sup>-2</sup>, depending

on location and the set of P:B ratios applied to the measured standing stocks. The range of values within any scenario demonstrated that one can expect substantial spatial variation in the amount of nekton production from intertidal marshes, even within a limited geographic region. The amount of material at the base of the food web (e.g. vascular plant detritus and benthic algae) that is ultimately available to nekton populations through trophic interactions sets the upper limit to the production that can be supported. An independent initial 'ball park' estimate of nekton production expected from 1250 g dw m<sup>-2</sup> of annual marsh primary production (4.7 g dw m<sup>-2</sup>, Fig. 1), following the application of bioenergetic constraints within the food web, was consistent with the high end of the range of nekton production values estimated from P:B ratios applied to empirical nekton standing stocks from the flume weir samples.

Physical constraints (e.g. tidal frequency and duration of flooding) on accessibility of marsh resources also contribute to controlling the amount of intertidal production available to aquatic consumers. To some degree, these constraints are reflected in structure of the landscape as represented by the measure of creek drainage density (intertidal creek edge within 200 m of a site), which was a good predictor of nekton production (Fig. 5). This measure may have combined the

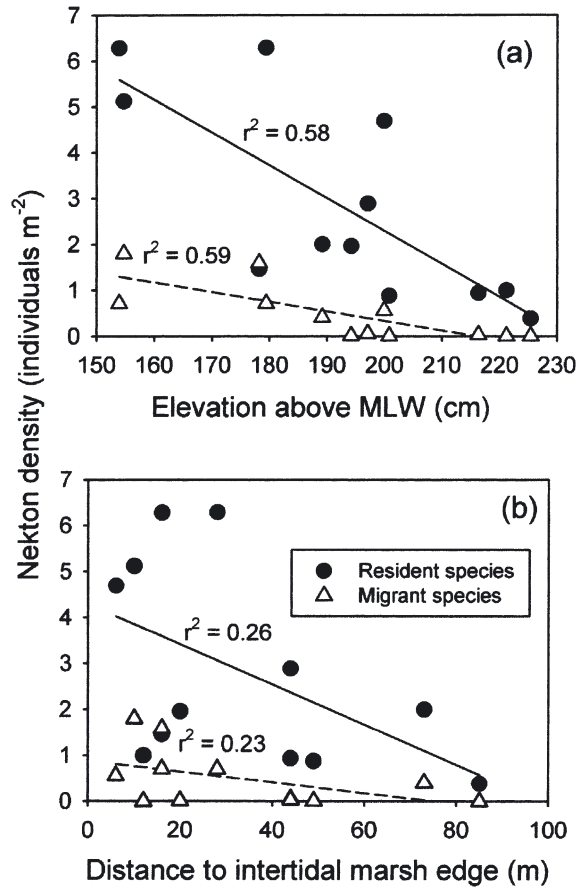


Fig. 4. Mean densities of resident and migrant nekton in relation to (a) intertidal elevation above mean low water (MLW);  $p = 0.004$  for residents and migrants, and (b) distance from the vegetated marsh edge;  $p = 0.09$  for residents and  $p = 0.116$  for migrants

effects of intertidal elevation and proximity to tidal channel, which, when considered as independent factors, were weaker predictors of nekton abundance and, presumably, production (Fig. 4). More complex creek-drainage networks offer greater potential for low-tide aquatic refugia that may be used by nekton as staging areas between flood-tide forays on the vegetated marsh surface (Kneib 1995).

Estimates of nekton annual production from the preferred intermediate set of P:B ratios ranged from ca. 0.12 to 2.88 g dw m<sup>-2</sup> and were similar to values from other studies that used the total area of intertidal marsh as the basis for the estimate (Table 1). Considerably higher production estimates reported for some systems often included an inherent assumption that all of the nekton production originated from only a portion of the habitat adjacent to the marsh, such as a tidal creek or the vegetated marsh edge. Sufficient information to estimate production corrected for the entire area of vegetated intertidal marsh that may have contributed to the production of nekton was not always available. However, in the few cases where it was possible to correct for total area, one can see that values which initially appeared to differ substantially from those estimated from the Sapelo Island data are actually quite similar. For example, Weinstein et al. (1984) and Weinstein (1983) estimated the annual production of juvenile spot *Leiostomus xanthurus* from tidal creeks in Virginia to average ca. 4.4 g dw m<sup>-2</sup>, but when extended to the entire area of tidal marsh, production of spot was 0.38 g dw m<sup>-2</sup>. Similarly, production of grass shrimp in South Carolina was estimated by Sikora (1977) to be 10.8 g dw m<sup>-2</sup> of creekbank area,

