Detecting larval export from marine reserves


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Marine reserve theory suggests that where large, productive populations are protected within no-take marine reserves, fished areas outside reserves will benefit through the spillover of larvae produced in the reserves. However, empirical evidence for larval export has been sparse. Here we use a simple idealized coastline model to estimate the expected magnitude and spatial scale of larval export from no-take marine reserves across a range of reserve sizes and larval dispersal scales. Results suggest that, given the magnitude of increased production typically found in marine reserves, benefits from larval export are nearly always large enough to offset increased mortality outside marine reserves due to displaced fishing effort. However, the proportional increase in recruitment at sites outside reserves is typically small, particularly for species with long-distance (on the order of hundreds of kilometers) larval dispersal distances, making it very difficult to detect in field studies. Enhanced recruitment due to export may be detected by sampling several sites at an appropriate range of distances from reserves or at sites downstream of reserves in systems with directional dispersal. A review of existing empirical evidence confirms the model’s suggestion that detecting export may be difficult without an exceptionally large differential in production, short-distance larval dispersal relative to reserve size, directional dispersal, or a sampling scheme that encompasses a broad range of distances from the reserves.

Whereas the conservation benefits of marine reserves are clear (1), continuing debate about whether reserves can also benefit fisheries remains a major roadblock to successful implementation of reserves worldwide (2–6). At the center of this debate is the suggestion that larvae from highly productive populations in marine reserves may move outside reserves and enhance populations in harvested areas (7, 8). A few studies have demonstrated spatial and/or temporal patterns of recruitment or abundance that suggest larvae exported from reserves can enhance nearby fished populations (9–18). However, the larval export effect remains controversial (3), in part because empirical evidence remains limited (6). In contrast, researchers have accumulated a convincing body of evidence for enhanced biomass, density, size, and biodiversity inside reserves (1) as well as an abundance of mobile adults beyond their borders (19–21).

Inherent difficulties in collecting and interpreting the data needed to document larval export may explain the relative scarcity of empirical evidence. Benefits from larval export may be widespread but very diffuse, and the signal of export may be too weak to detect relative to the high spatial and temporal variability of recruitment (22–24). Even when recruitment patterns suggest a larval export effect, the data are difficult to interpret unless studies employ a before–after–control–impact (BACI) design, because both temporal and spatial patterns in recruitment may be driven by natural variability (24).

Whereas debate about larval export often centers on whether export occurs, we know that reserves often lead to dramatic increases in larval production (25–27) and that larvae disperse on scales far larger than typical reserve sizes (1, 28), suggesting that some export of larvae produced in reserves is nearly certain. The more relevant questions include how much export occurs, on what spatial scales, and under what conditions, and whether it provides a benefit to fished areas sufficient to outweigh the increased mortality that may result from displaced effort when closing an area to fishing. There are a number of spatially explicit theoretical models addressing the interplay of reserve configuration and dispersal characteristics on marine reserve effects (5, 29–33), but very few studies couple theoretical predictions with an empirical test of the spatial patterns, magnitude, or scale of increased recruitment due to larval export (13). In addition, many of these models do not account for the effects of displaced fishing effort to predict the net benefits of reserves (34), although there is growing attention to this effect in the theoretical literature (32, 35, 36).

A spatially implicit theoretical model suggests that, assuming broad dispersal via a common larval pool and a 3-fold increase in production, benefits from larval export can compensate for displaced fishing effort, or “fishery squeeze,” with up to 50% of a coastline in reserves (24). In addition, even for short-distance dispersers, reserves can provide a net benefit to fished areas as long as the mean dispersal scale is no shorter than half the width of reserves (24).

To extend this approach, and to investigate reasons for the scarcity of empirical demonstrations of larval export from reserves, we provide a spatially explicit model to quantify the relative magnitude, scale, and spatial and temporal signal of larval export, with biological parameters based on recent empirical observations that also incorporate density dependence in settlement, heterogeneous habitat, and oceanographic currents, all of which are common in marine systems and may be critical determinants of reserve effects (5, 29).

A framework coupling review of existing empirical findings with theoretical predictions that address fishery squeeze, reserve configuration, and larval dispersal scale can advance our current understanding of larval export from reserves. Although there are only a few studies that provide empirical evidence for larval export, these studies can be used to test the predictions of spatially structured theoretical evaluations of larval export. We review existing empirical evidence for larval export and compare these data with results from our model, to reveal commonalities among findings from larval export studies, explore the challenges in detecting larval export effects in the field, and evaluate theoretical predictions in light of empirical data.

Results

Recruitment Before and After Reserve Establishment. We determined whether larval export is great enough to offset fishery squeeze across a range of dispersal scales, reserve sizes, and proportions of the coastline placed in reserves. In general, the increase in recruitment due to larval export, integrated across

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the area outside of reserves, was greater than the decrease in recruitment due to fishery squeeze for most combinations of mean dispersal scale (10, 50, or 250 km), reserve size (10 or 100 km), and percentage of coastline in reserves (0–60%), leading to a net increase in recruitment outside reserves (Fig. 1A and B). Only for short-distance dispersers (mean dispersal scale = 10 km) in 100-km reserves was larval export insufficient to offset the decline in recruitment due to fishery squeeze (Fig. 1B).

Overall, the increase in recruitment due to larval export from reserves was greatest when the mean dispersal scale was longer than the reserve length, because for short dispersers in large reserves, most of the extra larval production was retained inside reserves. Across most combinations of reserve size and dispersal scale, benefits initially increased with an increasing proportion of coastline placed in reserves, because of the greater enhancement of larval production throughout the system, but then declined with very high proportions of coastline in reserves, due to an increased fishery squeeze effect. Peak benefits resulted from protecting ~40% of the coastline in reserves.

Next, we asked whether larval export is likely to be detected in field studies across the same range of conditions, by examining the percentage of change in recruitment expected at the reserve edge after implementation. Change in recruitment at the edges of reserves was between 0 and 45% for all of the combinations of reserve size, percentage of coastline in reserves, and mean dispersal scale explored here (Fig. 1C and D). This change in recruitment is small relative to scales of natural variability in recruitment as reported in prior studies, which may limit the ability to detect this effect in field studies (Challenges of Measuring and Monitoring Larval Export in Discussion).

Patterns were very consistent across the different dispersal kernels (Figs. S1–S3). The model with heterogeneous habitat distribution behaved similarly to the continuous habitat model, but results were driven by the proportion of suitable habitat protected in reserves (Fig. S4; SI Text). We found that advection can increase both the magnitude and the detectable signal of larval export (Fig. S5), and that results varied with the strength of density dependence and fishing mortality rates (SI Text; Figs. S6–S8).

