Quantifying fish and mobile invertebrate production from a threatened nursery habitat

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Summary

1. Quantification of ecosystem services is increasingly valuable for conservation and restoration decision-making. Structured habitats serve as nursery grounds by enhancing juvenile fish and mobile crustacean survival and abundance. This service is challenging to quantify due to ontogenetic shifts in habitat use by many species.

2. We reviewed available literature on the increased abundance of juvenile fish and mobile crustaceans in a key nursery habitat – *Crassostrea virginica* reefs in the USA. We modelled the growth and mortality of the enhanced species using three different natural mortality (M) estimates to provide estimates of the gross and net lifetime production and uncertainty that can be attributed to the habitat.

3. Recruitment of nineteen and twelve species were found to be enhanced by the addition of *C. virginica* reefs to previously unstructured habitat in the Gulf of Mexico and the South Atlantic and Mid-Atlantic USA, respectively. This increased recruitment is estimated to result in a mean lifetime enhancement in production of 397 ± 115 (1 SD) g m^{-2} year^{-1} in the Gulf of Mexico and 281 ± 56 g m^{-2} year^{-1} in the South Atlantic and Mid-Atlantic.

4. The two regions differed with regard to the identity of the enhanced species and their degree of augmentation. Thus, our results highlight the inadequacy of applying regional estimates of ecosystem services to global scales. Furthermore, estimates of total enhancement varied by up to a factor of 2·8 across the three methods of M estimation.

5. Our estimates are quantitative predictions of the ecological benefits derived from the restoration or conservation of a threatened habitat, and advance the field of restoration science beyond qualitative statements that just predict direction of benefit (e.g. increased or decreased). Quantification of the uncertainty in the production estimates further increases their utility for decision-makers.

6. *Synthesis and applications.* Our results can be applied to the restoration or conservation of nursery habitats where habitat is limiting the recruitment of fish species. Quantitative estimates of fisheries productivity enhancement by habitats can be used by managers to determine the expected return on investment in restoration activities, provide testable predictions for monitoring programs and communicate the value of restoring or conserving habitat.

Key-words: coastal, *Crassostrea virginica*, ecosystem service valuation, fisheries, habitat restoration, nursery habitat, oyster reef, recruitment, restoration scaling, uncertainty

Introduction

Advancing a wider societal recognition of the ecological importance of biogenic habitats has been a major accomplishment of conservation science over the last couple of decades (Turner & Daily 2008). This growing understanding has been sufficient to stimulate the conservation and small-scale restoration of critical habitats; however, as habitat loss continues to increase, so too does the need for larger and more costly conservation and

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restoration efforts. Qualitative predictions of benefits where only direction is hypothesized fail to provide strong arguments for costly endeavours and do little to advance the science of restoration (Powers & Boyer 2014). Therefore, quantitative assessments of the ecological benefits and the economic value of services are needed to ensure that decision-makers have the appropriate tools to prioritize conservation and scale the benefits of habitat restoration efforts relative to natural resource damage assessments (Peterson & Lipcius 2003).

The lack of models to quantify benefits is a problem ubiquitous across many ecosystem services. While ecological studies often quantify services at fine temporal and spatial scales, few scale up services to units meaningful for policy and management (Turner & Daily 2008). Furthermore, they rarely incorporate measures of uncertainty in their provision, with some notable exceptions (e.g. Hutchison *et al.* 2013). Basing models on meta-analyses is one solution to bridging the gap from fine- to coarser-scale application of studies.

Structured coastal habitats such as oyster reefs, seagrass meadows and saltmarshes have been shown to support enhanced abundances of juvenile fish and invertebrates compared to adjacent unstructured areas (Heck, Hays & Orth 2003). This enhancement is the product of both higher settlement rates of larvae (Eckman 1987) and lower post-settlement mortality of newly settled individuals (Heck, Hays & Orth 2003), which can strongly regulate fish and benthic invertebrate populations (Ólafsson, Peterson & Ambrose 1994; Steele 1997). Assuming the supply of larvae does not limit population size (see review by Caley *et al.* 1996), nursery habitats can mediate the population dynamics of enhanced fish (Juanes 2007). Recognition of this important function of structured habitats and their role as foraging areas for older age classes of fish has resulted in efforts to protect them. Quantification of the augmentation in fish productivity across scales and over time, and estimates of the uncertainty in this service are now needed to guide decision-making, which often seeks to maximize the return on investment of restoration and conservation activities.

Oyster reefs provide a model system for quantifying the magnitude of, and regional variability in, augmented fish productivity by nursery habitats. Eastern oyster *Crassostrea virginica* (Gmelin, 1791) is a biogenic habitat-building species capable of forming substantial reefs as a result of gregarious settlement patterns, in areas that predominately lack structure. They are well-studied nursery habitats. Moreover, oyster reefs have suffered declines in excess of 90% in many estuaries (zu Ermgassen *et al.* 2012), so that the availability of this habitat likely limits the productivity of many fish species in these estuaries. Furthermore, oyster reefs are currently the focus of substantial restoration efforts and finfish and crustacean fisheries enhancement are frequently cited as grounds for restoration investment (Coen & Luckenbach 2000; Grabowski & Peterson 2007). This methodology could,

however, be applied to any structured habitat fulfilling the following conditions: (i) the current extent is limiting the productivity of species that utilize it as juveniles; and (ii) there is adequate sampling of densities of juvenile size classes of fish and mobile crustaceans both on and off the habitat of interest.

The stochastic nature of fish populations and the difficulty in sampling a large area or range of locations makes it challenging to derive quantitative estimates for fish and invertebrate enhancement by nursery habitats. Ontogenetic shifts in habitat use further complicate the process of attributing fish production to specific habitats (Mumby 2006). Here we conducted a meta-analysis to determine which species are enhanced by eastern oyster reefs in two separate ecoregions: (i) the northern Gulf of Mexico and (ii) South Atlantic and Mid-Atlantic coasts of the USA. We then modelled enhancement of fish production and biomass that can be attributed to the nursery function of this habitat over the lifetimes of the enhanced species (i.e. including their growth even if they have moved off of the reef). Similar approaches have been used in a range of structured habitats (e.g. Watson, Coles & Lee Long 1993; Peterson, Grabowski & Powers 2003; Powers *et al.* 2003; Blandon & zu Ermgassen 2014), although these previous efforts have quantified neither the uncertainty around the estimated enhancement in fish production nor the gross and net production. Incorporating uncertainty surrounding point estimates is a critical step in assisting the translation of ecosystem service estimates into policy and management actions (Ruckelshaus *et al.* 2014). We discuss the potential utility of our approach and the value of adopting an ecoregional-scale approach to estimating enhanced fish production derived from threatened nursery habitats. We also briefly examine the evidence for enhancement of later life-history stages of fish by this structured habitat.

