



Contents lists available at [ScienceDirect](#)

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres



Short communication

Adapting the steepness parameter from stock–recruit curves for use in spatially explicit models

J. Wilson White*

Dept. Wildlife, Fish, and Conservation Biology, University of California, Davis, Bodega Marine Laboratory, PO Box 247, Bodega Bay, CA 94923, USA

ARTICLE INFO

Article history:

Received 9 October 2009
Received in revised form
12 December 2009
Accepted 15 December 2009

Keywords:

Compensation ratio
Population persistence
Spatially explicit metapopulation model
Steepness

ABSTRACT

To inform the design of MPA networks and ensure that they will meet stated goals, spatially explicit metapopulation models are often used to simulate the response of fished species to MPA implementation. Typically, such models are simply spatial extensions of traditional, nonspatial population models used in fisheries management. A common assumption used in making this transition is that $R'(0)$, the slope at the origin of the nonspatial, population-wide egg–recruit relationship (often termed the steepness or compensation ratio), can be used to estimate α , the slope at the origin of the small-scale settler–recruit relationship used in spatially explicit models. This assumption is not always correct. In particular, the value of $R'(0)$ often implicitly accounts for a variety of processes spanning the egg–recruit transition, including larval mortality and advection away from suitable habitat. If a spatial model accounts for some of those loss processes explicitly, such as by using an oceanographically realistic dispersal matrix, it becomes necessary to adjust the estimate of α upwards to avoid double-counting those losses. Here I present a simple correction involving the dominant eigenvalue of the dispersal matrix that adjusts the value of $R'(0)$ to avoid this error. Applying this correction factor ensures that a spatially explicit model will predict population collapse at the same level of fishing implied by a large-scale estimate of $R'(0)$.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

As marine protected areas (MPAs) become a more common tool for marine conservation and fisheries management (Lubchenco et al., 2003; Leslie, 2005; Lester et al., 2009), there is increasing interest in the use of spatially explicit metapopulation models to forecast the effects of MPAs on fished populations (reviewed by Gerber et al., 2003; Pelletier and Mahévas, 2005; Botsford et al., 2008, 2009). Such models can be used in a strategic context, to obtain general relationships between MPA design and population dynamics (e.g., Botsford et al., 2001) or in a tactical context, to project the population consequences of proposed MPAs in a particular location (e.g., Meester et al., 2004; Little et al., 2007; Walters et al., 2007; Kaplan et al., 2009; White et al., in press).

The use of tactical population dynamic models for MPA design can be especially valuable (Pelletier et al., 2008). While strategic modeling efforts have produced general guidelines for MPA design (Botsford et al., 2001; Gaines et al., 2003; Neubert, 2003; Kaplan and Botsford, 2005; Kaplan, 2006; McGilliard and Hilborn, 2008), the success of a particular MPA or MPA network will be sensitive to the details of habitat distribution, the spatial configuration of MPAs, lar-

val connectivity, adult movement, and fishing fleet behavior in that geographical location (Botsford et al., 2008; Pelletier et al., 2008). Thus site-specific models will be useful for projecting MPA effects when one or more key assumptions of more general strategic models are violated. Furthermore, spatially explicit model predictions should be invaluable in an adaptive management setting. In that case, model projections can be compared to subsequent empirical observations of MPA effects to determine whether MPAs have had the desired effect on populations of interest (Walters, 1997; Pelletier et al., 2008).

The models used for this type of analysis are typically spatially explicit extensions of nonspatial population models developed for conventional fisheries management (e.g., Kaplan et al., 2006, 2009; Walters et al., 2007; White et al., in press; reviewed by Pelletier and Mahévas, 2005; Pelletier et al., 2008). Here I identify and propose a solution for a crucial oversight that is often made when making the transition from nonspatial population models to spatial metapopulation models.

2. Theory

For many marine species, population dynamics can be effectively summarized by the relationship between egg production and subsequent recruitment (Fig. 1; Sissenwine and Shepherd, 1987; Botsford, 2005; Botsford and Hastings, 2006). The saturating nature

* Tel.: +1 707 875 1927; fax: +1 707 875 2009.
E-mail address: jwwhite@ucdavis.edu.

