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Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design

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Abstract. Demographic connectivity is a fundamental process influencing the dynamics and persistence of spatially structured populations. Consequently, quantifying connectivity is essential for properly designing networks of protected areas so that they achieve their core ecological objective of maintaining population persistence. Recently, many empirical studies in marine systems have provided essential, and historically challenging to obtain, data on patterns of larval dispersal and export from marine protected areas (MPAs). Here, we review the empirical studies that have directly quantified the origins and destinations of individual larvae and assess those studies' relevance to the theory of population persistence and MPA design objectives. We found that empirical studies often do not measure or present quantities that are relevant to assessing population persistence, even though most studies were motivated or contextualized by MPA applications. Persistence of spatial populations, like nonspatial populations, depends on replacement, whether individuals reproduce enough in their lifetime to replace themselves. In spatial populations, one needs to account for the effect of larval dispersal on future recruitment back to the local population through local retention and other connectivity pathways. The most commonly reported descriptor of larval dispersal was the fraction of recruitment from local origin (self-recruitment). Self-recruitment does not inform persistence-based MPA design because it is a fraction of those arriving, not a fraction of those leaving (local retention), so contains no information on replacement. Some studies presented connectivity matrices, which can inform assessments of persistence with additional knowledge of survival and fecundity after recruitment. Some studies collected data in addition to larval dispersal that could inform assessments of population persistence but which were not presented in that way. We describe how three pieces of empirical information are needed to fully describe population persistence in a network of MPAs: (1) lifetime fecundity, (2) the proportion of larvae that are locally retained (or the full connectivity matrix), and (3) survival rate after recruitment. We conclude by linking theory and data to provide detailed guidance to empiricists and practitioners on field sampling design and data presentation that better informs the MPA objective of population persistence.

Key words: larval dispersal; local retention; marine reserves; self-recruitment.

Introduction

Demographic connectivity is a fundamental process structuring the dynamics of spatially distributed populations (Hanski 2002, Hastings and Botsford 2006). Consequently, quantitative estimates of connectivity between habitat patches are essential to the successful design of spatial networks of protected areas (Williams

et al. 2005). This is particularly true in benthic marine systems, where many species have a pelagic larval stage that allows potential large-scale dispersal among habitat patches (Cowen and Sponaugle 2009). In coastal marine systems, marine protected areas (MPAs) are increasingly being used as a strategy to protect biodiversity or maintain sustainable fisheries (Halpern 2003, Gerber et al. 2005, Fogarty and Botsford 2007, Wood et al. 2008). MPAs created for biodiversity conservation and fishery management may differ in optimal design (Halpern 2003, Hastings and Botsford 2003), but they have a common, fundamental objective: maintaining the persistence of populations. For example, protecting biodiversity requires that populations of each species avoid

extinction and that a predator's prey and mutualists persist (Baskett et al. 2007). Maintaining sustainable fisheries yield requires that populations of harvested species inside MPAs persist so that they can provide yield through spillover, including both larval export and adult movement out of MPAs.

In the last decade or so, a strong theoretical literature has emerged providing generalized design principles for MPAs in the context of population persistence (e.g., Mangel 1998, Botsford et al. 2001, 2009*a*, Gaines et al. 2003, Gerber et al. 2003, White et al. 2010*a*, Grüss et al. 2011, Blowes and Connolly 2012). This literature emphasizes that patterns of population connectivity, typically facilitated by larval dispersal in coastal currents, critically influence persistence. In essence, patterns of larval dispersal and population connectivity determine whether a particular reserve configuration produces a spatial distribution of survival and reproductive rates that are adequate for persistence. Larval dispersal patterns are also one of the largest sources of uncertainty in determining the effectiveness of MPAs, and are notoriously difficult to measure empirically due to the small size and high dispersal potential of larvae (Levin 2006, Pineda et al. 2007, Cowen and Sponaugle 2009).

Fortunately, rapidly evolving technologies have made it possible to overcome the enduring challenge of determining where recruits were born, and essential data on connectivity patterns are now obtainable (Lopez-Duarte et al. 2012). Recent empirical studies, however, often do not measure the quantities that are needed to determine population persistence, or if the correct quantities are measured, they are not described in terms of persistence theory (Botsford et al. 2009*b*). There remains, therefore, a distinct need to align empirical and theoretical studies to address the core ecological goal of MPA management (i.e., population persistence) and advance the science of MPA design (Botsford et al. 2009*a, b*, Steneck et al. 2009).

Our goals here were to (1) review the empirical studies that have quantified the origins and destinations of larvae while assessing their relevance to determining population persistence, and (2) provide detailed guidance to empiricists and practitioners for field sampling design that better addresses population persistence and informs MPA design. We begin by briefly reviewing the theoretical basis for how larval dispersal influences population persistence, and then we review empirical studies on connectivity in marine systems while assessing their contribution to persistence evaluation. We conclude with suggestions for better linking theory and data and designing empirical studies that more explicitly address population persistence.

THE THEORY OF PERSISTENCE IN SPATIALLY STRUCTURED POPULATIONS

The approach to evaluating persistence of a population that is distributed over space depends on whether patch extinctions are a dominant feature. In a "classic" metapopulation, such as the well-studied Glanville fritillary butterfly metapopulation in Finland (Hanski 2002), dispersal among patches is infrequent and individual patches often go extinct before being recolonized. Such metapopulations will persist if the recolonization rate exceeds the extinction rate. Although the classic framework describes many terrestrial metapopulations quite well, it is less effective for most marine metapopulations because dispersal during the larval stage leads to much greater connectivity among patches and local extinctions are rare (Kritzer and Sale 2006). In classic metapopulations, dispersal between patches is crucial for persistence because patches become extinct. In marine metapopulations, recruitment back to the local population through local retention and other connectivity pathways is crucial. The central question regarding population persistence in marine metapopulations is whether the population growth rate is positive at low abundance for either the entire metapopulation or a portion of it (Armsworth 2002, James et al. 2002, Hastings and Botsford 2006, Bode et al. 2008, Botsford et al. 2009*b*, Blowes and Connolly 2012). The key to answering this question requires following the flow of individuals through development (i.e., ages or stages) and across space. Demographic rates are likely to vary among patches, so one must account for both connectivity and within-patch dynamics (Figueira 2009). In this section, we briefly review the theory of persistence in spatially structured populations with the goal of highlighting the quantities that empirical studies should measure to address questions about persistence. We begin by explaining persistence in the simple, nonspatial case before expanding the theory to include multiple patches.

Persistence in a single, closed population

Population persistence is achieved through replacement. That is, each adult must, on average, replace itself with one offspring during its lifetime (i.e., each mating pair must produce on average ≥2 offspring during their lifetime and the offspring must survive and reproduce). To see how, first consider a single, closed population with no emigration or immigration. One can determine whether replacement is achieved by calculating the net reproductive rate of the population, which is the average number of offspring that an individual contributes to the population over that individual's lifetime (denoted as R_0 in age-structured populations with no density dependence). Note that R_0 is the product of the survival from birth to a given age and the fecundity at that age, summed across all ages (Table 1; Caswell 2001). A population will persist and increase only if $R_0 > 1$.