Materials and methods

UNDERLYING ASSUMPTIONS

To quantitatively estimate the annual enhancement of fish and mobile invertebrate production by structured habitats, we assumed that the structured habitat of interest was limiting. Therefore, the addition of this habitat reduces a survival bottleneck by enhancing settlement and decreasing post-settlement mortality on the newly settled individuals (Peterson 1986), consequently resulting in enhanced recruitment. We refer to recruitment in an ecological context, where survival to census is based on a relatively early life stage (0·5 or 0·25 years of age), rather than at the date of maturity or entry into the fishery, as would be the case in a fisheries definition.

There is significant evidence that oyster reef habitat in the USA is greatly reduced in extent and quality (zu Ermgassen *et al.* 2012). Such dramatic losses have similarly been noted for many other structured marine habitats (e.g. Bromberg & Bertness 2005; Burke *et al.* 2011). Where oyster reefs have been lost in the Gulf of Mexico and on the South Atlantic and Mid-Atlantic coast of

the USA, they have most frequently been replaced by soft sediments. We therefore assumed that soft sediments were not limiting in these systems, and hence that the presence or restoration of oyster reefs did not decrease the populations of species utilizing soft sediment habitats.

STUDY SELECTION AND DATA HANDLING

We conducted a comprehensive literature search for studies reporting fish and mobile invertebrate abundance on oyster reef and in an unstructured control habitat. Twelve studies from the Mid and South Atlantic and nineteen studies from the northern Gulf of Mexico were identified (Fig. 1). Data from the two coasts were managed separately as they represent different fish stock management areas with different spawning stock biomass targets, and are two largely distinct ecosystems with differing levels of fish diversity (i.e. Gulf of Mexico > Mid and South Atlantic). We used these two regions to reveal if ecosystem services associated with nursery habitats are consistent or vary across biogeographic regions. The location and duration of each study were noted, along with the sampling effort and sampling technique (see Table S1, Supporting information for details). We extracted fish and mobile crustacean abundance from both oyster reef and control habitat and converted these to densities.

Only sampling methodologies suitable for catching the target species (demersal fish and crustaceans) were retained in the data set. Data were parsed according to the size of the individuals caught or deemed likely to be caught with each sampling methodology. Small drop and pop-up nets, seines and habitat trays select primarily for young of year individuals (Bloomfield & Gillanders 2005), whereas size-class data were examined for species captured in lift nets and otter trawls to determine which age classes were represented in the data set. Gillnets were used to sample primarily older age classes. Thus, we were able to separate abundance estimates into two life stages: juveniles and older age classes. The documented densities of juveniles were deemed to represent on average 0·5-year-old individuals based on examination of size information where available and on the timing of sampling. Shrimp species brown shrimp *Farfantepenaeus aztecus* (Ives, 1891), white shrimp *Litopenaeus setiferus* (Linnaeus 1767) and blue crab *Callinectes sapidus* (Rathbun, 1896) were exceptions to this assumption as they are known to move on from structured nursery grounds before 6 months of age (Parrack 1979; Pattillo *et al.* 1997). We therefore assumed a mean age of 0·25 years for these species.

Pop-up nets, drop nets and habitat trays likely sample all age classes for a small number of primarily benthic species known to be resident on structured habitat such as gobies, blennies and
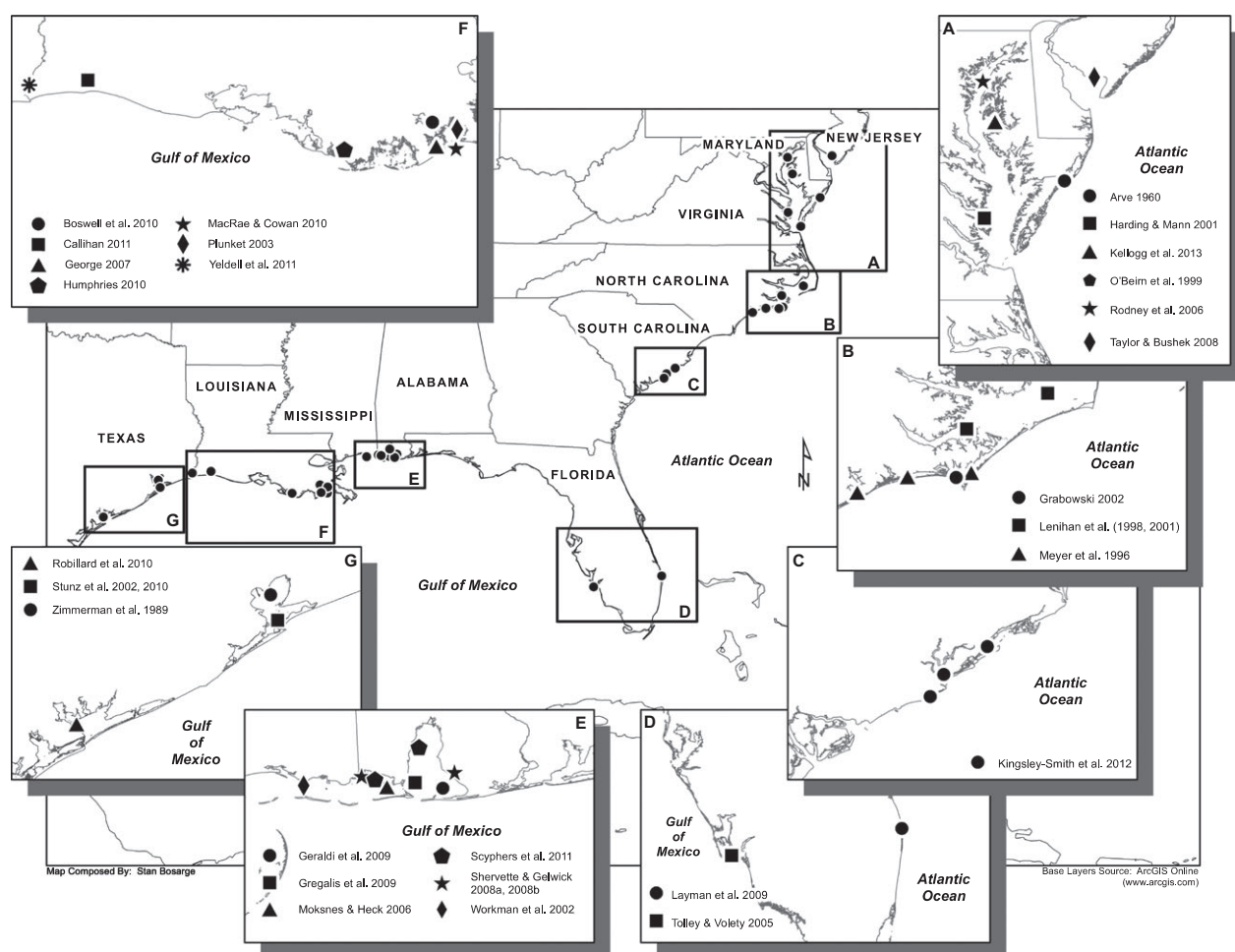