Table 6. Summary of annual nekton production estimate (g dry weight m<sup>-2</sup>) scenarios at 6 tidal marsh sites on Sapelo Island, GA using the indicated production to biomass (P:B) ratio values. Overall average annual production includes all sites. See Table 2 for site abbreviations

Nekton group	LD1-L	LD1-H	LD2-L	LD2-H	MD1-L	MD1-H	MD2-L	MD2-H	UD1-L	UD1-H	UD2-L	UD2-H	Mean
<b>Scenario 1: P:B ratio = 2.0 for all species</b>													
Residents	0.269	0.106	1.116	1.069	0.750	0.461	1.131	1.618	1.882	0.392	0.810	1.001	0.884
Migrants	<0.001	<0.001	0.008	0.032	1.477	0.050	0.617	0.278	0.369	0.013	1.051	0.185	0.340
Total	0.270	0.107	1.124	1.101	2.227	0.511	1.748	1.896	2.251	0.405	1.861	1.186	1.224
<b>Scenario 2: P:B ratio = 2.0 for fishes, 5.0 for <i>Palaemonetes pugio</i>, 3.0 for <i>Litopenaeus setiferus</i> (recommended)<sup>a</sup></b>													
Residents	0.326	0.115	1.207	1.239	0.814	0.525	1.558	2.081	1.955	0.409	1.232	1.064	1.044
Migrants	<0.001	<0.001	0.011	0.038	2.070	0.074	0.663	0.364	0.538	0.018	1.433	0.247	0.455
Total	0.327	0.116	1.218	1.277	2.884	0.599	2.221	2.445	2.493	0.427	2.665	1.311	1.499
<b>Scenario 3: P:B ratio = 3.0 for fishes, 5.0 for <i>Palaemonetes pugio</i>, 5.0 for <i>Litopenaeus setiferus</i></b>													
Residents	0.442	0.165	1.735	1.716	1.168	0.734	1.981	2.736	2.872	0.599	1.496	1.543	1.432
Migrants	<0.001	<0.001	0.017	0.061	3.401	0.122	1.016	0.590	0.891	0.029	2.340	0.402	0.739
Total	0.443	0.166	1.752	1.777	4.569	0.856	2.997	3.326	3.763	0.628	3.836	1.945	2.171

<sup>a</sup>The preferred scenario uses P:B ratios that match most closely those from the literature for the small fishes and shrimp that predominated in samples from the intertidal marsh (see 'Production:biomass ratios')

