

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 downcurrent 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.

spillover | marine protected areas | recruitment | dispersal | fisheries

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 magnitude, scale, and spatial and temporal signal of larval export, with biological parameters based on recent empirical data. We also incorporate density dependence at 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

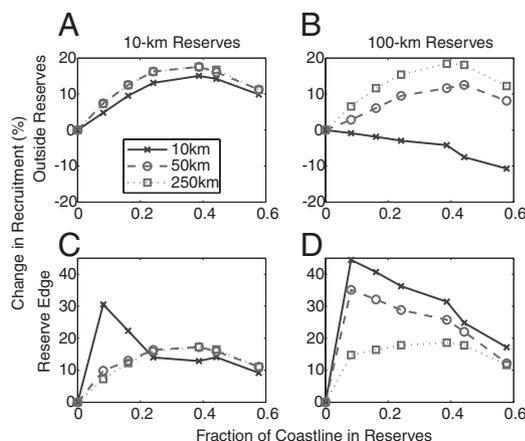


Fig. 1. Change in recruitment outside reserves after the onset of protection, based on a Laplacian dispersal kernel, (A) integrated across the area outside reserves for networks of 10-km reserves, (B) integrated across the area outside reserves for networks of 100-km reserves, (C) just outside reserve 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 mean dispersal distances: $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$.

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. 2A). 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

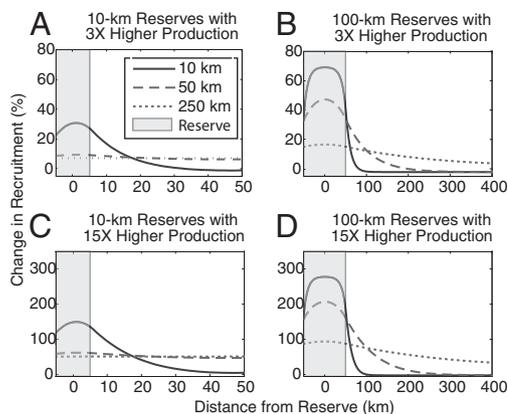


Fig. 2. Change in recruitment with distance from one reserve within a network. Shown are (A) 10-km reserves with a 3-fold increase in production, (B) 100-km reserves with a 3-fold increase in production, (C) 10-km reserves with a 15-fold increase in production, and (D) 100-km reserves with a 15-fold increase in production. Results are shown for three different mean dispersal distances, 10% of the coastline in reserves, $F = 0.4$, $\alpha = 0.5$, and $\beta = 0$.

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 environmental 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 ungulate 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 dif-