Fig. 1. Map showing the locations of the 31 studies used in the meta-analysis. Full citations of included studies can be found in Table S1.

toadfish. In these cases, year 0·5 density was back-calculated using the same size-dependent mortality model as applied for further calculations in each case. For these species, standard error was estimated for the 0·5 year class by determining the ratio of the mean across all age classes to the total standard error and applying the ratio to the 0·5 year mean.

Catch efficiency varies substantially both across species and across sampling methodologies (Rozas & Minello 1997). While reported catch efficiencies for methodologies included in this study range from 7 to 100%, the majority of samples, particularly for juvenile stages, were undertaken using methodologies with efficiencies in excess of 50% (Rozas & Minello 1997). Given the range of sampling methodologies included in our meta-analysis, we did not apply correction factors to the data. Neither did we apply correction factors for differences in efficiency across habitat types. While many of the samples were collected by small-scale enclosure gears and hence should be similarly effective across habitat types, some included gears have lower efficiencies on structured habitats (Rozas & Minello 1997). Our reported differences in fish and crustacean densities between oyster reefs and soft sediments are therefore likely underestimated and hence form the basis of a conservative estimate of enhancement by oyster reefs.

The vast majority of data were included as reported, as they sampled sufficiently small areas to be confident that the differences between on-reef and control samples could be attributed to the reef that was present. For a subset of sampling methodologies (e.g. seine and M-traps) we applied correction factors to the data to reflect the area of oyster reef sampled (see Appendix S1, Supporting information for further details).

The 31 studies represented variable sampling frequencies. Therefore, in order to reflect the level of confidence in each reported value, data were combined to represent independent sampling events, or were weighted by the number of independent sampling events they represented. We defined independent sampling events as samples that were collected in different bays or estuaries, or in different seasons (defined as: Spring = March, April and May; Summer = June, July and August; Autumn = September, October and November; Winter = December, January and February). Many fish species migrate out of estuaries during the winter months as part of their ontogenetic habitat change (e.g. Darcy 1983; Ross & Moser 1995), so that densities within the nursery habitats may not represent juvenile enhancement in winter months. Therefore, samples taken in the winter season were excluded and were not included as independent events where data were represented as annual means.

To determine which species were enhanced by oyster reef, a series of criteria were applied to each species: (i) there must be life-history information indicating the species benefits from structured habitats; (ii) the weighted mean of the within-habitat minus the control density must be positive; (ii) the species must be more abundant within the habitat than in the control in more than half of the independent sampling events; and (iv) the species must be represented by data from at least two geographically independent estuaries. Species fulfilling all of these criteria were deemed to be enhanced by the presence of oyster reef.

PRODUCTION CALCULATIONS

The enhancement in production that can be attributed to the presence of oyster reef habitat was determined by applying known growth and mortality relationships to the enhanced density of juveniles on the structured habitat, where the term 'enhanced density' refers to the weighted mean of the density within the habitat minus the density in the unstructured control.

The number of surviving individuals at time t, $N(t)$, was calculated from $dN/dt = -M(t) N$, where $M(t)$ is the species-specific and size-dependent natural mortality. Size-dependent mortality was computed as $M(t) = M (L_m/L(t))$, following Lorenzen (2000), where $L(t)$ is the length at time t and L_m is the length of recruitment to the fishery, or length at maturity if age or length of recruitment to the fishery was unavailable. Estimates of M found in the literature were assumed to represent the natural mortality at size L_m. In cases where L_m was unknown, it was calculated from L_{inf} (Froese & Binohlan 2000). M is still frequently assumed to be constant across the life history of a fish in many fisheries assessments. For comparison, we therefore also computed results using a constant M, in which case $N(t) = N_{0.5} \times e^{(-M \times (t-0.5))}$, where $N_{0.5}$ is the density enhancement at 0·5 years. Finally, a recent review by Kenchington (2014) suggested that the model $\ln(M) = 0.55 - 161\ln(L) + 1.44(\ln(L_{inf}) + \ln (K)$, developed by Gislason *et al.* (2010), showed promise but recommended further investigation of its applicability. We have also included results computed using this estimate of mortality. The Lorenzen model is widely accepted in the literature and is regularly used by fishery managers. Thus, we have used the results based on the Lorenzen model as our baseline, but we present results from all three models as an indicator of model uncertainty arising from M estimation.

Given $N(t)$, the rate of production was computed as $dP/dt = N(t) dW/dt$, where P is production, W is weight and t is time. Integrated over time, this formula gives an estimate of gross production (P_g) including both living individuals and individuals that died in the intervening time period. The growth rate, dW/dt, was computed using the von Bertalanffy growth equation to compute the mean length of individuals at a given age and applying published length–weight relationships (see Table S2) to convert this to weight as a function of time. Gross production from a single recruitment event was computed by integrating this production rate from year 0·5 (year 0·25 for shrimp and blue crab) to the estimated maximum life span (t_{max}) for each species. This calculation is also equivalent to the annual production in a steady state, assuming annual recruitment and that time since restoration $\geq t_{max}$ of the longest-lived species. As an alternative metric, net production (P_n) was computed by calculating the number, N_i, of additional individuals in each age class, i, multiplied by the increment in mass in that age class, $W_i - W_{i-1}$.

