Spatially Coupled Larval Supply of Marine Predators and Their Prey Alters the Predictions of Metapopulation Models

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abstract: Oceanographic forces can strongly affect the movement of planktonic marine larvae, often producing predictable spatial patterns of larval delivery. In particular, recent empirical evidence suggests that in some coastal systems, certain locations consistently receive higher (or lower) larval supplies of both predators and their prey. As a consequence, rates of settlement and predation may be coupled spatially, a phenomenon I term the "coupled settlement effect." To investigate the metapopulation consequences of this phenomenon, I created discrete-time, patch-based analytical and simulation models with a common larval pool and uneven larval supply among patches. Using two complementary measures of subpopulation value as a basis of comparison, I found that models with and without the coupled settlement effect yielded strikingly different predictions. When prey and predator larval supplies were not coupled, patches supplied with a larger proportion of the larval pool made a greater contribution to the metapopulation. When settlement of prey and predator was strongly coupled, however, the opposite was true: subpopulations with lower rates of larval supply (above some minimum) were more essential to metapopulation persistence. These considerations could facilitate more effective selection of sites for protection in marine reserves.

Keywords: metapopulation, predator-prey interactions, source-sink dynamics, spatially coupled dispersal.

The dynamics of many animal populations are strongly influenced by the spatial distribution of predators (Hassell and May 1974; Holt 2002). This is especially true of species in fragmented or spatially discontinuous habitats in which

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both predators and prey are found in discrete patches linked by dispersal into metapopulations. For example, the absence of predators from certain patches can provide refuge habitat that stabilizes the prey metapopulation (Murdoch et al. 1992), while high rates of predator immigration into a particular patch may greatly depress and/or destabilize the local prey population (Holt 2002).

Most theoretical investigations of predator-prey metapopulations center on scenarios in which predator dispersal is either random and diffusive (e.g., Hassell et al. 1994; Hosseini 2005; Amarasekare 2006) or behaviorally directed, so that predators actively search for prey (e.g., Holt 1985; Murdoch et al. 1992; Bernstein et al. 1999; Jackson et al. 2004). In either case, prey population dynamics are shaped by the resulting spatial heterogeneity in predation rates (Briggs and Hoopes 2004). However, neither dispersal assumption is likely to hold for systems in which movement is strongly affected by the advective physical forces, such as wind (Bell et al. 2005) or flowing water (Fagan 2002), a dispersal scenario that is rarely examined in the terrestrial metapopulation literature (but see Lett et al. 2003, 2005). This scenario is particularly relevant for benthic marine metapopulations (Kritzer and Sale 2004) in which dispersal between patches of adult habitat is achieved by planktonic larvae whose movement is driven predominately by oceanic currents (Norcross and Shaw 1984; Shanks 1995). Consequently, theoretical investigations of marine metapopulation dynamics must invoke specific assumptions regarding the specific type of dispersal being modeled, for example, well-mixed larval pools (Roughgarden et al. 1985) versus alongshore advection (Alexander and Roughgarden 1996). In some cases, oceanographic data have been used to create detailed simulations of larval trajectories (James et al. 2002; Gilg and Hilbish 2003; Cowen et al. 2006). Regardless of the level of oceanographic detail used, the majority of these efforts have taken a single-species (i.e., prey) perspective and assumed that within-patch predation rates are spatially invariant, so prey population dynamics are shaped only by patterns of larval delivery (James et al. 2002; Cowen et al. 2006; Karlson 2006; Mumby and Dytham 2006; for notable

exceptions, see Gaines and Lafferty 1995; Connolly and Roughgarden 1999). However, the importance of predator movement to population dynamics of species in both terrestrial and aquatic systems suggests that marine metapopulation models could profit from a consideration of trophic interactions.

Although specific modeling approaches may vary, the goals of most metapopulation studies are generally the same: to identify those patches that are most important to the stability, persistence, or abundance of the metapopulation (Carr et al. 2003). In many cases, the objective is to inform decisions regarding the placement of reserve areas. For marine reserves, placement recommendations vary depending on the specific goals of the reserve (Halpern and Warner 2002; Hastings and Botsford 2003) but commonly emphasize the importance of sites where oceanographic conditions favor consistently high larval supply of target species (Roberts et al. 2003). When the primary reserve goal is biodiversity conservation, protected sites should receive enough locally produced larvae for the reserve population to be self-sustaining (Botsford et al. 2003; Roberts et al. 2003). With this need in mind, it is usually suggested that reserves be placed near oceanographic retention zones or spawning grounds in order to maximize larval delivery (Shepherd and Brown 1993; Warner et al. 2000; Sala et al. 2002). A second common goal is the enhancement of local fisheries by the export of larvae from reserves to fished zones (Halpern and Warner 2002). In this case, retention of all larvae in the reserve is undesirable (Roberts et al. 2003), and some high-settlement sites may remain unprotected in order to maximize the biomass available for harvest (Crowder et al. 2000; Parnell et al. 2006). These recommendations follow from the predictions of single-species metapopulation models (Gerber et al. 2003) and generally rely on the observation that even when mortality in reserves is compensatory and density dependent (Hixon and Webster 2002), adult population density will be positively correlated with the level of recruitment, at least over a wide range of recruit densities (Hixon et al. 2002).

The importance ascribed to the sites with high rates of larval replenishment in existing marine metapopulation models may be an artifact of the single-species approach and the accompanying assumption of spatially uniform mortality rates. New recruits of many marine organisms suffer heavy mortality soon after settling to the benthos (Glynn 1988; Hixon 1991), and in most cases, the predators responsible for this mortality also have planktonically dispersed larvae. Oceanographic forces often affect larvae of different species in similar ways, so taxonomically diverse assemblages of fish and invertebrate larvae are commonly concentrated in coastal eddies and retention zones (Boehlert and Mundy 1993; Wing et al. 1998; Nishimoto

and Washburn 2002). Coastal areas near such oceanographic features generally experience consistently high settlement of many different species (Cowen and Castro 1994; Swearer 2000; Connolly et al. 2001; Valles et al. 2001; Mace and Morgan 2006). Consequently, certain habitat patches are likely to be settlement hotspots for both predators and their prey, and predation rates may be higher in these patches as a result. For example, at the Caribbean island of St. Croix, leeward reefs near an oceanographic convergence experience consistently higher settlement of both bluehead wrasse (*Thalassoma bifasciatum*) and its major predator, the coney (*Cephalopholis fulva*), relative to more exposed, windward reefs (Hamilton et al. 2006; White 2007). As a result, bluehead wrasse recruits experience strong, density-dependent mortality immediately after settlement on the leeward, high-settlement reefs but not on the windward, low-settlement reefs (fig. 1; White 2007).

Metacommunity models predict that a high rate of predator immigration will depress the prey density in a patch (Holt 2002), but single-species models of marine metapopulation dynamics do not incorporate the potential for higher predator densities in patches with high rates of larval supply, a phenomenon I term the "coupled settlement effect." Here I construct a series of simple metapopulation models to illustrate the importance of accounting for spatial correlations in the dispersal of predators and their prey and the resulting spatial variation in predation rates. While not as sophisticated as many recent models grounded in oceanographic flow simulations, these models permit a straightforward examination of the consequences of coupled settlement. A common goal of metapopulation modeling is to identify key "source" subpopulations, so I compare models with and without the coupled settlement effect on the basis of their predictions regarding the importance of a focal deme to the larger metapopulation. Although the models describe a nonexploited system, I used measures of subpopulation importance that would be useful in assessing the costs and benefits of including a particular site in a reserve network.