Spatial Patterns in Recruitment. The spatial gradient of recruitment with distance from reserves varied with dispersal scale, reserve length, and the production differential. With production inside reserves set to triple the production outside, there was a noticeable decline in recruitment with increasing distance from 10-km reserves for short-distance dispersers, whereas recruitment was virtually flat across a range of distances from the reserve for medium (mean dispersal = 50 km) and long-distance (mean dispersal = 250 km) dispersers (Fig. S4). Near 100-km reserves, there were stronger declines in recruitment for species with 10- to 50-km dispersal scales (Fig. 2B). Additionally, there was a greater percentage of change in recruitment throughout the domain for networks of 100-km reserves than for networks of 10-km reserves. Recruitment was nearly flat across the domain for long-distance dispersers in both cases, due to the high diffusion of larvae for these species. Finally, the declines occurred on a larger spatial scale for networks of 100-km reserves. The spatial extent of these declines suggests that the benefits of export are widespread near large reserves, but also that field studies would need to cover tens to hundreds of kilometers to capture the scale of the export effect.

For corresponding reserve lengths and dispersal scales, spatial patterns in recruitment were qualitatively similar for both production differentials we examined (Fig. 2). However, the magnitude of the change in recruitment was far higher where the production differential was large (Fig. 2C and D). With a 15-fold differential in production inside the reserve compared to outside, and a network of 100-km reserves, the large percentage of change in recruitment after reserve establishment (up to nearly a 300% increase inside reserves and a 200% increase at reserve edges) makes it likely that field studies could detect the temporal signal of larval export if any data were available from before reserve designation (Fig. 2D). In the absence of before data, however, elevated recruitment throughout the domain after reserve establishment makes the spatial signal of larval export difficult to detect, particularly for long-distance dispersers.

Discussion

This synthesis provides a unique approach to generate and test qualitative theoretical predictions of the effects of marine reserves on fished populations through larval export, accounting for fishery squeeze, for a variety of dispersal parameters and reserve design scenarios. It couples predictions of the scale of recruitment subsidies from marine reserves with analyses of existing empirical data on larval export, providing a context for understanding results of prior empirical evidence. Results from
our model support Halpern et al.’s (24) conclusions that benefits from larval export are sufficient to offset fishery squeeze for most conditions. Not surprisingly, larval export benefits are predicted to be of greatest magnitude and easiest to detect when the differentials in production inside relative to outside reserves are exceptionally large. However, modeling results suggest that spillover effects may be greatest, but most difficult to detect, in cases where dispersal distances are long relative to reserve size. A review of existing empirical evidence is consistent with the implications of these theoretical findings: that detecting larval export in field studies is likely to be very challenging except when the increase in production within reserves is exceptionally large (9–12, 15–18, 37), the mean dispersal scale is not too long relative to reserve size (9–11, 13, 14), or sampling designs take advantage of directional dispersal and employ a suite of sampling sites at the appropriate spatial scale (9, 12, 13, 15–18, 37).

**Challenges of Measuring and Monitoring Larval Export.** Recruitment in marine systems is highly variable and is influenced by numerous factors including larval supply (38), larval delivery (39, 40), oceanographic conditions (41), biogeography (42), and postsettlement mortality (43). Variance in recruitment and other aspects of environment and variability may have important, potentially nonlinear effects on demographic processes. Environmental heterogeneity may interact with dispersal, and both play an important role in shaping spatial patterns of community structure (44–46), with their relative influence varying with spatial scale (46, 47). Environmental heterogeneity facilitates coexistence and affects mean population size (48–51), whereas dispersal and dormancy allow populations to cope with heterogeneity in space and time (44). Both temporal and spatial heterogeneity affect demographic processes, possibly in opposing directions; for example, in unagulate populations, temporal heterogeneity has been shown to strengthen density-dependent processes whereas spatial heterogeneity weakened them (52). In marine systems, recruitment variability has important demographic consequences (49, 50) and interacts with environmental heterogeneity and patterns of dispersal to shape spatial and temporal patterns. In this study, we focus on the influence of dispersal, particularly as it pertains to the benefits and the detectable signal of larval export from marine reserves, but an extension of this study explicitly exploring environmental heterogeneity and recruitment variability would be valuable.

For the purposes of this study, we addressed natural variability in recruitment by comparing the predicted change in mean recruitment due to larval export predicted by our model with the magnitude of natural variability in recruitment, reported as a coefficient of variation (CV), found in prior studies (22, 23). Inherent in this comparison is the assumption that the CV is independent of mean recruitment (i.e., the standard deviation of recruitment increases linearly with mean recruitment). The independence of CV and mean recruitment has been confirmed in a meta-analysis of recruitment time series (22).

The magnitudes of recruitment subsidy predicted by our model would be difficult to detect in field studies, because the proportional increases in recruitment are small compared to an average temporal and spatial coefficient of variation in recruitment of ~150–200% (22, 23). The magnitude of recruitment subsidy that may be detected in field studies depends on a multitude of factors and is not addressed quantitatively in this study. However, given the high inherent variability in recruitment, it is likely that the power to detect the magnitudes of larval export modeled here would be quite low in most study systems (see Fig. S9 and SI Text for an exploration of statistical power). Our model demonstrates the qualitative relationships among differentials in production, larval dispersal scale, and reserve size. With very large changes in production inside reserves relative to outside, both the benefits of larval export and the ability to detect it are enhanced. However, for a given production differential, the conditions that favored the greatest benefits from larval export—long-distance dispersal relative to reserve size and an intermediate fraction of coastline in reserves—also led to the most widespread but diffuse reserve benefits, thereby obscuring the signal of those benefits. This inverse relationship between the magnitude of overall export benefits and the strength of the detectable signal of export presents a formidable obstacle to understanding larval export benefits through empirical studies.

Even with an appropriate array of sampling sites, the spatial signal of larval export may be detectable only if the scale of dispersal is short relative to reserve size or if local oceanography increases the magnitude of larval export to certain areas. Unless data from before reserve protection are available or baseline recruitment levels can be estimated, larval export may be difficult to detect even in cases where it has more than doubled recruitment near reserves. Incorporating both spatial and temporal gradients in sampling can greatly improve statistical power to detect change. Whenever possible, studies should include time series of data from several sites along a distance gradient from reserves. Comparing changes over time in the slope of the relationship between recruitment and distance from reserves, as well as changes in absolute recruitment, can help distinguish regional reserve effects from environmental variation and allow quantification of the scale and magnitude of export. Unfortunately, the process of reserve designation often does not allow adequate time to collect sufficient data before implementation. In addition, in many cases the study design proposed here will be prohibitively expensive and time-consuming to conduct over appropriate spatial and temporal scales. However, a few in-depth case studies, sampled on appropriate scales and focused on systems where effects are likely to be detectable, can help test and refine our predictive theoretical framework, which in turn can be used to inform the design of marine reserve networks. The increased signal of larval export in advective systems suggests that empirical studies designed to sample downstream of reserves in areas with strong currents may be better able to detect the larval export effect than those conducted in systems without directional dispersal. In addition, where data are available, using oceanographic models will help to increase detection of larval export, particularly for long-distance dispersers, by identifying potential areas of retention or advection as priorities for sampling.