In a population with age structure, where survival, growth, and fecundity depend on the age of the organism, but not on population density, the dynamics can be represented by a Leslie matrix. The growth rate of the population is then given by the dominant

TABLE 1. Definitions of terms used throughout the text.

Term	Definition	Mathematical definition
R_0	the average number of recruits into the first age class produced during an individual's life that contribute to the population	$\sum_{a=1}^{A} l(a)f(a)$ where $l(a)$ is survival from birth to age a, $f(a)$ is fecundity at age a, and A is age at death
Lifetime egg production (LEP)	the average number of eggs (cf. R_0) produced during an individual's life, beginning from recruitment (includes survival from recruitment to maturity)	$\sum_{a=1}^{A} l(a)f(a)$ where $l(a)$ is survival from recruitment to age a, and $f(a)$ is fecundity at age a, and A is age at death
Local retention (LR)	fraction of offspring produced by a population that also recruits into that population	$\text{LR} = \dfrac{\text{Recruits from site } i}{\text{Reproductive output from site } i}$
Self-recruitment (SR)	fraction of recruitment to a site comprised of individuals born in that site	$\text{SR} = \dfrac{\text{Recruits from site } i}{\text{Total recruitment at site } i}$
Self-persistence	occurs when local populations persist independently due to local retention	$\text{LEP} \times \text{LR} > 1$
Network persistence	occurs when local populations persist through closed loops of connectivity between all or some local populations in the network (hence metapopulation persistence)	$\lambda_m > 1$ where λ_m is the largest real eigenvalue of the realized connectivity matrix $\mathbf{C}$ (see Appendix A for more detail)
Connectivity matrix	a matrix with origins as columns and destinations as rows, filled with the probability (p) that an offspring produced at a given origin recruits to a given destination (subscripts)	$\begin{bmatrix} p_{11} & p_{12} & \cdots & p_{ji} \\ p_{21} & p_{22} & \cdots & p_{ji} \\ \vdots & \vdots & \ddots & \vdots \\ p_{ij} & p_{ij} & \cdots & p_{ii} \end{bmatrix}$

eigenvalue of the Leslie matrix, which is denoted as λ (Caswell 2001). A population will be increasing if $\lambda > 1$ (in which case $R_0 > 1$) and decreasing if $\lambda < 1$ (in which case $R_0 < 1$). Thus, persistence can also be determined from the equivalent age-dependent survival and reproductive terms that comprise the Leslie matrix (Caswell 2001). Note that the two quantities that reflect whether a population is increasing (λ and R_0) are in different units: λ has the advantage that it is in units of the annual multiplier of abundance, while R_0 has the advantage that it explains the increase in terms of the replacement of individuals.

In introducing the theory of persistence for a single population, we have thus far ignored the possibility of density dependence, essentially assuming that when discussing persistence one is concerned with whether a population that is at low density will increase in abundance or continue to decline to extinction. Therefore, the theory of persistence, as we have presented it so far, implicitly assumes that densities are too low for density-dependent dynamics to be very important, and the persistence criterion ($R_0 > 1 \Leftrightarrow \lambda > 1$) is correct. It is straightforward, however, to account for density-dependent recruitment (i.e., density-dependent survival of juveniles or larvae recruiting into the adult population) in the persistence criterion (Sissenwine and Shepherd 1987). Even with density dependence, it is ultimately the density-independent survival rate (i.e., the survival rate at very low recruitment) that is important for persistence, because the behavior of the population at low densities is what matters for persistence. Thus, there is still a replacement threshold above which lifetime reproduction will supply sufficient replacement to allow the population to persist. The basic theory we present also assumes there are no Allee effects (density depensation), environmental stochasticity, or demographic stochasticity, although these are easily accounted for and they do not change the replacement logic for persistence (Caswell 2001).

Persistence in a network of connected populations

To address the question of persistence when there is dispersal between patches, the replacement concept for a single, closed population can be extended by accounting for the movement of individuals among patches. The population dynamics of the network can then be described in terms of the survival of individuals over time (i.e., the transitioning through the age structure) within patches and movement over space (i.e., the transitioning through the spatial structure) between patches. There are two non-mutually exclusive ways by which a marine metapopulation in a system of MPAs can persist (see Appendix A for a mathematical description of this issue; Botsford et al. 2001, Hastings and Botsford 2006): (1) Local populations can persist independently (self-persistence), or (2) even if there is no self-persistent population, persistence can be achieved through closed loops of connectivity among all or some local populations in the network (network persistence; Table 1).
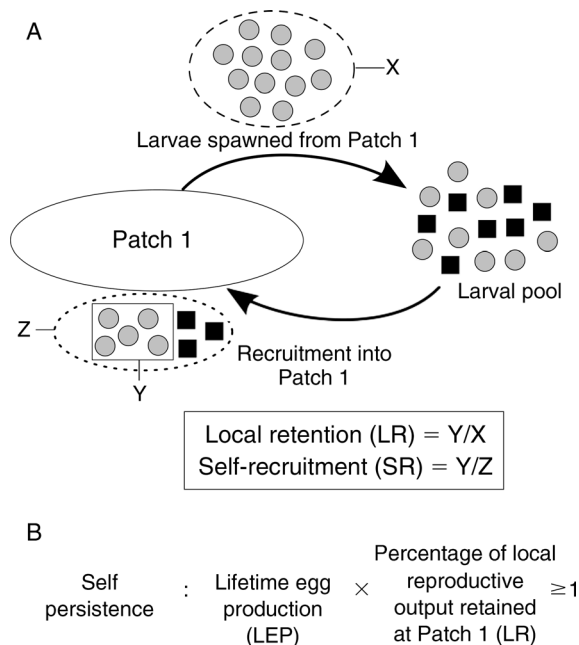
A

Larvae spawned from Patch 1

Patch 1

Larval pool

Recruitment into
Patch 1

Local retention (LR) = Y/X
Self-recruitment (SR) = Y/Z

B

Self   : Lifetime egg × Percentage of local ≥ 1
persistence   production   reproductive
                     (LEP)   output retained
                                      at Patch 1 (LR)

FIG. 1. (A) Representation of local retention and self-recruitment in a marine protected area. Both local retention and self-recruitment include the number of recruits originating from Patch 1, but the difference lies in the denominator (Table 1). Local retention refers to fraction of larvae spawned from Patch 1 (X) that also recruit back into Patch 1 (Y). Self-recruitment refers to the fraction of recruitment into Patch 1 (Z) composed of recruits spawned from patch 1 (Y). (B) Only local retention, not self-recruitment, appears in the assessment of population persistence (see also Fig. 2 and Appendix A). The gray circles and black squares represent individual larvae.