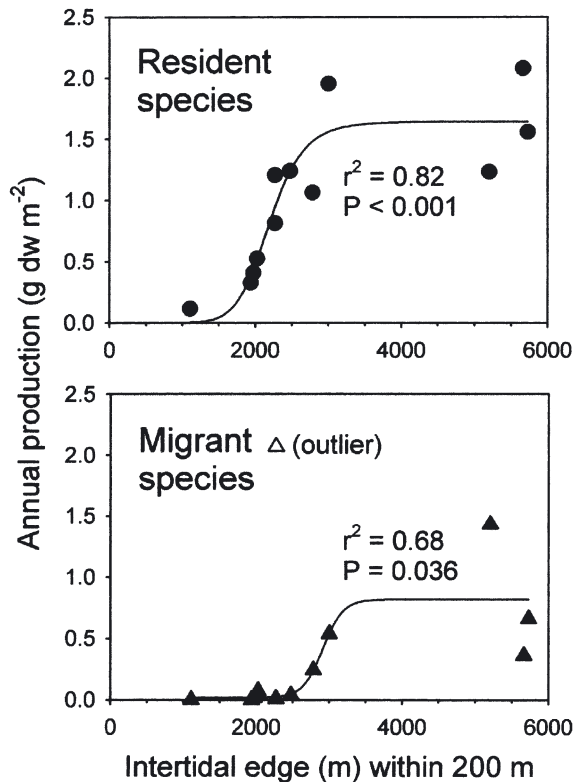


Fig. 5. Relationships between spatial variation in production of resident and migrant nekton estimated from production to biomass (P:B) ratios in Scenario 2 (see Table 6) and landscape complexity measured as the amount of intertidal marsh edge within a 200 m radius of the sampling site (see text for equations)

but was  $0.67 \text{ g dw m}^{-2}$  when adjusted for the intertidal area drained by the marsh creek from which shrimp were sampled. If estuarine nekton production is attributed to intertidal production, then the standing-stock biomass must be calculated on the basis of the entire area providing the trophic support.

Nekton densities, standing stocks and production estimates from Sapelo Island were substantially lower than those reported from marshes in parts of the Gulf of Mexico. Most of the density estimates reported from Texas and Louisiana have been based on collections from  $2.6$  and  $1 \text{ m}^2$  drop traps used at, or very near, the edges of marsh vegetation and do not account for standing stocks or production of nekton attributable to the interior intertidal marsh plain. In many cases, these marshes comprised a complex, reticulated pattern of vegetated patches (i.e. almost entirely edge) such that 'marsh edge' was assigned the status of a separate habitat (e.g. Minello et al. 2003). Because such marsh systems are surrounded by shallow subtidal water, and perhaps are adjacent to seagrass beds, it can be very difficult to determine their relative contribution to the production of estuarine nekton. It is also possible that

nekton production associated with some marshes in the Gulf of Mexico is substantially greater per unit area than in other regions because of substantial allochthonous nutrient inputs discharged from the Mississippi River (Chesney et al. 2000). In contrast, all samples collected by flume weirs in the present study would be classified as representing the marsh 'interior' by the definitions used in Minello (1999), Rozas & Zimmerman (2000) and Minello et al. (2003). The sites had neither a source of substantial allochthonous nutrient inputs nor areas of submerged aquatic vegetation as alternative sources of primary production to support nekton.

Deegan et al. (2000) recently considered the available evidence for the tenets that salt marsh habitats are associated with enhanced growth rates, reduced mortality rates and greater abundance of nekton compared to other estuarine environments. Their focus was on juveniles of migrant species, and also considered the potential mechanisms by which salt marsh food webs support nekton production. They concluded that there was no difference in growth rates of species associated with tidal marshes compared to other estuarine and coastal areas if one adjusted for effects of temperature. Higher temperatures were associated with shallow waters of the estuary and this factor alone could explain higher growth rates in juvenile nekton associated with intertidal wetlands. If growth rates per se are not enhanced by the presence of vegetated intertidal habitat, then the principal contribution of vegetated wetland habitat to estuarine nekton production might be through reduced mortality or greater trophic support for populations at higher densities. Evidence for the contention that mortality rates are generally lower in marshes compared to other estuarine environments was mixed, but Deegan et al. (2000) recognized that accurate measures of mortality rates are extremely difficult and there is a paucity of reliable estimates on which to base any general conclusions regarding the refuge value of tidal marshes. The strongest evidence connecting intertidal primary production to production of estuarine nekton remains in studies of diet and tissue analyses, which continue to link nekton production primarily to a mixture of detritus and benthic algae originating from tidal marshes.

There has been considerable debate over the issue of attaining habitat equivalency with respect to the restoration or creation of natural marsh functions. Whether engineered habitats can match the functioning of natural systems, and the length of time required to do so, seem to depend largely on what function is being considered (e.g. Simenstad & Thom 1996). The development of substrata containing a high organic content, and benthic assemblages that match those of natural marshes or reference sites, may require a considerable time (e.g. Moy & Levin 1991, Craft et al.