Appropriate expectations are the key to focusing research that will advance our knowledge of larval export. Due to the inherently diffuse nature of export benefits and the trade-offs between the detectable signal of export and its overall benefit to fished areas, we may be unlikely to amass a comprehensive database that quantifies export benefits across a broad range of biological parameters and reserve characteristics, as researchers have done for responses within reserves (1).

**Optimal Design of Reserve Networks for Larval Export.** Our results confirm the results of previous models that offer guidelines for designing reserve networks to realize the full potential of larval export benefits. In accordance with Halpern et al.’s (24) findings, we find that reserves should be no larger than about twice the target species’ dispersal scale to ensure that enough larvae are exported to offset fishery squeeze. Our findings may seem difficult to reconcile with models suggesting that populations in reserves any smaller than the mean dispersal scale of a target species cannot persist, but persistence in smaller reserves is possible when the assumption of zero larval production outside reserves is relaxed (30). Clearly, there are trade-offs between sustainability within reserves and export of production to areas outside reserves, but networks of variably spaced reserves on the scales of 10–100 km² can meet both conservation and fisheries enhancement goals (8).

The optimal fraction of coastline protected in reserves in our model was ~35–40%, in agreement with many other theoretical
studies of reserves (30, 53). From a political perspective, such large fractions of coastline in reserves are still unlikely in most parts of the world. However, both our model and empirical evidence show that benefits from export will accrue even with smaller fractions of coastline in reserves. Importantly, our patchy habitat model suggests that where habitat distribution is highly heterogeneous, reserve designation processes need to consider the proportion of habitat that will be closed to fishing, not only the proportion of coastline, to adequately predict the effects of both enhanced production and displaced fishing.

In systems with directional dispersal, larger reserves and a greater proportion of coastline in reserves may be optimal. The model's finding that directional dispersal enhances the benefits of reserves confirms previous empirical work (5, 29). Directional dispersal makes it possible for even large reserves to produce net benefits from species with low diffusive dispersal. Without advection, most extra larval production for short-distance dispersers is retained in reserves, but strong advection allows much of the extra larvae to be exported, even if the larval diffusion scale is very short. In addition, because more of the larvae produced in reserves are exported, the benefits of export increase with increasing fractions of coastline placed in reserves. A greater proportion of coastline in reserves leads to more enhanced larval production, and enough of the extra production is exported due to advection to offset the additional fishery squeeze effect.

Dispersal scale parameters, including the scales of diffusion and advection, are difficult to estimate in the field, and these parameters remain poorly understood for most species, which may present an obstacle to determining optimal reserve design. In some cases, diffusion and advection parameters may be directly estimated using oceanographic flow field models and/or drifter or dye studies. More often, basic knowledge of oceanographic conditions (e.g., the presence of advection currents, retention features such as eddies, etc.) and planktonic larval duration are used to estimate first-order approximations of mean larval dispersal scales, including diffusion and advection parameters (54–57).

With typical larval neighborhood sizes on scales of tens to hundreds of kilometers for most marine fish and invertebrates (4), and a median size of only ∼3.3 km² for existing reserves (1), net benefits from the export of larvae outside reserves should be the rule rather than the exception—a finding that mirrors Halpern et al.'s (24) conclusion. However, dispersal scales are highly variable, particularly among invertebrates (28), and larval export benefits should not be expected for species with particularly low dispersal potential, such as macroalgae, brooding corals, abalone, or tunicates (57).

Empirical Evidence of Larval Export from Marine Reserves. Existing empirical evidence for larval export (Table S1) (9–18) is consistent with the results of our modeling study, which suggest that larval export will be difficult to detect with dispersal distances that are long relative to reserve size and without either exceptionally strong production differentials, numerous sampling sites at the appropriate spatial scale, or strongly directional dispersal. Many studies of larval export focus on reserves with exceptionally high production relative to adjacent fished areas. Overall, in five of six reserves where evidence for larval export was found and data on the biological response within reserves were available, the magnitude of increased abundance, biomass, or production was at least an order of magnitude higher inside reserves than outside. A note of caution is necessary here. The results of the model and the empirical observations suggest that systems where larval export is detectable are also those that exhibit large differentials in biomass. However, this does not imply any particular threshold production differential that would allow detection of reserve effects. The ability to detect this effect depends not only on the predicted change in mean recruitment due to larval export, but also on recruitment variability and sampling design.

Other studies providing evidence of larval export have sampled sites downcurrent from reserves or measured recruitment at a gradient of distances from reserves to determine whether there is a detectable spatial signal of larval export (Table S1). Data from reserves in South Africa suggest that for short-distance dispersers, recruitment does decline with increasing distance from reserves as predicted in the model, allowing for the detection of a larval export effect that could probably not be discerned without spatial data (9, 14) (Fig. S10; SI Text).

Among studies that have found evidence for larval export, planktonic larval durations (PLDs) of focal species are generally shorter, and reserve sizes far larger, than among reserve studies in general (Table S1) (1). Notably, all studies reporting evidence of larval export to date focus on mollusks (Table S1). In contrast, Lester et al. (1) found more studies of biological responses inside reserves for fish than for invertebrates and about as many studies of arthropods and other invertebrate groups as of mollusks. This bias is most likely driven by taxonomic differences in dispersal scale, as well as differences in adult mobility. On average, teleost fish and crustaceans spend about twice as long in the plankton as bivalves and gastropods (58). Whereas the average PLDs for crustaceans and teleosts are ∼40 days (58), all but one of the species exhibiting evidence of larval export had PLDs shorter than a month. The exception, the deep sea scallop, is protected in an extraordinarily large reserve in Georges Bank (∼17,000 km²; Table S1), so that its dispersal scale is probably quite short relative to the reserve length. Differences in adult mobility may also drive the greater representation of mollusks in this data set, because any increase in abundance outside reserves can be attributed to larval export for mollusks with sedentary adults, whereas abundance of fish and crustaceans must be measured soon after settlement to distinguish larval export effects from spillover of the relatively mobile juveniles or adults. Although the taxonomic bias is easily explained, it underscores the limitations of the empirical data set. Fish and crustaceans are among the most commercially important and heavily exploited marine taxa and, given their relatively high larval dispersal scales, are excellent candidates for fisheries benefits through larval export. However, as noted earlier, export may be hardest to detect for these species that have the potential for the greatest benefits from export.