Life-history parameters were drawn from www.fishbase.org (Froese & Pauly 2011) or the literature. In some cases, species-specific data were unavailable and related proxies were used (see Table S2). Three different species-specific estimates *of M* were used: a static M from the literature or estimated to the nearest year using Hoenig's equation (Hoenig 1983), M as estimated by Gislason *et al.* (2010), and M as estimated by Lorenzen (2000). Where t_{max} was unavailable, it was estimated using Beverton (1992), either using published age of first maturity or, where unavailable, estimated age of first maturity (Froese & Binohlan 2000). Where there was evidence in the literature of sexual dimorphism or significant differences in life-history parameters between coasts, separate growth equations were used (see Table S2). When applying different growth parameters to each sex, we assumed a 1 : 1 sex ratio at sampling.

To compute the uncertainty around our calculations of the enhancement in fish production, the enhanced density was modelled as a normal distribution, modified such that if a negative value was drawn from the distribution, the density was set to zero. This results in a mixed probability distribution, with a continuous probability distribution for positive enhancements, plus a nonzero probability that the enhancement is the discrete value of zero. The parameters of the normal distribution were chosen such that the mean and standard deviation of the mixed distribution matched the mean and standard error determined from the raw data on juvenile densities (Table 1). The appropriate parameters for the normal distribution were found numerically using the Hybrid root-finding algorithm. Negative enhancement values were truncated because the presence of reef does not lead to a decrease in fish abundance, but not all fish are present at all sites and may therefore have zero abundance.

Estimates of enhanced productivity and uncertainty were calculated using each of the three estimates of M. In each case, one hundred thousand samples were drawn independently from the modelled distribution of enhancements and the mean, standard deviation and lower and upper quartiles of the distribution of productivity enhancements were computed for each fish species, and for all species combined. Due to the lack of available scientific knowledge regarding variability in other life-history parameters, all other life-history parameters were assumed to be invariant.

ENHANCED UTILIZATION OF STRUCTURED HABITAT BY OLDER AGE CLASSES

Species that had enhanced levels of utilization of reef habitat at older life-history stages were identified using similar criteria to those applied to determine recruitment enhancement: (i) the species must have a life history that indicates it benefits from structured habitats; (ii) the species must be more abundant on than off the structured habitat in more than half of the independent sampling events in the data set; and (iii) the species must be represented by data from at least two geographically independent estuaries. As fish abundance could not be standardized across sampling methodologies, the percentage of fish encountered on-reef as opposed to off-reef was determined for each independent sampling event, and a mean percentage across all studies calculated. This estimate provided a measure of the mean percentage time spent on-reef vs. off-reef for enhanced species. These species or life stages were not included in our calculations of production enhancement because more research needs to be conducted on the absolute densities of these fish on reefs and the bioenergetic benefit derived from oyster reefs vs. other habitats before the contribution of reefs can be quantified.

Results

Nineteen species (15 fish, four crustacean) and 12 species (11 fish, one crustacean) were found to be recruitment-enhanced in the Gulf of Mexico and South Atlantic and Mid-Atlantic coasts, respectively (Table 1). An additional five fish species on the Gulf of Mexico and two fish species on the South Atlantic and Mid-Atlantic coast were found to preferentially use oyster reef habitat over unstructured controls during older life stages (Table 2). Recruitment-enhanced species included numerous demersal fish such as sheepshead *Archosargus probatocephalus* (Walbaum, 1792), and pinfish *Lagodon rhomboides* (Linnaeus, 1766), as well as resident species such as gulf toadfish, *Opsanus beta* (Goode & Bean, 1880) and oyster toadfish *Opsanus tau* (Linnaeus, 1766), whereas species utilizing the habitat at older age classes included important sport fish such as red drum *Sciaenops ocellatus* (Linnaeus, 1766), and black drum *Pogonias cromis* (Linnaeus, 1766), on the Gulf of Mexico coast and black sea bass *Centropristis striata* (Linnaeus, 1758), and striped bass *Morone saxatilis* (Walbaum, 1792), on the South Atlantic and Mid-Atlantic coast.

Seven species were enhanced by the addition of reef habitat on both the Gulf of Mexico and South Atlantic and Mid-Atlantic coasts (Table 1). The degree of enhancement, however, differed between coasts both within species and in total (Fig. 2). Oyster reef habitat on the Gulf of Mexico results in approximately 397 ± 115 (1 SD) g m^{-2} year^{-1} more P_g than on unstructured controls, whereas oyster reef habitat on the South Atlantic and Mid-Atlantic coast results in an additional 281 ± 56 g m^{-2} year^{-1} of fish and mobile crustacean P_g. While sheepshead was the single largest contributor to production on the Gulf of Mexico coast (37% P_g, 145 g m^{-2} year^{-1}), oyster toadfish was the single largest contributor on the South Atlantic and Mid-Atlantic coast (41% P_g, 115 g m^{-2} year^{-1}). Production was dominated by just a handful of species on each coast, with just four species accounting for 72% P_g on the Gulf of Mexico coast and 80% P_g on the South Atlantic and Mid-Atlantic coast. Of the most productive species, only sheepshead and oyster toadfish were important on both coasts (Table 1). Production by most species was characterized by high inter-regional variability. For example, pinfish accounted for just 1 g m^{-2} year^{-1} (0·2%) P_g on the South Atlantic and Mid-Atlantic coast, but 33 g m^{-2} year^{-1} (8%) P_g on the Gulf of Mexico coast.

The enhanced fish and mobile crustacean production reported represents the P_g attributed to enhanced recruitment of species to 1 m^2 of oyster reef habitat on a yearly basis when $t \geq t_{max}$ of the longest-lived species. On the Gulf of Mexico coast, this is 16 years, whereas on the South Atlantic and Mid-Atlantic coast, this is 21 years (see Table S2). The majority of this production, however, can be attributed to the reef within just 2 years of reef creation (54% P_g on the Gulf of Mexico coast and 52% P_g on the South Atlantic and Mid-Atlantic coast; Fig. 2).