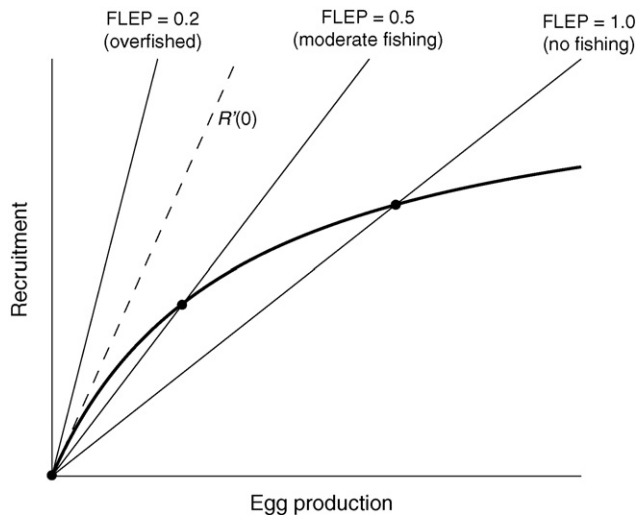


Fig. 1. Typical form of the egg–recruit relationship in marine populations. The relationship between egg production and subsequent recruitment is saturating because of post-settlement density-dependent mortality. The equilibrium density of recruits can be found at the intersection of the egg–recruit curve and a line with slope $1/\text{FLEP}$; several representative examples are shown. The dashed line shows the slope at the origin of the egg–recruit curve, $R'(0)$; if $1/\text{FLEP} > R'(0)$, the equilibrium recruit density is zero and the population collapses. Here, $R'(0) = 1/0.35$, so the population is not persistent for the $\text{FLEP} = 0.2$ case. This curve describes the large-scale relationship represented by nonspatial fishery models. For a spatial model, a similar curve would describe the relationship between larval settler density and subsequent recruit density.

of the curve in Fig. 1 reflects density-dependent resource competition among juveniles. The equilibrium density of recruits is found at the intersection of the egg–recruit curve with a line of slope $1/(\text{lifetime egg production})$ drawn through the origin (Botsford, 2005). The value of lifetime egg production (LEP) reflects all post-recruitment processes, including growth, mortality, harvest, and fecundity, integrated over the average lifespan of a new recruit (LEP is essentially equivalent to eggs per recruit, EPR, or spawning stock biomass per recruit, SSB/R , both of which are commonly used in the fisheries literature). Fishing reduces LEP from its natural, unfished maximum, thus increasing $1/\text{LEP}$ and shifting the equilibrium recruit density to the left along the egg–recruit curve. If $1/\text{LEP}$ exceeds the slope at the origin of the egg–recruit curve, termed $R'(0)$, the equilibrium density is zero and the stock collapses due to overfishing. That is, the population is persistent if $\text{LEP} > 1/R'(0)$. This relationship is the basis for the use of biological reference points derived from LEP in conventional fisheries management (Goodyear, 1993; Mace and Sissenwine, 1993), and most nonspatial models used in stock assessments and other fisheries contexts incorporate some version of this framework (Hilborn and Walters, 1992; Martell et al., 2008). When estimating $R'(0)$ it is common practice to scale both LEP and recruitment by their respective maximum values, so that the horizontal axis becomes FLEP, the fraction of unfished LEP (O’Farrell and Botsford, 2005), and the persistence threshold is $\text{FLEP} = 1/R'(0)$. This formulation of $R'(0)$ is also referred to as the compensation ratio because it is the ratio of recruit survival in the unfished state to survival at near-zero population densities (Goodyear, 1980). For convenience the slope can also be parameterized in terms of steepness, h ; $R'(0) = 4h/(1-h)$ (Hilborn and Walters, 1992). Regardless of the terminology, the slope of the egg–recruit curve is a fundamental population parameter, and considerable effort has been devoted to estimating its value for various fished populations (e.g., Myers et al., 1999; Dorn, 2002).