1999). However, as long as aquatic connections with the open estuary are maintained, marshes that have been created or restored are populated by nekton relatively quickly and early indications suggest that fishes do not discriminate between natural and excavated wetland channels (Whitman & Gilmore 1993, Zedler et al. 1997, Williams & Zedler 1999). Clearly, the immediate appearance of nekton at a new site is driven by immigration from elsewhere and not new production from the restored or created habitat. However, once a source of primary production is established and begins to be processed through detrital or herbivorous trophic pathways, it will lead to secondary production. Most estuarine nekton species are opportunistic and remarkably flexible in their dietary choices (Kneib 1997), and so will quickly begin to forage on whatever prey sources become established. Initial concerns about the development of a suitable prey base for nekton that forage in restored or created marshes (e.g. Moy & Levin 1991, Allen et al. 1994) seem to have given way to a recognition that vegetated intertidal habitats can rapidly (within 1 to 3 yr) develop prey resources useful to both resident and migrant nekton (Shreffler et al. 1992, Fell et al. 1998, James-Pirri et al. 2001). Assuming that restored or created tidal wetland develop a level of primary production typical of the region in which they are established, and the site is engineered in a way that allows access to nekton (i.e. adequate connection to the estuary and sufficient edge for the free flow of organisms and materials between intertidal and subtidal portions of the environment), then there should be every expectation that nekton production from the restored/created site has potential to rapidly match that of natural systems. In practice, many marsh restoration projects have taken considerably longer to achieve functional parity with natural systems, including the development of benthic prey communities (e.g. Craft et al. 1999), and may not meet the assumptions of appropriate site selection and engineering. Furthermore, the net enhancement of nekton production from a created or restored tidal marsh depends on the pre-project contribution of the candidate site to nekton production in the estuary. The conversion of a site that may already be contributing substantially to the trophic support of nekton populations (e.g. a productive mudflat with rich communities of benthic algae and associated invertebrate prey populations) will not provide the same net benefit as restoring a site that had previously been altered in a way that removed or reduced its communication with the estuary (e.g. impounded or diked marsh).

The findings presented here suggest that the amount of available primary production as modified by bioenergetic constraints operating through food web interactions will set the upper limit on the amount of nekton

production from marshes in a region, but that relatively small additions of marsh/creek edge may enhance nekton production up to a threshold level, above which no additional enhancement should be expected. Site-specific bioenergetic and landscape constraints should guide the development of realistic expectations and success criteria for marsh restoration efforts designed to enhance estuarine nekton production.

*Acknowledgements.* The original data on nekton densities, standing stocks and landscape measurements from marshes on Sapelo Island, Georgia were from research supported by the National Science Foundation under Grant Nos. DEB-9629621 and OCE-0308777. Additional support for the analysis of portions of the data presented here was provided by the National Oceanic & Atmospheric Administration (NOAA) through a contract with Industrial Economics. L. DiPinto and T. Penn provided guidance and comments on an earlier version of the data synthesis, and 3 anonymous reviewers kindly contributed suggestions that improved the manuscript. Any opinions, findings, and conclusions or recommendations expressed here are those of the author and do not necessarily reflect the views of the National Science Foundation or any other government or private organization. This paper is Contribution No. 925 of the University of Georgia Marine Institute.

#### LITERATURE CITED

- Abraham BJ (1985) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic): mummichog and striped killifish. Biological Report 82(11.40) TR EL-82-4. US Fish and Wildlife Service, Washington, DC
- Allen EA, Fell PE, Peck MA, Geig JA, Guthke CR, Newkirk MD (1994) Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. *Estuaries* 17:462-471
- Allen LG (1982) Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. *Fish Bull* 80:769-790
- Agostinho AA, Penczak T (1995) Populations and production of fish in two small tributaries of the Paraná River, Paraná, Brazil. *Hydrobiologia* 312:153-166
- Banise K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. *Ecol Monogr* 5:355-379
- Benaka LR (ed) (1999) Fish habitat: essential fish habitat and rehabilitation. Proc Sea Grant Symp on Fish Habitat: 'Essential Fish Habitat' and Rehabilitation, Hartford, CT, Aug 26-27, 1998. American Fisheries Society, Bethesda, MD
- Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7(4A):460-468
- Carlton JT, Hodder J (2003) Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. *Mar Ecol Prog Ser* 256:271-286
- Chapman DW (1978) Production in fish populations. In: Gerking SD (ed) Ecology of freshwater fish production. John Wiley and Sons, New York, p 5-25
- Chapman VJ (1960) Salt marshes and salt deserts of the world. Leonard Hill, London
- Chesney EJ, Baltz DM, Thomas RG (2000) Louisiana estuar-