This model expands upon prior theoretical findings that larval export can offset fishery squeeze for a variety of reserve design scenarios (24) by adding a spatial component that explicitly addresses the role of dispersal scale and reserve size. The synthesis of model results and a review of empirical findings helps explain the limitations of existing empirical evidence for the larval export effect and underscores the difficulty in detecting larval export benefits in field studies, particularly for long-distance dispersers, despite the potential of long-distance dispersers to realize great overall benefits from larval export. This synthesis study does not consider the economic costs and benefits of reserves (59) and does not incorporate many of the complexities that may affect larval export benefits, such as adult movement (36) and spawning behaviors (60), heterogeneous oceanographic connectivity within a region (61, 62), natural sources of recruitment variability (23, 39, 40, 42), and species interactions (63). In data-rich regions, reserve designation processes will benefit from incorporating all available economic and biological information and detailed oceanographic models to select reserve sites that will optimize larval export benefits. In addition, an explicit exploration of natural variability would be a useful extension to this model. However, the broad framework provided here can be used to produce general predictions about spatial and temporal changes in recruitment, set realistic expectations for empirical studies, and provide guidelines both for designing reserve networks and for crafting monitoring studies to detect export.
Materials and Methods

We developed a spatially explicit model to determine how increased biomass in marine reserves translates to enhanced larval production and to estimate the export of larval outside reserve boundaries in an idealized linear coastline domain (see SI Text for detailed methods). The model accounts for increased fishing mortality in exploited areas after reserve designation due to displaced effort (fisheye squeeze) and incorporates density-dependent settlement and spatially structured larval dispersal. Results reported here assume an instantaneous fishing mortality rate of 0.4, an intracohort density-dependent coefficient of 0.5, and no intercohort density dependence (see SI Text for more explanation of assumptions and parameters and an exploration of various fishing mortality and density-dependence parameters). To explore the effects of export for scales of increased production that are most relevant to real systems, we modeled a 3-fold production differential, based on the median increase in biomass found in a recent meta-analysis of no-take marine reserves (1) (SI Text). We used the model to generate qualitative predictions of both temporal and spatial patterns of recruitment shaped by larval export.

We estimated the magnitude of larval export by comparing recruitment (defined as the number of larvae surviving postsettlement) outside reserve areas before and after reserve designation. We calculated the percentage of change in recruitment integrated across the area outside reserves (a measure of the overall benefit due to larval export); this measure was consistent for a wide range of domain sizes (SI Text). We also calculated the percentage of change in recruitment predicted by our model with a Laplacian dispersal kernel for a range of reserve network configurations, for species with short-distance (10 km), moderate (50 km), or long-distance (250 km) mean dispersal scales. We tested the robustness of these general patterns by comparing the above results with the change in recruitment outside reserves generated from a Gaussian dispersal kernel (i.e., a normal distribution of probability of dispersal distances—see SI Text), as well as dispersal kernels derived for coral, fish, and lobster in the Caribbean that accounted for local oceanographic variability (see Fig. S1). We also used a discrete version of the model to test the effects of patchy habitat and advection on larval export benefits.

Carefully designed studies may detect the export effect by sampling several sites at the appropriate range of distances from reserves (9). In addition, in most existing reserve studies, before–after data are not available (1), so spatial patterns of recruitment are often the only metric used to explore the larval export effect. Therefore, we used the spatial pattern of recruitment to investigate the power of various sampling designs and to characterize the spatial scale of benefits from larval export.

Although a 3-fold increase in production in reserves is a reasonable assumption given a median of a 3-fold increase in biomass in reserves (1), several empirical studies that found evidence of larval export also found production increases that are differentials of an order of magnitude or more (Table S1). To characterize how the magnitude of increased production inside reserves affects spatial patterns of recruitment, we explored patterns of recruitment with a 3-fold as well as a 15-fold increase in production, for both 10- and 100-km reserves and a range of dispersal scales. Because our assumption of equal production throughout the domain before reserve establishment leads to equal recruitment everywhere (excepting domain boundaries) before reserves are established, the change in recruitment directly reflects patterns of recruitment across space after reserve establishment.

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Supporting Information

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Detailed Methods of Model

This model compares recruitment before and after reserve establishment, assuming biomass has reached an equilibrium state, and does not address transient dynamics. In a recent global meta-analysis of the ecological effects of marine reserves, Lester et al. (1) found a median increase in biomass of 200% inside marine reserves. Most studies included in the meta-analysis compare values inside and outside reserves, with no before–after component. In a review of the reserve studies that do use a before–after–control–impact (BACI) design, Lester et al. (1) found no evidence that biomass (or any other metrics) decreased outside reserves after the onset of protection. However, in the model, we made the conservative assumption that displaced fishing effort from closing a reserve area to fishing results in higher fishing mortality rates outside reserves after implementation (fishery squeeze), such that the instantaneous fishing mortality rate outside reserves is

$$F_{\text{outside}} = \frac{F}{1-R},$$  \[S1\]

where $F$ is the instantaneous fishing mortality rate before reserves are set aside and $R$ is the proportion of the coastline in reserves (2). Therefore, after reserve implementation, biomass was assumed to be reduced by a factor of $e^{-F/2\pi}$ due to displaced fishing effort.

To determine how increased biomass in reserves translates to potential larval export, we estimated both how reproductive output scales with biomass and the fate of any increased reproductive output. The relationship between increased biomass and increased reproductive output depends in part on relative fecundity (egg weight per body weight). Relative fecundity may decrease with increasing age or body size in a few species (3). In most cases, however, relative fecundity either is constant (4–6) or increases with increasing biomass (7–9), suggesting that biomass increases in reserves may lead to even greater enhancement of reproductive output. The effects of reserves on reproductive output also depend on whether changes in biomass are driven mainly by increased abundance or increased sizes, whether individuals outside reserves are largely below reproductive size, and how density-dependent effects modify fecundity inside reserves as density increases. Therefore, studies that measure changes in both biomass and reproductive output in marine reserves provide the most useful estimates of the relationship between the two response variables. Several studies have examined changes in both biomass and reproductive output in reserves. Changes in reproductive output were similar in magnitude to changes in biomass for rockfish (10), spiny lobster (11), coral reef fish (12), and scallop (13), whereas reproductive output increased more than biomass for snail (14), limpet (15), grouper (16), and two species of snapper (17, 18). Although there is evidence that for some species changes in biomass may lead to disproportionately large increases in reproductive output, in this model we conservatively assumed that reproductive output scales linearly with biomass. This assumption suggests that the 200% increase in biomass found in reserves should lead to a 200% increase in production inside reserves relative to outside. To model the spatial distribution of production, we make the simplifying assumption that before reserve implementation, production everywhere in the domain is equal (although this assumption is relaxed in more complex extensions of the model, detailed below). After reserves are designated, production outside reserves is