For self-persistence, a single local population will persist if individuals can produce enough offspring to replace themselves, as described in the previous section for a single population. Extending the same logic to multiple populations where some larvae will potentially disperse, losses due to emigration need to be accounted for. Replacement for self-persistence therefore depends on the proportion of the total reproductive output of a population that also recruit back into that population, a quantity called *local retention* (LR; Fig. 1, Table 1; Botsford et al. 2009b). To translate the local retention fraction into the currency of persistence, the logic of replacement can be followed. To define reproductive output in a system with larval dispersal, we use lifetime egg production (LEP), which is the product of survival from recruitment to a given age and the fecundity at that age, summed across all ages (this is analogous to R_0, but in terms of eggs produced, rather than recruits into the population; Table 1). Self-persistence requires that the multiplication of lifetime egg production (LEP) by the local retention fraction (LR) be greater than one at low density, i.e., LEP × LR > 1. This calculation is the spatial analogue of the nonspatial criterion that $R_0 > 1$. In a metapopulation in which one local subpopulation

meets the self-persistence criterion, connectivity between subpopulations, regardless of its magnitude, is not necessary for persistence.

Note that LEP accounts for survival from recruitment to death, while LR implicitly accounts for survival from egg to recruitment (see section *Linking theory and data* for examples). Thus, the local retention fraction does not determine persistence by itself. Persistence requires that any losses during the larval stage be compensated for by lifetime egg production. For a given local retention fraction, a population of long-lived, highly fecund individuals (high LEP) may self-persist, but a population of short-lived, low-fecundity individuals (low LEP) may not. In the context of MPA design, the self-persistence criterion suggests that, to ensure a single MPA is self-persistent, it should be in a location with high enough LEP (survival, fecundity, or both) and LR (local retention) for LEP × LR > 1 (White et al. 2010a).

The other form of persistence, network persistence, occurs when connectivity creates sufficient closed loops for replacement (Gerber et al. 2005, Hastings and Botsford 2006). Populations can still persist even when the local retention fraction in all populations is less than the critical value allowing self-persistence (Fig. 2; Appendix A). Network persistence takes advantage of additional pathways for replacement in addition to local retention. The additional pathways can be most simply illustrated in a metapopulation with two patches (Fig. 2). In the case of two populations, population 1 supplies a fraction of its larvae to population 2 (p_{21}), which supplies a fraction of its larvae to population 1 (p_{12}; Fig. 2). This forms a loop by which an individual in population 1 does not replace itself entirely with its own offspring (i.e., via local retention, LR = p_{11}), but rather over time with its grand-offspring (the offspring of the focal individual's dispersed offspring) on the return loop from population 2 (Hastings and Botsford 2006). Note that connectivity from population 1 to population 2 does not contribute to network persistence unless there is also a return loop of connectivity from population 2 to population 1. The actual persistence criterion derived by Hastings and Botsford (2006; see Appendix A) has the convenient interpretation that the amount of replacement provided by the shared loop between populations must compensate for the combined shortfalls in self-persistence of each local population. A similar logic applies for cases where the number of patches is greater than two, although the mathematical expressions become complicated rapidly as the number of patches increase (see Hastings and Botsford 2006).

We can describe metapopulations with multiple patches, or subpopulations, in terms of a matrix, say **C**, with elements C_{ij} = $LEP_i × p_{ij}$ terms (the "realized" connectivity matrix; Fig. 3). Mathematically, the requirement for network persistence is $\lambda_m > 1$, where λ_m is the largest real eigenvalue of this **C** matrix (Hastings and Botsford 2006, White 2010). Thus, for this spatial matrix description, as for the Leslie matrix, there are two ways

to determine persistence: the actual rate of growth λ_m and the criterion in Hastings and Botsford (2006), which is similar to R_0 in explaining how replacement determines persistence in nonspatial populations.

Description of spatial variability in LEP becomes important in an MPA network context where patches in MPAs are likely to have higher reproduction and survival than patches outside of MPAs subject to fishing mortality. If one knows the spatial pattern of connectivity and LEP, then one can determine whether a network of MPAs should persist. This criterion is particularly important for species with moderate or large dispersal distances, because it quickly becomes impractical to design a single MPA large enough to be self-persistent (Gaines et al. 2003, White et al. 2010a). In reality, connectivity and LEP all likely vary over time. Stochasticity in connectivity can decrease (Watson et al. 2012) or increase (Williams and Hastings 2013) metapopulation growth rates.

The important conclusion for our purposes here is that, even in spatially distributed local populations connected by the dispersal of larvae, the currency for population persistence is still replacement. For a single, isolated local population, local retention is crucial. For more complex networks, replacement needs to be tracked through multiple connectivity pathways. To fully understand the persistence of populations in a network of MPAs, the crucial information needed is the connectivity matrix (the fraction of larvae produced at each location that recruits to each location; see section *The connectivity matrix*) and an estimate of the LEP of each population (Fig. 3; Botsford et al. 2009b, White 2010).

Local retention vs. self-recruitment

As we describe in our review of empirical studies, many studies of marine population connectivity report metrics related to what is often called *self-recruitment*, which is the fraction of all recruits to a location that originated from local parents (Table 1, Figs. 1 and 3; e.g., Jones et al. 1999, Botsford et al. 2009b). Because the numerators are the same, self-recruitment is often assumed to say something about local retention, which is the fraction of *local reproductive output retained* at the focal site (Figs. 1 and 3). The key difference is in the denominators. For self-recruitment, the denominator is total recruitment to a site (including larvae originating from elsewhere), while for local retention, the denominator is total reproductive output of the site (Figs. 1 and 3). Note that nowhere in the logic for replacement and persistence described up to this point (or expressions in Appendix A) does the fraction of self-recruitment appear because it does not describe recruitment back to the natal population (i.e., replacement).