- ine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecol Appl* 10:350–366
- Condrey RE, Gosselink JG, Bennett HJ (1972) Comparisons of the assimilation of different diets by *Penaeus setiferus* and *P. aztecus*. *Fish Bull* 70:1281–1292
- Craft C, Reader J, Sacco JN, Broome SW (1999) Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecol Appl* 4:1405–1419
- Curran CA, Newell SY, Paerl HW (1995) The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Mar Ecol Prog Ser* 121:99–116
- Dai T, Wiegert RG (1996) Estimation of the primary productivity of *Spartina alterniflora* using a canopy model. *Ecography* 19:410–423
- D'Avanzo CD, Valiela I (1990) Use of detrital foods and assimilation of nitrogen by coastal detritivores. *Estuaries* 13: 20–24
- Darnell RM (1967) Organic detritus in relation to the estuarine ecosystem. In: Lauff GH (ed) *Estuaries*. American Association for the Advancement of Science Publ 83, Washington, DC, p 376–382
- Deegan LA, Garritt RH (1997) Evidence for spatial variability in estuarine food webs. *Mar Ecol Prog Ser* 147:31–47
- Deegan LA, Peterson BJ, Portier R (1990) Stable isotopes and cellulase activity as evidence for detritus as a food source for juvenile Gulf menhaden. *Estuaries* 13:14–19
- Deegan LA, Hughes JE, Rountree RA (2000) Salt marsh ecosystem support of marine transient species. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*, Kluwer Academic Publishers, Dordrecht, p 333–365
- Downing JA, Plante C (1993) Production of fish populations in lakes. *Can J Fish Aquat Sci* 50:110–120
- Fell PE, Weissbach SP, Jones DA, Fallon MA and 5 others (1998) Does invasion of oligohaline tidal marshes by reed grass, *Phragmites australis* (Cav.) Trin. ex Steud., affect the availability of prey resources for the mummichog, *Fundulus heteroclitus* L.? *J Exp Mar Biol Ecol* 222: 59–77
- Franz DR (2001) Recruitment, survivorship, and age structure of a New York ribbed mussel population (*Geukensia demissa*) in relation to shore level—a nine year study. *Estuaries* 24:319–327
- Gilmore RG, Cooke DW, Donohue CJ (1982) A comparison of the fish populations and habitat in open and closed salt marsh impoundments in east-central Florida. *Northeast Gulf Sci* 5:25–37
- Gilmore RG, Donohue CJ, Cooke DW (1983) Observations on the distribution and biology of east-central Florida populations of the common snook, *Centropomus undecimalis* (Bloch). *Fla Sci* 46:313–336
- Gleason DF, Wellington BM (1988) Food resources of post-larval brown shrimp (*Penaeus aztecus*) in a Texas salt marsh. *Mar Biol* 97:329–337
- Harrington RW Jr, Harrington ES (1961) Food selection among fishes invading a high subtropical salt marsh: from onset of flooding through the progress of a mosquito brood. *Ecology* 42:646–666
- Harrington RW Jr, Harrington ES (1982) Effects on fishes and their forage organisms of impounding a Florida salt marsh to prevent breeding by salt marsh mosquitoes. *Bull Mar Sci* 32:523–531
- Herke WH, Knudsen PA, Rogers BD (1992) Effects of semi-impoundment of Louisiana marsh on fish and crustacean nursery use and export. *N Am J Fish Manage* 12:151–160