Quantifying the Value of a Subpopulation

The role played by individual demes in a metapopulation context is commonly described in terms of sources and sinks (reviewed inmean larvalDias 1996; Runge et al. 2006). The definitions of these terms vary by author but are often framed in terms of self-sustainability: sources would persist in isolation, but sinks would not (Pulliam 1988; Armsworth 2002). This definition is favored because the presence of a self-sustaining source is sufficient for the persistence of a metapopulation; if at least one deme is a self-sustaining source, that deme (and, by extension, the metapopulation) will persist even if the remaining sinks
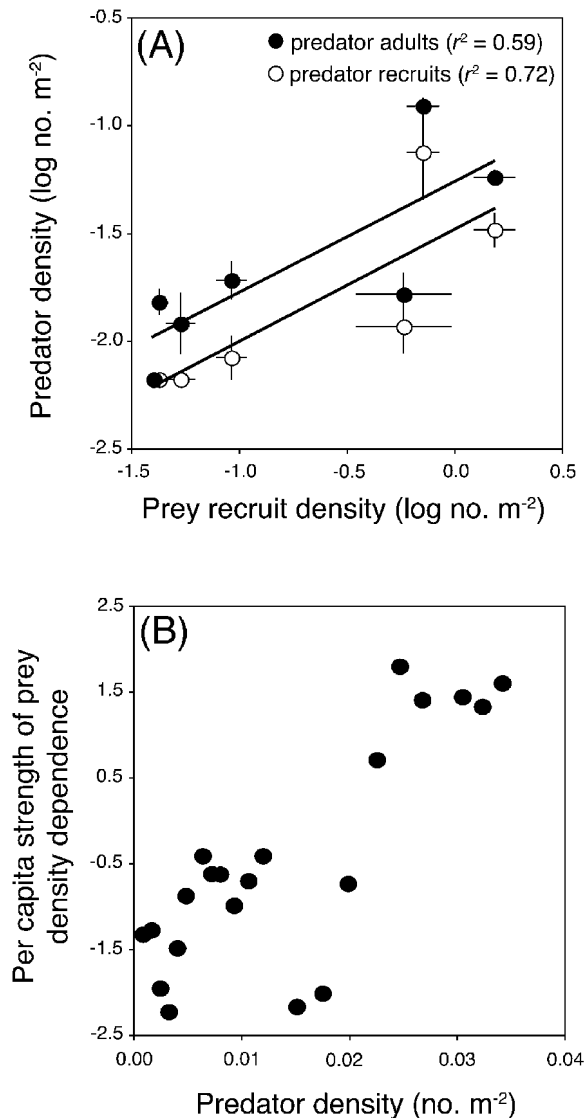
Figure 1: Empirical evidence for the coupled settlement effect for a coral reef fish (bluehead wrasse *Thalassoma bifasciatum*) and its predator (coney grouper *Cephalopholis fulva*) from White (2007). *A*, Relationship between mean prey recruitment and mean recruitment and adult density of the predator on seven reefs at St. Croix, U.S. Virgin Islands, in June–September 2003. Reefs were separated by distances greater than typical distances moved by adult coneys, so the pattern of adult predator abundance reflects long-term trends in recruitment. Error bars are 1 SE. *B*, Per capita strength of density-dependent prey mortality (measured as the slope of the density-mortality relationship and equivalent to $1/\gamma$ in eq. [6]; Schmitt and Holbrook 2007) as a function of predator density. Independent estimates of transect-wide mortality and settler density were obtained on three transects at each of five St. Croix reefs in two months in 2005; points indicate a running average of the slope of the (approximately linear) density-mortality relationship as a function of predator density. Each point represents the slope calculated using the transect-wide density and mortality estimates from a subset of seven transects with similar predator densities; adjacent points have overlapping subsets.

become extinct (Armsworth 2002). However, under this criterion, a self-sustaining source need not export individuals to any other patch and so may not be sufficient for the persistence of a multiple-patch metapopulation. Futhermore, a metapopulation may consist entirely of non-self-sustaining demes if interdeme connectivity is sufficient (Hastings and Botsford 2006). The focus of this article is on the contribution of a focal subpopulation to the larger metapopulation, so I eschew potentially uninformative self-replenishment-based definitions of source-sink status in favor of two alternative metrics of patch value (sensu Ovaskainen and Hanski 2003) drawn from network graph theory (Urban and Keitt 2001).

The first metric is a point estimate of the net reproductive contribution of subpopulation i to the metapopulation, which I term the "export ratio" E_i. Consider a network of equal-sized subpopulations $i = 1 \dots m$ that are separated by barriers to adult movement but linked by the exchange of dispersing larvae. Each subpopulation has a population density n_i and per capita fecundity β_i (for convenience, all variables and parameters used in this article are summarized in table 1). Larvae spawned in subpopulation i disperse to subpopulation j with probability ϕ_{ij}; in transit they have survivorship η_S. The net reproductive contribution of patch i in a given time interval is the difference between the total number of larvae produced in i recruiting anywhere in the metapopulation and the number of larvae produced anywhere in the metapopulation recruiting to i, which is most conveniently represented as a log ratio:

$$E_i = \log \frac{\sum_{j=1}^{m} n_i \beta_i \eta_S \phi_{ij}}{\sum_{j=1}^{m} n_j \beta_j \eta_S \phi_{ji}}. \tag{1}$$

By this criterion, "source" subpopulations that produce more larvae than they receive will have $E_i > 0$, while "sinks" will have $E_i < 0$. In a reserve context, E_i addresses the goal of fishery enhancement, capturing the degree to which reserves export larvae to exploited populations. This measure is analogous to network flux (Urban and Keitt 2001) and is similar to patch contribution metrics used by other authors (Tuck and Possingham 2000; Figueira and Crowder 2006; Runge et al. 2006; Samhouri 2007).

The second metric considers the consequences of removing subpopulation i from the metapopulation, thus capturing both the importance of the total reproductive output of i and its potential function as a stepping-stone linking other sources and sinks. A less formal version of this approach was taken by James et al. (2002). Using the same notation as above, let the mean population density of the metapopulation at equilibrium be

Table 1: Symbols and parameter values used in population models

Symbol	Value	Description (units)
ϕ		Proportional larval supply
π		Larval supply correlation
n		Local prey density (fish m^{-2})
N		Metapopulation-wide prey density (fish m^{-2})
S		Prey settler density (fish m^{-2})
R		Prey recruit density (fish m^{-2})
γ		Maximum recruit density (recruits m^{-2})
α		Subpopulation area (m^2)
η_S	1.7×10^{-10}–2.6×10^{-1}	Prey larval survivorship[a]
η_{P1}	1.7×10^{-12}–2.6×10^{-3}	Predator larval survivorship[b]
$\eta_{P2}\psi$	.015	Mean predator density–open population model (predators m^{-2})[c]
$\overline{P}$	.015	Mean predator density–metapopulation model (predators m^{-2})[c]
β	1.1×10^{6}–3.0×10^{6}	Prey reproductive rate (larvae adult^{-1})[d]
δ_S		Settler survivorship
δ_A	.39–.96	Adult survivorship[e]
δ_γ	.14–.51	Density-independent settler survivorship[f]
K_δ	51	Density-independent survivorship scaling factor (predator^{-1})[g]
K_γ	17–109	Density-dependent survivorship scaling factor (predator^{-1})[h]

Note: Unless otherwise noted, parameter values were randomly drawn from uniform distribution defined by range of values. Values not given for state variables, independent variables, and variables not used in numerical simulations.