Methods for Literature Review

To what extent do empirical studies of larval dispersal, especially those motivated by applications to
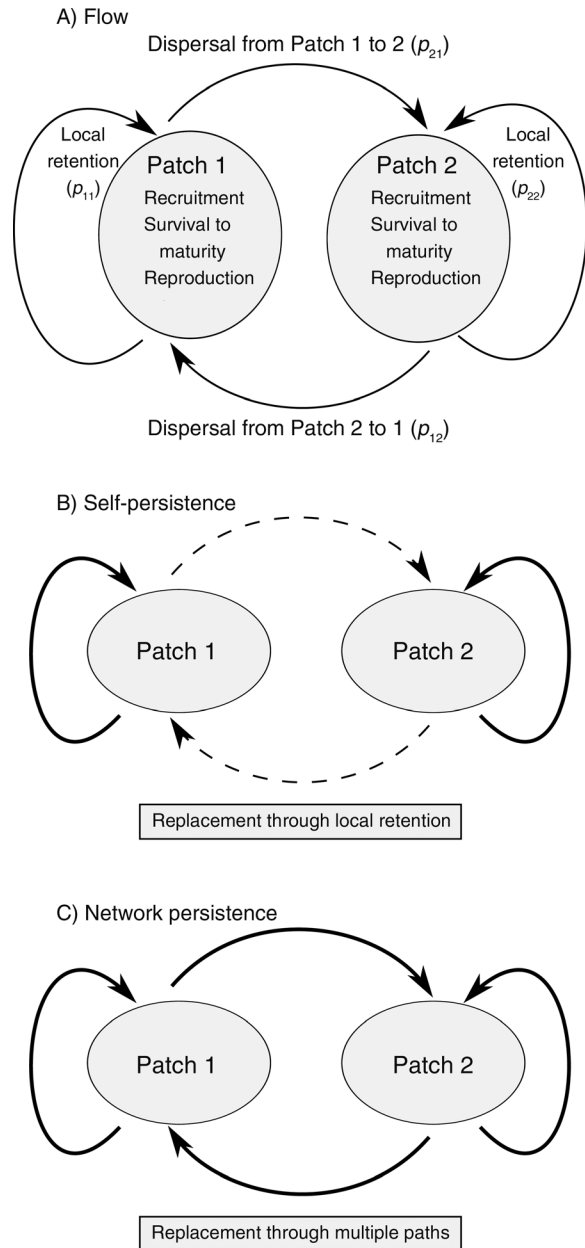

FIG. 2. Two routes to persistence when there are multiple patches: self-persistence and network persistence. The two-patch case is used here for illustration, but the logic extends to multiple patches. (A) The flow of individuals between patches (p_{ij} and p_{ji}) and their survival and reproduction (LEP) within patches. (B) Self-persistence, where local populations persist independently due to local retention (solid lines), even though connectivity may still occur (dashed lines). (C) Network persistence, where local populations persist through both local retention and closed loops of connectivity between patches (solid lines). Note that only the connectivity that leads to closed loops of replacement contributes to persistence.

MPA design, inform questions of population persistence in light of the existing theory for persistence in marine metapopulations? To answer this question, we first searched the primary literature for all studies that
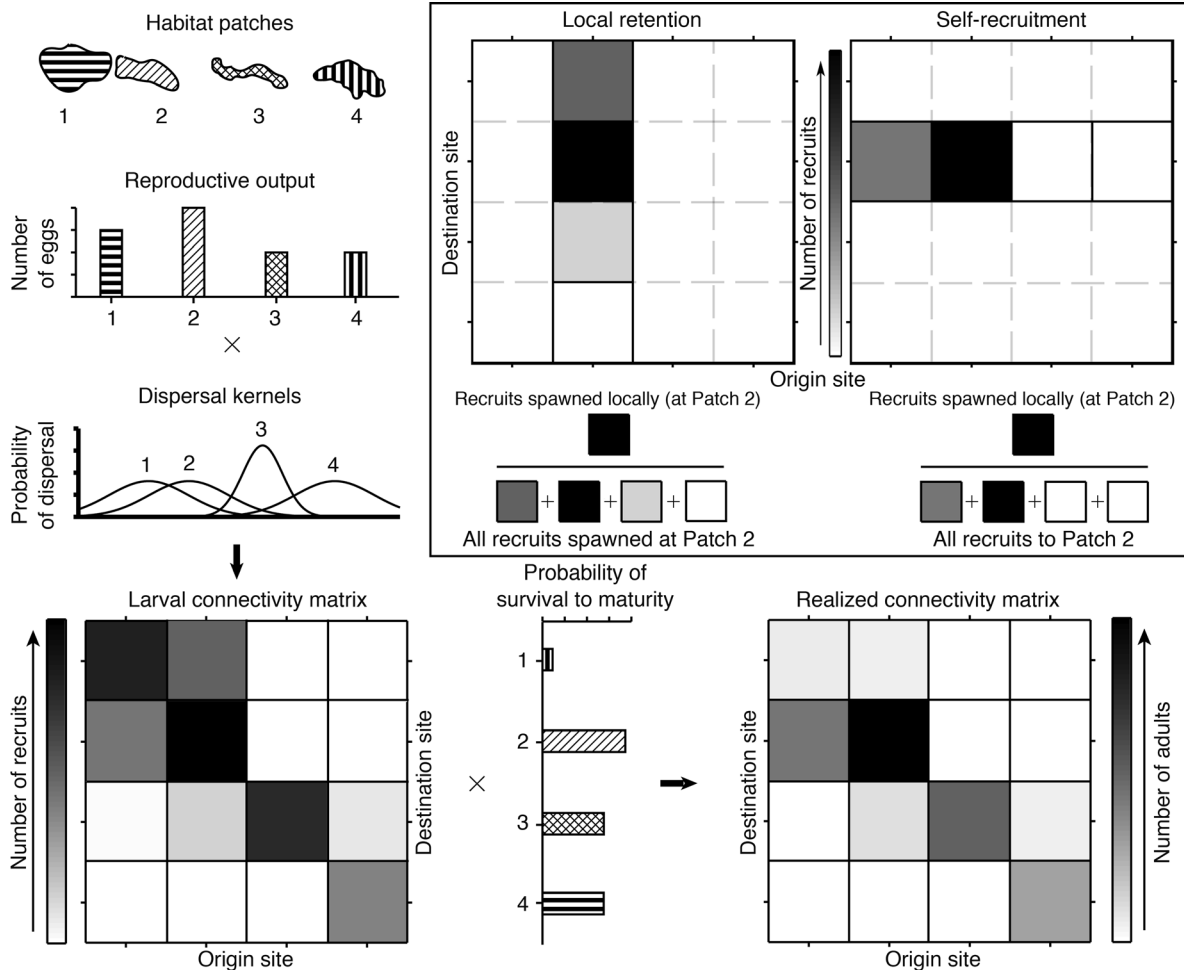
FIG. 3. Data needed to fully inform assessments of population persistence. Starting from the upper left, a hypothetical spatially structured network of populations within a heterogeneous habitat leads to differential reproductive output among patches. Larvae originating at each patch disperse over the landscape according to a dispersal kernel, which is shaped by hydrodynamic processes in the coastal ocean. Translating the continuous-space dispersal kernels to the discrete patch landscape gives a larval connectivity matrix. The realized connectivity matrix (C) is the larval connectivity matrix multiplied by the patch-specific survival from recruitment to maturity. Inside the box on the upper right is shown how one can calculate the local retention or self-recruitment fraction from a connectivity matrix (see also Fig. 1). Note that these metrics have the same numerator, but a different denominator (Table 1). See also Botsford et al. (2009b).

empirically estimated the origins and destinations of larvae. To perform the search, we used the ISI Web of Knowledge database with the search terms "marine connectivity," and "self-recruitment," or "local retention." The search was performed on 15 October 2012. To ensure we did not miss any relevant papers that were not found in the database search, we also searched the literature cited in recent reviews of marine population connectivity (e.g., Cowen and Sponaugle 2009, Lopez-Duarte et al. 2012) for studies that empirically measured dispersal pathways. Our search resulted in a total of 146 references. From this list we selected the publications that made empirical measurements of the origins and destinations of larvae. We excluded studies that measured dispersal pathways only via biophysical

models or studies that inferred connectivity using spatial genetic structure in neutral markers. The latter were excluded because standardized estimates of variance in allele frequencies among populations (such as F_{ST}) can rarely be used to accurately estimate the number of migrants (Whitlock and McCauley 1999, Hedgecock et al. 2007) and do not assign recruits to their origin. We also excluded studies for which data on origins of settlers were not presented in the paper or where origins were only differentiated by habitat type (e.g., estuarine vs. open coast) rather than specific geographic locations. Based on these criteria, our search resulted in a total of 21 papers that provided empirical measurements of the origins and destinations of larvae (Table 1).