- Hettler WF Jr (1989) Nekton use of regularly-flooded salt-marsh cordgrass habitat in North Carolina, USA. *Mar Ecol Prog Ser* 56:111–118
- Hullar MAJ, Fry B, Peterson BJ, Wright RT (1996) Microbial utilization of estuarine dissolved organic carbon: a stable isotope tracer approach tested by mass balance. *Appl Environ Microbiol* 62:2489–2493
- James-Pirri MJ, Raposa KB, Catena JG (2001) Diet composition of mummichogs, *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (USA) salt marsh. *Estuar Coast Shelf Sci* 53:205–213
- Kneib RT (1978) Habitat, diet, reproduction and growth of the spotfin killifish, *Fundulus luciae*, from a North Carolina salt marsh. *Copeia* 1978:164–168
- Kneib RT (1986) The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Am Zool* 26:259–269
- Kneib RT (1987) Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68:379–386
- Kneib RT (1991) Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Mar Ecol Prog Ser* 75:29–38
- Kneib RT (1993) Growth and mortality in successive cohorts of fish larvae within an estuarine nursery. *Mar Ecol Prog Ser* 94:115–127
- Kneib RT (1994) Spatial patterns, spatial scale and feeding in fishes. In: Stouder DT, Fresh KL, Feller RJ (eds) *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia, p 171–185
- Kneib RT (1995) Behaviour separates potential and realized effects of decapod crustaceans in salt marsh communities. *J Exp Mar Biol Ecol* 193:239–259
- Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. *Oceanogr Mar Biol Annu Rev* 35: 163–220
- Kneib RT (2000) Salt marsh ecoscapes and production transfers by estuarine nekton in the southeastern United States. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 267–291
- Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Mar Ecol Prog Ser* 106:227–238
- Kneib RT, Newell SY, Hermeno ET (1997) Survival, growth and reproduction of the salt-marsh amphipod *Uholorchestia spartinophila* reared on natural diets of senescent and dead *Spartina alterniflora* leaves. *Mar Biol* 128:423–431
- Knudsen EE, Paille RF, Rogers BD, Herke WH (1989) Effects of a fixed-crest weir on brown shrimp *Penaeus aztecus* growth, mortality, and emigration in a Louisiana coastal marsh. *N Am J Fish Manage* 9:411–419
- Kruczynski WL (1999) The importance of coastal wetlands: why do we need them? *Association of Southeastern Biologists Bull* 46:246–272
- Kruczynski WL, Ruth BF (1997) Fishes and invertebrates. In: Coultas CL, Hsieh YP (eds) *Ecology and management of tidal marshes*. St. Lucie Press, Delray Beach, FL, p 131–173
- Kruczynski WL, Subrahmanyam CB, Drake SH (1978) Studies on the plant community of a north Florida salt marsh. Part I. Primary productivity. *Bull Mar Sci* 28:316–334
- Kurz RC, Fenwick RW, Davis KA (1998) A comparison of fish communities in restored and natural salt marshes in Tampa Bay, Florida. Tech Rep, Southwest Florida Water Management District, Tampa, FL
- LaSalle MW (1996) Assessing the functional level of a constructed intertidal marsh in Mississippi. Tech Rep WRP-RE-15, US Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS



