Sustainable exploitation and management of autogenic ecosystem engineers: application to oysters in Chesapeake Bay

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Abstract. Autogenic ecosystem engineers are critically important parts of many marine and estuarine systems because of their substantial effect on ecosystem services. Oysters are of particular importance because of their capacity to modify coastal and estuarine habitats and the highly degraded status of their habitats worldwide. However, models to predict dynamics of ecosystem engineers have not previously included the effects of exploitation. We developed a linked population and habitat model for autogenic ecosystem engineers undergoing exploitation. We parameterized the model to represent eastern oyster (*Crassostrea virginica*) in upper Chesapeake Bay by selecting sets of parameter values that matched observed rates of change in abundance and habitat. We used the model to evaluate the effects of a range of management and restoration options including sustainability of historical fishing pressure, effectiveness of a newly enacted sanctuary program, and relative performance of two restoration approaches. In general, autogenic ecosystem engineers are expected to be substantially less resilient to fishing than an equivalent species that does not rely on itself for habitat. Historical fishing mortality rates in upper Chesapeake Bay for oysters were above the levels that would lead to extirpation. Reductions in fishing or closure of the fishery were projected to lead to long-term increases in abundance and habitat. For fisheries to become sustainable outside of sanctuaries, a substantial larval subsidy would be required from oysters within sanctuaries. Restoration efforts using high-relief reefs were predicted to allow recovery within a shorter period of time than low-relief reefs. Models such as ours, that allow for feedbacks between population and habitat dynamics, can be effective tools for guiding management and restoration of autogenic ecosystem engineers.

Key words: Chesapeake Bay, United States; Crassostrea virginica; *ecosystem-based management; effects of fishing on habitat; oyster restoration; sustainable harvest.*

INTRODUCTION

Species that create, modify, or maintain habitat are classified as ecosystem engineers and have the potential to be disproportionately important to ecosystem structure and function (Jones et al. 1994). By structuring their environment, ecosystem engineers can have impacts on both the abundance and biodiversity of species in the resulting habitat (Wilby et al. 2001, Wright et al. 2002). Given their importance in many marine and estuarine ecosystems, it is essential to understand how ecosystem engineers respond to disturbances, and if disturbed, how long it will take habitat to recover to predisturbance levels. Fishing is one such disturbance that may impact ecosystem engineers either directly or indirectly, and these impacts can have system-wide effects due to the link between ecosystem engineers and the habitat they create. However, the effects of exploitation on habitat are often not considered in management (Pikitch et al.

2004), but in many systems the scale of the engineering makes it important to evaluate the effects of fishing on habitat specifically (Hastings et al. 2007). Ecosystem engineers that produce their own habitat (autogenic engineers), such as corals or oysters, are particularly important in systems dominated by soft-bottom substrates (Hastings et al. 2007), and can be especially vulnerable to harvest and other disturbances. Coral and oyster reefs not only provide substrate for organisms to grow (both conspecifics and heterospecifics), but also provide shelter from predators (Gutiérrez et al. 2003, Peterson et al. 2003, Grabowski et al. 2005).

Across the globe, oysters play an essential role as ecosystem engineers in estuaries (Gutiérrez et al. 2003) and are also the target of directed fisheries. Many of the methods used to harvest oysters damage the oyster reef, and declines in oyster populations and reef habitats have been observed worldwide (Beck et al. 2011). Because oyster reefs are the primary habitat for larval oyster settlement, fishing not only removes adults from the population, but also has the potential to reduce the productivity of the population by removing habitat (Lenihan and Peterson 1998, Beck et al. 2011). In

addition to their role in creating habitat (Peterson et al. 2003, Grabowski et al. 2005, 2007), oysters provide important ecosystem services including nutrient cycling (Dame and Libes 1993, Fulford et al. 2007) and transfer of energy between pelagic and benthic components of the food web (Baird and Ulanowicz 1989, Porter et al. 2004), making the restoration of depleted oyster populations essential for rehabilitating many coastal and estuarine systems (Beck et al. 2011).

Management and restoration of oysters present unique challenges, as evidenced by the worldwide decline of oyster stocks and the oyster reef habitats they create (Beck et al. 2011). Eastern oysters (*Crassostrea virginica*) in the Chesapeake Bay have undergone a drastic decrease in abundance over the past century due to overfishing (Rothschild et al. 1994, Jackson et al. 2001, Wilberg et al. 2011), disease (Andrews 1988, Burreson and Ragone Calvo 1996), and habitat loss (Rothschild et al. 1994, Smith et al. 2005). Currently, the population is estimated to be at <1% of virgin abundance (Newell 1988, Jackson et al. 2001, Wilberg et al. 2011), making substantial restoration efforts necessary if the population is to recover. Based on the recommendations of a recent Executive Order (2010, no. 13 508), the U.S. Army Corps of Engineers is currently planning a new initiative aimed at restoring self-sustaining oyster populations to 20 Chesapeake Bay tributaries by 2025.

Previous restoration efforts for oysters in the Chesapeake have not been successful in stabilizing or increasing the population, in part, because of the lack of theoretical tools available to guide efforts (Mann and Powell 2007). Several factors currently inhibit oyster restoration, including harvest, which has continued even on some sanctuary reefs where fishing is prohibited (Paynter et al. 2010). Habitat is decreasing through increased natural mortality, siltation, and harvest (Rothschild et al. 1994, Smith et al. 2005, Wilberg et al. 2011). Additionally, two diseases, MSX and dermo, continue to negatively affect oyster population growth in Chesapeake Bay (Burreson and Ragone Calvo 1996, Ford and Tripp 1996). Although studies have quantified the effect of harvest practices on reefs (Lenihan and Peterson 1998, 2004) and abundance (Wilberg et al. 2011), no studies have explicitly linked these effects on habitat within a modeling framework. A general model of the dynamics of ecosystem engineers was developed by Gurney and Lawton (1996), but it did not include effects of exploitation. An alternative model was developed to link mortality, growth, and reef accretion for oysters (Powell and Klinck 2007, Mann et al. 2009), but it did not include effects of habitat on population dynamics. Additionally, previous efforts assumed that fishing had no direct effect on the underlying habitat (Powell and Klinck 2007).