In order to represent MPA effects in any tactical situation, it is necessary to move to a model that is explicitly spatial. In making the transition from nonspatial to spatial models, one must make two

major adjustments to the basic model framework outlined above. First, connectivity among locations must be represented in a spatially explicit way, such as using a dispersal matrix (Botsford et al., 2008, 2009). By contrast, nonspatial models implicitly assume that all portions of a population are equally well connected via some sort of a larval pool. Second, it is necessary to assume that the density dependent process represented by the saturating egg–recruit curve (Fig. 1) is spatially distributed, so that a similar curve describes the density-dependent survival of settlers within each model cell. Given these two adjustments, a simple example of a spatially explicit model would be:

$$S_{i,t} = \sum_{j=1}^n D_{ji} N_{j,t} \phi$$

$$R_{i,t} = f_i(S_{i,t}) = \frac{\alpha_i}{1 + \beta_i S_{i,t}} S_{i,t}$$

$$N_{i,t+1} = R_{i,t} + N_{i,t} e^{-(M+F_i)}$$
(1)

where $S_{i,t}$ is the density of settlers in cell i (out of n cells) at time t , $R_{i,t}$ is recruit density, and $N_{i,t}$ is adult density. D_{ji} is an element of the dispersal kernel and gives the probability of dispersal from cell j to i . ϕ is per-capita fecundity; M is natural mortality, F_i is the fishing mortality rate in cell i , and function $f_i(S)$ is a Beverton–Holt function with initial slope α_i and asymptotic maximum α_i/β_i . The density-dependent Beverton–Holt parameter β_i may vary over space, reflecting variation in habitat availability or predator density (e.g., Osenberg et al., 2002; White, 2008). The Beverton–Holt slope α_i may also vary over space, though there has been little empirical attention to this possibility, and it is typically assumed that it takes on a constant value α , as in the nonspatial version. I will make the same assumption here, unless otherwise noted.

More complex, age-structured versions of Eq. (1) are commonly used (e.g., Walters et al., 2007), and Kaplan et al. (2006) showed that the steady-state equilibrium for such models can be found rapidly by iterating this system of equations:

$$S_i = \sum_{j=1}^n D_{ji} R_j \text{FLEP}_j$$

$$R_i = f_i(S_i) = \frac{\alpha}{1 + \beta_i S_i} S_i$$
(2)

where the effects of fishing, natural post-settlement mortality, and age-dependent fecundity are now encapsulated by the value of FLEP_i in each cell i . The formulation given in Eq. (2) makes the parallel between the nonspatial and spatial models quite clear, because population persistence in Eq. (2) depends on the value of FLEP_i (and its spatial distribution) relative to α , just as persistence in the nonspatial case depends on the value of FLEP relative to $R'(0)$. Consequently, it is standard practice to parameterize α , the slope of the Beverton–Holt settler–recruit relationship in Eq. (2), using an estimate of $R'(0)$ derived from the large-scale, nonspatial stock–recruit or egg–recruit relationship (Kaplan et al., 2006, 2009; Little et al., 2007; Walters et al., 2007; McGilliard and Hilborn, 2008). However, this approximation may be biased in some cases.

Consider the rationale for describing population dynamics in terms of the egg–recruit relationship. It is exceedingly difficult to observe and measure larval movement, survival, and settlement, and there are virtually no data on these processes for most species. By contrast, it is more straightforward to measure egg production and recruitment over multiple years and estimate the slope at the origin of the egg–recruit relationship (assuming the egg production data extend sufficiently close to zero). Therefore it is possible to obtain an empirical estimate for $R'(0)$ and thus for the value of FLEP that leads to population collapse. However, it is important to be mindful of the suite of processes that are subsumed within the egg–recruit relationship: given X eggs, $R(X)$ will survive the larval

period, avoid advection into open water, return to suitable habitat, and successfully recruit to the adult population. Thus one could decompose $R'(0)$ into its component processes:

$$R'(0) = r_1 r_2 r_3 \dots r_n \quad (3)$$

where the n values of r_i each represent the probability of surviving one of the series of processes (larval mortality, advection, finding suitable habitat, settlement, etc.) spanning the egg–recruit transition.