Net production (P_n) was enhanced by oyster reefs by 289 ± 102 g m^{-2} year^{-1} in the Gulf of Mexico and 218 ± 47 g m^{-2} year^{-1} on the South Atlantic and Mid-Atlantic coast (Table 1). The contribution of enhanced shrimp species tended to zero by the end of year one as a result of their high mortality rates.

Table 1. Mean enhancement (year 0·5 ind m⁻²), gross annual production (P_g) both including and excluding uncertainty in natural mortality (M), and net annual production (P_n) of fish and mobile crustaceans on oyster reef relative to unstructured control habitat on the Gulf of Mexico and Mid and South Atlantic coasts

Coast	Species	Common name	Number of samples (positive samples)	Number of estuaries	Mean year 0·5 ind m⁻² (SE)	Mean P_g constant M g m⁻² year⁻¹ (SD)	Mean P_g Gislason M g m⁻² year⁻¹ (SD)	Mean P_g Lorenzen M g m⁻² year⁻¹ (SD)	Mean P_n Lorenzen M g m⁻² year⁻¹ (SD)
Gulf of Mexico	Fish								
	Archosargus probatocephalus	Sheepshead	2 (2)	2	0·139 (0·101)	138·4 (99·9)	51·3 (37·0)	145·1 (104·8)	133·6 (96·5)
	Bairdiella chrysoura	Silver perch	15 (14)	4	0·501 (0·481)	28·0 (26·9)	23·0 (22·1)	41·0 (39·5)	29·5 (28·4)
	Bathygobius soporator	Frillfin goby	4 (4)	2	0·024 (0·009)	2·3 (0·9)	1·4 (0·5)	2·0 (0·7)	1·4 (0·5)
	Chaetodipterus faber	Spadefish	5 (4)	2	0·006 (0·004)	4·2 (3·1)	1·2 (0·9)	3·0 (2·2)	2·3 (1·7)
	Chasmodes bosquianus	Striped blenny	7 (7)	2	0·076 (0·039)	0·3 (0·1)	0·2 (0·1)	0·2 (0·1)	0·1 (0·1)
	Ctenogobius boleosoma	Darter goby	13 (10)	5	0·234 (0·169)	0·5 (0·4)	0·4 (0·3)	0·5 (0·3)	0·2 (0·2)
	Gobiesox strumosus	Skilletfish	12 (12)	5	0·959 (0·420)	3·2 (1·4)	2·3 (1·0)	3·1 (1·4)	1·4 (0·6)
	Gobiosoma bosc	Naked goby	15 (15)	6	1·920 (0·488)	2·3 (0·6)	1·1 (0·3)	2·2 (0·6)	1·4 (0·3)
	Hypsoblennius hentz	Feather blenny	10 (10)	4	0·074 (0·020)	0·3 (0·1)	0·2 (0·1)	0·2 (0·1)	0·1 (0·04)
	Hypsoblennius ionthas	Freckled blenny	4 (4)	2	0·392 (0·269)	1·4 (0·9)	1·0 (0·7)	1·3 (0·9)	0·8 (0·5)
	Lagodon rhomboides	Pinfish	11 (9)	4	0·415 (0·209)	35·0 (17·6)	31·8 (16·0)	33·2 (16·7)	22·6 (11·4)
	Leiostomus xanthurus	Spot	6 (5)	3	0·342 (0·167)	18·4 (9·0)	9·7 (4·7)	17·9 (8·7)	11·7 (5·7)
	Opsanus beta	Gulf toadfish	11 (11)	5	1·325 (0·527)	51·8 (20·6)	0·05 (0·02)	41·9 (16·6)	39·4 (4·3)
	Orthopristis chrysoptera	Pigfish	5 (4)	2	0·044 (0·018)	5·3 (2·1)	3·8 (1·6)	5·8 (2·4)	4·7 (1·9)
	Prionotus spp.	Searobin	5 (3)	2	0·012 (0·015)	4·1 (5·0)	0·7 (0·9)	2·2 (2·7)	1·6 (1·9)
	Crustaceans								
	Callinectes sapidus	Blue crab	30 (23)	8	7·418* (6·731)	6·2 (5·6)	0·7 (0·6)	4·9 (4·5)	3·2 (2·9)
	Farfantepenaeus aztecus	Brown shrimp	11 (7)	4	1·036* (0·627)	7·3 (4·4)	16·0 (9·6)	7·0 (4·2)	NA
	Litopenaeus setiferus	White shrimp	9 (8)	4	4·640* (2·726)	25·1 (14·8)	53·8 (31·8)	24·2 (14·3)	NA
	Menippe mercenaria	Stone crab	4 (4)	2	1·936 (0·214)	232·2 (25·6)	4·8 (0·5)	61·4 (6·8)	39·4 (4·3)
					Total	566·2 (109·5)	203·3 (57·0)	397·2 (115·4)	289·5 (102·0)
Atlantic	Fish								
	Archosargus probatocephalus	Sheepshead	8 (7)	3	0·072 (0·048)	60·4 (40·2)	29·9 (19·9)	59·6 (39·7)	54·0 (36·0)
	Chasmodes bosquianus	Striped blenny	5 (5)	3	5·824 (1·431)	20·0 (4·9)	14·5 (3·6)	19·4 (4·7)	8·7 (2·1)
	Fundulus majalis	Striped killifish	20 (11)	5	0·015 (0·019)	0·08 (0·10)	0·03 (0·03)	0·06 (0·07)	0·04 (0·05)
	Gobiesox strumosus	Skilletfish	8 (8)	3	6·837 (2·184)	23·1 (7·4)	16·7 (5·4)	22·2 (7·1)	10·0 (3·2)
	Gobiosoma bosc	Naked goby	12 (12)	5	24·863 (6·877)	29·8 (8·2)	14·2 (3·9)	28·0 (7·7)	17·7 (4·9)
	Lagodon rhomboides	Pinfish	32 (21)	6	0·009 (0·224)	0·8 (19·3)	0·7 (17·6)	0·7 (18·3)	0·5 (12·5)
	Lutjanus griseus	Grey snapper	11 (7)	4	0·010 (0·007)	10·9 (7·6)	0·4 (0·3)	5·6 (3·9)	5·1 (3·5)
	Mycteroperca microlepis	Gag	4 (3)	2	0·014 (0·009)	34·6 (22·3)	17·6 (11·4)	23·3 (15·0)	19·3 (12·4)
	Opsanus tau	Oyster toadfish	6 (6)	3	1·187 (0·400)	128·2 (43·1)	26·7 (9·0)	114·7 (38·5)	93·5 (31·4)
	Orthopristis chrysoptera	Pigfish	8 (5)	4	0·026 (0·027)	3·1 (3·3)	2·3 (2·4)	3·5 (3·6)	2·8 (2·9)
	Paralichthys lethostigma	Southern flounder	11 (7)	4	0·001 (0·008)	0·5 (3·1)	0·4 (2·7)	0·6 (3·7)	0·5 (2·9)
	Crustaceans								
	Farfantepenaeus aztecus	Brown shrimp	11 (9)	4	0·034* (0·008)	0·2 (0·1)	0·5 (0·1)	0·2 (0·1)	NA
					Total	311·8 (60·3)	124·1 (30·7)	280·8 (55·6)	218·9 (47·4)

