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

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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^2 of restored oyster reef in the southeast United States is expected to yield an additional 2.6 kg yr^{-1} 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^{-2}, 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

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 gatropods, 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, Breitburg 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
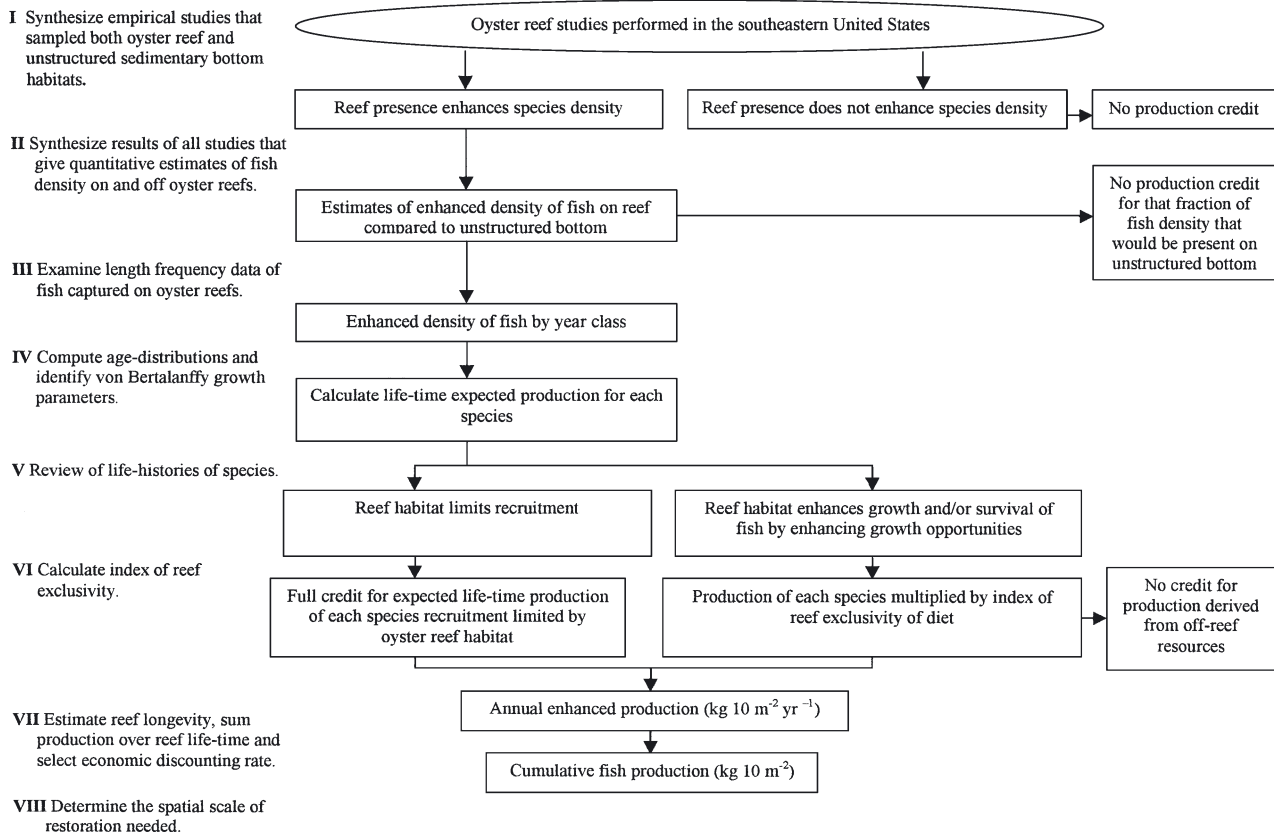

Fig. 1. Flow diagram illustrating our approach to calculating expected enhancement of fish and mobile crustacean production resulting from the restoration of oyster reefs in the southeastern USA

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^2 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^2). 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^2 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
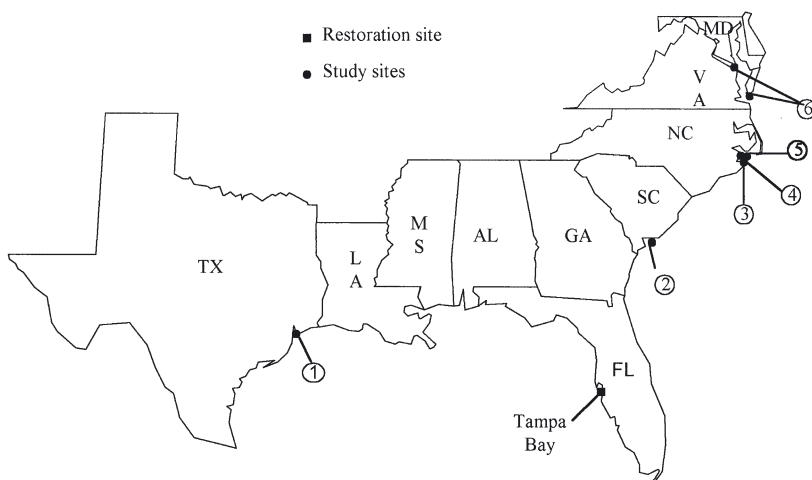