Within a spatial metapopulation model, it is possible to explicitly represent some of the processes implicitly contained within $R'(0)$ in Eq. (3). For example, consider a rocky reef fish population along a coastline containing both rocky- and soft-bottom habitat. It is reasonable to expect that some of that species' larvae disperse to non-habitat (i.e., soft-bottom) locations, where they do not survive. In a nonspatial model, that larval loss is one of the processes r_i represented by $R'(0)$ in Eq. (3). In a spatial model, that loss could be represented explicitly by the larval dispersal matrix (the $n \times n$ matrix \mathbf{D} of dispersal probabilities D_{ji} , as in Eqs. (1)–(2)), which will specify the fraction of larvae that are lost to non-habitat locations. Thus it would be improper to use $R'(0)$ as an estimate of α , because that would effectively double-count process r_i . Instead, one would ideally use $\alpha = R'(0)/r_i$. Depending on the complexity of the method used to estimate \mathbf{D} , the spatial model could include explicitly a range of the processes implied by Eq. (3), including offshore advection and larval mortality, and the value of α would need to be corrected to account for each of these.

As a practical matter, we lack independent estimates of the probabilities r_i , so it is difficult to apply the desired correction to $R'(0)$. Rather the only value that has empirical support is $R'(0)$ itself, which has been derived from observations of the egg–recruit relationship of an actual population. However, it is reasonable to expect that as estimates of the dispersal kernel become more realistic (e.g., moving from an idealized, one-dimensional dispersal kernel to a dispersal matrix estimated from the output of a numerical circulation model) and account for more of the processes implicitly described by $R'(0)$, the value of α should be reduced so as not to double-count those processes in the spatial population model. I now propose a method to accomplish this and demonstrate its validity.

3. Methods

The key empirical result that should be preserved in the spatial population model is that the population collapses if $\text{FLEP} < 1/R'(0)$. If one considers population dynamics at low density (i.e., near the point of collapse), it is reasonable to ignore density-dependent processes and use a linear approximation to the nonspatial model, so that $R_{t+1} = R'(0) \times R_t \times \text{FLEP}$ (e.g., Hastings and Botsford, 2006). Similarly, a linearized version of the spatial model can be written using matrix notation as

$$\mathbf{R}_{t+1} = \mathbf{A} \cdot [\mathbf{D} \times (\mathbf{R}_t \cdot \mathbf{L})] \quad (4)$$

where \mathbf{A} is an $n \times 1$ vector of the slope α_i at each location, \mathbf{R} is an $n \times 1$ vector of the recruit density at each location, \mathbf{D} is an $n \times n$ matrix of dispersal probabilities D_{ji} , and \mathbf{L} is an $n \times 1$ vector of FLEP_i at each location; \times represents matrix multiplication and \cdot represents elementwise (Hadamard) multiplication. Making the assumption that α and FLEP are constant across space (i.e., scalars), representing the scenario implied by the nonspatial model, Eq. (4) becomes

$$\mathbf{R}_{t+1} = \alpha \mathbf{D} \times \mathbf{R}_t \text{FLEP} \quad (5)$$

Defining matrix $\mathbf{C} = \alpha \times \mathbf{D} \times \text{FLEP}$, then the dynamics are $\mathbf{R}_{t+1} = \mathbf{C} \times \mathbf{R}_t$. Because \mathbf{C} has only non-negative entries, the

Perron–Frobenius theorem applies and the population will persist (i.e., \mathbf{R}_t will increase over time rather than decreasing towards zero) if λ_C , the dominant eigenvalue of \mathbf{C} , is greater than 1 (Caswell, 2001; Hastings and Botsford, 2006). Equivalently, λ_D , the dominant eigenvalue of \mathbf{D} , must be greater than $1/(\alpha \text{FLEP})$, and the population does not persist if $\text{FLEP} < 1/(\alpha \lambda_D)$. Therefore, in order to preserve the result that the population is not persistent if $\text{FLEP} < 1/R'(0)$, one must parameterize the slope of the settler–recruit function to be