- Levin LA, Boesch DF, Covich A, Dahm C and 8 others (2001) The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4:430–451
- Lewis RR III (1992) Coastal habitat restoration as a fishery management tool. In: Stroud RH (ed) *Stemming the tide of coastal fish habitat loss*. National Coalition for Marine Conservation, Savannah
- Lowe-McConnell RH (1987) *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge
- McIvor CC, Rozas LP (1996) Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States. In: Nordstrom KF, Roman CT (eds) *Estuarine shores: evolution, environments and human alterations*. John Wiley & Sons, New York, p 311–334
- McTigue TA, Zimmerman RJ (1991) Carnivory vs herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). *J Exp Mar Biol Ecol* 151:1–6
- Mendelssohn IA, Morris JT (2000) Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 59–80
- Meredith WH, Lotrich VA (1979) Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). *Estuar Coast Mar Sci* 8:99–118
- Meyer DL, Townsend EC, Murphy PL (1996) The evaluation of restored wetlands and enhancement methods for existing restorations, Final Report. Office of Habitat Conservation, National Oceanic and Atmospheric Administration, Silver Spring, MD
- Minello TJ (1999) Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. *Am Fish Soc Symp* 22:43–75
- Minello TJ, Rozas LP (2002) Nekton in Gulf coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecol Appl* 12:441–455
- Minello TJ, Zimmerman RJ (1992) Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. *Mar Ecol Prog Ser* 90:273–285
- Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Mar Ecol Prog Ser* 246:39–59
- Mitsch WJ, Gosselink JG (1993) *Wetlands*, 2nd edn. Van Nostrand Reinhold, New York
- Montague CL, Wiegert RG (1990) Salt marshes. In: Myers RL, Ewel JJ (eds) *Ecosystems of Florida*. University of Central Florida Press, Orlando, p 481–516
- Morgan MD (1980) Grazing and predation of the grass shrimp *Palaemonetes pugio*. *Limnol Oceanogr* 25:896–902
- Moy LD, Levin LA (1991) Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. *Estuaries* 14:1–16
- Newell SY, Porter D (2000) Microbial secondary production from salt marsh-grass shoots, and its known and potential fates. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 159–185
- Nixon SW, Oviatt CA (1973) Ecology of a New England salt marsh. *Ecol Monogr* 43:463–498
- Odum EP (2000) Tidal marshes as outwelling/pulsing systems. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 3–7
- Odum WE, Heald EJ (1972) Trophic analyses of an estuarine mangrove community. *Bull Mar Sci* 22:671–738
- Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374:255–257
- Pérez-España H, Galván-Magaña F, Abitia-Cárdenas LA (1998) Growth, consumption, and productivity of the California killifish in Oho de Liebre Lagoon, Mexico. *J Fish Biol* 52:1068–1077
- Peterson GW, Turner RE (1994) The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262
- Prinslow TW, Valiela I, Teal JM (1974) The effect of detritus and ration size on the growth of *Fundulus heteroclitus* (L.). *J Exp Mar Biol Ecol* 16:1–10
- Reagan RE (1985) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico): red drum. Biol Rep 82(11.36) TR EL-82-4. US Fish and Wildlife Service, Washington, DC
- Rey JR, Shaffer J, Tremain D, Crossman RA, Kain T (1990) Effects of re-establishing tidal connections in two impounded subtropical marshes on fishes and physical conditions. *Wetlands* 10:27–45
- Rountree RA, Able KW (1992) Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. *Estuaries* 15:171–185
- Rozas LP (1992) Comparison of nekton habitats associated with pipeline canals and natural channels in Louisiana salt marshes. *Wetlands* 12:136–146
- Rozas LP (1995) Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18:579–590
- Rozas LP, Minello TJ (2001) Marsh terracing as a wetland restoration tool for creating fishery habitat. *Wetlands* 21:327–341
- Rozas LP, Reed DJ (1993) Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Mar Ecol Prog Ser* 96:147–157
- Rozas LP, Zimmerman RJ (2000) Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). *Mar Ecol Prog Ser* 193:217–239
- Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar Ecol Prog Ser* 99:1–16
- Schooley JK (1981) Fish secondary production and ecosystem efficiency in a Florida estuary. *Estuaries* 4:281–282
- Shreffler DK, Simenstad CA, Thom RM (1992) Foraging by juvenile salmon in a restored estuarine wetland. *Estuaries* 15:204–213
- Sikora WB (1977) The ecology of *Palaemonetes pugio* in a southeastern salt marsh ecosystem with particular emphasis on production and trophic relationships. PhD dissertation, University of South Carolina, Columbia
- Simenstad CA, Thom RM (1996) Functional equivalency trajectories of the restored Gog-Le-Hi-Te Estuarine wetland. *Ecol Appl* 6:38–56
- Stiven AE, Hunter JT (1976) Growth and mortality of *Littorina irrorata* Say in three North Carolina marshes. *Chesap Sci* 17:168–176
- Sullivan MJ, Currin CA (2000) Community structure and functional dynamics of benthic microalgae in salt marshes. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 81–106
- Teal JM (1962) Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624
- Teal JM, Howes BL (2000) Salt marsh values: retrospection from the end of the century. In: Weinstein MP, Kreeger DA