Fig. 2. Southeastern USA, with the sites of empirical studies used in our synthesis noted by filled circles and the targeted restoration site, Tampa Bay, FL, noted by the filled square. Numbers identify the location and sources of data: (1) Galveston Bay, TX, Minello & Zimmerman (1989); (2) Charleston 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 m² drop-sampler	Summer and Fall 1988	Zimmerman et al. (1989)
Inlet Creek, SC Toler's Cove, SC	Intertidal Intertidal	None None	Yes (3) Yes (3)	3 (Oct 1994) 3 (Oct 1994)	24 m² lift net	Spring, Summer and Fall 1995	Wenner et al. (1996)
New River, NC White Oak River, NC Back Sound, NC	Intertidal Intertidal Intertidal	Yes (6) Yes (6) Yes (6)	Yes (6) Yes (6) Yes (6)	6 (Aug 1992) 6 (Aug 1992) 6 (Aug 1992)	Block & fyke nets, $\frac{1}{4}$ m² excavations	Nets: Spring, Summer and Fall 1993, 1994 at all sites Excavations: Fall 1992, Spring and Summer 1993 and 1994 at all sites	Meyer et al. (1996)
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 West Bay, NC	3, 4, 6 m 3 m	Yes (4) Yes (8)	None None	4 (Jun 1993) 8 (Jul 1996)	Gill nets, fish traps and diver census	Monthly Summer and Fall 1996 Spring and Summer 1997	Lenihan et al. (1998, 2001)
Piankatank 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 occured 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 m² 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:

$$S_i = S_o \times e^{(-M_i \times i)} \qquad (1)$$

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:

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

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

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

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_∞	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	Savage & Sullivan (1978), Sullivan (1979), French 1999
Stone crab	0.70	0.30	3	14.0	0.173	−0.397	0.1170	3.30	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), Serafy 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 m² 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 ½ 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:

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

where L_∞ (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:

$$W_i = a \times L_i^b \qquad (5)$$

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):

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

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^2 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):

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

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^2 of oyster reef for a particular species, was calculated by:

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

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^2 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. $10 \, m^{-2}$)	IRE	Grouping	Annual increase in secondary production (kg $10 \, m^{-2} \, yr^{-1}$)
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[a]	0.16	–	RE	0.293
Black sea bass	0.39	0.75	G	0.046
Spottail 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