[a] Larval mortality rates used by Cowen et al. (2000) were converted to monthly survivorships assuming a larval duration of approximately 30 d (the model time step). Values were sampled from uniform distribution of $\log \eta_S$ and then back transformed.

[b] Fixed at $0.01\eta_S$ to match empirical relationship between *Thalassoma bifasciatum* settler density and *Cephalopholis fulva* density at St. Croix, U.S. Virgin Islands (White 2007).

[c] Mean density of *C. fulva* at St. Croix (White 2007).

[d] Calculated from range of values given by Caselle et al. (2003), assuming that per capita fecundity is constant.

[e] Monthly survivorships calculated from range of weekly mortality rates for *T. bifasciatum* at San Blas, Panama (Warner and Chesson 1985).

[f] 95% confidence interval on density-independent component of per capita *T. bifasciatum* settler mortality (White 2007).

[g] This value is scaled so that $\delta_S = 0.23$ in the case with $\pi = 0$; this corresponds to the mean density-independent survivorship observed for *T. bifasciatum* settlers at St. Croix (White 2007).

[h] 95% confidence interval on slope of relationship between density-dependent component of *T. bifasciatum* recruit mortality and *C. fulva* density (White 2007).

$$N_\bullet^* = \frac{1}{m} \sum_{i=1}^{m} n_i^*,$$

where the bullet subscript indicates that all subpopulations are present. If subpopulation i is deleted from the metapopulation so that all individuals dispersing to i die immediately on arrival (this could be imagined to be some type of "scorched earth" harvesting), the equilibrium density of the metapopulation will be $N_{\bullet-i}^*$ (where the mean is still taken over all m patches). Now I define the deletion index D_i as a function of the ratio between these two values:

$$D_i = 1 - \frac{N_{\bullet-i}^*}{N_\bullet^*}.$$

This index produces a continuum rather than a binary classification, and subpopulations with higher values of D_i make a larger contribution to the metapopulation. At the extremes, $D_i = 1$ indicates a patch that is essential for

metapopulation persistence; this could be termed a "global source." Under most conditions, the minimum value of D_i is 0, although strongly overcompensatory density dependence could theoretically produce $D_i < 0$. In a reserve context, this metric addresses both the biodiversity goal (will the species persist if the focal patch is overexploited?) and the fishery enhancement goal (will population densities in other patches be higher if a focal patch is left unexploited?).

Metapopulation Models

Marine metapopulation models are frequently framed around the well-studied life history of small-bodied reef fish (James et al. 2002; Cowen et al. 2006). My effort follows suit and reflects to a large degree the empirical relationship between predator recruitment and prey mortality observed in *Thalassoma bifasciatum* and *Cephalopholis fulva* (White 2007). Nonetheless, the general results should be broadly applicable to any system in which small,

short-lived prey are vulnerable to a longer-lived, generalist predator. Here I consider a series of metapopulation models of increasing complexity; for simplicity and analytical tractability, I begin with a single prey subpopulation nested within a larger metapopulation (cf. Roughgarden et al. 1985) before moving on to simulation models of entire metapopulations.

Many reef fish spawn and settle in monthly pulses (Robertson 1991, 1992), so the models operate in discrete time. The length of each time step corresponds to the interval between spawning and recruitment, spanning the pelagic larval period and the initial bout of heavy mortality that occurs at the time of settlement.

Analytical Model of an Open Local Population

In this initial scenario, a subpopulation receives S_t settling larvae per unit area at each time t, and a negligible fraction of these larvae were spawned locally. Larval delivery is a function of some physical factor ϕ, so that $S_t = \eta_S \phi$, where η_S is a constant. A fraction δ_S of the settlers survive the initial bout of mortality to recruit into the adult population, after which they have per capita survivorship δ_A. The adult population density n_i follows the equation

$$n_{t+1} = \delta_S S_t + \delta_A n_{i,t}.$$

Assuming constant larval supply, so $S_t \equiv S$, this system reaches a globally stable steady state at

$$n^* = \frac{\delta_S S}{1 - \delta_A}. \tag{2}$$

Reef predators are generally omnivorous (Randall 1967), and predatory fishes are usually longer lived and have lower annual reproductive investment than their prey (Shuter et al. 2005), so predator dynamics should be slower than and independent of the dynamics of any one prey species. Indeed, Murdoch et al. (2002) showed that a wide variety of generalist predatory fishes exhibited population fluctuations inconsistent with strong coupling to the dynamics of their prey. As such, I preserve the simplicity of the models presented here by avoiding an explicit treatment of predator dynamics. Instead, a subpopulation is assumed to have constant predator density P, which could represent the combined density of multiple predatory species. This density will be a function of larval supply, which may be driven by the same physical factor ϕ that delivers prey larvae. Alternatively, predator settlement may be unrelated to ϕ if, for example, predator larvae differ markedly from prey in swimming ability or behavioral response to oceanographic cues. Therefore, it is convenient to express

P in terms of the relative proportions of individuals delivered by different physical processes:

$$P = \pi \eta_{P1} \phi + (1 - \pi) \eta_{P2} \psi, \tag{3}$$

where ψ_i is some alternative process that does not affect prey larvae, π is the proportion of predators delivered by ϕ, and the η_P are constants of proportionality. Hereafter, π will be used as a proxy for the strength of the coupled settlement effect. Equation (3) can be recast in terms of S:

$$P = \frac{\pi \eta_{P1}}{\eta_S} S + (1 - \pi) \eta_{P2} \psi, \tag{4}$$

where $\pi \eta_{P1} / \eta_S$ describes the slope of the relationship between predator density P and prey settlement. Predator density could affect prey mortality in any number of ways, but mortality is often most intense immediately after settlement, so I focus on cases in which δ_S is a function of P. There is no evidence that predators affect the settlement of reef fish larvae (Almany 2003), so I consider postsettlement predation only.

In this open local population scenario, it is not possible to calculate D. Calculating E is also problematic; the denominator of equation (1) is equal to S, but without explicit consideration of the rest of the metapopulation, there is no sensible way to calculate "export." However, for an open population, it is informative to consider the size of the population relative to the larval import, on the assumption that the number of exported larvae (whatever their destination) is roughly proportional to population size. Consequently, for this scenario I define a revised metric, $E' = \log(n/S)$, which is equivalent to equation (1) with the unspecified terms related to export removed. While the actual values of E and D are unknown, it is possible to investigate the effect of changes in π on the relative value of E'.