Eastern oysters in the Chesapeake Bay are just one example of an exploited ecosystem engineer for which a lack of understanding of the interplay between habitat dynamics and harvest has resulted in failure to achieve management and restoration goals (Beck et al. 2011). Successful science-based management and restoration of oyster populations and the habitat and ecosystem services they provide depends on developing decision support tools to integrate habitat and population dynamics with the effects of harvest. Here we develop a general model explicitly linking the effects of exploitation and habitat dynamics for ecosystem engineers, and apply the model to management and restoration activities for eastern oysters in Chesapeake Bay.

METHODS

We constructed a differential equation model for the dynamics of ecosystem engineers tailored after Gurney and Lawton (1996), with a simplified description of the habitat dynamics. The model includes processes such as individual growth, reproduction, shell decay, and the response of these processes to fishery and restoration activities. We parameterized the model based on previous studies and applied it to estimate the effects of several management and restoration options on eastern oyster in Chesapeake Bay.

Model

Our model is based on a simplified version of that in Gurney and Lawton (1996) with additional effects of fishing on the population and habitat. The population dynamics follow a logistic function in which population growth is limited by available habitat and fishing:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{H}\right) - FN \qquad (1)$$

where t is time, N is abundance (individuals), r is the intrinsic rate of increase (individuals per individual per year), H is available habitat (individuals), and F is the instantaneous fishing mortality rate (year^{-1}). Given the model formulation, habitat determines carrying capacity, so habitat and abundance are in the same units. The rate of change in available habitat is an increasing function of population size offset by the amount of habitat relative to the maximum potential total amount of habitat and degradation from "natural" sources and fishing:

$$\frac{dH}{dt} = qN\left(1 - \frac{H}{T}\right) - (\delta + pF)H \qquad (2)$$

where q is the maximum per capita rate of habitat production (individuals per individual per year), T is the maximum potential habitat (individuals), p is a scalar to convert fishing mortality to a rate of habitat destruction (fishing mortality^{-1}), and δ is the rate of habitat loss due to non-fishing sources (year^{-1}). The effect of fishing is to decrease abundance and habitat. The original Gurney and Lawton (1996) ecosystem engineer model also included a process to allow for a lag between when

habitat was lost and when it could be recolonized. Our model did not include that term because there is not a mechanistic reason why recently lost habitat could not be immediately recolonized for oysters.

The model has two equilibrium states. The first is the trivial equilibrium with abundance and habitat equal to zero:

$$N_e = H_e = 0 \tag{3}$$

where N_e is equilibrium abundance, and H_e is equilibrium habitat. In the second equilibrium, abundance depends on available habitat and fishing mortality relative to the intrinsic rate of increase:

$$N_e = H_e(1 - F/r). \tag{4}$$

As with the typical logistic model, a positive equilibrium abundance is obtained if $F < r$, $H_e > 0$, and $r > 0$. Equilibrium habitat depends on the total potential habitat, the rate of habitat loss, the rate of habitat destruction caused by fishing, the maximum per capita rate of habitat production, and fishing mortality relative to the intrinsic rate of increase:

$$H_e = T\left(1 - \frac{\delta + pF}{q(1 - F/r)}\right). \tag{5}$$

Habitat has a positive equilibrium if $T > 0$ and $q > (\delta + pF)/(1 - F/r)$ (i.e., the maximum rate of habitat production exceeds the rate of habitat loss at a given level of fishing). In order for fishing to be sustainable, both abundance and habitat must retain positive equilibrium values. This occurs when $F < r$, the usual condition for population sustainability in the logistic model, and, $F < (q - \delta)/(q/r + p)$ the requirement for sustainable habitat.

Equilibrium catch (C_e) during one unit of time is the product of fishing mortality and equilibrium abundance:

$$C_e = FN_e. \tag{6}$$

The fishing mortality rate that maximizes sustainable yield, F_{MSY}, can be determined by substituting Eqs. 4 and 5 into Eq. 6, differentiating with respect to F, and solving for F when the first derivative equals zero. The result is similar to the well-known $F_{MSY} = r/2$ for the simple logistic model with fishing and no habitat effects:

$$F_{MSY} = \frac{r}{2}\left(\frac{q - \delta}{q + rp}\right). \tag{7}$$

Note that F_{MSY} increases as r increases, but habitat loss from fishing or nonfishing sources act to reduce F_{MSY}. Thus, as a general rule, autogenic ecosystem engineers will have lower F_{MSY} values than nonecosystem engineers for a given r.

Application to Chesapeake Bay oysters

We applied our model to eastern oysters in upper Chesapeake Bay to understand potential effects of current fishery management and habitat restoration practices. We also used the model to estimate the effects of a moratorium on oyster harvest, which was recommended by Wilberg et al. (2011), and to identify ways to improve the effectiveness of habitat restoration. While habitat generally refers to a suite of environmental characteristics, we use the term here to represent hard substrate, which is the primary habitat component directly modified by oysters. To apply the model to Chesapeake Bay eastern oysters, we needed to identify plausible values for each of the model parameters and initial conditions for abundance and available habitat.

We used a combination of values from the literature and a grid search approach to identify plausible sets of parameters and initial conditions that matched recent dynamics of eastern oysters in upper Chesapeake Bay. Wilberg et al. (2011) estimated that abundance in 1980 was at 3.8% of its precommercial fishing level and that the average fishing mortality rate during 1980–2008 was 0.29 yr⁻¹. They also estimated that abundance and habitat decreased at rates of 7.7 and 4.1% per year on average, respectively. These values constrained the potential parameter space, but the model was still underdetermined because we had two equations with five unknowns. We developed potential ranges for habitat and the other parameters and applied a grid search algorithm (described in the following paragraphs) to identify sets of parameters that matched the observed rates of decline in habitat and abundance.