$$\alpha = \frac{R'(0)}{\lambda_D} \quad (6)$$

This correction ensures that any larval loss explicitly accounted for in \mathbf{D} (such as larval mortality, advection offshore, or dispersal to non-habitat, or any other process implied by Eq. (3)) is not implicitly accounted for by α . For this correction to account for dispersal to non-habitat, \mathbf{D} must represent the failure to settle in non-habitat as a dispersal probability of zero. The magnitude of the correction in Eq. (6) will depend on how many of the suite of possible processes r_i are explicitly accounted for in \mathbf{D} . If no larval loss processes are represented by \mathbf{D} (e.g., if \mathbf{D} consists of a dispersal kernel that integrates to one along an infinite coastline with homogenous habitat; Botsford et al., 2001), then $\lambda_D = 1$ and $\alpha = R'(0)$. Note that it should be possible to adjust this correction factor for the case in which α is known to vary spatially (as implied by vector \mathbf{A} in Eq. (4)), but the connection to a large-scale aggregate estimate of $R'(0)$ is less clear and I do not pursue that special case here.

To demonstrate the use of the correction in Eq. (6), I simulated the dynamics of population occupying a one-dimensional coastline with heterogeneous habitat, using the model given in Eq. (2). The coastline consisted of spatial units that were classified as either suitable habitat or non-habitat. Larval dispersal among cells was modeled using a Gaussian dispersal kernel, so that the probability of dispersal from cell j to cell i , D_{ji} , was a function of the distance between i and j and given by a normal distribution with a mean of zero and a standard deviation, d , that defined the mean dispersal distance in one direction (Largier, 2003). Larvae were assumed to die if they dispersed to non-habitat cells, a process that was represented by setting $D_{ji} = 0$ for all non-habitat cells i . The dispersal matrix \mathbf{D} thus accounted for some larval loss that would be implicitly included in $R'(0)$ in a nonspatial model. This is a relatively simple example intended for illustrative purposes (although it similar to the representation of \mathbf{D} used in several recent tactical MPA models; Kaplan et al., 2006, 2009; White et al., in press). In a more sophisticated setting, \mathbf{D} might be estimated using output from a numerical circulation model (e.g., Paris et al., 2007), and more larval loss processes (the r_i in Eq. (3)) would be represented explicitly.

Coastlines with a range of habitat heterogeneities were represented using a spatial domain with a total of 20 linear units of which a fraction p were a contiguous string of habitat cells and the remainder were non-habitat cells (i.e., 12 habitat cells followed by 8 non-habitat cells would be a $p = 60\%$ coastline). Values of p ranged from 60 to 100%, which is similar to the range of rocky reef habitat coverage used in a one-dimensional model of the California coast (Kaplan et al., 2009). To avoid edge effects the coastline was made circular. Modeled species had dispersal distances of $d = 0.5, 1, 5,$ and 10 spatial units. All species were assumed to have a persistence threshold of $1/R'(0) = 0.35$. This corresponds to a Goodyear compensation ratio of $\kappa = 1/0.35 = 2.86$, and a steepness of $h = 0.42$, similar to estimates of steepness for several eastern Pacific rockfishes (Dorn, 2002). In other words, this is an estimate of $R'(0)$ that one might obtain from typical fisheries data.

For each combination of dispersal distance d and level of habitat coverage, p , I determined the minimum value of FLEP for which the population was persistent. This was done using the dispersal-