TABLE 2. Results from a literature search on studies that empirically estimated the origins and destinations of larvae from coastal benthic marine species.

Reference	Study system, taxa	Method	Metric presented
1) Swearer et al. (1999)	tropical, fish	natural microchemistry	self-recruitment
2) Christie et al. (2010a)	tropical, fish	parentage analysis	self-recruitment
3) Hogan et al. (2012)	tropical, fish	genetic assignment tests	self-recruitment, local retention, connectivity matrix
4) Christie et al. (2010b)	tropical, fish	parentage analysis	self-recruitment
5) Beldade et al. (2012)	tropical, fish	parentage analysis	self-recruitment
6) Jones et al. (1999)	tropical, fish	tag microchemistry	self-recruitment
7) Harrison et al. (2012)	tropical, fish	parentage analysis	self-recruitment
8) Jones et al. (2005)	tropical, fish	tag microchemistry, parentage analysis	self-recruitment
9) Almany et al. (2007)	tropical, fish	tag microchemistry	self-recruitment
10) Planes et al. (2009)	tropical, fish	tag microchemistry, parentage analysis	self-recruitment, connectivity matrix
11) Saenz-Agudelo et al. (2009)	tropical, fish	parentage analysis, genetic assignment tests	self-recruitment
12) Saenz-Agudelo et al. (2011)	tropical, fish	parentage analysis, genetic assignment tests	self-recruitment, connectivity matrix
13) Berumen et al. (2012)	tropical, fish	parentage analysis	self-recruitment
14) Buston et al. (2011)	tropical, fish	parentage analysis	dispersal distance
15) Saenz-Agudelo et al. (2012)	tropical, fish	parentage analysis	self-recruitment
16) Carreras-Carbonell et al. (2006)	temperate, fish	genetic assignment tests	self-recruitment
17) Swearer and Shima (2010)	temperate, fish	natural microchemistry	self-recruitment
18) Becker et al. (2007)	temperate, invertebrate	natural microchemistry	self-recruitment
19) Carson et al. (2010)	temperate, invertebrate	natural microchemistry	self-recruitment
20) Carson et al. (2011)	temperate, invertebrate	natural microchemistry	local retention, connectivity matrix
21) Wood and Gardner (2007)	temperate, invertebrate	genetic assignment tests	self-recruitment

Note: Papers are grouped by taxon and study region.

For each paper, we assessed its objective, study system (temperate vs. tropical, fish vs. invertebrates), geographic location, sampling effort, spatial scale of study (number of sites, patch size, inter-patch distance), type of method used to estimate origins and destinations of larvae (natural microchemistry, microchemistry tags, genetic assignment tests, or parentage analysis), and metrics calculated that related to connectivity and persistence (self-recruitment, local retention, connectivity matrix). Finally, we highlighted additional metrics that the authors could have estimated (with existing data or with additional sampling) to better inform population persistence.

Review of Empirical Studies

Missing from most of the papers was any measure of replacement. Yet, every study (except Swearer and Shima 2010) mentioned the relevance of their results to management or MPA design. Nearly every study reporting empirical estimates of the origins and destinations of recruits presented estimates of self-recruitment (Table 2). Only one study reported local retention directly (Hogan et al. 2012). Four studies reported connectivity matrices (Table 2). One study reported estimates of the origin and destination of individuals in terms of dispersal distances (Buston et al. 2011).

The studies we reviewed used a variety of terms to mean the same thing. Self-recruitment was often called "local recruitment," "local replenishment," "self-replenishment," or "self-seeding." Some studies referred to the term "self-recruitment," but correctly measured local retention. The range of terminology used made it difficult to understand which metric was actually reported. Furthermore, the derivation of the numbers used to calculate self-recruitment was often not clearly presented. Among those studies that did clearly present a metric, estimates of self-recruitment ranged from 0% to 96%, covering nearly the entire range of possibilities. The values of self-recruitment were not easily comparable between studies because the spatial scale (i.e., distance between patches) at which self-recruitment was calculated varied from ~0.2 km (among patch reefs within Kimbe island; Planes et al. 2009) to ~1200 km (among oceanic islands off New Zealand; Wood and Gardner 2007).

Many studies were only conducted at a single site and many of the study species likely disperse beyond that site. This would limit a study to calculating local retention, which can only permit a determination of self-persistence rather than network persistence. Several

studies did estimate connectivity matrices (Planes et al. 2009, Carson et al. 2011, Saenz-Agudelo et al. 2011, Hogan et al. 2012), and one study did link connectivity matrices with demographic processes to understand population persistence of two mussel species between two 30–40 km stretches of coast in southern California (Carson et al. 2011). Parameterizing a formal population model with empirical measurements of connectivity and within-patch demographic processes, as in Carson et al. (2011), is a particularly informative way to understand population persistence.

LINKING THEORY AND DATA

Gathering the necessary data to link empirical measurements with the logic of persistence is often difficult, but there are multiple approaches to do so. The biggest challenge has been estimating the connectivity matrix. The studies we reviewed have been a valuable start to overcome this challenge. However, the quantities reported need to be changed, and additional data needs to be collected, to be useful in determining persistence. The next step of informing population persistence for MPA design is to ensure that empirical methods properly account for all components of replacement, i.e., the survival and reproduction of individuals throughout their life, as well as the fate of larvae leaving each location. Recall that lifetime egg production (LEP) is the probability of survival from recruitment to a given age multiplied by the fecundity at that age, summed across all ages. Survival and fecundity, therefore, are two empirical components that are needed to estimate LEP. Empirical estimates of survival and fecundity will often provide a snapshot in time and this needs to be remembered when making statements about population persistence. In short, to fully understand population persistence in a network of MPAs, three pieces of empirical information are needed: (1) connectivity matrix, (2) per capita fecundity of populations, and (3) survival of recruits.