Several studies have quantified rates of habitat loss for eastern oysters. Natural habitat loss for Chesapeake Bay oysters is likely dominated by the processes of shell dissolution, siltation, and degradation by other organisms. Mann et al. (2009) estimated that the dissolution rate of oyster shell was ~0.35 yr⁻¹. Powell et al. (2006) estimated shell loss rates of 0.05–0.37 yr⁻¹ with a mean of 0.18 yr⁻¹ in Delaware Bay (Powell and Klinck 2007). Based on their results, we used 0.05–0.4 yr⁻¹ as a potential range for δ in the grid search.

Fishing has long been known to alter oyster reefs, but conversions to relate fishing mortality to a rate of habitat destruction have not been developed and likely depend on the method of fishing (Hargis and Haven 1999, Kennedy and Sanford 1999, Lenihan and Peterson 2004). Most forms of oyster fishing act to disaggregate the reef matrix, which spreads shell over a larger area and may make it more prone to siltation (Hargis and Haven 1999, Lenihan and Micheli 2000, Lenihan and Peterson 2004). The spreading of shell may also move a certain amount of shell to areas that cannot become oyster habitat due to physical conditions of the bottom. Lenihan and Peterson (1998, 2004) estimated that reef height was reduced by 0.3 m after only two hours of dredging or tonging, the two primary methods for oyster harvest in upper Chesapeake Bay. The reefs in their experiments were ~1 m high piles of unconsolidated shell, and thus were probably more susceptible to destruction from fishing than natural reefs (Lenihan and Peterson 1998). Given the size of the reefs in their

study and the achieved fishing mortality rate, the p parameter in our model should be ~0.2 for "restored" habitat. However, this value probably overestimates the effect of fishing gear on natural oyster reefs. DeAlteris (1988) estimated that Wreck Shoal in Virginia lost between 1.2 and 1.8 m of reef height during a 130-year period, approximately 9–14 mm/yr. A $p \approx 0.05$ would be consistent with the findings of DeAlteris (1988) if the fishing mortality rate were about 0.2 yr^{-1} for Wreck Shoal. Therefore, the range we considered for the scaling parameter (p) was 0–0.1.

The maximum per capita rate of habitat production depends on how quickly oysters grow shell and on how much habitat is necessary for an individual oyster. The amount of habitat necessary for an oyster is the size of an oyster. While this can vary depending on the oyster's orientation, the shell height of a market-sized oyster is ~7.5 cm. DeAlteris (1988) assumed that an oyster produces about 2.5 cm of shell yr^{-1}, which would result in a q of 0.33 yr^{-1}. We used a range of 0.05–0.5 for q.

The intrinsic rate of increase is the most difficult parameter for which to define a range. This parameter includes the effects of recruitment and natural and disease mortality. We were unable to separate disease mortality from the recruitment and other natural mortality sources because estimates were not available from the pre-disease period in Chesapeake Bay. We used estimates from a highly productive tributary in lower Chesapeake Bay to specify the maximum potential r. Harding et al. (2011) estimated that four age-0 oysters were produced per adult in the Piankatank River. Correcting the age-0 per adult for an approximate 40% survival to the adult stage results in an estimate of $r = 1.6$. We used −0.2 as the minimum for r, as this was below the estimated decline of −0.077 yr^{-1} of oysters in the Maryland portion of Chesapeake Bay (Wilberg et al. 2011). We included a negative lower bound for r because it is possible that such a continued long-term population decline could occur in the absence of fishing as a result of the effects of disease. For available habitat, we used a range from slightly lower to ~2.5 times higher than the estimated relative abundance of oysters.

We used a simple grid search over plausible values of the parameters and habitat to determine combinations that matched the observed decline in abundance of 7.7% per year and 4.1% per year in habitat during 1980–2008 (Wilberg et al. 2011). To implement the grid search, we estimated the relative rate of decline in abundance, $1/N \; dN/dt$, and habitat, $1/H \; dH/dt$, for all combinations of the parameters and variables (Table 1). For the purposes of our model, we assumed that $T = 1$, which scales the population and habitat relative to the unfished state. We selected combinations of parameters that resulted in rates of decline within ±10% of those from Wilberg et al. (2011). We also considered sets of parameters within 5% and 15% of the observed rates of decline, but results were about the same, with slightly fewer combinations of parameters within 5% and slightly more within 15%.

TABLE 1. Variables and parameters used in the grid search to identify sets that matched recent observed declines.

Parameter	Minimum	Maximum	Increment
δ	0.05	0.4	0.05
p	0	0.1	0.01
q	0.1	0.5	0.05
r	−0.2	2.0	0.2
H	0.02	0.2	0.02

Notes: Parameters included in the grid search were the natural rate of habitat loss (δ), the effect of fishing on habitat (p), the per capita rate of habitat production (q), the intrinsic rate of increase (r), and the relative amount of habitat (H). The minimum and maximum identify the lowest and highest values considered in the grid search, and the increment identifies the spacing of values that were used.

Our approach to parameter estimation and projections implies that environmental conditions affecting oyster population dynamics, such as temperature, salinity, and disease mortality, will be the same during the projection period as during 1980–2008 on average.

We calculated equilibrium conditions and projected the population for 50 years using all the sets of parameters that matched the observed rates of population and habitat decline under three fishing scenarios. The first scenario was the continuation of the average fishing mortality during 1980–2008, $F = 0.29$. The other two scenarios involved decreasing fishing mortality to F_{MSY}, and implementing a fishery moratorium (i.e., $F = 0$). For each set of parameters under each scenario, we calculated F_{MSY} and equilibrium abundance, habitat, and catch. For projections, starting abundance was set at 2009 relative abundance, 0.3% based on Wilberg et al. (2011). Initial habitat was set at 0.64% based on the ratio of 1980 habitat to abundance estimated from the grid search and the 1980 abundance of 3.8%.