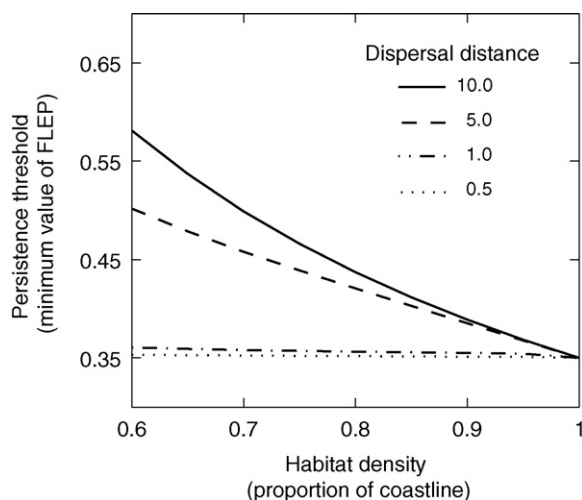


Fig. 2. Coast-wide value of FLEP (fraction of unfished lifetime egg production) at which a spatially explicit population model predicts population collapse (defined as nonzero density of recruits in at least one model cell at equilibrium). Models were run for species with a range of dispersal distances on coastlines with a range of habitat heterogeneity. Habitat density describes the proportion of the coastline that was suitable settlement habitat. Model species all had a nonspatial, coast-wide persistence threshold of $1/R'(0) = 0.35$. Actual persistence thresholds in the spatial model were calculated without the proposed correction to α , the slope at the origin of the settler–recruit curve. When the proposed correction was applied to α , all model runs matched the targeted threshold of 0.35, regardless of dispersal distance (not shown).

per-recruit method of Kaplan et al. (2006) to find the equilibrium density of recruits in each cell, \mathbf{R} . Persistence was defined as at least one nonzero element of \mathbf{R} at equilibrium. I determined the persistence threshold using both the commonly used approximation $\alpha = R'(0)$ and the corrected version from Eq. (5).

4. Results and discussion

When $R'(0) = 1/0.35$ (the nonspatial persistence threshold) was used as a direct estimate of α , the simulation model indicated (erroneously) that the FLEP required for population persistence was greater than 0.35 whenever the coastline had less than 100% habitat coverage (Fig. 2). Furthermore, the increase in the minimum FLEP threshold estimated by the simulation model was much greater for longer dispersal distances. This phenomenon is a consequence of a nonzero fraction of spawned larvae effectively dying when they dispersed to non-habitat cells. For short dispersal distances, most larvae settled in the cells where they were spawned, and there was little effect of the non-habitat cells. As dispersal distances increased, larger proportions of larvae spawned in each cell were lost to non-habitat cells, and the model indicated that greater larval production (FLEP) was required for persistence. By contrast, when the corrected estimate of α from Eq. (5) was used, the persistence threshold was always the correct value: FLEP = 0.35.

These model results reveal that if $1/R'(0)$ had been estimated (nonspatially) as 0.35 for a population with spatially heterogeneous habitat (i.e., less than 100% of the coastline is covered with suitable habitat), a corresponding spatial model would predict that the population would collapse even for values of FLEP > 0.35. Thus, without the proposed correction, the spatial analogue of a nonspatial model would produce strikingly different predictions regarding population persistence. Specifically, species with longer dispersal distances would be erroneously predicted to be more vulnerable to fishing than shorter distance dispersers, especially along coastlines with patchy habitat distributions. Following from this one could also expect biased predictions regarding the level

of FLEP corresponding to maximum sustainable yield or other quantities.

It is worthwhile to consider the possible effects of error in estimating λ_D . Even sophisticated representations of \mathbf{D} , such as from numerical ocean circulation models, may introduce unexpected errors into estimates of dispersal, and thus population persistence. For example, one might generally expect λ_D derived from circulation models to overestimate the loss of larvae due to physical advection because such models often poorly resolve extreme nearshore areas where larvae may be retained (Largier, 2003) and may not perfectly represent larval behaviors that can be crucial to retention and onshore transport (Paris et al., 2007). The predictions of such models are also sensitive to poorly known quantities such as larval mortality rates, although it is unclear whether typical estimates of larval mortality are biased in a particular direction. However, if larval losses were overestimated, the value of λ_D would be erroneously high, producing lower estimates of the minimum value of FLEP needed for population persistence in simulation models. Large downward errors in λ_D could cause population models to predict that a population could support erroneously high levels of fishing (low FLEP), so the correction factor should be used with that caution in mind.