I explore the dynamics of the open local population for two different scenarios: first, the highly illustrative but relatively unrealistic case of density-independent postsettlement mortality; second, the case of strong postsettlement density dependence, which is more representative of most reef fish populations studied to date (Hixon and Webster 2002; Osenberg et al. 2002).

Case 1: Density-Independent Mortality. In the simplest scenario, δ_S is independent of prey density but linearly related to predator density:

$$\delta_S = 1 - k_\delta P, \tag{5}$$

where k_δ is a constant describing the (linear) functional

response of the predator. Because P and S are both functions of ϕ when $\pi \neq 0$, this effectively makes prey mortality strongly dependent on prey density, despite the nominally density-independent local dynamics (fig. 2A). Combining equations (2), (4), and (5) and simplifying yields

$$n^* = \frac{[(-k_\delta \pi \eta_{P1})/\eta_S]S^2 + [1 - k_\delta \psi \eta_{P2}(1 - \pi)]S}{1 - \delta_A}.$$

If $\pi = 0$ (i.e., predator and prey settlement are uncoupled), the S^2 in the numerator of the right-hand side dis-

appears and n^* is an increasing function of S. However, if $\pi > 0$, n^* is a quadratic function of S. This function is negatively concave for all values of S, with a maximum at $S = \eta_S[1 - k_\delta \eta_{P2}(1-\pi)\psi]/(2k_\delta \eta_{P1}\pi)$. As S increases from 0, population size increases from 0 to the maximum; if larval supply increases further, the subpopulation declines to extinction (fig. 2C). This counterintuitive relationship between larval supply and local population size is the essence of the coupled settlement effect.

The magnitude of π has a strong effect on the export ratio. When $\pi = 0$, E' is constant for all values of S. When $\pi > 0$, E' is substantially higher than in the $\pi = 0$ case at low values of S but then declines at an accelerating rate as S increases (fig. 2E).
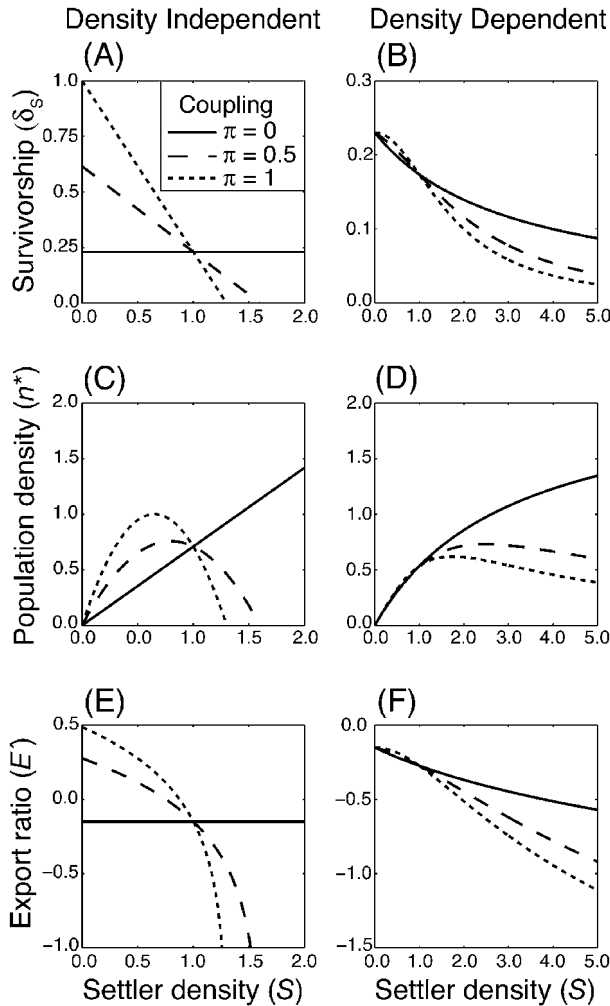
Case 2: Density-Dependent Mortality. The details of the relationship between S, π, and E' change only slightly as the model becomes more realistic. Most reef fish experience strong density-dependent mortality at the time of settlement (Hixon and Webster 2002), and in most cases this mortality can be approximated well by a Beverton-Holt relationship (Schmitt et al. 1999; Osenberg et al. 2002). In discrete time, this can be expressed as

$$\delta_S = \frac{\delta_\gamma}{1 + (\delta_\gamma/\gamma)S},$$

where δ_γ represents density-independent survivorship and γ represents the maximum possible density of recruits. In the continuous-time version of this function, the maximum recruit density is inversely proportional to the per capita density-dependent mortality rate (Osenberg et al. 2002), which can be strongly affected by local predator density. In order to approximate the empirical relationship between predator density and the density-dependent mortality rate documented by Schmitt and Holbrook (2007) and White (2007; also see fig. 1B), I made the maximum recruit density inversely proportional to predator density:

$$\gamma = \frac{1}{k_\gamma P_i}. \tag{6}$$

If there is correlated settlement ($\pi > 0$), the positive relationship between P_i and S causes γ to be inversely proportional to S as well. As with parameter k_δ in equation (5), the parameter k_γ describes the predators' functional response. Model results are quite sensitive to the strength of this response; for all results shown here, I used values estimated from empirical data (e.g., fig. 1B plots $1/\gamma$ vs. P for the *T. bifasciatum–C. fulva* system; the slope of that relationship corresponds to k_γ. Also see table 1).

Figure 2: Effect of larval supply correlation ϕ on the dynamics of an open population with density-independent (*A, C, E*) or density-dependent (*B, D, F*) survivorship. *A, B,* Per capita survivorship δ_S; *C, D,* equilibrium population density n^*; *E, F,* export ratio E' for a population with the indicated density of settlers S (higher values of E indicate greater export). Population densities are dimensionless and scaled by the factor $\eta_2 \eta_S \psi/\eta_1$. Mean values from table 1 were used for all parameters.

With density-dependent settler mortality and $\pi = 0$, n^* increases with S to an asymptotic maximum of $\gamma/(1 - \delta_\Lambda)$. When $\pi > 0$, the expression for n^* is quite complex but has a relationship with S similar to that of the density-independent case. As S increases from 0, n^* rises to a maximum at $S = (\eta_S/\delta_\gamma k_\gamma \eta_{P1} \pi)^{1/2}$ before declining toward extinction. Unlike the density-independent case, there is an inflection point in n^* to the right of the maximum, and n^* approaches 0 asymptotically with increasing S (fig. 2D).

The behavior of the export ratio E' differs from the density-independent scenario. When mortality is density dependent, E' declines with S, even when $\pi = 0$. This is a straightforward consequence of the maximum density imposed by the Beverton-Holt function: as S increases, a smaller proportion of settlers survive to enter the adult population, reproduce, and contribute larvae to the metapopulation. When $\pi > 0$, populations with higher S have lower maximum densities than populations with lower S, so E' declines more steeply with S (fig. 2F). In both the density-independent and density-dependent cases, P (and thus E') is the same for all values of π at $S = \eta_S\eta_{P1}\psi/\eta_{P2}$. Models not accounting for the coupled settlement effect will underestimate E' for populations with values of S less than this value and overestimate E' for populations with S greater than this value.