- (eds) Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, p 9–19
- Thayer GW, Colby DR, Hettler WF Jr (1987) Utilization of the red mangrove prop root habitat by fishes in South Florida. *Mar Ecol Prog Ser* 35:25–38
- Turner RE (1977) Intertidal vegetation and commercial yields of penaeid shrimp. *Trans Am Fish Soc* 106:411–416
- Valiela I, Wright JE, Teal JM, Volkmann SB (1977) Growth, production and energy transformations in the salt-marsh killifish *Fundulus heteroclitus*. *Mar Biol* 40:135–144
- Vose FE, Bell SS (1994) Resident fishes and macrobenthos in mangrove-rimmed habitats: evaluation of habitat restoration by hydrologic modification. *Estuaries* 17:585–596
- Wang SB, Houde ED (1995) Distribution, relative abundance, biomass and production of bay anchovy *Anchoa mitchilli* in the Chesapeake Bay. *Mar Ecol Prog Ser* 121:27–38
- Warburton K (1979) Growth and production of some important species of fish in a Mexican coastal lagoon system. *J Fish Biol* 14:449–464
- Webb SR, Kneib RT (2002) Abundance and distribution of juvenile white shrimp *Litopenaeus setiferus* within a tidal marsh landscape. *Mar Ecol Prog Ser* 232:213–223
- Weinstein MP (1983) Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*) along a tidal creek-seagrass meadow coenocline. *Can J Fish Aquat Sci* 40:1633–1638
- Weinstein MP, Litvin SY (2000) The role of tidal salt marsh as an energy source for marine transient and resident finfishes: a stable isotope approach. *Trans Am Fish Soc* 129:797–810
- Weinstein MP, Walters MF (1981) Growth, survival and production in young-of-the-year populations of *Leiostomus xanthurus* Lacepede, residing in tidal creeks. *Estuaries* 4: 185–197
- Weinstein MP, Scott L, O'Neill SP, Seigfried RC II, Szedlmayer ST (1984) Population dynamics of the spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River Estuary, Virginia. *Estuaries* 7(4A):444–450
- Weisberg SB, Lotrich VA (1982) The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: an experimental approach. *Mar Biol* 66:307–310
- Welsh BL (1975) The role of grass shrimp, *Palaemonetes pugio*, in a tidal marsh ecosystem. *Ecology* 56:513–530
- Whitman RL Jr, Gilmore RG Jr (1993) Comparative evaluation of fisheries community structure and habitat relationships in natural and created saltmarsh ecosystems. Tech Rep, Southwest Florida Water Management District, Tampa, FL
- Williams GD, Zedler JB (1999) Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: relative influence of channel morphology and restoration history. *Estuaries* 22:702–716
- Zedler JB, Williams GD, Desmond JS (1997) Wetland mitigation: can fishes distinguish between natural and constructed wetlands? *Fisheries* 22:26–28
- 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 Academic Publishers, Dordrecht, p 293–314

*Editorial responsibility: Charles Peterson, (Contributing Editor), Morehead City, North Carolina, USA*

*Submitted: July 10, 2003; Accepted: October 21, 2003  
Proofs received from author(s): December 4, 2003*

# Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations

Charles H. Peterson<sup>1,\*</sup>, Romuald N. Lipcius<sup>2</sup>

<sup>1</sup>Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA

<sup>2</sup>School of Marine Sciences, The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062, USA

**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

*Resale or republication not permitted without written consent of the publisher*

## 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 (Spurduto 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 microalgal 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 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 alterniflora* 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.

*Acknowledgements.* Support for preparing this paper was provided by the NOAA Damage Assessment Center.

#### 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
- Elmqvist 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  $^{13}\text{C}/^{12}\text{C}$  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
- Peterson 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, sea-duck, 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

*Editorial responsibility: Ronald Kneib,  
Sapelo Island, Georgia, USA*

*Submitted: October 4, 2003; Accepted: November 25, 2003  
Proofs received from author(s): December 8, 2003*