*Denotes densities at year 0·25.

Table 2. Species that show enhanced utilization of oyster reefs at later life stages

	Species	Common name	Total number of samples (positive samples)	Number of estuaries represented	Proportion of individuals caught on oyster
Gulf Coast	*Menticirrhus americanus*	Southern kingfish	21 (11)	3	52%
	Paralichthys lethostigma	Southern flounder	14 (13)	2	82%
	Pogonias cromis	Black drum	16 (11)	3	75%
	Rhinoptera bonasus	Cownose ray	12 (10)	3	82%
	Sciaenops ocellatus	Red drum	14 (11)	2	69%
Atlantic Coast	*Centropristis striata*	Black sea bass	3 (2)	2	63%
	Morone saxatilis	Striped bass	2 (2)	2	93%
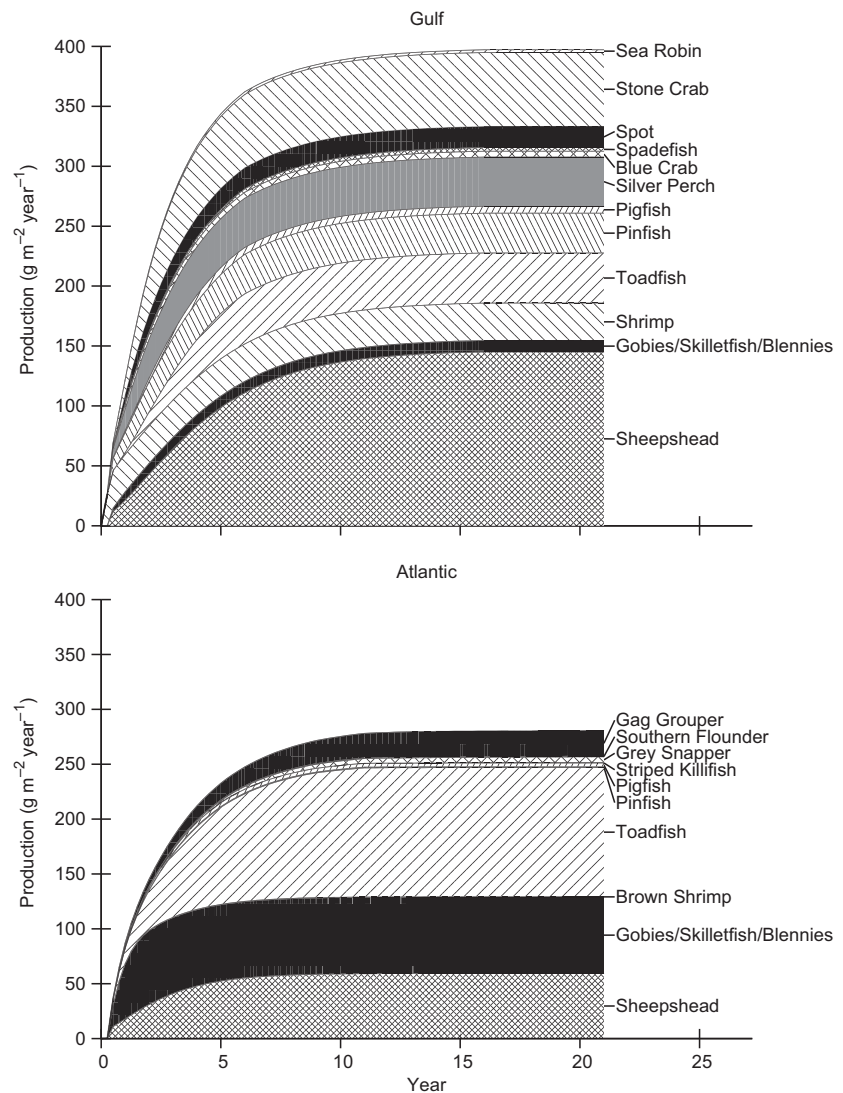
Fig. 2. Gross production (g m^{-2} year^{-1}) of fish and mobile crustacean species attributed to the enhancement of recruitment to oyster reefs as compared to an unstructured control over time.