Numerical Simulations of Metapopulation Dynamics

In order to fully capture the effects of coupled settlement on the value of a patch within a metapopulation, it becomes necessary to model the dynamics a full metapopulation. Such models no longer afford easily interpretable analytical solutions, so I used numerical simulations to characterize the relationship between S_i, π, and subpopulation value (defined by the export ratio E_i and deletion index D_i).

Consider an entire metapopulation consisting of m subpopulations $n_1 \ldots n_m$, each with area α. The metapopulation is closed to external inputs of larvae, so it is necessary to introduce a parameter for per capita fecundity β. At each time t, the $\alpha n_{i,t}$ adult fish in population i produce $\alpha\beta n_{i,t}$ larvae, which then enter a larval pool with the offspring of all other subpopulations. The size of the larval pool is

$$L_t = \alpha\beta \sum_{i=1}^{m} n_{i,t}$$

As before, each subpopulation is associated with a parameter ϕ_i that describes the intensity of larval supply to that location. In the context of an entire metapopulation, ϕ_i is most easily defined as the fraction of the larval pool delivered to subpopulation i. Thus, the number of settlers per unit area arriving at each population is $S_{i,t} = \phi_i\eta_S L_{i,t}/\alpha$, where η_S now represents larval survivorship and the sum of ϕ_i across all populations is unity. This formulation is equivalent to having an $m \times m$ connectivity matrix Φ, with elements ϕ_{ij} defining the proportion of larvae produced at i that disperse to j; but in this case, each row of Φ is identical, so that each subpopulation receives the same fraction ϕ_i of larvae from each subpopulation. This type of connectivity scheme is appropriate for some but not all marine metapopulations; I outline the justification for this approach in the "Discussion."

Now that ϕ_i has been recast as a proportion, the expression for the local density of predators (eq. [3]) must be revised. Defining $\overline{P}$ to be the mean density of predators across all subpopulations, the predator density in subpopulation i is now

$$P_i = \pi\phi_i m\overline{P} + (1 - \pi)\overline{P}.$$

Under this definition, P_i exhibits the same behavior as in the case of density-dependent mortality: when $\pi = 0$, $P_i = \overline{P}$ for all subpopulations i; when $\pi > 0$, P_i approaches $m\overline{P}$ as ϕ_i increases toward unity and approaches 0 as ϕ_i shrinks toward 0. Because variation in ϕ_i (and, by extension, S) is of most interest here, this assumes that the only spatial variation in P_i is due to the oceanographic process represented by ϕ_i. The strength of the coupled settlement effect is still indicated by π, but the slope of the relationship between P_i and S_i changes slightly and is now $\pi m\overline{P}/\eta_{P1}$. Postsettlement mortality remains density dependent, which ensures that the metapopulation has a stable nonzero equilibrium (Armsworth 2002), and the intensity of density dependence is a function of predator density, as in the open population model (eq. [3]).

In this model, γ_i effectively sets the spatial scale of the simulation by defining the maximum number of recruits in a unit of area, so the absolute value is less meaningful than the relative difference in γ_i among demes within the same metapopulation. For the purpose of parameterizing the model for simulations, I used units of fish/m² for γ_i. Biologically reasonable values were assigned to the other demographic parameters by using published data for *T. bifasciatum* (table 1). I created 100 unique parameter sets by taking uniform random draws from the range of plausible values for each parameter and then used each parameter set to simulate model dynamics across the range of π and ϕ_i. For each π-ϕ_i combination, I report the mean value of D_i and E_i taken across all 100 parameter sets. Simulations were run for 500 time steps, sufficient time for the model to reach equilibrium (to calculate D_i, an

additional set of 500 step simulations were run with the focal population deleted).

I focused on the dynamics of the simplest possible metapopulation, which consists of two subpopulations, n_1 and n_2; the results can be extended to larger, multipatch metapopulations without a loss of generality (see appendix). Taking subpopulation 1 as the focal deme, mean D_1 and E_1 were calculated for values of ϕ_1 ranging from 0.01 to 0.99.

Simulation Results

The dynamics of the simulated metapopulations were largely similar to those of the open population model with density-dependent mortality. When predator and prey settlement were uncoupled ($\pi = 0$), equilibrium population density n_i^* was constant for most values of larval supply ϕ_1 (fig. 3A), but when $\pi > 0$, n_i^* was highest at low values of ϕ_1 and decreased with increasing ϕ_1 (as in the density-dependent open population, $n_i^* = 0$ when $\phi_1 = 0$ and then quickly rises to a maximum; this behavior is only barely visible for $\pi = 0$ and $\pi = 0.5$ in fig. 3A). Changes in the export ratio E_1 were nearly identical to the open population case: E_1 declined with increasing larval supply for all values of π, but when $\pi > 0$, E_1 was higher for low-settlement populations (indicating greater relative larval export and more sourcelike behavior) and lower for high-settlement populations (indicating lower relative larval export and more sinklike behavior; fig. 3B). The effect of coupled settlement on the metapopulation contribution of subpopulation 1 was even more evident in the values of the deletion index D_1 (fig. 3C). When settlement was uncoupled ($\pi = 0$), D_1 increased modestly and monotonically with ϕ_1, indicating that the population receiving greater larval supply was more important to the metapopulation. For $\pi = 0.5$ or 1, by contrast, D_1 was highest for low values of ϕ_1 and declined with increasing ϕ_1, so importance of a patch declined as larval supply increased. This decline was not monotonic, however. At extreme values of ϕ, the low-settlement subpopulation received so little larval supply that it was no longer completely self-sustaining, causing a slight upturn in the deletion index of the high-settlement subpopulation and a corresponding downturn in the deletion index of the low-settlement subpopulation. Nonetheless, the value of D_1 when settlement was coupled ($\pi > 0$) remained far below that of the uncoupled case ($\pi = 0$) for all high values of ϕ_1. The values of n_i^*, E_1, and D_1 were the same for all values of π only at $\phi_1 = 1/m = 0.5$, when larval supply to both demes was exactly equal.

For all metapopulations, the export ratio E_i was less than 0 (indicating net larval import) for large values of larval supply (ϕ_i), regardless of the degree of larval coupling (fig.
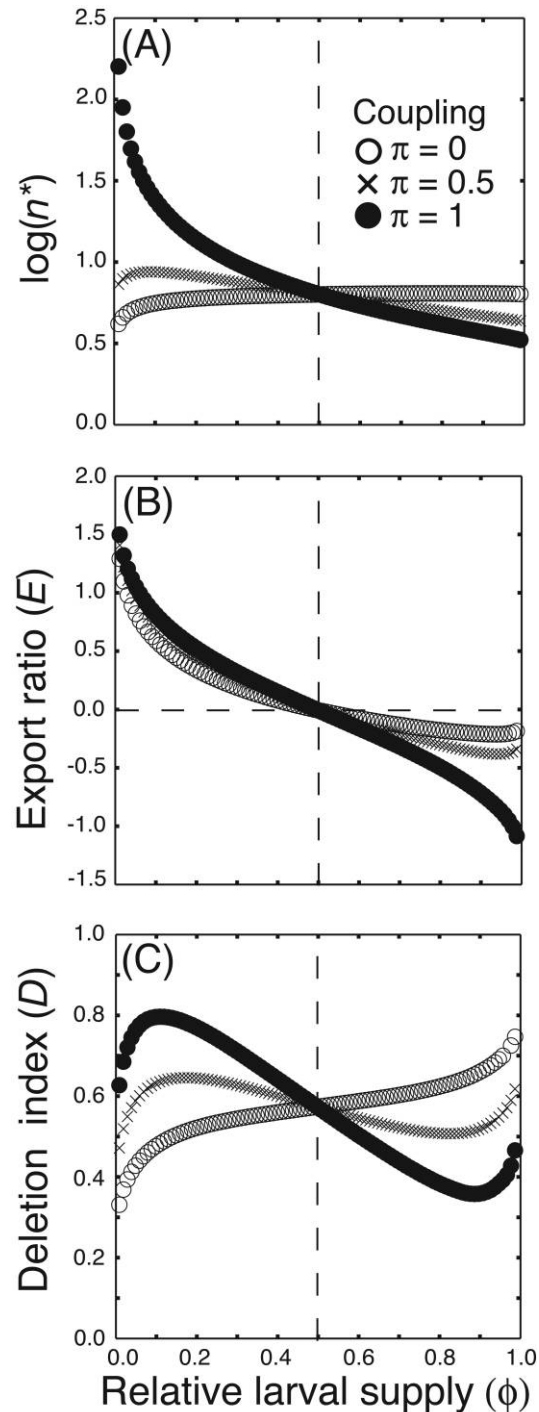