These three elements are likely to vary over time, and (2) and (3) are also likely to depend on age (or size, or some other structuring variable). Elements (2) and (3) include survival from recruitment to maturity, as well as survival and fecundity integrated over the reproductive life span of an average individual. Note that (2) and (3), when estimated over the average life span of individuals, approximate LEP. Connectivity matrices alone, or a single estimate of local retention, or any estimate of self-recruitment, are inadequate to fully describe population persistence in a network of MPAs. Next, we describe the connectivity matrix and how to estimate local retention. In the section *Case Study* below and in Appendix B, we then illustrate how to integrate empirical measurements of connectivity (or local retention), fecundity, and survival to inform self-persistence. In the case studies, the survival of recruits to maturity is unknown, but we can estimate what that value would need to be in order to maintain self-persistence.

The connectivity matrix

The connectivity matrix has origin locations along the columns and destination locations along the rows (Fig. 3). Note that the terms "source" and "sink" have a different meaning (see Pulliam 1988, Figueira 2009) than the terms "origin" and "destination" and should not be used to label a connectivity matrix. The cells of the "potential" connectivity matrix represents the probability that an offspring produced at a given origin location returns to recruit at that same location in a given time step (diagonals cells of the matrix, denoted as $p_{ii} = LR$) or disperses to recruit to another location (off-diagonals of the matrix, denoted as p_{ij}; Table 1). Each column represents the probabilities among destinations corresponding to the dispersal kernel from a particular origin (Fig. 3). When connectivity matrices are calculated via particle tracking in hydrodynamic models, the probabilities account for processes (physical and sometimes behavioral) influencing larval movement and successful settlement, but they may or may not include larval mortality or spatially variable egg production (Pineda et al. 2007, Watson et al. 2010). When connectivity matrices are quantified from field studies, as in the studies we reviewed, the probabilities necessarily include egg production, transport (physical and behavioral), larval mortality, and settlement, as well as typically including any early post-settlement mortality that occurred before sampling or counting by the researcher. Note that the elements of some "observed" connectivity matrices reported in empirical papers are presented as absolute numbers of individuals (Planes et al. 2009, Saenz-Agudelo et al. 2011), rather than probabilities or proportions. The "realized" connectivity matrix, which is required for determining persistence, contains total reproductive output in each patch, the movement of larvae between patches, and the subsequent survival to maturity within patches (Gerber et al. 2005, Pineda et al. 2007, Hamilton et al. 2008, Burgess et al. 2012). Empirical estimates of the realized connectivity matrix may also be a snapshot of the realized connectivity matrix **C** we described in the section above on *Persistence in a network of connected populations*.

Estimating local retention

An estimate of local retention requires an estimate of the reproductive output of the population (i.e., the denominator in the local retention fraction of Figs. 1 and 3). Because many estimates of local retention are a snapshot in time, so too are empirical estimates of reproductive output (i.e., it need not be integrated over the lifetime as in LEP). For the purpose of estimating local retention, reproductive output can be estimated in two ways. The first way is to sum the total number of recruits originating from a focal site across all destination sites comprising the connectivity matrix (see *Case study* below). The second way to calculate reproductive output is to estimate mean fecundity of individuals and

TABLE 3.   Connectivity matrix of panda clownfish *Amphiprion polymnus* in Bootless Bay, Papua New Guinea, for the case study.

Desti-nation	No. juveniles sampled	Origin								Fraction SR	Fraction LR	No. recruits per adult	No. local recruits per adult
		BA (57)	LO (37)	MO (29)	TA (48)	LI (31)	MN (13)	BE (57)	FI (62)				
BA	70	4	0	1	1	0	1	1	0	0.057	0.308	0.228	0.070
LO	69	3	3	2	1	1	2	1	1	0.043	0.375	0.216	0.081
MO	70	1	3	1	3	2	2	0	1	0.014	0.125	0.275	0.0344
TA	59	0	0	1	16	1	1	0	1	0.271	0.593	0.563	0.334
LI	42	1	1	0	3	0	0	1	1	0	0	0.161	0
MN	10	1	0	0	0	0	1	1	0	0.10	0.125	0.615	0.0769
BE	102	3	1	1	1	1	1	7	1	0.068	0.583	0.211	0.123
FI	68	0	0	2	2	0	0	1	3	0.044	0.375	0.129	0.0484
Total	490	13	8	8	27	5	8	12	8				

Notes: These data are adapted from Table 1 of Saenz-Agudelo et al. (2011). The origin and destination site abbreviations are those used in Saenz-Agudelo et al (2011). Numbers in parentheses show the numbers of breeders sampled at the origin. Connectivities were calculated using parentage analysis (see *Case study*). Fraction SR is the fraction of self-recruitment reported in Saenz-Agudelo et al. (2011). Fraction LR is the fraction of local retention that we calculated, which is the number of recruits that originated from a given population divided by the total number of all recruits produced by the given population. The number of recruits per adult was calculated from the total number of recruits originating from a population (sum of columns) divided by the number of breeding adults sampled. The number of local recruits per adult per time was calculated by multiplying the fraction of local retention by the number of recruits per adult.

multiply it by the number of breeding individuals (see case study in Appendix B).

The one study reporting direct estimates of local retention (Hogan et al. 2012) estimated the total reproductive output of a local population by summing the number of recruits across seven sites that originated from a particular site. In other words, for each origin population, the authors summed the number of recruits from that population to all sampled populations. This measure of reproductive output essentially estimates the effective contribution of one site to all sites. For the summed number of recruits across multiple sites that came from a particular site to be a reasonable measure of reproductive output, the number of sites sampled needs to be a high percentage of the total number of sites (habitat patches) accessible to larvae. If a site contributes substantial numbers of recruits to unsampled sites, then summing recruit numbers across sampled sites may not indicate the reproductive output of the local population very accurately. Nonetheless, the approach used by Hogan et al. (2012) is a useful way to begin providing estimates of connectivity that inform population persistence and MPA design.

Some of the studies reporting self-recruitment collected data that could be used to estimate local retention. For example, parentage analysis studies (Table 1) also conducted surveys of adult population densities, because knowing the percentage of the adult population sampled is typically required (Christie 2010, Jones et al. 2010). A crude estimate of total reproductive output of the population could be obtained by assuming realistic, constant per capita fecundity and multiplying it by the estimate of adult population size. Another approach is to calculate the relationship between body size and fecundity (Beldade et al. 2012). Reproductive output can then be estimated more accurately by using the estimates of population size, the body size frequency distribution of the population, and the size–fecundity relationship.

A common issue was that the number of adults and recruits sampled were often presented without the spatial scale or effort of sampling, so a quantitative estimate of abundance was unknown. To estimate local retention, adult and recruit abundances need to be quantitatively estimated at the spatial scales at which local retention is inferred. Therefore, in addition to collecting samples for assignment tests, surveys of adult and recruit densities would be a valuable step towards properly informing assessments of persistence.