The moratorium scenarios provide a description of the expected response in the sanctuaries, but we were also interested in the effect from marine protected areas (MPAs) that would be necessary to allow a sustainable fishery at historical levels outside the MPAs. In 2010 in Maryland, ~25% of oyster reefs were designated as no-take MPAs in which no oyster fishing is allowed (i.e., sanctuaries). For a sessile species like eastern oyster, an increase in abundance within a sanctuary may lead to a larval subsidy, or spillover effect, to areas outside the MPAs (Crowder et al. 2000, Halpern and Warner 2002). While a larval spillover may not occur for retentive areas or areas from which all larvae are exported to unsuitable habitat (North et al. 2010), a larval subsidy is the only way MPAs could provide a direct benefit to oyster fisheries in outside areas. Experience with MPAs in other regions and species indicates that fishing effort is often displaced to new areas, which means that fishing mortality may increase in areas outside the MPA (Dinmore et al. 2003, Zhang and Smith 2011). In our model, a spillover effect can be approximated as an increase in r. We estimated the spillover effect necessary to allow sustainable fisheries in areas outside the
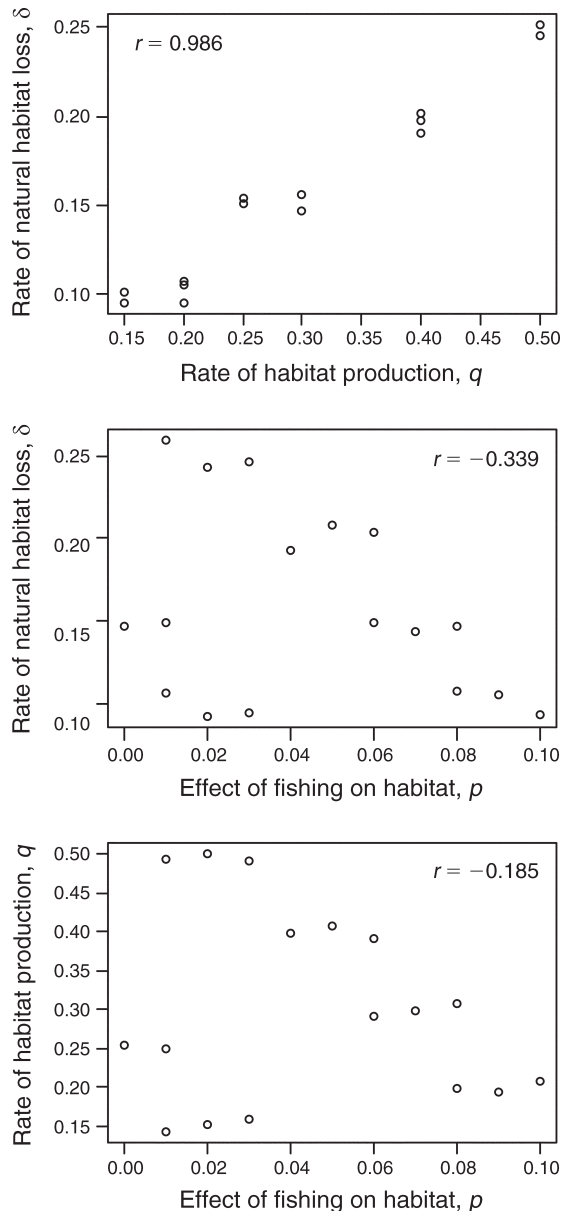
FIG. 1. Correlations between the rate of natural habitat loss (δ), per capita rate of habitat production (q), and the effect of fishing on habitat (p) from all of the parameter combinations that were within 10% of the observed rates of population and habitat decline during 1980–2008. Estimated correlation coefficients (r) are shown. A small random jitter is included to show all of the points.

sanctuaries using the average fishing mortality rate during 1980–2008 and the 2008 estimate, $F = 0.22$, and the average parameters identified from the grid search. We also considered scenarios with 25% increases in F outside the MPAs to represent potential displacement of fishing effort from MPA areas.

The model can be also used to compare efficacy of alternative habitat restoration options. Ideally, pilot studies would be conducted in which several proposed

restoration methods were tested at a small scale, and the results of those studies would be used to estimate parameters of the model. As a demonstration, we developed sets of parameter values to represent three restoration scenarios: high relief (reef height about 1 m), low relief (reef height about 0.2 m), and traditional (reef height <0.1 m). For the low-relief scenario, we used the average parameter values with average values from the grid search ($r = 0.4$, $q = 0.3$, and $\delta = 0.16$) under the assumption that the average values represent a low-relief state because there are few, if any, high-relief oyster reefs in upper Chesapeake Bay. For the high-relief scenario, we relied primarily on a study conducted in North Carolina in which reefs of different sizes were constructed and monitored (Lenihan 1999). Survival rates were approximately 40% higher, sedimentation rates 70% lower, and growth rates 50% higher on 1 m high reefs than low-relief reefs (Lenihan 1999). To represent these effects we adjusted the parameters of the low-relief scenario by these percentages to create values for the high-relief scenario ($r = 0.56$, $q = 0.51$, and $\delta = 0.05$). Our last scenario represented expected population change under the traditional practice: maximizing area covered by spreading shell as thinly as possible. For this scenario, we used the same values for r and q as in the low-relief scenario, but increased δ to 0.4 based on observed rates of shell burial from shell stocking efforts in upper Chesapeake Bay (Smith et al. 2005). We projected the population using these sets of parameter values to estimate the effects of reef relief on the trajectory of oyster abundance.

RESULTS

We calculated the relative rates of decline in abundance and habitat for 79 200 sets of parameters, and only 17 sets were within 10% of the estimated rates from Wilberg et al. (2011). In all 17 sets, the population growth rate, r, and the habitat in 1980, H, were relatively low, at 0.4 and 0.08, respectively. The other three parameters differed among cases, but were within relatively narrow ranges (Table 1). Among the sets of parameters δ and q were strongly negatively related, with $\delta < q$, which indicated that specific combinations could achieve the same overall rates of decline (Fig. 1). The effect of fishing on habitat (p) had the widest range of relative estimates (0.01–0.09) among the parameters, which indicates that there was relatively little information in the data to estimate it. Neither δ nor q was strongly correlated with p. We used all 17 sets of parameters to explore the potential dynamics under our three fishing mortality scenarios.