$$P_{\text{outside}} = P_{\text{before}} e^{-F/2\pi},$$  \[S2\]

where $P_{\text{outside}}$ represents production outside reserves, which is reduced due to fishery squeeze, and $P_{\text{before}}$ is the production everywhere before reserves are put in place. Production inside reserves is modeled as

$$P_{\text{inside}} = 3 P_{\text{before}} e^{-F/2\pi},$$  \[S3\]

where $P_{\text{inside}}$ is the production inside reserves, represented as 200% (or 3-fold) higher than production outside.

The fate of increased reproductive output depends on larval transport and larval survival. We modeled larval dispersal with a Laplacian (double exponential decay) dispersal kernel (19, 20),

$$K_{Laplacian}(x, y) = \frac{d}{2} e^{-d(x-y)^2},$$  \[S4\]

where $K_{Laplacian}(x, y)$ is the probability a larva from site $x$ arrives at site $y$, and the mean scale of dispersal via diffusion is $\frac{d}{2}$. The number of larvae arriving at each site was determined by multiplying production by the dispersal kernel and integrating over the domain.

To model postsettlement survival, we allowed for both intercohort and intracohort density dependence at settlement. Intercohort density dependence may be driven by territorial adults or cannibalism, whereas intracohort density dependence typically results from competition among settling larvae, for example, for refuge space (21). Several studies of fisheries species have found that the Gompertz (log-linear) model of density dependence matches empirical data more closely than the Ricker model (22–25). We modeled both intercohort and intracohort density dependence with the Gompertz model,

$$N_{t+1} = L_t e^{-m - \alpha \log N_t} - \beta \log N_t,$$  \[S5\]

where $N_t$ is the number of postsettlement individuals at time $t$, $L_t$ is the number of larvae at time $t$, $m$ is the density-independent instantaneous mortality rate for settling larvae, $\alpha$ is the intercohort density-dependence coefficient, and $\beta$ is the intracohort density-dependence coefficient.

Various Dispersal Kernels. To test the robustness of our results to various dispersal kernels, we also ran the model using both a Gaussian kernel and simulated dispersal kernels for Caribbean coral, fish, and lobster, in addition to the Laplacian dispersal kernel. Gaussian dispersal was modeled with the equation

$$K_{Gaussian}(x, y) = \frac{e^{-(x-y)^2/2\beta^2}}{\beta \sqrt{2\pi}},$$  \[S6\]

where the mean diffusive dispersal distance is calculated as $\beta \sqrt{2/\pi}$.

Dispersal trajectories for coral, fish, and lobster were generated from simulations of a detailed oceanographic circulation model with 1,915 spawning release sites across the Caribbean, incorporating life history information for each species, with monthly releases for 2 years. The resulting data were scaled to kernels describing the likelihood of arrival as a function of distance from a source site.
such that the probabilities across the domain scaled to 1 (Fig. S1), and sixth-order polynomials were fit to the simulated kernels using MATLAB. Finally, for comparison with the Gaussian and Laplacian kernels, we estimated the mean dispersal scale of coral, fish, and lobster from the derived kernels, using the relationship

\[
\delta = 2 \int_0^\infty |\text{dist}| K_{\text{poly}}(\text{dist}),
\]

where \(\delta\) is the mean dispersal scale, and \(K_{\text{poly}}\) is the polynomial function calculated above, describing the probability of larval arrival as a function of \(\text{dist}\), the distance from a source site.

Results from the model with a Gaussian dispersed kernel were nearly identical to results from the Laplacian model, for corresponding dispersal scales and reserve lengths (Fig. S2). We calculated mean dispersal distances of \(\sim 100, 150,\) and 350 km from the kernels describing dispersal in Caribbean corals, fish, and lobsters, respectively. The proportional change in recruitment predicted by our model using these kernels was very similar to results from the Laplacian and Gaussian models with similar dispersal scales (Fig. S3).

**Habitat Distribution and Advection.** On real coastlines, appropriate habitat for a particular species is rarely continuous across large spatial scales. The availability and quality of suitable habitat for adults and settlers is an important driver of connectivity (26) and may be critical to predicting and interpreting the effects of larval export in reserve systems. In addition, larval dispersal is not merely diffusive, as modeled above, but frequently also has a strong advective component, due to directional currents (27). Therefore, we examined the effects of both habitat distribution and advective currents using a discrete version of our model.

We investigated how reserve protection affects recruitment under more complex conditions by applying a discrete version of our model that allows for varying habitat distributions and advective currents. For the discrete model, we used the double geometric dispersal kernel, a discrete analog for exponential decay, and added a parameter to describe dispersal by advection as well as diffusion.

\[
K_{\text{Geom}}(x, y) = \frac{(1 - D) e^{-\gamma x + \alpha y} + D}{2},
\]

where the mean diffusive dispersal distance is \(\frac{\sqrt{D}}{\beta}\), and the mean advection distance is given by \(a\).

To vary habitat, we randomly assigned patches of suitable and unsuitable habitat across the domain so that a predetermined proportion of the coastline consisted of suitable habitat, with a minimum patch size of 1 km. To explore the effects of biased reserve siting, with more suitable habitat in reserves, we allowed for the proportion of habitat inside the reserve to differ from the proportion of habitat outside. We calculated the number of larvae arriving at each site by summing the contribution from each patch in the domain,

\[
L_y = \sum_x P_x K_{\text{Geom}}(x, y),
\]

where \(L_y\) is larval arrival at any location \(y\), \(P_x\) is larval production at location \(x\), and \(K_{\text{Geom}}(x, y)\) is the probability distribution of settlement given in Eq. S8. Next, we applied density dependence as in the continuous model (Eq. S5) to determine postsettlement recruitment at each site. We assumed that larvae require adult habitat for successful settlement; therefore, only larvae arriving at a site containing suitable habitat were assumed to survive.

Where habitat is patchily distributed, the proportion of suitable habitat may differ inside versus outside reserves, potentially confounding reserve effects (26). To explore this possibility, we ran our model with 80% of the area in reserves designated as habitat, whereas only 50% of the area outside reserves was habitatable. In contrast to the model with continuous habitat, the benefits from larval export in the patchy model were increased for small fractions of coastline in reserves, but declined more quickly with an increasing fraction of coastline in reserves (Fig. S4 A and B). Unlike the continuous model, in the patchy model overall benefits outside reserves peaked with \(\sim 30\%\) of the coastline in reserves, and when \(60\%\) of the coastline was in reserves, there was no net benefit from export for any of the modeled dispersal scales.