Case study

To illustrate how to present connectivity statistics that better inform persistence, we first focus on a study that reported a connectivity matrix for the panda clownfish, *Amphiprion polymnus* (Saenz-Agudelo et al. 2011). Saenz-Agudelo et al. (2011) provided a connectivity matrix, derived from parentage analyses, showing the number of recruits at each of eight sites that came from each of those sites in Bootless Bay, Papua New Guinea. To know, for example, whether Loloata South Bank, called site "BA" in Saenz-Agudelo et al. (2011), was self-persistent, an informative first step would be to calculate local retention, which is the number of recruits that originated from local parents (=4) divided by the number of recruits originating from site BA (Table 3; see also Table 1 in Saenz-Agudelo et al. 2011). Assuming that all possible destination sites were sampled (which was not the case in Saenz-Agudelo et al. 2011, but we ignore that for the sake of illustration and note that this assumption would inflate estimates of local retention in practice), the latter can be estimated as the sum of recruits from site BA across all destination sites (sums of each column in their connectivity matrix), which equals 13. The value 4/13 gives a local retention fraction of 0.31. Contrast this with the self-recruitment value presented by the authors, 0.057, which is the number of recruits that originated from local parents (=4)
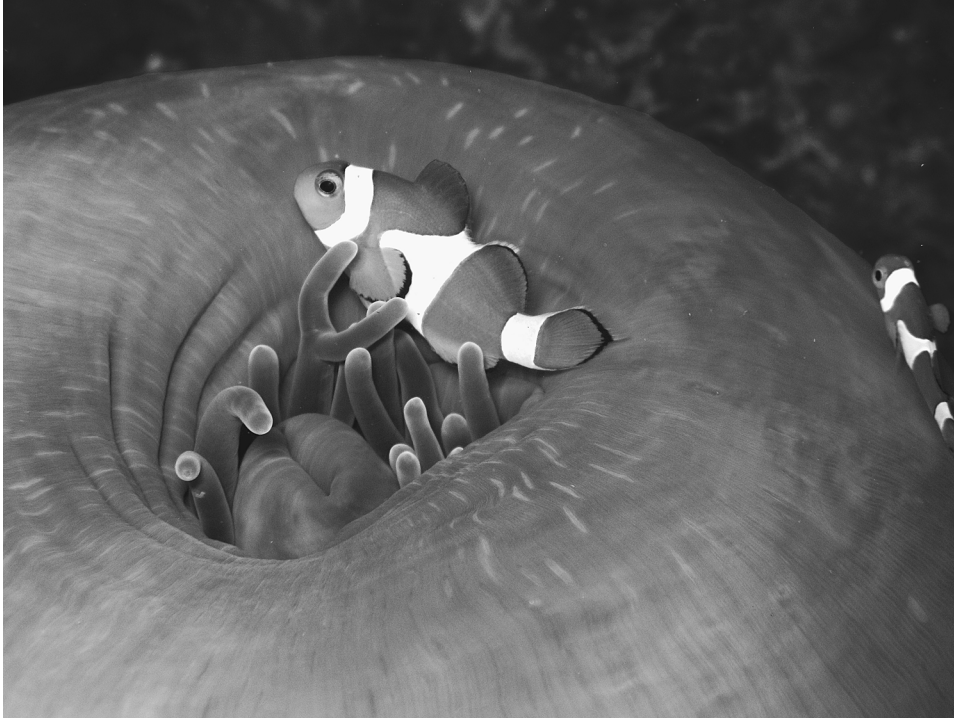
PLATE 1.   *Amphiprion ocellaris* at Semporna, Borneo, Malaysia. Species in the genus *Amphiprion* have proved to be very useful in studies on connectivity. Photo credit: E. V. Sattherthwaite.

divided by the total number of juveniles sampled at that site (=70). The requirement for self-persistence is LEP × LR, so next we need an estimate of LEP. We do not know the survival and fecundity of individuals over their life span, but we do have a snapshot of reproductive output that we can use to make a statement about persistence. To estimate the number of recruits produced per adult over a single time period (assuming all adults and juveniles were randomly sampled in the local population and all local populations were sampled), we assume that 57 adults produced 13 recruits over a period of three months (sampling interval in Saenz-Agudelo et al. [2011]) across all sites to infer that the average number of recruits an adult produces is $13/57 = 0.23$. Therefore, the number of recruits able to replace adults over this period of time is 0.31 (local retention fraction) × 0.23 (average number of recruits an adult produces) = 0.07.

So what does 0.07 local recruits per time interval say about self-persistence? For those recruits to replace the adults, we need to close the lifecycle "loop" and know something about the survival of recruits to maturity. If we assume, for the sake of illustration, that the local retention fraction and the average number of recruits produced per adult remain constant over time, and that all juveniles survive to maturity, then it will take $1/0.07 = 14$ three-month reproductive periods (assuming that is the length of time from egg production to recruitment; Saenz-Agudelo et al. 2011) for each adult to produce one

offspring that recruits locally. Therefore, one could infer that site BA will not self-persist if parents do not, on average, survive and reproduce for at least 42 months (14×3 months) after the onset of reproduction (longer if reproduction is seasonal). Because survivorship of recruits to adulthood is undoubtedly <1, it will take >14 reproductive periods for each adult to replace itself through self-persistence because not all recruits will survive to reproduce. For comparison, note that the life span of similar species of *Amphiprion* spp. is typically $\sim10–17$ years (Buston and García 2007), making self-persistence likely in this case. It is, of course, possible that site BA could persist through network persistence, even if it does not self-persist. It is also likely that that the local retention fraction and the average number of recruits produced per adult varies over time, which would necessitate longer term data collection on the order of the generation time of the members of the population.

The difficult reality

The illustrative example above (and in Appendix B) is deliberately simplistic, does not reflect actual predictions, and only concerns self-persistence; but it demonstrates how commonly collected data can better inform issues of population persistence than that provided by estimates of self-recruitment. The case study in the previous section and in Appendix B show that, while it is possible to collect the necessary data, the existing data

still fall short of properly assessing persistence. The inadequacy of existing data is evidenced by our need to make certain assumptions, such as the assumption that all possible destination sites were sampled in the case study, and that there was no temporal variation in local retention, fecundity, or survival. The difficult reality is that additional data on connectivity among patches and demographic rates within patches are required over larger spatial and temporal scales. If empirical data are to inform persistence-based MPA design, there needs to be a change in focus from self-recruitment to local retention, and a commitment to studies that aim to understand temporal variation in the local retention fraction, survival, and fecundity.

