



Using an individual-based model to quantify scale transition in demographic rate functions: Deaths in a coral reef fish

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ABSTRACT

Scientifically informed population management requires quantitatively accurate demographic rate functions that apply at the spatial scale at which populations are actually managed, but practical constraints confine most field measurements of such functions to small study plots. This paper employs an individual-based population growth model to extrapolate the death rate function in a well-studied coral reef fish, the bridled goby *Coryphopterus glaucofraenum*, from the scale of 2 m × 2 m coral reef “cells” at which it was measured to the larger scale of an entire coral reef. Density dependence in the whole-reef function actually proves stronger than in the local function because high goby density occasionally arises in local patches with few refuges from predators, producing very high mortality there. This IBM-based approach extends the reach of scale transition theory by examining considerably more realistic models than standard analytical methods can presently handle.

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1. Introduction

Spatial heterogeneity in natural habitats creates much of the interest of the science of ecology. It also creates difficulty in understanding the mechanisms that drive population dynamics and community structure (Wiens, 1989; Hewitt et al., 2007). Practical constraints force field investigators to measure demographic rates in small study areas of typically homogeneous habitat. However, the demographic rates that drive the dynamics of populations necessarily apply to larger areas of usually heterogeneous habitat. Thus, understanding the mechanisms that drive population dynamics requires some way to draw inferences about demographic rates on large spatial scales from measurements made at much smaller spatial scales (e.g., Rastetter et al., 1992, 2003; Chesson, 1998b; Moorcroft et al., 2001; Englund and Cooper, 2003; Melbourne and Chesson, 2005, 2006; Melbourne et al., 2005; Sato et al., 2007).

Developing this understanding has considerably more than just academic interest. Management decisions regarding endangered

species or species of economic concern usually focus on protected patches of habitat that form a network with other similar patches throughout a species' fragmented range, and these decisions can determine the global persistence or extinction of species or the economic viability of commercial harvests. Interest centers on the dynamics of a species' metapopulation comprised of the collection of populations that occupy discrete local patches of habitat dynamically interconnected by dispersal (Chesson, 2001). Understanding metapopulation dynamics necessarily begins with an appreciation of the dynamics of each local population whose habitat is typically both heterogeneous and considerably larger than study plots of practical size.

Two analytical approaches have produced considerable qualitative insight into spatial population dynamics. The scale transition theory of Chesson (1996, 1998a,b) and especially Chesson et al. (2005) approximates demographic rate functions by second order Taylor expansions and then averages resulting quantities over space. The equations so produced relate the spatial mean of population abundance to the spatial means, variances, and covariances of assorted spatially varying quantities. Unfortunately, however, so far this method has been applied only to populations lacking any kind of physiological structure (*sensu* Metz and Diekmann, 1986), and its use is easiest in temporally constant environments.

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Furthermore, although this approach emphasizes effects of population dispersion through space, it does not connect population dispersion to the dispersal histories of individual organisms. The second analytical approach (Bolker and Pacala, 1997; Levin and Pacala, 1997; Pacala and Levin, 1997; Bolker et al., 2000; Dieckmann and Law, 2000; Keeling et al., 2000; Law and Dieckmann, 2000a,b; Bolker, 2003; Law et al., 2003) does follow individual dispersal histories by the use of moment closure techniques. Unfortunately, the resulting approximations usually involve such complicated algebra that generalizing this approach to include population physiological structure and temporal environmental variation seems impossible. Thus, although both analytical approaches have produced considerable qualitative insight, neither presently appears able to confront detailed and genuinely realistic descriptions of nature, even qualitatively. The task of constructing, from small scale measurements, reasonably quantitatively accurate estimates of demographic rate functions that apply at large spatial scales seems likely, therefore, to require a fresh approach.

One possibility is to employ a detailed, empirically based computer model of local processes to produce “data” that might arise in a large and heterogeneous landscape, and then to fit simple aggregated functions to these data statistically that describe the same processes but on the larger spatial scale. Williams et al. (1997) successfully applied this idea to forest trees, capturing 96% of fine-scale model behavior in a coarse-scale model that ran several orders of magnitude faster.

An ideal initial formulation for such a program is a very detailed individual-based model (IBM) that incorporates empirically based descriptions of all processes in which organisms engage during their lifetimes. Such a model follows the fates of all individuals at all spatial locations and permits calculating from these fates the realized population demographic rates that apply at any spatial scale of interest. MacNally (1997) has used an IBM to address a related problem involving population dynamics through space.

