Appendix A: Density independent development and comparison to previous theory.

Previous models of open, space limited populations with density independent development rate (i.e., fixed maturation delay) differ from our model in the form of the density dependent feedback from established adults to settlers. These models typically assume that adults occupy some area of the benthos which simply restricts establishment of settlers to any remaining free space. The density dependence therefore occurs only at the instant of settlement, rather than throughout the maturation delay as we assumed in our model. Furthermore, space limitation implies a fixed upper bound on adult density, where all space is occupied and beyond which no new settlers can establish. By contrast, in our model juvenile mortality increases with adult density, but settlement occurs at a constant rate. Here we show that without density dependence in development rate (i.e., no competition among juveniles) our model predicts qualitatively equivalent effects of settlement rate and maturation delay on stability. In particular, our model is consistent with two key predictions from theory for space limited populations (see Bence & Nisbet 1989): 1) Increasing settlement rate destabilizes the equilibrium adult density; and 2) For any settlement rate, the equilibrium adult density is stable for sufficiently short or long development delays. This comparison reveals the underlying mechanisms driving instability, which we use to interpret the results of our model with density dependent maturation delay in the Results section.

Without density dependence in the development rate (b_{ij}=0 for all i and j), the maturation delay is constant ($\tau_q(t)$=1/θ_q, see Eq. 5). The only source of density dependence is the effect of adult density on juvenile survival (α_q>0 in Eq. 4). We begin with the simplest case in which there is no demographic heterogeneity, and we arbitrarily assume all settlers are of the high quality type (p_h=1). We conduct a standard stability analysis by linearizing the model equations around the equilibrium to find the characteristic equation:

$$\lambda^2 + \delta_a \lambda + \alpha_h \delta_a N_a^* \left(1 - e^{-\lambda \tau_h}\right) = 0 \qquad \text{(A.1)}$$

We then solve this equation numerically to find pairs of parameter values (τ_h, S) for which the real part of the eigenvalue is 0 (Fig. A1a).

For any value of the maturation delay the equilibrium can be destabilized by sufficiently high settlement rate (large S, Fig. A1a). However, for values of S large enough that instability is possible, extremely short and long maturation delays result in a stable equilibrium (small and large τ_h, Fig. A1a). The mechanisms underlying the transition from stable to unstable equilibrium are identical to those described by Bence and Nisbet (1989): high settlement rate allows juveniles to overshoot the equilibrium during the maturation delay, after which high adult density (with the associated juvenile mortality) pushes juvenile density below its equilibrium, and this results in sustained oscillations. Extreme values of the maturation delay prevent the adult-juvenile feedback because there is either little time for juvenile buildup and mortality (small τ_h) or few juveniles surviving to adulthood (large τ_h), regardless of settlement rate.

Addition of demographic heterogeneity does not alter the general qualitative predictions when development rate is density independent. If the development rates of high and low quality juveniles are within the range for which an unstable equilibrium is possible, sufficiently high settlement rate leads to cyclic dynamics for any mixture of quality types (p_h; Fig. A1b).)

LITERATURE CITED

Bence, J. R., and R. M. Nisbet. 1989. Space-limited recruitment in open systems: the importance of time delays. Ecology 70:1434–1441.

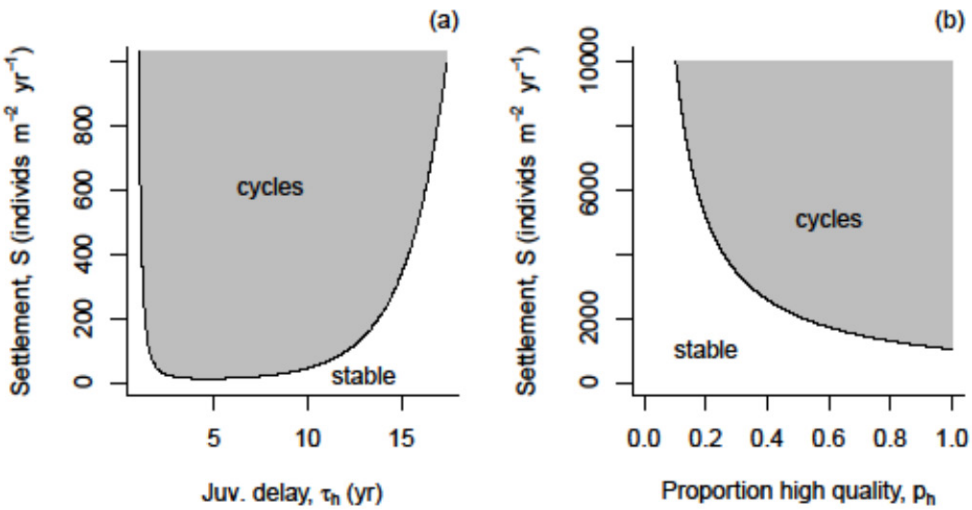

FIG. A1. Stability boundaries for the model with density independent development and a) single juvenile quality type; b) two juvenile quality types with development delays τ_h=1 and τ_l=2 years (for θ_h=1 and θ_l=0.5 year^{-1}, as in Table 1). Shaded areas indicate regions of parameter space in which the equilibrium is unstable.