The challenges of collecting the necessary data likely force researchers to choose species with characteristics lending themselves to the methods used to estimate connectivity, and species in which measurements of survival and fecundity can more easily be obtained (see Plate 1). The practical challenges in estimating connectivity have perhaps, at least in part, caused the disproportionate number of studies on tropical fish species (Table 2). Most of the tropical fish species used in the studies we reviewed lay benthic egg masses from which pelagic larvae emerge and, compared to other species, generally have small population sizes, short life spans, clearly defined habitat patches, and small adult home ranges. Such characteristics more easily allow census and microchemistry tagging of the entire population, as well as the collection of tissue samples or otoliths from both recruits and adults. Now that the promise of these methods to inform MPA design has been made clear in relatively tractable systems, researchers will need to develop new methods and overcome some logistical hurdles in order to guide MPA planning for other species and study systems.

What does self-recruitment tell us?

As should be clear from theory presented in this paper, the self-recruitment fraction reveals nothing about population persistence (Appendix A). Self-recruitment (e.g., Figs. 1 and 3) does not reveal how much a local population relies on larval dispersal from other local populations, or why connectivity is important for population persistence. A patch with a given amount of self-recruitment may persist independently (if the fraction of locally derived recruits is sufficient for replacement) or persist only as a result of connectivity loops through other patches. The important point is that self-recruitment does not express a quantity relevant to either self-persistence or network persistence.

Self-recruitment can be considered as the complement of "openness" (openness = 1 – self-recruitment; Hixon et al. 2002). Openness is an ad hoc quantity used to represent the relative influence of recruits from other patches on the recruitment to a focal patch, so is likely to be related to how rapidly an extirpated patch will recover in the presence of nearby populations at normal levels (Roberts 1997, Pinsky et al. 2012). However, if MPAs are designed for network persistence, then openness is a redundant metric because network persistence implies that a single patch will recover from local extinction (Hastings and Botsford 2006). Pinsky et al. (2012) used calculations of openness for particular spatial patterns of populations to show how high fractions of self-recruitment (i.e., low openness) could arise from short dispersal distances and wide patch spacing. Their analysis showed how high levels of self-recruitment could be commonly observed in coral reef landscapes, but did not directly address whether populations would persist at each location. Earlier models have shown how persistence in MPA networks is determined by the combination of patch size, patch spacing, and dispersal distances (Botsford et al. 2001, Gerber et al. 2005, Moffitt et al. 2009, White et al. 2010a). These earlier models did not calculate openness because that specific quantity does not arise in the analysis of persistence (Appendix A). Openness, however, could be calculated from plots showing which dispersal distances will persist for a specific patch size and spacing, such as Fig. 3 in Botsford et al. (2001). It is possible that openness is a useful metric to quantify some aspects of metapopulation dynamics, such as rates of recovery, but to date no quantitative study has investigated how recovery rates should influence MPA design. Openness, like self-recruitment, is not relevant to persistence-based MPA design.

Finally, there may be other questions for which self-recruitment could be informative. If recruits that originated from nonlocal parents are phenotypically or genetically dissimilar to recruits originating from local parents, then the percentage of self-recruitment may be important for questions of gene flow, artificial propagation programs, and the evolution of traits. Such questions are still relevant to MPAs, especially if phenotypic or genetic differences between recruits from local and nonlocal sources influence local demographic rates (Holt and Gomulkiewicz 1997, Baskett et al. 2013, Burgess et al. 2013).

A Way Forward

Better integration of estimates of connectivity among patches with estimates of demographic rates within patches will improve our ability to address the question of how spatial management can maintain the persistence of populations. In the context of MPAs, empirical estimates of larval dispersal, obtained through genetic assignment tests, parentage analysis, or microchemical tagging should be combined with estimates of population size, survival, and fecundity within patches. Furthermore, it would be fruitful to combine empirical estimates of larval dispersal, measurements of within patch demography, and biophysical models of larval dispersal. Empirical estimates of larval dispersal require substantial effort and still only provide a snapshot of population dynamics. Biophysical models are used to

estimate connectivity over larger and longer scales than currently feasible in empirical studies (e.g., James et al. 2002, Cowen et al. 2006, Treml et al. 2007). We deliberately did not include studies using biophysical models in our review, because such models are rarely validated with field data (except see Sponaugle et al. 2012). A promising approach would be to combine empirical estimates of larval dispersal with biophysical models to validate, or ground-truth, the results from biophysical models, and then to estimate connectivity at sites and years where field sampling of recruit origins was not undertaken. The usage and interpretation of biophysical models depends on the representation of larval behaviors, the spatial resolution of the model, and other considerations. The inclusion of small-scale flow features (order of hundreds of meters to a few kilometers) in circulation models can increase the predicted return of larvae to their natal population, which may have a large impact on predicted population persistence (Nickols et al. 2012). Large-scale circulation models that neglect such features (often having relatively coarse spatial resolution of 1 km per cell or more) may overestimate connectedness of populations and underestimate the ability of some populations to self-persist.

Designing MPAs is complicated and time-consuming, and often suffers from a shortage of relevant empirical information (Saarman et al. 2013). There have been efforts towards handling this shortage by developing decision theory in the absence of perfect empirical information (Halpern et al. 2006, Bottrill et al. 2008, White et al. 2010b), and developing approaches for designing MPAs based on representative areas that capture community- and ecosystem-level characteristics (Leslie et al. 2003, Fernandes et al. 2005) without considering whether populations will persist. The current state of the art in persistence-based MPA design is to use spatially explicit population models with connectivity estimates drawn from biophysical circulation simulations (White et al. 2013). In the meantime, the tools and data needed to obtain direct empirical estimates of larval connectivity to "ground-truth" the biophysical models, or to use in locations where circulation models are not available, are increasingly within reach. The studies we reviewed are important for providing direct estimates of larval dispersal, revealing the capabilities of larvae to return to their natal origin, as well as documenting the large variation in dispersal among species and locations. The next step is to evaluate how such patterns of dispersal influence persistence of each species. Simply documenting larval export from MPAs is not enough to understand how, or if, MPAs achieve their ecological objective. The same patterns of connectivity may have different impacts on species that differ in demographic rates, and vice versa. Therefore, estimates of self-recruitment or larval connectivity matrices alone are inadequate for predicting population persistence. Instead, connectivity matrices should be combined with information on population size, repro-

ductive output, and survival within patches (giving a realized connectivity matrix) of multiple species before any generalities can be revealed. Such a task requires great effort and will be relatively easier for some species compared to others. An important and achievable first step will be for future studies to change the focus from estimating self-recruitment to estimating local retention. Estimating realized connectivity matrices requires additional data beyond the origins and destinations of individuals (described by larval connectivity matrices), but such additional data are not beyond the scope of current capabilities, as evidenced by the two case studies (in the section *Case study* and in Appendix B). Ultimately, our ability to accurately predict marine metapopulation persistence in a network of MPAs will require an interdisciplinary approach with participation from oceanographers, ecological empiricists, and population modelers.

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Supplemental Material

Appendix A

Mathematical description of persistence in spatially structured populations (*Ecological Archives* A024-016-A1).

Appendix B

Empirical example of how to calculate local retention without the full connectivity matrix (*Ecological Archives* A024-016-A2).