The models displayed substantially different equilibrium conditions depending on the set of parameter values and the fishing mortality scenario, but equilibrium conditions were not strongly affected by p (Table 2). The small effect of p on the results was because the product of p and F was about an order of magnitude lower than the effects of δ and q (0.003–0.026 yr^{-1} for p

TABLE 2.   Equilibrium conditions of abundance and habitat under three scenarios that depict different fishing levels for sets of parameters that matched the observed rates of decline for abundance and habitat during 1980–2008.

Parameter			F 1980–2008		F_{MSY}				Moratorium ($F = 0$)	
δ	q	p	N_e	H_e	F	N_e	H_e	C_e	N_e	H_e
0.10	0.15	0.01	0	0	0.065	0.167	0.199	0.011	0.33	0.33
0.10	0.15	0.02	0	0	0.063	0.167	0.198	0.011	0.33	0.33
0.10	0.15	0.03	0	0	0.062	0.167	0.197	0.010	0.33	0.33
0.10	0.20	0.08	0	0	0.086	0.250	0.319	0.022	0.50	0.50
0.10	0.20	0.09	0	0	0.085	0.250	0.317	0.021	0.50	0.50
0.10	0.20	0.10	0	0	0.083	0.250	0.316	0.021	0.50	0.50
0.15	0.25	0.00	0	0	0.080	0.200	0.250	0.016	0.40	0.40
0.15	0.25	0.01	0	0	0.079	0.200	0.249	0.016	0.40	0.40
0.15	0.30	0.06	0	0	0.093	0.250	0.325	0.023	0.50	0.50
0.15	0.30	0.07	0	0	0.091	0.250	0.324	0.023	0.50	0.50
0.15	0.30	0.08	0	0	0.090	0.250	0.323	0.023	0.50	0.50
0.20	0.40	0.04	0	0	0.096	0.250	0.329	0.024	0.50	0.50
0.20	0.40	0.05	0	0	0.095	0.250	0.328	0.024	0.50	0.50
0.20	0.40	0.06	0	0	0.094	0.250	0.327	0.024	0.50	0.50
0.25	0.50	0.01	0	0	0.099	0.250	0.332	0.025	0.50	0.50
0.25	0.50	0.02	0	0	0.098	0.250	0.332	0.025	0.50	0.50
0.25	0.50	0.03	0	0	0.098	0.250	0.331	0.024	0.50	0.50

Notes: Abundance is N_e, and habitat is H_e. The three scenarios were: fishing mortality at the average of 1980–2008 (*F* 1980–2008); fishing mortality at maximum sustainable yield (F_{MSY}); and a fishing moratorium ($F = 0$). In all sets, $r = 0.4$. Equilibrium catch (C_e) was zero for the *F* 1980–2008 and moratorium scenarios. Parameters are as defined in Table 1. See *Methods* for details on calculating equilibrium conditions.

$\times$ *F* and 0.1–0.5 yr^{-1} for δ and q). Based on the formulated model and the parameter sets, oysters were unable to persist in the ecosystem when fishing mortality rates were at their 1980–2008 average (Fig. 2). The average fishing mortality rate during 1980–2008 (0.29 yr^{-1}) resulted in extirpation of the population (i.e., $N_e = H_e = 0$). Fishing mortality rates above 0.12 to 0.20 yr^{-1} were predicted to cause extirpation of the population (i.e., were not sustainable). Decreasing fishing mortality to F_{MSY} or imposing a moratorium allowed the population to have positive stable equilibrium values for abundance and habitat. F_{MSY} was between 0.06 and 0.1 yr^{-1} and depended on the specific set of parameters. Fishing at F_{MSY} resulted in equilibrium abundance at half the unexploited level and equilibrium habitat at 35–40% lower levels than the moratorium scenario.

As would be expected for a reef-building organism, the transitory dynamics were fairly slow. None of the models was expected to reach equilibrium abundance within 50 years. In most cases it took between 200 and 500 years to reach stable abundance and habitat for the F_{MSY} scenario. The 1980–2008 fishing scenario resulted in a monotonic decline in abundance and habitat (Fig. 2A, B). For abundance, both the F_{MSY} and moratorium scenarios resulted in fairly rapid increases in population size during the first 10 years (Fig. 2C, E). Habitat continued to decline during the first several years, followed by an increase (Fig. 2D, F). The moratorium scenario resulted in abundance and habitat levels 2–3 times higher than the F_{MSY} scenario after 50 years (Fig. 2E, F).

While harvest sanctuaries will likely have a positive effect on abundance and habitat within the protected areas (Fig. 2E, F), they would need to have a substantial spillover effect to allow fisheries outside of sanctuaries to become sustainable. To achieve sustainability, *r* would have to increase by 67% in the 1980–2008 average *F* scenario and 26% in the 2008 *F* scenario (Table 3). If fishing effort was displaced by implementation of the sanctuaries, the subsidy from sanctuaries would need to be even greater to achieve sustainability. Reaching sustainability would require an increase in *r* of 60% in the displaced 2008 *F* scenario and 115% in the displaced 1980–2008 average scenario.

Differences in parameters reflecting high-relief, low-relief, and traditional habitat restoration produced substantial differences in production and rates of recovery (Fig. 3). Oysters in the high-relief habitat scenario increased fairly rapidly toward their equilibrium abundance level. In contrast, oysters in the low-relief habitat scenario had an equilibrium abundance 48% lower than the high-relief scenario and a substantially lower population growth rate. The traditional method for shell stocking in Maryland did not result in a sustainable population. The high-relief scenario reached 95% of equilibrium abundance in about one-third the time of the low-relief scenario, about 35 years and 90 years, respectively.