It is important to note that the correction proposed here is appropriate only when $R'(0)$ has been empirically estimated in a large-scale, nonspatial context by analyzing a population-wide egg–recruit or stock–recruit relationship (e.g., Myers et al., 1999; Dorn, 2002). Alternatively, if α were estimated directly from a settler–recruit relationship measured at a small spatial scale comparable to the individual cells in spatial model, no correction would be necessary because the estimate of the slope parameter would not implicitly include larval loss processes. While direct estimation of α is possible when data are available, such as for some coral reef species (e.g., White, 2008), the assumption that $\alpha = R'(0)$ has been the norm in most fishery applications (Little et al., 2007; Walters et al., 2007; Kaplan et al., 2009). As such, future fisheries studies should employ the correction factor applied here (e.g., White et al., in press), especially as more sophisticated representations of larval connectivity, larval mortality, and other processes become increasingly available and can provide explicit representations of the various processes in Eq. (3) (Botsford et al., 2009).

In light of the results presented here, re-examination of some prior model results may be called for. In particular, spatially explicit models of coastlines with heterogeneous habitat that directly parameterized α from nonspatial estimates of $R'(0)$ may have somewhat underestimated recruit survival and overestimated the persistence threshold, especially for widely dispersing species (e.g., Walters et al., 2007; Kaplan et al., 2009). That said, the general result presented by Kaplan et al. (2009) remains entirely correct: given a constant value of α and heterogeneous settlement habitat, longer distance dispersers require greater FLEP for persistence. The caveat is that such results should be interpreted as representing the case in which similar values of α have been estimated at small scales for both long- and short-distance dispersers. If, on the other hand, similar values of $R'(0)$ were estimated for long- and short-distance dispersers, then the correction factor should be applied to α to ensure that a spatial model recaptures the same persistence threshold [i.e., $1/R'(0)$] evident in the natural population. Unfortunately, as Kaplan et al. (2009) noted, both large- and small-scale estimates of this crucial demographic parameter are sorely lacking. Given the importance of α to population persistence and conservation planning, additional research effort to estimate its value for key species would be welcome. In the meantime, the procedure proposed here should ensure that large-scale estimates are not misused in their application to small-scale problems.

Acknowledgements

Thanks to L. Botsford, E. Moffitt, and two anonymous reviewers for helpful comments on the manuscript. This work benefited from discussions with A. Rassweiler and was supported by a grant to L. Botsford from the Resource Legacy Fund Foundation. This publication is a contribution of the Bodega Marine Laboratory, University of California at Davis.