Accounting for size-dependent mortality substantially reduced the estimated total production relative to considering natural mortality as a constant (Table 1, Fig. 3). This difference was, however, primarily driven by substantial changes in a small number of species, namely stone crab *Menippe mercenaria* (Say, 1818) on the Gulf of Mexico coast (3·8 times greater production under static M) and gag grouper *Mycteroperca microlepis* (Goode & Bean, 1879) on the South Atlantic and Mid-Atlantic coast (1·5 times greater production under static M). Production estimates for nine of the 19 species on the Gulf of Mexico coast and five of the 12 species on the South Atlantic and Mid-Atlantic coast changed by less than 10% (Table 1). Meanwhile, incorporating the Gislason *et al.* (2010) model into our model framework consistently resulted in lower or similar estimates of production relative to using the
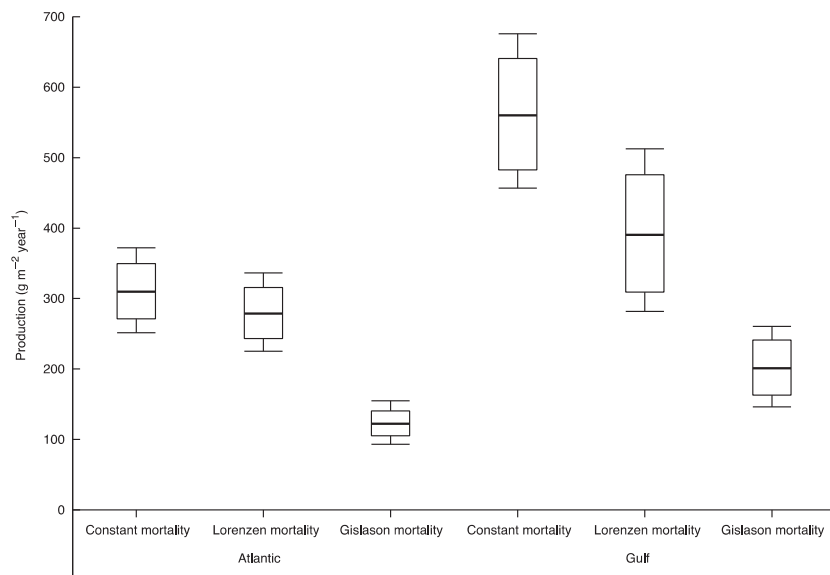
Fig. 3. Mean, upper and lower quartile and minimum and maximum estimated enhancement of gross production (P_g) of fish and mobile crustacean production in both the Gulf of Mexico and the Mid and South Atlantic region of the USA at t_{max} of the longest-living species, as modelled using constant- and size-dependent natural mortality.

Lorenzen Model for all species aside from the shrimp (Table 1). Overall, total production was a factor of 2·0- and 2·3-fold lower using Gislason's rather than Lorenzen's model in the Gulf of Mexico and the South Atlantic and Mid-Atlantic, respectively (Fig. 3).

Discussion

Here we provide quantitative estimates of the enhancement of fish and mobile invertebrates attributable to the restoration or conservation of limiting habitats. While we have used the case study habitat of eastern oyster reefs, many habitats of conservation importance such as seagrass meadows and saltmarshes are similarly represented in numerous small-scale studies of fish or invertebrate density across paired habitat and control sites (e.g. Bloomfield & Gillanders 2005), and would fulfil the criteria required to apply this methodology. Application of the methodology need not be limited to nearshore habitats, but could similarly be applied to offshore habitats such as deep water corals, boulder and cobble bottom, or relic oyster shell bars and ridges (e.g. Szedlmayer & Howe 1997), as long as the criteria of significant habitat limitation and availability on and off habitat species density data are met. The ability to quantify the lifetime enhancement across a whole community, as well as on a species-by-species basis (Table 1), and to include estimates of uncertainty around these values, would be valuable to conservation and fisheries managers seeking to determine the potential gains from management interventions and habitat restoration.

While this methodology has broad applicability across a range of habitats, its application is limited to habitats that are rare enough to be limiting fish populations. This underlying assumption critically underpins the representation of enhancement as a constant value per unit area. While it could be expected that the enhancement of fish production increases near linearly as areal extent is added to a nursery habitat with limited areal extent, at some unknown point habitat will cease to be the limiting factor to juvenile recruitment and enhancement (Fig. 4). At this point, it would no longer be appropriate to apply our estimated values of enhancement. The exact nature of the relationship between habitat extent and fisheries enhancement is currently unknown. Further research is necessary to elucidate the true nature of the relationship between areal habitat extent and fish production. There are currently no universal guidelines available for managers to assess the extent to which habitat is limiting fish populations and thus predict how restoration might vary among estuaries with different levels of existing habitat. The application of these results to areas with extensive habitat remaining should therefore be avoided, and care should be taken when applying this methodology to extensive restoration efforts. Given the highly degraded nature of oyster reef habitats in the USA we, however, feel that these results can be confidently applied to our case study habitat.

At first glance, our method did not yield substantially different results from a previous attempt to quantify the fish and mobile crustacean enhancement by oyster reefs in the USA, which estimated the net production enhancement as 260 g m^{-2} year^{-1} (Peterson, Grabowski & Powers 2003). However, Peterson, Grabowski & Powers (2003) used a static M in deriving their production estimates. If our static M model results are compared with their results, we find that our approach estimated twice the previously estimated production in the Gulf of Mexico (Fig. 3). This illustrates the impact of incorporating more realistic estimates of mortality that are size-based relative to previous gross production estimates derived from this habitat. Other methodological advances include incorporating uncertainty from the density data, refined criteria for inclusion of a species, and a much larger number of studies (31 as opposed to six included in the meta-analysis). As a result, we can have greater confidence in our estimates.
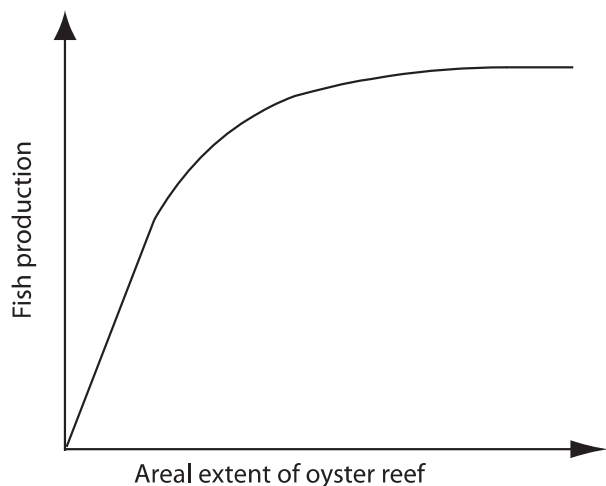
Fig. 4. A theoretical relationship between oyster reef extent and fish production. In the early part of the curve, when habitat is limiting, there is a near-linear relationship between area and fish production. As the extent of oyster reef habitat increases, however, the return in fish production per unit area begins to decrease and eventually asymptotes when habitat no longer limits fish production.

The differences between productivity estimates derived using each of the three mortality estimators further illustrates the sensitivity of fisheries modelling to estimates of natural mortality, which remains poorly understood. A static M appears to result in overoptimistic estimates of production. Yet, even the two size-dependent methods resulted in a 2·0- and 2·3-fold difference in total gross productivity in the Gulf of Mexico and South Atlantic and Mid-Atlantic, respectively. For many species, the Gislason model predicts higher mortality rates (typically a factor of 1–2) than those estimated by the Lorenzen model. However, for some species, the predicted mortalities are very different. For example, estimated mortality of *O. beta* differs by a factor of 6·6 and 3·0 for females and males, respectively. The difference in fish production enhancement derived using these models provides an indication of the size of the uncertainty in the results that arises from incomplete knowledge of the natural mortality of fish enhanced by oyster reefs.