Where suitable habitat is concentrated in reserves, the proportion of suitable habitat closed to fishing increases more quickly than the proportion of coastline closed to fishing, thereby increasing both enhanced larval production and the fishery squeeze effect. For example, with the heterogeneous habitat distribution modeled here, placing \(60\%\) of the coastline in reserves closes >70% of suitable habitat to fishing. Similarly, the patchiness of the habitat also increases the detectable signal of larval export when small fractions of the coastline are protected, but the change in recruitment at reserve edges declines with greater proportions of coastline in reserves (Fig. S4 C and D). Overall, the patchy habitat model behaves similarly to the continuous habitat model, but results are driven by the proportion of suitable habitat placed in reserves, rather than the proportion of coastline.

We examined the effect of advection on larval export by running the model with 100% suitable habitat both inside and outside reserves, and a mean advection distance of 50 km in addition to a range of diffusive dispersal distances. With strong advection, there were greater net benefits from larval export for short-distance dispersers, particularly in large reserves, compared to the models with no advection (Fig. S5 A and B). Whereas most extra larval production for short-distance dispersers was retained in reserves without advection, strong advection allowed many of the extra larvae to be exported, even if the diffusion scale was very short. In addition, the benefits of export increased with increasing fractions of coastline placed in reserves. A greater proportion of coastline in reserves led to more enhanced larval production, and enough of the extra production was exported due to advection to offset the additional fishery squeeze effect. The signal of larval export was also more detectable when advection was included, particularly for greater proportions of coastline in reserves (Fig. S5 C and D). As with the overall benefit to fish habitat, the greater increase in recruitment at reserve edges was driven by enhanced export of extra production due to advection. The results of the advection model suggest that in systems with strongly directional currents, greater benefits from larval export are possible, a conclusion that mirrors previous theoretical findings (27). In addition, the increased signal of larval export in advective systems suggests that empirical studies designed to sample downstream of reserves in areas with strong currents may be better able to detect the larval export effect than those conducted in systems without directional dispersal.

**Model Parameters.** We ran the model with Laplacian and Gaussian kernels across a 1,000-, a 5,000-, and a 10,000-km domain (i.e., the spatial scale over which simulations take place) and found no major differences due to domain size. Our kernels for coral, fish, and lobster were not well defined beyond 1,000 km, so in both the continuous model and the discrete model simulations, we used a 1,000-km domain for all of the results shown. Our domain included 100-km buffers on each end of the coastline, which contributed to total production in the system, but were not included in the calculation of overall change in recruitment outside reserves, to reduce the effect of propagule loss due to absorbing boundaries in the model. We ran each model across a range of possible parameters (0–1) for each of the density-dependence coefficients and the instantaneous fishing mortality rate. Results were qualitatively similar across the range of parameters, except that in models with intercohort density dependence, recruitment was suppressed to lower values inside
reserves than outside due to high adult densities inside, a pattern that has been found for highly territorial limpets inside reserves (15). We discuss how larval export effects varied with levels of fishing mortality (F), intracohort density-dependent coefficient (\( \alpha \)), and intercohort density-dependent coefficient (\( \beta \)) below (Effects of Fishing Mortality and Density Dependence). Throughout the remainder of this paper, we show results for an array of realistic dispersal scales (25) and reserves sizes (1), for an instantaneous fishing mortality rate of \( F = 0.4 \) and density-dependence parameters of \( \alpha = 0.5 \) and \( \beta = 0 \), values within the range found for fisheries species in previous studies (29).

**Effects of Fishing Mortality and Density Dependence.** We examined how varying fishing mortality and density-dependence coefficients affects changes in recruitment due to larval export. We modeled changes in recruitment after reserve establishment for three levels of instantaneous fishing mortality rates: \( F = 0.2, F = 0.4 \) (used throughout the rest of this paper), and \( F = 0.8 \). These rates span the range of fishing mortality rates found in real fisheries throughout the world (30). We used a moderate mean dispersal distance of 50 km, intracohort density-dependence coefficient \( \alpha = 0.5 \), and intracohort density-dependence coefficient \( \beta = 0 \) for these simulations (not discussed in the main text, under these conditions, recruitment increases after reserve establishment with up to 60% of the coastline placed in reserves, with peak benefits occurring at ~40% of the coastline in reserves (Fig. S6). The net benefits of reserves are even greater with a low fishing mortality rate of \( F = 0.2 \). At this lower fishing mortality rate, the benefits increased with an increasing proportion of the coastline in reserves (Fig. S6). However, with a high fishing mortality rate (\( F = 0.8 \)), there was little change in recruitment with up to ~30% of the coastline in reserves, and the net change recruitment was negative with greater than ~30–40% of the coastline in reserves (Fig. S6). A fishing mortality of \( F = 0.8 \) combined with about a third of the coastline in reserves represents a possible threshold of fishery squeeze impacts, beyond which the benefits of larval export cannot offset squeeze (although this threshold may be reached at various combinations of \( F \), dispersal distance, reserve size, and proportion of coastline in reserves). The reduced benefits of larval export in a system with high fishing mortality rates result from the increased pressure on fished populations outside reserves due to fishery squeeze, because the impact of fishery squeeze is proportional to fishing mortality. This contrasts with results of models assuming a reduction in overall fishing effort due to reserve establishment rather than a realloation of effort, which generally found that marine reserve benefits increased with increasing fishing effort outside reserve borders (31). An instantaneous fishing mortality rate of 0.8 (equivalent to an annual fishing mortality rate of ~0.55) is higher than typical exploitation rates found in fisheries worldwide, and such fishing mortality rates are unlikely to be sustainable in most systems with or without closed areas (30). However, marine reserves can be an important tool used in combination with reductions in effort and other management tools to help reduce exploitation rates to sustainable levels (30).