ferential, 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 ($\sim 17,000$ 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 larvae 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 (fishery 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 *Fig. S6–S8* and *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 at the reserve edge (where the detectable signal of export is often the strongest), mirroring a response variable typically measured in larval export studies with a before–after design. We examined changes 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 (*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 or biomass 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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- Lester SE, et al. (2009) Biological effects within no-take marine reserves: A global synthesis. *Mar Ecol Prog Ser* 384:33–46.
- Stobutzki IC (2001) Marine reserves and the complexity of larval dispersal. *Rev Fish Biol Fish* 10:515–518.
- Hilborn R, et al. (2004) When can marine reserves improve fisheries management? *Ocean Coast Manage* 47:197–205.
- Palumbi SR (2004) Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Annu Rev Environ Resour* 29:31–68.
- Gaylord B, Gaines SD, Siegel DA, Carr MH (2005) Marine reserves exploit population structure and life history in potentially improving fisheries yields. *Ecol Appl* 15: 2180–2191.
- Sale PF, et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* 20:74–80.
- Gell FR, Roberts CM (2003) Benefits beyond boundaries: The fishery effects of marine reserves. *Trends Ecol Evol* 18:448–455.
- Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol Appl* 13:5117–5137.
- Pelc R, Baskett ML, Tanci T, Gaines S, Warner RR (2009) Quantifying larval export from South African marine reserves. *Mar Ecol Prog Ser* 394:65–78.
- Tawake A, et al. (2001) Harvesting clams and data: Involving local communities in monitoring can lead to conservation success in all sorts of unanticipated ways: A case in Fiji. *Conserv Biol Pract* 2:32–35.
- Tawake A, Gell F, Roberts C (2002) *The Fishery Effects of Marine Reserves and Fishery Closures*, eds Gell F, Roberts C (WWF-US, Washington, DC), pp 59–62.
- Murawski SA, Brown R, Lai HL, Rago PJ, Hendrickson L (2000) Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bull Mar Sci* 66:775–798.
- Cudney-Bueno R, Lavin MF, Marinone SG, Raimondi PT, Shaw WW (2009) Rapid effects of marine reserves via larval dispersal. *PLoS One* 4:e4140.
- Hockey PAR, Branch GM (1994) Conserving marine biodiversity on the African coast—implications of a terrestrial perspective. *Aquat Conserv: Mar Freshw Ecosyst* 4:345–362.
- Stoner AW, Mehta N, Ray-Culp M (1998) Mesoscale distribution patterns of Queen Conch (*Strombus gigas* Linnaeus) in Exuma Sound, Bahamas: Links in recruitment from larvae to fishery yields. *J Shellfish Res* 17:955–969.
- Stoner AW, Ray M (1996) Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: Effects of a marine fishery reserve on adults, juveniles, and larval production. *Fish Bull (Wash D C)* 94:551–565.
- Beukers-Stewart BD, Vause BJ, Mosley MWJ, Brand AR (2004) Evidence for larval export of scallops from a small closed area off the Isle of Man. *ICES Annual Science Conference*, Vigo, Spain (Copenhagen, ICES), p. 262.
- Beukers-Stewart BD, Vause BJ, Mosley MWJ, Rossetti HL, Brand AR (2005) Benefits of closed area protection for a population of scallops. *Mar Ecol Prog Ser* 298:189–204.
- McClanahan TR, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol Appl* 10:1792–1805.
- Roberts CM, Bohnsack JA, Gell F, Hawkins JP, Goodridge R (2001) Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923.
- Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT (2004) Marine reserve benefits local fisheries. *Ecol Appl* 14:597–606.
- Eckert G (2003) Effects of the planktonic larval period on marine population fluctuations. *Ecology* 84:372–383.
- Navarrete SA, Broitman BR, Menge BA (2008) Interhemispheric comparison of recruitment to intertidal communities: Pattern persistence and scales of variation. *Ecology* 89:1308–1322.
- Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecol Appl* 14: 1248–1256.
- Branch GM, Odendaal F (2003) The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biol Conserv* 114:255–269.
- Manriquez PH, Castilla JC (2001) Significance of marine protected areas in central Chile as seedling grounds for the gastropod *Concholepa concholepa*. *Mar Ecol Prog Ser* 215:201–211.
- Willis TJ, Millar RB, Babcock RC (2003) Protection of exploited fish in temperate regions: High density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J Appl Ecol* 40:214–227.
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* 84:2007–2020.
- Gaines SD, Gaylord B, Largier JL (2003) Avoiding current oversights in marine reserve design. *Ecol Appl* 13:532–546.
- Botsford LW, Hastings A, Gaines SD (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol Lett* 4:144–150.
- Lockwood DR, Hastings A, Botsford LW (2002) The effects of dispersal patterns on marine reserves: Does the tail wag the dog? *Theor Popul Biol* 61:297–309.
- Kaplan DM, Botsford LW (2005) Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. *Can J Fish Aquat Sci* 62:905–912.
- White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries management. *Oikos* 116:2039–2043.
- Gerber LR, et al. (2003) Population models for marine reserve design: A retrospective and prospective synthesis. *Ecol Appl* 13:547–564.
- Botsford LW, et al. (2009) Connectivity, sustainability, and yield: Bridging the gap between conventional fisheries management and marine protected areas. *Rev Fish Biol Fish* 19:69–95.
- Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 17:1039–1054.
- Fogarty MJ, Botsford LW (2007) Population connectivity and spatial management of marine fisheries. *Oceanography (Wash DC)* 20:112–123.
- Grour-Colvert K, Sponaugle S (2009) Larval supply and juvenile recruitment of coral reef fishes to marine reserves and non-reserves of the upper Florida Keys, USA. *Mar Biol* 156:277–288.
- Pineda J, Hare J, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography (Wash DC)* 20:22–39.