Figure 3: Effect of larval supply correlation, π, on relative patch importance in two-deme metapopulations. Each point is the equilibrium value of (A) log equilibrium population density n^*, (B) export ratio E, or (C) deletion index D for a subpopulation with the indicated value of proportional larval supply ϕ_i. Vertical dashed lines indicate the mean value of ϕ. The horizontal dashed line indicates $E = 0$, the boundary between net larval export and net larval import.

3*B*). This was a consequence of density-dependent mortality in these subpopulations (the same phenomenon was evident in the open local population with density-dependent mortality; fig. 2*F*). When $\pi = 0$, these high-settlement subpopulations were the most important demes in the metapopulation (as indicated by D_i) despite their low values of E_i. This seeming disparity between E_i and D_i reflects a fundamental difference between the two measures: E_i describes only the relative efficiency of larval production (regardless of its overall magnitude), while D_i is a measure of the absolute contribution to population density in the metapopulation. It was striking, then, that these complementary measures were in accord when $\pi > 0$; high-settlement populations had low values of both E_i and D_i relative to those of lower-settlement subpopulations.

Discussion

It is well known that the dynamics of predator-prey interactions can be strongly affected by the existence of spatial refuges that predators cannot access (Sih 1987). Released from predation, the prey populations in refuges have increased reproductive success and can replenish high-predation patches elsewhere in the metapopulation (Murdoch et al. 1992). Metapopulation models often incorporate refuges to represent some sort of habitat unsuitable for predators, but a similar effect is produced when physical forces distribute predators unevenly through the metapopulation. This phenomenon was first noted by Lett et al. (2003, 2005), who studied a Nicholson-Bailey model of host-parasitoid dynamics in a system with fixed migration rates between patches. They found that the stability and equilibrium density of the host population were often maximized when the hosts and parasitoids dispersed in opposite directions, so that most hosts tended to arrive at patches with few parasitoids. However, they acknowledged that such divergent dispersal patterns were unlikely to be found in nature (Lett et al. 2003, 2005). Here I investigated the opposite situation, which is far more likely to occur in environments with physical forcing: predators and prey tend to disperse in the same direction. Furthermore, I focused on the effects of coupled dispersal on measures of patch value that are particularly relevant for conservation planning and the placement of marine protected areas (Roberts et al. 2003), and one of the primary results of this article was the development of two novel metrics for patch value. When prey and predator dispersal were strongly coupled ($\pi = 1$) in the reef fish metapopulations modeled here, the few settlers arriving at low-settlement patches were effectively entering a predation refuge where they could maintain a much greater adult population density and have increased value to the metapopulation. This effect is unique to a system with physically forced dispersal

and would not occur if prey were able to emigrate from high-density patches (Amarasekare 2004) or if predators could redistribute themselves after depleting the prey in a patch (Bernstein et al. 1999; Jackson et al. 2004). Scenarios without dispersal coupling ($\pi = 0$) recapture the type of system more commonly examined in metapopulation models (reviewed in Briggs and Hoopes 2004), in which high-settlement subpopulations were more valuable to the metapopulation. The opposite was true when $\pi > 0$: both the export ratio and the deletion index decreased with proportional larval supply. This contrast is the second primary result of this article: metapopulation models not accounting for the coupled settlement effect in systems where it exists will incorrectly predict the relative metapopulation value of subpopulations.

The key feature of the coupled settlement effect is most easily visualized in the unimodal settler-adult relationship in the open population model (fig. 2*C*, 2*D*): subpopulations receiving a very small proportion of the larval pool experience approximately density-independent mortality, while subpopulations with high proportional larval supply experience intense density-dependent mortality. The unimodal shape and resemblance to a Ricker stock-recruitment function (Hilborn and Walters 1992) makes it tempting to think of this phenomenon in terms of overcompensating density dependence. It is important to note, however, that this relationship does not describe the temporal relationship between settlement and mortality within a single population (as a Ricker function does) but rather variation in mortality across a spatial gradient of settlement. With the coupled settlement effect, mortality is a function of the average larval supply at a site, not the density of any particular prey cohort. Recruit mortality within each cohort is always a saturating Beverton-Holt function that produces dynamic stability (Armsworth 2002). The importance of this distinction becomes evident if one considers the consequences of allowing prey larval supply to vary stochastically through time while keeping local predator densities a function of the mean larval supply. In this scenario, sporadic large pulses of larvae to sites with high mean supply will experience strong density-dependent mortality, while large pulses at sites with low mean supply will experience low density-independent mortality. These low-settlement sites will thus be able to store large settlement pulses (Warner and Chesson 1985), buffering them against future settlement failures. Consequently, sites with low mean larval supply could be important reservoirs of reproductive adults.

Larval pools are a common feature of marine metapopulation models (Roughgarden and Iwasa 1986). This approach probably assumes an unrealistic degree of mixing and homogeneity (Flowers et al. 2002; Planes et al. 2002) and is clearly an inappropriate description of highly di-

rectional systems with stepping-stone dispersal (Carr and Reed 1993). Nonetheless, it can capture the essential features of systems in which frequent current shifts facilitate bidirectional larval exchange among multiple subpopulations, as in the uniform metapopulation scenario (e.g., Southern California Bight; Carr and Reed 1993; Selkoe et al. 2006), or in which currents favor larval accumulation and delivery to particular geographical locations, with limited or infrequent larval delivery to other sites in the metapopulation (e.g., headland accumulation zones: Botsford 2001; eddies and accumulation zones near oceanic islands: Lipcius et al. 2001; Harlan et al. 2002). It is important to recall that because my model assumes that all larvae are identical, larval mixing per se is not important, and the larval pool could be equally well described by a connectivity matrix of a particular form (see "Numerical Simulations of Metapopulation Dynamics"). In any case, the larval pool assumption provided a simple way to model the correlation between prey settlement and predator abundance without explicitly modeling predator dynamics, and using a more complex connectivity matrix would require a dynamic model of the predator population. The results of such a model would probably depend on the specifics of the connectivity matrix, but so long as there is some bidirectional dispersal between most patches and some patches tend to receive higher larval supply than others, the general patterns described here should hold.