Next we considered the effects of varying density-dependence parameters, with a focus on how the effects outside of reserve boundaries vary with the strength of density dependence. We explored the effects of intracohort density dependence (\( \alpha \)) on larval export benefits, assuming a mean dispersal distance of 50 km, instantaneous fishing mortality rate of 0.4, and no intercohort density dependence. Strong intracohort density dependence lessened the benefits of reserves, such that recruitment outside reserves increased no more than ~5% outside reserves with \( \alpha = 0.75 \) (Fig. S7). However, even with this strong rate of density dependence at settlement, reserves still led to a net increase in recruitment across a wide range of reserve sizes and proportions of coastline in reserves. In agreement with other scenarios explored in this paper, with both weak and strong intracohort density dependence, the net benefits outside reserve boundaries peaked at ~40% of the coastline in reserves. The greatest benefits, peaking at more than a 25% increase in recruitment outside reserve boundaries, occurred with relatively weak intracohort density dependence (\( \alpha = 0.25 \)) (Fig. S7). The increase in the benefits of reserves outside their boundaries with decreasing intracohort density dependence is not surprising. When intracohort density dependence at settlement is strong, competition between settling larvae increases mortality at settlement for large cohorts, reducing some of the benefit of enhanced recruitment near reserve boundaries.

Finally, we addressed the influence of intercohort density dependence on larval export benefits, for a species with a mean dispersal scale of 50 km, \( F = 0.4 \), and \( \alpha = 0.5 \). The benefits of larval export increased with increasing strength of intercohort density dependence (\( \beta \)) (Fig. S8). When \( \beta \) is high, adults reduce survival of settling larvae through competition or predation. Because fishery squeeze reduces adult populations outside reserves, the survival of settlers is enhanced outside reserves, which acts in combination with increased supply due to larval export to increase recruitment outside reserves. As a result of both increased supply and reduced intercohort density-dependent mortality, for both \( \beta = 0.3 \) and \( \beta = 0.6 \), the benefits of larval export increased with increasing fractions of coastline placed in reserves (Fig. S8).

**Power to Detect Changes in Recruitment.** We cannot predict the precise circumstances necessary to allow detection of enhanced recruitment due to larval export. The ability to detect these changes in recruitment will depend on the natural variability in recruitment, sample sizes, experimental design, and other factors beyond the scope of this study, in addition to the factors modeled here (i.e., production differential, mean larval dispersal scale, fishing mortality, and density dependence). Additionally, the causes and consequences of natural variability in recruitment are complex. Recruitment variability is likely to increase with mean recruitment and may also depend on factors such as regional oceanographic characteristics, habitat heterogeneity, larval behavior, larval mode, and planktonic duration (32, 33). Whereas it is not possible to conclusively determine when a change in recruitment resulting from larval export may be detected in the field, it is clear that the greater the difference is in mean recruitment relative to natural variability, the more likely that difference is to be detectable. In addition, it seems likely that for most study designs, modest increases in recruitment will be difficult to detect, given typical coefficients of variation in natural recruitment of ~150–200% (32, 33). To illustrate this, we examined the statistical power to detect changes in mean recruitment before compared to after reserve establishment, assuming a sample size of 25 replicates at each site and a standard deviation equal to 150% of the mean recruitment before the reserve is established (i.e., \( CV = 150% \)). The results of this analysis demonstrate that the statistical power to detect subtle changes given high natural variability is probably quite low; for example, in this theoretical scenario the power to detect an increase in recruitment of between 10 and 45%, as predicted for a broad suite of parameters in our model (Fig. 1), is \(<0.2 \) (Fig. S9). In other words, in this scenario, this change in recruitment would be detected \(<20\% \) of the time. It is important to emphasize that as the results of this analysis are qualitative, the above example does not suggest a particular threshold for the ability to detect changes in recruitment due to larval export, but merely emphasizes the challenges of detecting these changes in most systems, particularly when the dispersal scale is long relative to reserve size. Depending on characteristics of the system and study design, it may be possible to detect more subtle changes, potentially even in cases where the change in mean recruitment is less than the standard deviation.

**Comparison of Empirical and Theoretical Results: A Case Study.** The data presented in Pelc et al. (34) allow us to compare empirical spatial patterns in recruitment with the patterns predicted by our
model. We explored the patterns of recruitment for conditions mirroring those reported by Pelc et al. (34) in the Goukamma and Dwesa regions. To reflect conditions in Goukamma, we modeled a 3-fold increase in production in reserves, with a mean dispersal scale of ~4 km. To approximate the heterogeneous habitat distribution found in the reserve, we set the proportion of suitable habitat to 60% inside reserves and 20% outside reserves. For the Dwesa simulation, we modeled a 2.2-fold increase in production in reserves with fairly continuous habitat (90% suitable habitat both inside and outside reserves) and a mean dispersal scale of 12 km. In Goukamma, simulated patterns in recruitment were qualitatively similar to the empirical results, and the decline in recruitment occurred over a similar spatial scale of ~30 km from the reserve’s center (Fig. S10 A and B). However, the proportional increase in recruitment near the center of the reserve relative to outside was nearly two orders of magnitude in the actual data compared to just under a 4-fold increase in the simulations. The discrepancy may be due in part to either natural or density-dependent variation in settlement habitat quality. In the model, all patches along the coastline are either habitable or uninhabitable, but there is no variation in quality of habitable patches. However, just as there is a greater proportion of suitable habitat in the reserve, the available habitat may also be higher quality in the reserve, allowing for greater settlement or postsettlement survival of arriving larvae. Similarly, because mussel larvae settle directly into mussel habitat (35), the higher densities of adult mussels in the reserves may exacerbate differences in settlement through positive intercohort density dependence. Whereas relationships between settlement rates and adult mussel density have been found in other systems (35), Pelc et al. (34) did not find this correlation in their study. Overall, our simulations mirror their findings that despite possible natural gradients in production and/or recruitment, larval export from the high production population in the Goukamma reserve contributes to a steep decline in recruitment on a scale of ~30 km (34). However, it appears that our model may underestimate the magnitude and spatial signal of larval export for this system. Simulated patterns of recruitment in the Dwesa region match the available empirical data from the region fairly well (Fig. S10 C and D). In the empirical data, recruitment declined ~3-fold from inside the reserve to the farthest site, located ~22 km from the reserve center (Fig. S10C). In the simulated data, recruitment declined ~2-fold across the same spatial scale (Fig. S10D). Without empirical data from more distant sites, we cannot determine how well the actual recruitment levels near Dwesa match the simulations beyond ~22 km from the reserve center. However, our simulation suggests that recruitment near Dwesa continues to decline well beyond the farthest site sampled and is elevated above baseline (before reserve) recruitment rates within ~70 km of the reserve center. It appears from our simulations that the spatial scale of sampling was sufficient to capture the scale of the larval export effect near the Goukamma reserve, but too short to fully characterize the scale of export near the Dwesa reserve. Therefore, both the scale and the magnitude of the larval export effect in the Dwesa region are probably underestimated by using a highly conservative value for baseline recruitment (34).


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**Fig. S1.** Dispersal kernels for coral, fish, and lobster in the Caribbean.