References

- Botsford, L.W., 2005. Potential contributions of marine reserves to sustainable fisheries: recent modeling results. *Bull. Mar. Sci.* 76, 245–259.
- Botsford, L.W., Hastings, A., 2006. Conservation dynamics of marine metapopulations with dispersing larvae. In: Kritzer, J., Sale, P. (Eds.), *Marine metapopulations*. Elsevier, New York, pp. 411–429.
- Botsford, L.W., Hastings, A., Gaines, D., 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* 4, 144–150.
- Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B.J., Largier, J., O'Farrell, M.R., Ralston, S., Soulanille, Wepestad, E.V., 2008. Connectivity, sustainability and yield: bridging the gap between conventional fishery management and marine protected areas. *Rev. Fish. Fish.* 19, 69–95.
- Botsford, L.W., White, J.W., Coffroth, M.-A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold, S.R., Jones, G.P., 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28, 327–337.
- Caswell, H., 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Chicago.
- Dorn, M.W., 2002. Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock–recruit relationships. *N. Am. J. Fish. Manage.* 22, 280–300.
- Gaines, S.D., Gaylord, B., Largier, J.L., 2003. Avoiding current oversights in marine reserve design. *Ecol. Appl.* 13, S32–S46.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserves design: a retrospective and prospective synthesis. *Ecol. Appl.* 13, S47–S64.
- Goodyear, C.P., 1980. Compensation in fish populations. In: Hocutt, C.H., Stauffer, J.R. (Eds.), *Biological Monitoring of Fish*. Lexington Books, Lexington, MA, pp. 253–280.
- Goodyear, C.P., 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Can. Sp. Pub. Fish. Aquat. Sci.* 120, 67–81.
- Hastings, A., Botsford, L.W., 2006. Persistence of spatial populations depends on returning home. *Proc. Natl. Acad. Sci. (U.S.A.)* 103, 6067–6072.
- Hilborn, R., Walters, C.J., 1992. *Quantitative fisheries stock assessment and management: choice, dynamics and uncertainty*. Chapman and Hall, New York.
- Kaplan, D.M., 2006. Alongshore advection and marine reserves: consequences for modeling and management. *Mar. Ecol. Prog. Ser.* 309, 11–24.
- Kaplan, D.M., Botsford, L.W., 2005. Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. *Can. J. Fish. Aquat. Sci.* 62, 905–912.
- Kaplan, D.M., Botsford, L.W., Jorgensen, S., 2006. Dispersal per recruit: an efficient method for assessing sustainability in marine reserve networks. *Ecol. Appl.* 16, 2248–2263.
- Kaplan, D.M., Botsford, L.W., O'Farrell, M.R., Gaines, S.D., Jorgensen, S.J., 2009. Model-based assessment of persistence in proposed marine protected area designs for the central California coast. *Ecol. Appl.* 19, 433–448.
- Largier, J.L., 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.* 13, S71–S89.
- Leslie, H.M., 2005. A synthesis of marine conservation planning approaches. *Conserv. Biol.* 19, 1701–1713.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Aïramé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Little, L.R., Punt, A.E., Mapstone, B.D., Pantus, F., Smith, A.D.M., Davies, C.R., McDonald, A.D., 2007. ELFSim—a model for evaluating management options for spatially structured reef fish populations: an illustration of the “larval subsidy” effect. *Ecol. Mod.* 205, 381–396.
- Lubchenco, J., Palumbi, S.R., Gaines, S.D., Andelman, S., 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol. Appl.* 13, S3–S7.
- Mace, P.M., Sissenwine, M.P., 1993. How much spawning per recruit is enough? *Can. Sp. Pub. Fish. Aquatic Sci.* 120, 101–118.
- Martell, S.J.D., Pine III, W.E., Walters, C.J., 2008. Parameterizing age-structured models from a fisheries management perspective. *Can. J. Fish. Aquat. Sci.* 65, 1586–1600.
- McGilliard, C.R., Hilborn, R., 2008. Modeling no-take marine reserves in regulated fisheries: assessing the role of larval dispersal. *Can. J. Fish. Aquat. Sci.* 65, 2509–2523.
- Meester, G.A., Mehrotra, A., Ault, J.S., Baker, E.K., 2004. Designing marine reserves for fishery management. *Manage. Sci.* 50, 1031–1043.
- Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* 56, 2404–2419.
- Neubert, M.G., 2003. Marine reserves and optimal harvesting. *Ecol. Lett.* 6, 843–849.
- O'Farrell, M.R., Botsford, L.W., 2005. Estimation of change in lifetime egg production from length frequency data. *Can. J. Fish. Aquat. Sci.* 62, 1626–1639.
- Osenberg, C.W., St. Mary, C.M., Schmitt, R.J., Holbrook, S.J., Chesson, P., Byrne, B., 2002. Rethinking ecological inference: density dependence in reef fishes. *Ecol. Lett.* 5, 715–721.
- Paris, C.B., Chérubin, L.M., Cowen, R.K., 2007. Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar. Ecol. Prog. Ser.* 347, 285–300.
- Pelletier, M., Mahévas, S., 2005. Spatially-explicit fisheries simulation models for policy evaluation. *Fish. Fish.* 6, 1–43.
- Pelletier, D., Claudet, J., Ferraris, J., Benedetti-Cecchi, L., Garcia-Charton, J.A., 2008. Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. *Can. J. Fish. Aquat. Sci.* 65, 765–779.
- Sissenwine, M.P., Shepherd, J.G., 1987. An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* 44, 913–918.
- Walters, C.J., 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conserv. Ecol.* 1, 1. Available from <http://www.consecol.org/vol1/iss2/art1>.
- Walters, C.J., Hilborn, R., Parrish, R., 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Can. J. Fish. Aquat. Sci.* 64, 1009–1018.
- White, J.W., 2008. Spatially coupled larval supply of marine predators and their prey alters the predictions of metapopulation models. *Am. Nat.* 171, E179–E194.
- White, J.W., Botsford, L.W., Moffitt, E.A., Fischer, D.T., in press. Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. *Ecol. Appl.* doi:10.1890/09-0962.