Most predators on coral reefs have diverse diets (Randall 1967), and omnivory is a common strategy in many other systems as well (Polis and Strong 1996), so making predator densities independent of the abundance of a single prey species should be a reasonable approximation to reality (Murdoch et al. 2002). However, the effects reported here could differ in models incorporating a full complement of prey species and predator dynamics, especially if the predator population is size structured. In general, assuming additional prey species follow the same general spatial pattern of settlement, predators at high-settlement sites will have access to a greater and more consistent influx of prey, which should lead to higher predator survival, enhancing the general pattern presented here. This effect would be dampened if territoriality produced density dependence in the predator population, but numerical density dependence could be offset by a developmental response if per capita prey consumption increases with biomass in a size-structured predator population (Murdoch 1971). However, these predictions will also depend on the degree to which predators influence adult prey mortality rates. In this model, predator abundance affected only settler mortality, but if predators can accumulate biomass by feeding on both new settlers and adults, low-settlement sites may no longer accumulate high densities of adult prey. For example, a biomass-based model of

predator-prey dynamics suggests that the accumulation of predator biomass due to feeding outstrips the influx of biomass due to settlement (Sandin and Pacala 2005). All else being equal, this would negate spatial differences in predation created by larval delivery patterns. However, asymptotic limits on the size of individual fish should ensure that there is still a numerical constraint on the potential predation pressure at low-settlement sites, as in the model presented here. An additional consideration is the strength of the predator functional response, which was linear and given by the k parameters (k_δ and k_γ) in this model. If the relationship between predator density and predation rate were weak or rapidly asymptotic, there would be no effect of coupled settlement; indeed, the model results are just as sensitive to k as to the settlement coupling parameter π. However, the available field data suggest a substantial and approximately linear functional response (Schmitt and Holbrook 2007; White 2007), and empirically derived values were used in the results presented here.

This study was inspired by the observation of correlated settlement and predation rates in a coral reef fish metapopulation (White 2007), but this phenomenon may be a common feature of many metacommunities, both marine and terrestrial. Intertidal mussels along the California coast experience significantly higher predation rates at sites with high settlement of both mussels and their sea star predators, and mussel densities in these sites are similar to densities in locations with far lower settlement (Menge et al. 2004). Movement in riverine metacommunities is strongly affected by the intensity of stream discharge, which tends to concentrate resources and organisms in downstream confluences (Schlosser 1995; Power and Dietrich 2002). In turn, these wide, deep, downstream locations are thought to act as source populations that can recolonize upstream headwaters after disturbances (Osborne and Wiley 1992; Schlosser 1998). However, predator densities and predation rates also increase with downstream distance and stream size (Schlosser 1987; Power and Dietrich 2002), which could dilute the efficacy of larger stream regions as "sources" and may partially explain some mismatches between observed recolonization rates and single-species metapopulation model predictions (Gotelli and Taylor 1999). In some terrestrial metacommunities, interpatch dispersal is wind driven. Zooplankton and their invertebrate predators form aquatic metacommunities in the leaves of pitcher plants (*Sarracenia purpurea*; Miller and Kneitel 2005). Both predators and prey disperse among pitcher plants aerially, and larger plants are likely to receive higher inputs of both trophic levels (Heard 1994; Cáceres and Soluk 2002; Vanschoenwinkel et al. 2008), so these metacommunities may also be structured by coupled dispersal of predators and their prey. In

general, this sort of relationship should arise whenever certain patches are equally attractive to dispersing propagules of both species, either because of similar habitat preferences, in the case of active dispersers (e.g., van der Meijden and van der Veen-van Wijk 1997), or similar susceptibility to abiotic forcing, in the case of water- or wind-dispersers (e.g., Cowen and Castro 1994; Bell et al. 2005). It should be noted that many existing single-species metapopulation models with passive dispersal assume that larger patches receive more colonists and have lower extinction rates (e.g., Hanski and Ovaskainen 2003), but the extinction rates of those patches might be higher than expected if predators also colonize those patches at a high frequency. Alternatively, coupled dispersal is not likely to occur if predators and prey differ greatly in larval behavior or the seasonality of dispersal (in locations where currents vary seasonally) or if adult movement occurs on a scale large enough to disrupt patterns established at settlement (Kritzer and Sale 2006).

The source-sink concept is widely applied in metapopulation ecology, and the criteria used to differentiate sources and sinks can vary widely (Runge et al. 2006). For terrestrial studies, investigators generally calculate the difference between local birth and death rates (Pulliam 1988); in a marine context, this requires that a sufficient number of locally produced larvae return to replenish the natal population (Armsworth 2002; Hastings and Botsford 2006). Evidence is beginning to accumulate that shows populations often retain at least some fraction of locally produced larvae (Swearer et al. 2002), so that many populations may be self-replenishing as long as fecundity exceeds larval mortality by a sufficient margin (Byers and Pringle 2006). Indeed, most of the subpopulations simulated in this study were self-replenishing sources even when the values of D_i and E_i were quite low. The focus of this article, however, was on the contribution of a given subpopulation to an equilibrial metapopulation rather than a near-extinction metapopulation. This can be a crucial distinction; a self-replenishing source that contributes few recruits to the rest of the metapopulation would persist in isolation but cannot be relied on to replenish sinks where self-replenishment is low or mortality is high. Likewise, subpopulations for which local oceanography precludes larval retention and self-replenishment would be sinks under Armsworth's (2002) criterion but might be nonetheless essential to the persistence and equilibrial size of the larger metapopulation. Such subpopulations could occupy favorable habitat that permits them to export large numbers of larvae to other demes (garnering a high export ratio E_i; Figueira and Crowder 2006) or act as stepping-stones, linking distant patches through subsequent generations of dispersal (Hastings and Botsford 2006) and yielding a high value of deletion index D_i. Such considerations underscore the value of the export- and deletion-based statistics as measures of patch contribution. The examples I chose also highlight the complementarity of these statistics. A net larval exporter (high E_i) might not be as essential to metapopulation connectivity as a stepping-stone (high D_i), and vice versa, but taken together, the two statistics readily identify such distinct roles. One caveat is that demes with extremely low larval supply could produce a biologically insignificant number of larvae yet have a large value of E_i; in such cases, the near-zero value of D_i will be more informative. Nonetheless, in a conservation context, both metrics may provide more information than traditional source-sink definitions regarding the consequences of destroying or overharvesting a particular subpopulation and so may be more useful in matching reserve functions to desired goals (Halpern and Warner 2002).

