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

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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^2 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^{-2} yr^{-1}. 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

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 supported 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 m^{-2}); a: abundant (0.9 to 0.02 m^{-2}); rare species (<0.01 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
Archosargus probatocephalus	Sheepshead	Reef resident	Macroinvertivore, piscivore	A	a
Balistes capriscus	Gray triggerfish	Reef resident	Macroinvertivore	A	a
Caranx crysos	Blue runner	Brief visitor	Piscivore	A	a
Centropristis striata	Black seabass	Reef resident	Macroinvertivore	A	a
Chaetodipterus faber	Atlantic spadefish	Reef resident	Macroinvertivore	A	a
Clupeidae spp.	Herrings	Reef resident—transient occupant	Planktivore	R, J, A	ha
Decapterus punctatus	Round scad	Transient occupant	Planktivore	J, A	ha
Diplectrum formosum	Sand perch	Reef resident	Microinvertivore, macroinvertivore, piscivore	J, A	a
Diplodus holbrooki	Spottail pinfish	Reef resident	Herbivore, microinvertivore		a
Equetus umbrosus	Cubbyu	Reef resident	Microinvertivore	J, A	ha
Haemulon aurolineatum	Tomtate	Reef resident	Planktivore, microinvertivore	J, A	ha
Haemulon plumieri	White grunt	Reef resident	Planktivore, microinvertivore, macroinvertivore	J, A	ha
Halichoeres bivittatus	Slippery dick	Reef resident	Microinvertivore, macroinvertivore	J, A	a
Hypleurochilus geminatus	Crested blenny	Reef resident	Microinvertivore	R, J, A	a
Lutjanus griseus	Gray snapper	Reef resident	Macroinvertivore, piscivore	J, A	a
Mycteroperca microlepis	Gag grouper	Reef resident	Macroinvertivore, piscivore	A	a
Odontoscion dentex	Reef croaker	Brief visitor	Macroinvertivore, piscivore	J, A	a
Opsanus pardus	Leopard toadfish	Reef resident	Macroinvertivore	R, J, A	a
Orthopristis chrysoptera	Pigfish	Reef resident	Macroinvertivore, piscivore	A	a
Parablennius marmoreus	Seaweed blenny	Reef resident—transient occupant	Microinvertivore	R, J, A	a
Rypticus maculatus	Whitespotted soapfish	Brief visitor	Macroinvertivore	A	a
Scomberomorus maculatus	Spanish mackerel	Transient occupant	Piscivore	A	ha
Seriola dumerili	Greater amberjack	Transient occupant	Piscivore	A	a
Serranus subligarius	Belted sandfish	Reef resident	Microinvertivore, macroinvertivore	J, A	a
Synodus intermedius	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 pro-files: 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 (Ni), 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:

$$W_i = a \times L_i^b \tag{1}$$

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

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

The parameters L_∞ (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_∞ (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		r	D	Age-length and length-weight relationships					Source
	M	F			L_∞	K	t_0	a	b	
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[a]
Leopard toadfish	0.60	0.00	2	S	30.0	0.193	−0.180	0.0170[b]	4.98[b]	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)

[a] For annual species (blennies), production is calculated by multiplying fish density by average individual wet weight
[b] For leopard toadfish, length was converted to wet weight using the following exponential equation: $W_i = a \times e^{b \times L_i}$. 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^{-2})	IRE	Grouping	Annual increase in fish production (kg 10 m^{-2} yr^{-1})		
				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:

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

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^2 of artificial reef was calculated by:

$$AP = IRE \times \sum (P_i \times N_i) \tag{4}$$

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^2 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^{-1})	Expected change in biomass on reefs opened to fishing if fishing did not occur (%)	Expected biomass on open reefs in 1997 (kg reef^{-1}) if fishing did not occur	Observed biomass on reefs opened to fishing in 1997 (kg reef^{-1})	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 m^{-2} 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 m^{-2} 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 m^{-2} under Scenario 2, and 84 kg 10 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 m^{-2}) or 3 (~140 kg 10 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%

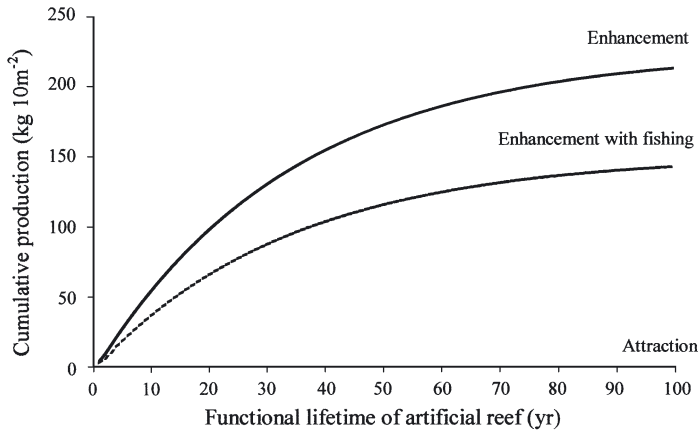| Scenario	Cumulative production (kg wet wt 10 m^{-2}) for given project lifespan				
	1 yr	2 yr	10 yr	20 yr	30 yr
1. Attraction	0.00	0.00	0.00	0.00	0.00
2. Enhancement	4.07	8.66	51.32	92.28	122.75
3. Enhancement with fishing	2.80	5.94	35.30	63.47	84.43

Fig. 1. Long-term projection of cumulative fish production per 10 m² 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⁻² 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 m² 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.

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