**Fig. S2.** Change in recruitment outside reserves after the onset of protection, based on Gaussian dispersal kernel, (A) integrated across the area outside reserves, for networks of 10-km reserves, (B) integrated across the area outside reserves, for networks of 100-km reserves, (C) just outside reserve boundaries, for networks of 10-km reserves, and (D) just outside reserve boundaries, for networks of 100-km reserves. Results are shown for three different dispersal distances, $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$.

**Fig. S3.** Change in recruitment outside reserves after the onset of protection, based on dispersal kernels for three different species derived from oceanographic simulations, (A) integrated across the area outside reserves, for networks of 10-km reserves, (B) integrated across the area outside reserves, for networks of 100-km reserves, (C) just outside reserve boundaries, for networks of 10-km reserves, and (D) just outside reserve boundaries, for networks of 100-km reserves. Results shown for $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$. 
Fig. S4. Change in recruitment outside reserves after the onset of protection, with 80% coastline in reserves habitable and 50% of coastline outside reserves habitable, (A) integrated across the area outside reserves, for networks of 10-km reserves, (B) integrated across the area outside reserves, for networks of 100-km reserves, (C) just outside reserve boundaries, for networks of 10-km reserves, and (D) just outside reserve boundaries, for networks of 100-km reserves. Results are shown for three different dispersal distances, $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$.

Fig. S5. Change in recruitment outside reserves after the onset of protection, with 50-km advection scale, (A) integrated across the area outside reserves, for networks of 10-km reserves, (B) integrated across the area outside reserves, for networks of 100-km reserves, (C) just outside reserve boundaries, for networks of 10-km reserves, and (D) just outside reserve boundaries, for networks of 100-km reserves. Results are shown for three different dispersal distances, $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$.

Fig. S6. Change in recruitment outside reserves after the onset of protection, (A) integrated across the area outside reserves, for networks of 10-km reserves, and (B) integrated across the area outside reserves, for networks of 100-km reserves. Results are shown for a mean dispersal scale of 50 km, three different instantaneous fishing mortality rates ($F$), $\alpha = 0.5$, and $\beta = 0$. 

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Fig. S7. Change in recruitment outside reserves after the onset of protection, (A) integrated across the area outside reserves, for networks of 10-km reserves, and (B) integrated across the area outside reserves, for networks of 100-km reserves. Results are shown for a mean dispersal scale of 50 km, $F = 0.4$, three different intracohort density-dependence coefficients ($\alpha$), and $\beta = 0$.

Fig. S8. Change in recruitment outside reserves after the onset of protection, (A) integrated across the area outside reserves, for networks of 10-km reserves, and (B) integrated across the area outside reserves, for networks of 100-km reserves. Results are shown for a mean dispersal scale of 50 km, $F = 0.4$, $\alpha = 0.5$, and three different intercohort density-dependence coefficients ($\beta$).

Fig. S9. Statistical power (1 – the probability of a type II error) as a function of percentage of change in mean recruitment, assuming a comparison between a site before and after reserve establishment, with a sample size of 25 and a standard deviation in recruitment equal to the mean recruitment before reserve establishment.
Table S1. Summary of empirical evidence for larval export from reserves

<table>
<thead>
<tr>
<th>Region</th>
<th>Species</th>
<th>PLD, days</th>
<th>Reserve size, km²</th>
<th>Change inside reserve</th>
<th>Type of evidence</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goukamma, South Africa</td>
<td>Brown mussel <em>Perna perna</em></td>
<td>10–20</td>
<td>40</td>
<td>3-fold increase in production</td>
<td>Decline in recruitment with distance</td>
<td>(34)</td>
</tr>
<tr>
<td>Dwesa, South Africa</td>
<td>Brown mussel <em>P. perna</em></td>
<td>10–20</td>
<td>39</td>
<td>22-fold increase in biomass</td>
<td>Decline in recruitment with distance</td>
<td>(34)</td>
</tr>
<tr>
<td>Dvesa, South Africa</td>
<td>South African eye limpet <em>Cymbula oculus</em></td>
<td>6</td>
<td>39</td>
<td>80-fold increase in production</td>
<td>No evidence of decline with distance</td>
<td>(15)</td>
</tr>
<tr>
<td>Tenerife, Spain</td>
<td>China limpet <em>Patella aspera</em></td>
<td>6</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Decline in recruitment with distance</td>
<td>(36)</td>
</tr>
<tr>
<td>Georges Bank, United States</td>
<td>Deep sea scallop <em>Placopecten magellanicus</em></td>
<td>32–56</td>
<td>17,000</td>
<td>14-fold increase in density</td>
<td>5-fold increase in adult abundance downcurrent of reserve</td>
<td>(37, 38)</td>
</tr>
<tr>
<td>Fiji</td>
<td>Clam <em>Anadara sp.</em></td>
<td>20–30</td>
<td>0.24</td>
<td>19-fold increase in density</td>
<td>8-fold increase downcurrent of reserve</td>
<td>(39, 40)</td>
</tr>
<tr>
<td>Gulf of California, Mexico</td>
<td>Rock scallop <em>Spondylus calcifer</em></td>
<td>&lt;28</td>
<td>18 (all reserves in network)</td>
<td>Unknown for adults. 40% increase in juvenile density</td>
<td>Increase downcurrent of reserve</td>
<td>(41)</td>
</tr>
<tr>
<td>Gulf of California, Mexico</td>
<td>Black murex snail <em>Hexaplex nigritus</em></td>
<td>&lt;28</td>
<td>18 (all reserves in network)</td>
<td>Unknown</td>
<td>3-fold increase downcurrent of reserve</td>
<td>(41)</td>
</tr>
<tr>
<td>Exuma Cays, Bahamas</td>
<td>Queen conch <em>Strombus gigas</em></td>
<td>25–30</td>
<td>456</td>
<td>30-fold increase in density</td>
<td>2- to 10-fold more early-stage veligers near reserve relative to far</td>
<td>(42, 43)</td>
</tr>
<tr>
<td>Isle of Man, United Kingdom</td>
<td>Great scallop <em>Pecten maximus</em></td>
<td>16–33</td>
<td>2</td>
<td>12-fold increase in reproductive output</td>
<td>Higher spat settlement near reserve than far; 5- to 10-fold increase in abundance of 2-yr olds at sites near but not far from reserves</td>
<td>(13, 44)</td>
</tr>
</tbody>
</table>

Fig. S10. Spatial patterns in recruitment inside and outside reserves from simulations compared to empirical data. Shown are (A) simulation of the Goukamma region, (B) data from the Goukamma region, (C) simulation of the Dwesa region, and (D) data from the Dwesa region. Empirical data are from Pelc et al. (34).