Accounting for correlated settlement effects should improve our ability to predict marine metapopulation dynamics in general but could also be quite important to conservation planning and reserve design. In the case of single-species management, the coupled settlement effect may temper the value ascribed to certain high-settlement sites by models assuming spatially constant predation (reviewed in Gerber et al. 2003). In reality, sites with lower settlement may be more useful as reserves because of their elevated reproductive potential (Caselle et al. 2003). This may be true even when the species of interest is a top predator, since most marine organisms are vulnerable to predation when they are young and small. However, for some marine predators, population dynamics are strongly influenced by cannibalism of recruits by older conspecifics (Claessen et al. 2004). The predictions of the models presented here are not likely to hold in that situation, and the spatially explicit metapopulation dynamics of a cannibalistic species would be a productive avenue for future research (Claessen et al. 2004; Olson et al. 2005). An attractive alternative to single-species conservation strategies is ecosystem-based management (EBM). Species interactions and spatial variability are nominally included in the EBM rubric but are rarely considered in practice (Arkema et al. 2006). This study provides additional evidence for the need to move beyond the single-species approach (Botsford et al. 1997). Indeed, other authors have recognized that because top predators are protected from harvest, reserves may have higher predation rates than surrounding habitat (Micheli et al. 2004; Baskett et al. 2006; Langlois et al. 2006). This extends the lesson noted by Crowder and colleagues (Crowder et al. 2000; Crowder and Figueira 2006; Figueira and Crowder 2006) that spatial variability in habitat quality and resource availability must be taken into account when evaluating subpopulation importance. The future of informed marine population ecology and conservation may lie in embracing the metacommunity concept (Guichard et al. 2005) and recognizing

the importance of oceanographically driven spatial variation in species interactions to the role individual patches play in the larger network.

APPENDIX

Simulation of Multiple-Deme Metapopulation Dynamics

The main text describes simulations of a simple, two-deme metapopulation, but those results can be extended to more complex metapopulations as well. To demonstrate this point, I present results for a 10-deme metapopulation.

To model the $m = 10$ scenario, I created $m \times m$ connectivity matrices Φ with elements ϕ_{ji}, as described in the main text. Each matrix had identical rows (in keeping with the larval pool assumption), so generating Φ simply involved randomly generating a single row vector of length 10, $\Phi = (\phi_1, \ldots, \phi_{10})$. The elements of ϕ sum to unity and define the proportional larval supply to each subpopulation; for brevity, I drop the subscript j and refer only to the value of ϕ_i for each subpopulation. Note that import and export connectivities to and from each patch are still explicitly defined in this case: a particular subpopulation q will have different rates of export to each other subpopulation ($\phi_{q1} = $ "ϕ_1"; $\phi_{q2} = $ "ϕ_2") but will have the same rate of import from every other subpopulation ($\phi_{1q} = \phi_{2q} = $ "ϕ_q").

Metapopulations with a range of larval supply configurations were simulated by drawing 10 values of ϕ_i uniformly on the interval (0, 1), with the constraint that they sum to unity. I generated 500 vectors ϕ; for each one, metapopulation dynamics were simulated using 100 parameter sets generated in the same way as in the two-deme case and with the strength of settlement coupling $\pi = 0$, 0.5, or 1. For each ϕ and each value of π, the mean values
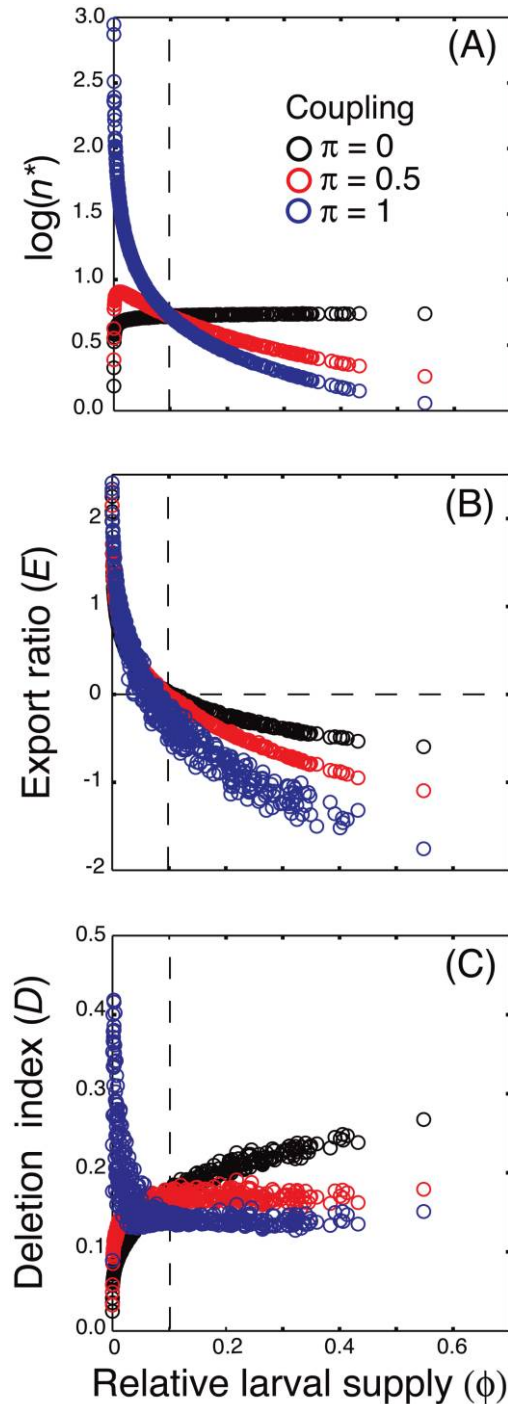

Figure A1: Effect of larval supply correlation, π, on relative patch importance in multiple-deme metapopulations. Each point is equilibrium value of (*A*) log population density n^*, (*B*) export ratio E_i, or (*C*) deletion index D_i for a subpopulation with the indicated value of ϕ_i. Vertical dashed lines indicate the mean value of ϕ. The horizontal dashed line indicates $E_i = 0$, the boundary between net larval export and net larval import.

of E_i and D_i (taken across all 100 parameter sets) were calculated for each subpopulation. To illustrate the behavior of E_i and D_i across the range of potential ϕ_i values, for each of the 500 connectivity vectors (ϕ), I present the mean values of both metrics for a single, randomly selected focal subpopulation n_i. The resulting relationship between ϕ_i and E_i (or D_i) taken across all simulations is identical to that present within each individual 10-deme metapopulation.

The effects of larval supply ϕ and settlement coupling π on mean population density n_1^*, export ratio E_i, and the deletion index D_i in the multiple-deme metapopulation were similar to those observed in the two-deme metapopulation. When larval supply was uncoupled ($\pi = 0$), E_i was highest at low values of ϕ_i and declined steadily (fig. A1B), and D_i increased monotonically with ϕ_i (fig. A1C). For $\pi > 0$, however, both E_i and D_i declined rapidly with ϕ_i, and D_i was highest for subpopulations with very low values of ϕ_i (fig. A1C).

As in the two-deme case, n_1^* in the multiple-deme metapopulation was equal for all values of π at the mean value of ϕ_i, which is $1/m$, or 0.1 for a 10-deme metapopulation (fig. A1A). However, the values of E_i and D_i were not equal for all π at this point (fig. A1B, A1C). Unlike the two-deme scenario, all subpopulations in the multiple-deme metapopulation did not have equal larval supply when the focal subpopulation had $\phi_i = 1/m$, and the presence of additional subpopulations with $\phi_i < 1/m$ depressed the values of E_i and D_i for that focal subpopulation. This effect was barely noticeable for $\pi = 0.5$ but quite pronounced for $\pi = 1$.

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