By incorporating the variability in the enhancement of juvenile fish and mobile crustacean densities into our estimates, our model allows managers to visualize and account for the stochastic variability in recruitment that would be expected in the wild (Table 1). The production enhancement attributable to habitat restoration will vary spatially and while our regional analysis captures that variability on a large scale, the variability expressed as uncertainty in our production estimates may be used to account for intraregion variability. The estimated variability arises from differences in initial density of species between sites and sampling events. Managers seeking to use our predicted enhancement values can therefore assess the likely benefit on the basis of species presence and relative abundance at the site of restoration, with benefits

likely to be lower where a species is rare relative to where it is abundant.

Also of relevance to managers is an understanding of how the estimated value accrues over time. Although the estimates given in Table 1 represent the annual production attributable to 1 m^2 of reef once $t > t_{max}$ of the longest-living individual, most of the production from a particular recruitment class can be attributed to the first 2 years (Fig. 2). This knowledge allows managers to include consideration of the time frames over which the benefits of an intervention such as restoration are accrued.

Of further relevance to managers is the ability to assess the enhancement of both the gross and net production. These values have different applications within management scenarios. Net production has application when considering the contribution of the habitat to commercial or recreational fisheries, whereas gross production allows for a more ecosystem-based approach to evaluating habitats. The difference between the two values provides an estimate of the biomass lost to the system, or in other words, an estimate of the wider ecosystem contribution of the enhanced recruitment (i.e. as prey for higher trophic levels).

Although the focus of our study was the quantification of recruitment-enhanced species, structured habitats may also benefit later life stages for a number of fish species (Powers *et al.* 2003). To fully quantify the degree to which species that utilize a habitat at a later life-history stage are enhanced, it is necessary to measure the impact of habitat use on growth rates or survival rates. Such studies are extremely difficult to undertake given the mobile nature of these species, although a few examples do exist (e.g. Stunz, Minello & Levin 2002). While our methodology does not allow us to quantify the production from such species, there is sufficient evidence in the literature to support the expectation that species that utilize the habitat at these later life stages, benefit from it (e.g. Brown *et al.* 2008). The list of species that were caught more frequently on oyster reef habitat than on the control (Table 2) is therefore also of use to managers in ascertaining the importance of this habitat.

A key finding from our production estimates is that the values associated with a given habitat differ regionally (Fig. 3). While many resident species (e.g. gobies, skilletfish and oyster toadfish) appear to be more abundant in the South Atlantic and Mid-Atlantic, total production and the species richness of the enhanced species was greater in the Gulf of Mexico (Fig. 2). Furthermore, crustaceans appear to be more enhanced by oyster reefs on the Gulf of Mexico coast (25% of the total P_g) than in the South Atlantic and Mid-Atlantic (<0·1% P_g; Table 1). In general, our results clearly illustrate significant species-level differences in enhancement by a single nursery habitat across regions. These differences are perhaps to be expected given that the Gulf of Mexico and South Atlantic and Mid-Atlantic are distinct biogeographic ecoregions

(Spalding *et al.* 2007) that also have different fisheries management policies.

Whereas most of the differences in production between coasts are likely the result of biogeographic differences in species distributions and coastal landscapes, the differences for a subset of species may be the result of inadequate sampling. The three species for which this appears to be the case are as follows: gag grouper in the Gulf, and stone crab and blue crab in the Atlantic. Gag grouper are not traditionally caught by the methods represented in our Gulf of Mexico data set and were therefore not represented despite their high abundance in Florida (Koenig & Coleman 1998). Stone crab were excluded from the South Atlantic and Mid-Atlantic estimates as they were not represented in a sufficient number of studies or estuaries, but were positively enhanced where they were found. Blue crab was excluded from our production estimates on the South Atlantic and Mid-Atlantic coast as we found no evidence of enhancement; however, this is likely due to Blue crab being poorly represented in the available studies on the South Atlantic and Mid-Atlantic coast. Thus, we would anticipate that the addition of further studies with appropriate sampling techniques may result in positive production estimates.

Ecosystem service estimates need to be conducted at scales appropriate to inform conservation and restoration decision-making. By drawing on data from many small-scale studies across a broader geographical area and across many years, the model outputs represent longer-term, larger-scale variability. Furthermore, while the majority of studies in our meta-analysis were conducted on small (i.e. <1 m^2) reefs, several sampled smaller areas within large natural reefs (e.g. Zimmerman *et al.* 1989; Plunket & La Peyre 2005). The enhancement estimated by applying our model is therefore likely representative of larger-scale units (e.g. ha) of relevance to managers, as long as the conditions of the model are not violated.

We have developed a model for quantifying the enhanced fish production and its uncertainty provided by limiting nursery habitats such as oyster reefs. Our results illustrate that oyster reefs substantially augment fish production in both the Gulf of Mexico and in the South Atlantic and Mid-Atlantic, but to varying degrees. Furthermore, the composition of augmented species varied greatly between regions, with likely ramifications for the fisheries services that these reefs provide. Consequently, we have demonstrated the limitation of applying regional estimates of the ecosystem service benefit, fish production, at larger spatial scales, and in particular, the practice of benefit transfer between different regions. While augmented fish production is an important ecosystem service often considered in oyster reef conservation and restoration efforts, oyster reefs are valued and managed for a suite of additional services including shoreline stabilization, anthropogenic nitrogen removal and seagrass habitat enhancement (Grabowski & Peterson 2007; Grabowski *et al.* 2012). A greater understanding of how each of these services varies at local and regional spatial scales is also needed to assist managers to maximize the return on investment in oyster reef habitat restoration and conservation efforts.

Data accessibility

Data included in the meta-analysis are available through the cited references listed in Table S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Extended methods describing correction factors applied in data handling.

Table S1. Summary of the studies used to determine fish and mobile crustacean enhancement.

Table S2. Life-history parameters of recruitment-enhanced species.