[a]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 $10 \, m^{-2}$) 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 butterfish) were collected in only a single study (striped bass and white perch in the VIMS studies; and weakfish, spadefish, and butterfish 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 $(2.57 \text{ kg } 10 \text{ m}^{-2})$, 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 $(0.653 \text{ kg } 10 \text{ m}^{-2})$, gobies $(0.644 \text{ kg } 10 \text{ m}^{-2})$, sheepshead $(0.586 \text{ kg } 10 \text{ m}^{-2})$ and gag grouper $(0.293 \text{ kg } 10 \text{ m}^{-2})$ 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% $(0.21 \text{ kg } 10 \text{ m}^{-2})$ after the IRE was applied to production estimates. Production of pigfish $(0.135 \text{ kg } 10 \text{ m}^{-2})$ and black seabass $(0.046 \text{ kg } 10 \text{ m}^{-2})$ 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
Large mobile crustaceans					
Farfantepenaeus duorarum	Pink shrimp	2	2	All mudflat – all reef	Not enhanced
Liptopenaeus setiferus	White shrimp	1	1	1.89	Not enhanced
Farfantepenaeus aztecus	Brown shrimp	1	0	All mudflat	Not enhanced
Callinectes sapidus	Blue crab	5	1	0.2 – all reef	Not enhanced
Menippe mercenaria	Stone crab	4	3	0.8 – all reef	Recruitment enhanced
Fish					
Anchoa hepsetus	Striped anchovy	1	0	0.1	Not enhanced
Anchoa mitchilli	Bay anchovy	2	2	0.3 – 18	Growth enhanced
Archosargus probatocephalus	Sheepshead	2	2	All reef	Recruitment enhanced
Bairdiella chrysoura	Silver perch	3	2	All mudflat – all reef	Not enhanced
Brevoortia patronus	Gulf menhaden	1	0	1.0	Not enhanced
Brevoortia tyrannus	Atlantic menhaden	2	0	All mudflat – 0.2	Not enhanced
Carcharhinus acronotus	Blacknose shark	1	0	All mudflat	Not enhanced
Carcharhinus limbatus	Blacktip shark	1	0	All mudflat – 0.1	Not enhanced
Centropristis striata	Black sea bass	2	2	0.5 – all reef	Growth enhanced
Chaetodipterus faber	Atlantic spadefish	1	0	All sand – all reef	Not enhanced*
Chasmodes bosquianus	Striped blenny	4	4	All reef	Recruitment enhanced
Chilomycterus schoepfi	Striped burrfish	1	0	All mudflat	Not enhanced
Cynoscion nebulosus	Speckled seatrout	2	1	All mudflat – all reef	Not enhanced*
Cynoscion regalis	Weakfish	1	1	0.4 – all reef	Not enhanced*
Cyprinodon variegatus	Sheepshead minnow	1	1	0.5 – all reef	Growth enhanced
Diplodus holbrooki	Spotail pinfish	1	1	1.64 – all reef	Growth enhanced
Eucinostomus argenteus	Spotfin mojarra	1	0	0.33	Not enhanced
Fundulus heteroclitus	Mummichog	3	1	0.32 – all reef	Not enhanced
Gobiesox strumosus	Skilletfish	1	1	All reef	Recruitment enhanced
Gobionellus boleosoma	Darter goby	2	0	All mudflat – 1.5	Not enhanced
Gobiosoma bosci	Naked goby	4	4	33 – all reef	Recruitment enhanced
Hypsoblennius hentz	Feather blenny	1	1	All reef	Recruitment enhanced
Lagodon rhomboides	Pinfish	4	1	All mudflat – all reef	Not enhanced
Leiostomus xanthurus	Spot	5	1	All mudflat – all reef	Not enhanced
Lucania parva	Rainwater killifish	2	1	1 – all reef	Not enhanced*
Lutjanus griseus	Gray snapper	2	2	4 – all reef	Recruitment enhanced
Membras martinica	Rough silversides	1	1	23	Growth enhanced
Menidia beryllina	Inland silversides	1	1	4.1	Growth enhanced
Menidia menidia	Atlantic silversides	1	1	All reef	Growth enhanced
Micropogonias undulatus	Atlantic croaker	3	0	All mudlfat – 1.2	Not enhanced
Monacanthus hispidus	Filefish	1	0	All mudflat – all reef	Not enhanced
Morone americana	White perch	1	1	All reef	Growth enhanced
Morone saxatilis	Striped bass	1	1	All reef	Not enhanced*
Mugil cephalus	Striped mullet	3	1	All mudflat – all reef	Not enhanced
Mugil curema	White mullet	1	1	1.8	Not enhanced*
Mycteroperca microlepis	Gag grouper	2	2	1 - all reef	Recruitment enhanced
Opsanus spp.	Toadfishes	4	4	0.4 – all reef	Recruitment enhanced
Orthopristis chrysoptera	Pigfish	4	3	All mudflat – all reef	Growth enhanced
Paralichthys albigutta	Gulf flounder	2	0	All mudflat – 0.3	Not enhanced
Paralichthys dentatus	Summer flounder	2	1	All mudflat – all reef	Not enhanced
Paralichthys lethostigma	Southern flounder	2	2	1 – 3.3	Growth enhanced
Peprilus spp.	Butterfish	1	1	All reef	Not enhanced*
Pogonias cromis	Black drum	1	0	0.66	Not enhanced
Pomatomus saltatrix	Bluefish	2	0	All mudflat – 0.5	Not enhanced
Sciaenops ocellatus	Red drum	2	1	All sand – all reef	Not enhanced*
Scomberomorus maculatus	Spanish mackerel	1	0	All sand	Not enhanced
Tautoga onitis	Tautog	2	2	2 – all reef	Recruitment enhanced
Trinectes maculatus	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 *Paleomonetes 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 kg yr^{-1}, the discounted cumulative production credit for 20 yr of reef function is 38.2 kg 10 m^{-2} of reef. For 30 yr, this credit increases to 50.4 kg 10 m^{-2}. By 100 yr, an asymptote of ca. 80 kg 10 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-
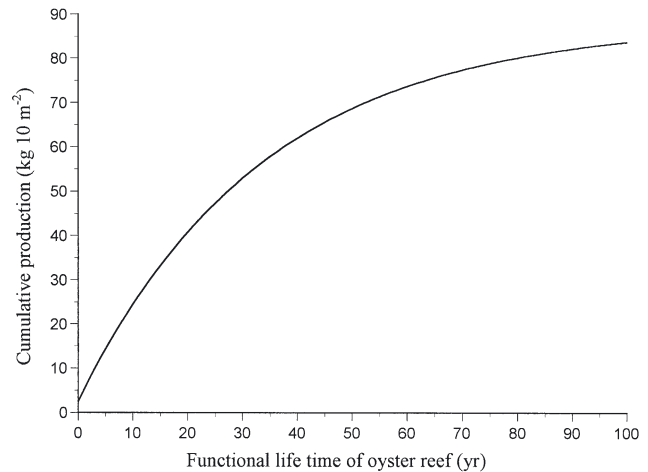

Fig. 3. Long-term projection of cumulative enhanced fish and mobile crustacean production per 10 m^2 of restored oyster reef habitat, discounted to adjust for annual depreciation of resources as a function of the functional lifetime of the reef. An annual discount rate of 3 % was applied

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.

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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