DISCUSSION

Exploitation has a stronger effect on autogenic ecosystem engineers than on species that do not create their own habitat because sustainable exploitation of autogenic engineers depends on sustainable habitat generation. The lack of resilience to fishing is evident in the world-wide decline of oyster populations (Beck et al. 2011). The decline of oyster populations is also likely due to the relative ease of maintaining a high fishing mortality rate on oysters because they are sessile, associated with reefs, and are often located in
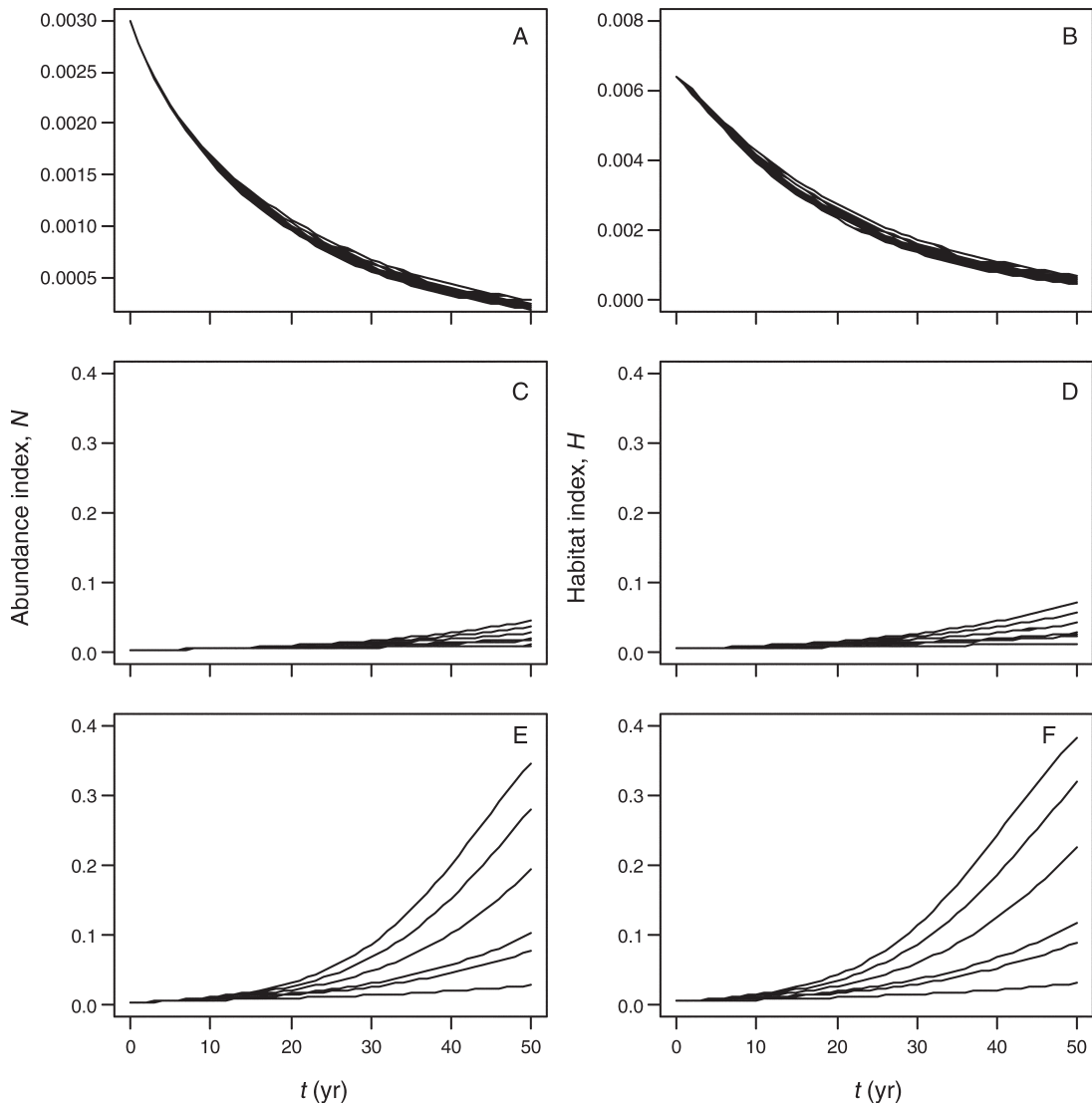
FIG. 2. (A, B) Projections of abundance (N) and habitat (H) under scenarios of average fishing during 1980–2008, (C, D) fishing at the rate that would achieve maximum sustainable yield, and (E, F) a moratorium. The different trajectories represent the different parameter combinations listed in Table 2. Note that the results strongly overlap because the parameter that describes the direct effect of fishing on habitat (p) has a relatively small effect on the dynamics and equilibrium conditions.

shallow waters (Beck et al. 2011). If the habitat requirement for oysters is ignored, they would seem to be an ideal group for supporting a fishery because they have relatively high fecundity, early maturation, and rapid growth. For reef-building organisms, it is likely that habitat production rates are the bottleneck for sustainable exploitation, making only relatively low exploitation rates sustainable. Because the net rate of habitat production will often be the factor limiting abundance, recovery from a highly degraded state is expected to take a long time.

We applied our model linking the effects of exploitation and habitat dynamics for ecosystem engineers to oysters in upper Chesapeake Bay, which suggested that historical fishing mortality rates were not sustainable. In

2010, Maryland increased the area of no-harvest oyster sanctuaries to ~25% of oyster habitat to protect productive oyster grounds, provide a source of larvae for areas outside the sanctuaries, and increase compliance with sanctuary boundaries, among other goals. While the new sanctuary program is a marked improvement in fishery management, substantial larval subsidy to areas outside the sanctuary would be necessary for the oyster fishery to become sustainable. This is not to say that sanctuaries will provide a larval subsidy to neighboring regions. The location of the sanctuary can have a substantial influence on whether it is a net source or sink of larvae, and will thus influence the effectiveness of any sanctuary to provide a larval subsidy to neighboring areas (North et al. 2010).

TABLE 3. Change in the intrinsic rate of increase (r) necessary for fishing to be sustainable outside sanctuary areas for a range of fishing mortality rates (F).