40. Porri F, McQuaid CD, Radloff S (2006) Spatio-temporal variability of larval abundance and settlement of *Perna perna*: Differential delivery of mussels. *Mar Ecol Prog Ser* 315:141–150.
41. Menge BA, Chan F, Nielsen KJ, Lorenzo ED, Lubchenco J (2009) Climatic variation alters supply-side ecology: Impact of climate patterns on phytoplankton and mussel recruitment. *Ecol Monogr* 79:379–395.
42. Broitman BR, et al. (2008) Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. *Ecol Monogr* 78:403–421.
43. Shanks AL (2009) Barnacle settlement versus recruitment as indicators of larval delivery. I. Effects of post-settlement mortality and recruit density. *Mar Ecol Prog Ser* 385:205–216.
44. Levin SA (1976) Population dynamic models in heterogeneous environments. *Annu Rev Ecol Syst* 7:287–310.
45. Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J Ecol* 94:181–195.
46. Freestone AL, Inouye BD (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87:2425–2432.
47. Seabloom EW, Bjornstad ON, Bolker BM, Reichman OJ (2005) Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. *Ecol Monogr* 75:199–214.
48. Whittaker RH, Goodman D (1979) Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. *Am Nat* 113:185–200.
49. Chesson PL, Warner RR (1981) Environmental variability promotes coexistence in lottery competitive systems. *Am Nat* 117:923–943.
50. Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *Am Nat* 125:769–787.
51. Levins R (1969) The effect of random variations of different types on population growth. *Proc Natl Acad Sci USA* 62:1061–1065.
52. Wang GM, et al. (2006) Spatial and temporal variability modify density dependence in populations of large herbivores. *Ecology* 87:95–102.
53. Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proc R Soc Lond Ser B Biol Sci* 270:1871–1878.
54. Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecol Appl* 13:571–589.
55. Siegel DA, Kinlan BP, Gaylord B, Gaines SD (2003) Lagrangian descriptions of marine larval dispersion. *Mar Ecol Prog Ser* 260:83–96.
56. Levin LA (2006) Recent progress in understanding larval dispersal: New directions and digressions. *Integr Comp Biol* 46:282–297.
57. Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:5159–5169.
58. Bradbury IR, Laurel B, Snelgrove PVR, Bentzen P, Campana SE (2008) Global patterns in marine dispersal estimates: The influence of geography, taxonomic category and life history. *Proc R Soc Lond Ser B Biol Sci* 275:1803–1809.
59. White C, Kendall BE, Gaines S, Siegel DA, Costello C (2008) Marine reserve effects on fishery profit. *Ecol Lett* 11:370–379.
60. Bradbury IR, et al. (2008) Discrete spatial dynamics in a marine broadcast spawner: Re-evaluating scales of connectivity and habitat associations in Atlantic cod (*Gadus morhua* L.) in coastal Newfoundland. *Fish Res* 91:299–309.
61. Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: Empirical evaluation and theoretical metapopulation recruitment dynamics. *Mar Freshw Res* 52:1589–1598.
62. Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522–527.
63. White JW (2008) Spatially coupled larval supply of marine predators and their prey alters the predictions of metapopulation models. *Am Nat* 171:E179–E194.