Appendix A

Effects of nonlinear functional forms in the density dependence of maturation rates

We expand our original analysis of constant (i.e., Type 0, m_t fixed at μ) and linearly density-dependent (i.e., Type I) maturation rates to explore four different functional forms of the juvenile maturation rate (Fig. A1). The Type I function, examined in the main text (eqn. A.1), assumes a proportional increase in juvenile maturation rate as harvest reduces adult abundance. However, if adult individuals respond to reduced population levels with increased rates of per capita resource use (i.e. increased ingestion rates), the greatest increase in juvenile maturation occurs only when high harvest mortality reduces adult abundance to low levels. Consequently, maturation rates mostly increase at very high levels of harvest (i.e., harvest-insensitive, Type II). In other situations, small declines in adult abundance driven at low harvest levels may yield a strong increase in maturation rates if per capita consumption rates are lower for juveniles than adults (i.e., harvest-sensitive, Type III). Thus, we have:

$$Type\,I: \quad m_t = m_{max} - \left(m_{max} - m_{min}\right)\frac{A_t}{K} \qquad \text{(A.1)}$$

$$Type\,II: \quad m_t = \frac{m_{max}K}{K + \left(\frac{m_{max}}{m_{min}} - 1\right)A_t} \qquad \text{(A.2)}$$

$$Type\,III: \quad m_t = m_{min} + \left(m_{max} - m_{min}\right)\sqrt{1 - \left(\frac{A_t}{K}\right)^{2\left(1-m_{min}\right)}}\,. \qquad \text{(A.3)}$$

In all cases, m_t fixed at its lowest value m_{min} when adult abundance exceeds a "carrying capacity" K for the population, and approaches a maximum rate of maturation m_{max} near $A_{t-1} = 0$.

As all three functional forms have the same value of m_{max} at very low abundance levels of the stage limiting maturation rates, populations with all three forms of density dependence in age at maturity collapse at the same harvest levels (h_c) in a constant environment. However, the maturation functions strongly differ in the effect of harvest on adult abundance (h_{half}) at low levels of juvenile survival (Fig. A2a), and especially when harvest targets adults (Fig. A2b). These results illustrate that whether the competition from adults experienced by maturing juveniles declines primarily at small, intermediate, or large reductions in adult abundance can have a strong effect on adult abundance, particularly under adult-targeted harvest. This may be of particular importance in fisheries management, although determining the functional form of density dependence in maturation rate (i.e., Type I, II, or III) may require long time series of the exploited population.

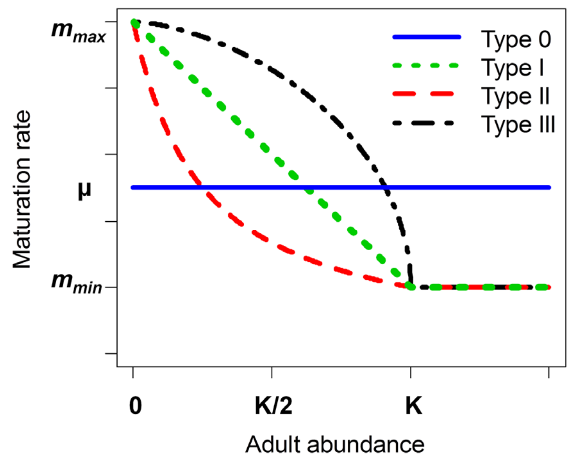

FIG. A1. Effect of adult abundance on juvenile maturation rate along the four functional forms of density-dependent maturation rate examined in the analysis.

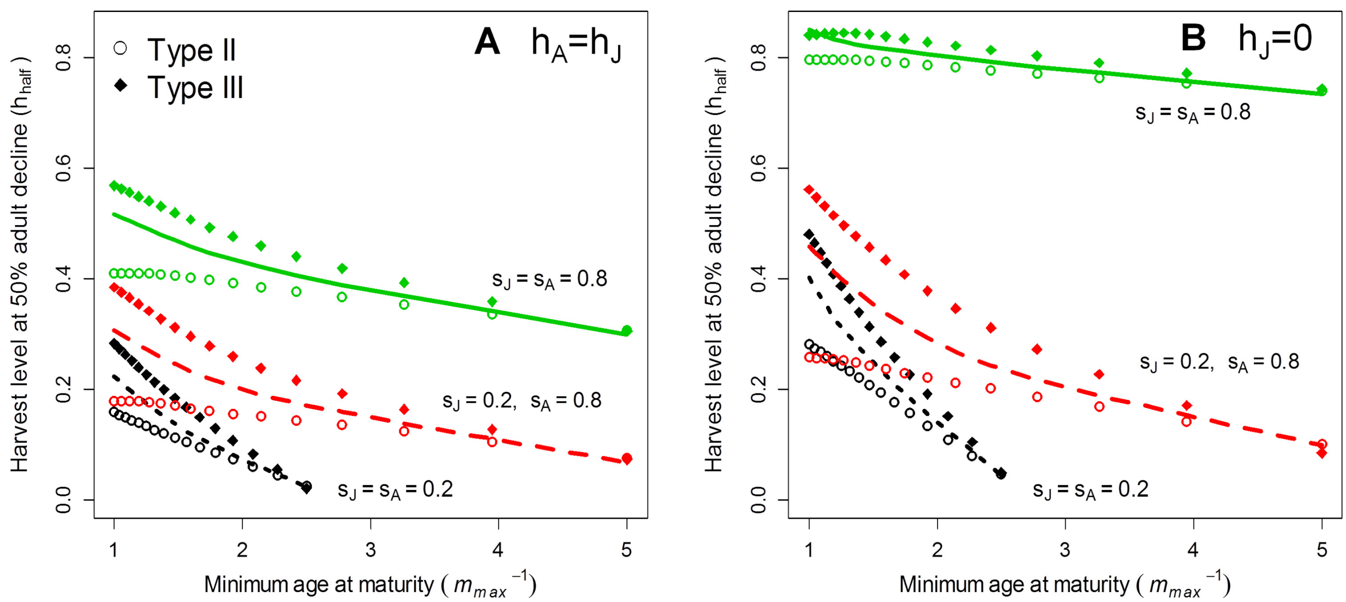

FIG. A2. Effects of the functional form of maturation rate and minimum age at maturity (maximum maturation rate m_{max}^{-1}) on the harvest level at which adult abundance declines by 50% compared to zero harvest (h_{half}) for harvest of both stages (A) and adults only (B). For each value of m_{max}, the values of h_{half} are given under the Type I (lines), Type II (open dots), and Type III (diamonds) functional forms of maturation rates. Differences in h_{half} among maturation functional forms at a given level of m_{max} are greatest when juvenile survival is low, minimum age at maturity is low (i.e., <2; m_{max}>0.5), and under adult-only harvest (B). Harvest targeting adults further reduces the importance of maturation functional forms under high adult survival. The results for the high juvenile, low adult survival (s_J=0.8, s_A=0.2) are nearly identical to high survival (s_J=s_A=0.8), and are omitted here for clarity. All parameters are as in Fig. 3.