Scenario	F	r	Increase in r (%)
Average 1980–2008	0.29	0.67	67
Displaced 1980–2008	0.36	0.86	115
2008	0.22	0.50	26
Displaced 2008	0.28	0.64	60

Notes: The base fishing mortality rates are the average during 1980–2008 and the value from 2008. The displaced scenarios assume that fishing mortality rates will be 25% higher in areas open to fishing after implementation of sanctuaries, due to redistribution of effort.

We were able to determine plausible ranges of parameter values using the grid search approach, whereby parameter combinations were selected based on the output of the model run matching observed trends in oyster abundance in recent years (Wilberg et al. 2011). The resulting values were within the ranges determined from the literature, and produced similar dynamics of future growth relative to their equilibrium levels. The parameter describing direct effects of fishing on habitat had the widest range of relative estimates, indicating that it is highly uncertain. Additionally, the carrying capacity associated with a certain amount of habitat may be underestimated for high-settlement areas if oysters require less habitat per individual at high densities because of changes in shell orientation or compensation in growth. The grid search we applied to estimate plausible parameter values for projections was relatively coarse. We conducted a sensitivity analysis that used a finer grid and identified many more sets of parameter values that could match the observed rates of decline in habitat and abundance. However, the additional parameter sets had similar mean responses to the treatments in our study, but wider variability. Despite the general agreement in model responses over the fine-scale grid search, the parameters of the model are still highly uncertain, as different combinations produced the same pattern of decline during 1980–2008. The primary difference among sets of parameters was the level of equilibrium abundance and habitat that would eventually return if fishing were reduced or halted. To refine the estimated response of the oyster population to management changes, future studies would need to better estimate rates of habitat loss and production. Additionally, our results are likely somewhat optimistic because substantial programs existed to enhance habitat with fresh and fossilized shell and to stock hatchery-reared oysters during 1980–2008 (Smith et al. 2005, Kennedy et al. 2011), but were not explicitly corrected for in the model. These activities should act to increase estimates of r and q, and decrease estimates of δ and p.

We projected oyster dynamics under a range of fishing mortality rates and habitat conditions reflecting differences in hard-bottom substrate, but several other factors have important effects on oyster dynamics. In particular, salinity, temperature, and disease prevalence all play substantial roles in causing the vital rates of oysters to vary over time (Shumway 1996). Because we calibrated the model to estimated population and habitat changes during 1980–2008, the parameters represent average conditions of temperature, disease, and salinity (as well as other environmental conditions) during that period. However, using only the average means that the variability in response is understated in our model. Additionally, if patterns of these variables changed through processes such as climate change, sea level rise, or development of increased resistance to disease, our projections may substantially differ in the time needed to observe a response.

Our model differed from previous approaches in that it included effects of habitat (i.e., hard-bottom substrate) on the population dynamics and direct effects of fishing on habitat. Gurney and Lawton (1996) developed a general model for the dynamics of ecosystem engineers, but their model did not include effects of exploitation. Powell and Klinck (2007) developed an age-structured model to link shell accretion rates to oyster dynamics for Delaware Bay. This model was further applied by Mann et al. (2009) to estimate minimum abundance necessary for oyster reef accretion to keep pace with sea level rise. While their model included effects of growth and mortality on shell production, population dynamics were independent of the habitat dynamics, and direct removal of oyster reef by fishing was not included. Managing oysters to achieve a constant shell budget has been proposed as a goal for sustainable oyster fisheries (Powell and Klinck 2007). All sustainable fishing mortality rates in our model achieve constant shell budgets, so maximizing
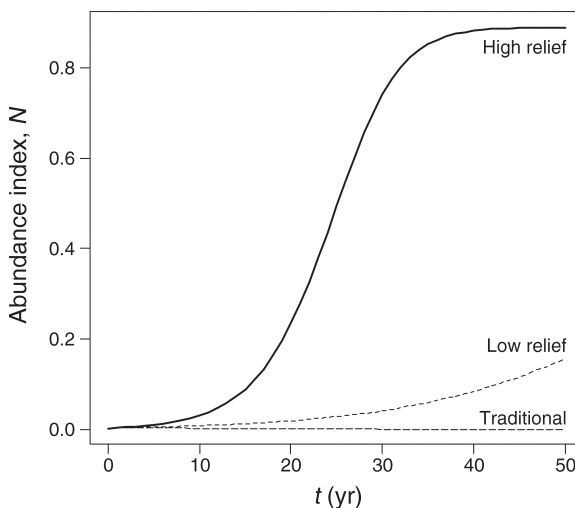

FIG. 3. Simulations of oyster abundance (N) under high-relief conditions (1 m high; solid line), low-relief conditions (0.2 m high; short dashed line), and traditional restoration (<0.1 m; long dashed line).

sustainable yield is congruent with the goal of a constant shell budget. Similar to Powell and Klinck (2007), our model also suggests that shell repletion programs should improve the sustainability of a fishery by providing additional substrate to replace that removed by fishing.

The projections are more useful for comparing the relative effects of alternative actions than making specific predictions about timing of recovery because the model is deterministic and assumes constant values for the parameters. Oyster recruitment has historically shown substantial interannual variability in Chesapeake Bay (Kimmel and Newell 2007, Wilberg et al. 2011), which would add considerable uncertainty to the length of time for recovery after restoration efforts. For example, the restoration of a reef complex in the Great Wicomico River, Virginia, benefited from a strong recruitment event shortly after completion (Schulte et al. 2009). Natural mortality also varies substantially among locations and over time (Wilberg et al. 2011), which would cause the intrinsic rate of increase to vary. Additionally, ocean acidification, resulting from increases in anthropogenic CO_2, has the potential to slow the shell growth of oysters and also increase the dissolution rate of nonliving oyster habitat (Waldbusser et al. 2011). The pH of marine waters is expected to increase (Orr et al. 2005), suggesting that our parameter values for shell growth and decay may decrease and increase, respectively. The average shell size of oysters interacts with the natural mortality rate because the size structure of the population will be truncated under high natural mortality rates. Thus, if mortality rates are high, oysters will contribute a smaller-sized shell to the reef, which may suffer a higher rate of degradation. Accounting for this process in our model would require that the r and δ parameters would be negatively related, such that high rates of natural mortality produce lower rates of increase (r) and higher rates of habitat loss (δ). The difference in dynamics between high- and low-relief reefs should also decrease over time as low-relief reefs eventually become high-relief reefs under unfished conditions. Because our model did not explicitly consider reef geometry, it does not allow for feedback between reef shape and rates of habitat accretion or population increase.