This paper illustrates this general IBM approach to spatial scaling by applying it to the death rate function in the bridled goby *Coryphopterus glaucofraenum*, a coral reef fish we have studied extensively in the Bahamas and the Caribbean (e.g., Forrester, 1995, 1999; Steele et al., 1998; Malone et al., 1999; Forrester and Steele, 2000, 2004; Forrester et al., 2002, 2006, 2008; Steele and Forrester, 2002, 2005; Finley and Forrester, 2003; Forrester and Finley, 2006). This goby species lives about 1 year, grows to nearly 50 mm in length, and spends its entire adult life within a home range of a few square meters' area, making it possible to follow tagged individuals for several months. We have tracked large numbers of tagged gobies in field experiments that measured parameter values in most of this goby's demographic rate functions. From these empirically measured functions, we construct an individual-based model of a population that occupies a hypothetical coral reef also constructed from rules based on field measurements.

We focus here specifically on deaths because our field experiments have demonstrated strong density dependence in deaths that we think plays a central role in regulating local populations. Goby deaths arise from density-dependent predation whose effect is mediated by the use of refuges (Forrester, 1995; Forrester and Steele, 2000, 2004; Steele and Forrester, 2002; Forrester and Finley, 2006). Goby refuges consist of crevices and structural irregularities in living and dead coral into which gobies rapidly retreat upon perceiving a predator. Field experimental data have permitted statistical fitting of several nonlinear instantaneous per capita death rate functions that describe this role of refuges (Samhuri et al., 2009).

In this paper, we formulate and employ an IBM (1) to determine how a mortality function that applies in small homogeneous experimental plots extrapolates to larger heterogeneous areas of reef and especially to a large reef as a whole; (2) to evaluate the strength of density dependence as the spatial scale increases to that of a whole

reef; (3) to develop a whole-reef scalar death rate function for use in a metapopulation model that emphasizes dispersal between hundreds of far-flung reefs and cannot afford to include spatially explicit demographic phenomena within each individual reef; and (4) to explore how variation in the amount of spatial heterogeneity in different reef features alters the whole-reef function.

This research employs the same basic philosophy as the diverse field applications of analytical scale transition theory by Melbourne et al. (2005), Melbourne and Chesson (2005, 2006), Bergström et al. (2006), and Englund and Leonardsson (2008). It also embraces some of the general thoughts on scaling in ecology expressed by Warner and Swearer (2001) and other authors in the volume on this subject by Gardiner et al. (2001); and, like Dunstan and Johnson (2005), Hölker and Breckling (2005), and Anderson et al. (2006), this work attempts to infer large-scale patterns from small-scale processes in which individual organisms engage.

The remainder of this paper is organized as follows. Section 2 describes the local death rate function that has been statistically fitted to experimental field data. Section 3 describes features of the IBM's formulation that figure most prominently in the simulations of this paper, and Section 4 describes general methods employed in analyzing the simulated data. Section 5 presents and interprets the reef-scale functions fitted statistically to whole-reef simulated data, and Section 6 discusses our various findings. Appendix A describes in nontechnical language all features of the IBM's formulation not explained in Section 3, postponing until Appendices B–D the few inescapable technical details involved. Together, Section 3 and the appendices constitute a full (and the first published) description of the whole IBM, and together they give the numerical values of all model parameters.

2. The local death rate function

Let x and R represent the number of gobies and of refuges, respectively, per m^2 of habitat, and let $y = x/R$. Statistical analysis (Samhuri et al., 2009) using the Akaike Information Criterion has revealed that the bridled goby instantaneous per capita death rate function in a field experiment involving small and relatively homogeneous patches of habitat is described best by the two-parameter function

$$f(y) = \max\{d_0, d_1 y\} = \begin{cases} d_0 & \text{for } y \leq d_0/d_1 \\ d_1 y & \text{for } y > d_0/d_1. \end{cases} \quad (1)$$

That is, this function has the strongest statistical support among the 9 candidate functions examined. The fitted constants $d_0 = 0.01387$ and $d_1 = 0.057891$ incorporate predator abundance implicitly. (These values differ slightly from those reported in the earlier paper. They arose from analysis of transformed data that slightly improves the statistical fit.) Fig. 1a displays this function (1) graphically.

We apply the generic term “musical chairs functions” to describe the class of all per capita death rate functions that depend on the ratio of prey individuals to refuges, because prey flight into refuges upon a predator's arrival resembles the scramble for chairs that takes place in the childhood game of musical chairs. We call f in (1) the piecewise musical chairs function because its density-independent and density-dependent components apply over different portions of the domain. When y is small, each foraging goby has access to as many refuges as it can use effectively, and increasing y causes no increase in deaths as long as this condition holds. As soon as y crosses the threshold d_0/d_1 , however, competition reduces each goby's access to refuges, and the death rate becomes directly proportional to the number of gobies per refuge present. A somewhat fuller explanation of this function's biological interpretation appears in Samhuri et al. (2009).

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