Our model represented a set of reefs, but the spatial dynamics of the population and fishery may not be captured well within it. In particular, our simulations of the current management approach using marine protected areas (MPAs) did not include the spatial distribution of MPAs in the system. For example, some areas experience extremely high fishing pressure, while other areas experience much lower fishing pressure. Additionally, differential production by oysters on different reefs caused by physical factors likely results in source–sink dynamics (Powers et al. 2009, Schulte et al. 2009, North et al. 2010). North et al. (2010) developed a model that explicitly considered larval transport among a spatial configuration of oyster reefs for Chesapeake Bay and found that the expected benefits of oyster restoration differed substantially among several regions due to patterns of larval transport.

Management programs to rehabilitate oyster habitat in upper Chesapeake Bay have occurred since at least the 1960s on a large scale (Kennedy and Breisch 1983, Smith et al. 2005). The primary method for habitat restoration in Maryland has been stocking areas with fresh or fossilized oyster shell. To maximize the area affected, repletion efforts have attempted to spread the shell as thinly as possible, one shell layer thick (Smith et al. 2005, Kennedy et al. 2011). However, when this method is employed, restored habitat is lost at a very fast rate, ~0.4 yr^{-1} (Smith et al. 2005). This average rate of habitat loss is more than double the rate observed in Delaware Bay (Powell et al. 2006). Although shell-stocking programs have likely had a positive effect on the fishery, they have not resulted in a stabilized or increasing oyster population in upper Chesapeake Bay (Wilberg et al. 2011), which is consistent with our modeling results.

The effects of fishing on habitat have been very important in reducing the productivity of oyster reefs (Lenihan and Peterson 1998). While laws are in place that require reef material (i.e., cultch) be returned to the reef (Kennedy and Breisch 1983), fishing still has a disruptive effect on habitat by disaggregating the substrate. Restoration efforts that use unconsolidated shell are very sensitive to effects of fishing (Lenihan and Peterson 1998, 2004). Powers et al. (2009) found that most restoration efforts that paired high-relief reefs with protection from fishing were successful in North Carolina. Thus, the goal of habitat rehabilitation should be habitat permanence instead of maximum area.

In addition to habitat permanence, optimal restoration efforts would benefit by focusing on practices that maximize the net rate of habitat production, $q - (\delta + pF)$. One promising option for improving restoration efforts is to build high-relief reefs. Reef height has been linked with increased growth and decreased sedimentation and burial through increased flow rates caused by greater three-dimensional structure (Lenihan 1999). Other potential effects of high-relief reefs are more equivocal; Gregalis et al. (2008) and Schulte et al. (2009) found recruitment increased with reef relief, while Lenihan (1999) did not find a significant effect of reef height. Similarly, Lenihan (1999) found higher survival on higher-relief reefs, but Gregalis et al. (2008) found no consistent difference associated with reef height. While these studies spanned only 1–2 year periods, Powers et al. (2009) followed up on several restoration efforts in North Carolina and found that most of them should be considered successes despite illegal fishing on most of the subtidal reefs. The parameters for our comparisons of different habitat restoration activities were primarily based on a study from North Carolina (Lenihan 1999). There are likely differences in survival, growth, and the environment

that mean that the results probably do not represent any individual Chesapeake Bay system well. However, the relative difference between our restoration scenarios should be robust because the primary driver of the differences among scenarios was the rate of habitat loss, which is dominated by sedimentation and burial in much of upper Chesapeake Bay (Smith et al. 2005) and relies on how the physical structure of high-relief reefs changes flow patterns (Lenihan 1999).

Oysters are at extremely depleted levels in Chesapeake Bay, and a moratorium has been suggested as a management measure to assist population recovery (Wilberg et al. 2011). Our analyses here support the use of a moratorium because it is the most rapid way to rebuild the population from its current low levels. While fishing at F_{MSY} also led to an increasing population in our model, there is substantial uncertainty about potential Alee effects given the extremely low stock size. Additionally, fishery management has recognized the perils associated with attempting to estimate and attain MSY (Larkin 1977), so precautionary management that implements target fishing mortality rates below F_{MSY} has been recommended (Mace 2001). One rule of thumb is that fishing at 75% of F_{MSY} still produces substantial yield, while also allowing a precautionary buffer in management (Restrepo et al. 1998). This would correspond to target fishing mortality rates of between 0.045 and 0.074 yr^{-1}, which represent 3–5 fold decreases in the fishing mortality rate over the 2008 level of 0.23 yr^{-1} (Wilberg et al. 2011). Our estimates of fishing mortality rates that would achieve maximum sustainable yield were very similar to those suggested by Powell and Klinck (2007) for eastern oysters in Delaware Bay, 5–7% per year.

Our model provides a tool for comparing oyster restoration strategies and for modeling the dynamics of exploited ecosystem engineers in general. If the goal of a restoration project is to maximize habitat or abundance, then fishing should not be allowed in the area being restored. Reducing the natural habitat loss rate should be possible by engineering reefs that have greater stability and greater height or relief. We acknowledge that habitat loss rates and intrinsic rates of increase likely differ among areas, which is why some regions in Chesapeake Bay have been more robust to fishing than others. Spatial differences in rates of habitat loss and source–sink dynamics should be considered before implementing restoration programs. Although others have suggested that oyster restoration may not be possible in Chesapeake Bay (Mann and Powell 2007), our model suggests that restoration could be successful if fishing was halted and improved methods were used to restore habitat. We maintain that substantial reductions in fishing mortality are necessary to make the oyster fishery in upper Chesapeake Bay sustainable and that a moratorium coupled with substantial habitat restoration is the most rapid path toward recovery.

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