

## 5. SINGLE-SEX APPROXIMATION

Most stock dynamic models either assume that population production scales with mature adult biomass or that individual fecundity increases (monotonically) with length or age. However, in a protogynous species, as individuals grow older and larger they change from female to male and thus traditional combined-sex models will overestimate the production of eggs at the population level. Similarly, traditional split-sex models (that assume males and females can occur in all age classes) cannot readily incorporate the absence of males in early age and size classes and the predominance of males in later ages and larger sizes. It is certainly preferable to consider the existence of sex change when relating spawning stock biomass and production to recruitment, abundance and landings.

We therefore developed, for the first time, a combined-sex (or single-sex) stock assessment model that includes a dome-shaped maturity function that incorporates both maturity and sex change. To confirm that the predicted population dynamics would be unaltered by combining sex change and maturity, we created two separate, parallel models. First, a split-sex sex-changing population where individuals are born female and mature and become male with a certain probability (Alonzo and Mangel 2004). Second, a combined-sex model that considers individuals starting at the same initial size as the split-sex population where cohort fecundity declines, simulating the sex change from female to male.

**5.1 Model Description:** We developed identical two-sex (i.e. sex-changing) and single-sex (i.e. combined-sex) models, where the sole difference between the two models resides in the maturity and fecundity functions. For growth, maturity, fecundity and mortality, we used the same parameters described in Section 3 and given in Table 3.1, see Table 5.1 for all model parameters. Both models use the difference equation-version of the von Bertalanffy growth equation (Equation 5.1, Figure 5.1 Gulland 1983) for length and weight estimates where  $L(a)$

$$L(a+1) = L(a) \exp(-k \exp(\varepsilon_g)) + L_\infty (1 - \exp(-k \exp(\varepsilon_g)))$$

$$W(a) = cL(a)^d$$
(5.1)

is the length at age in cm,  $k$  is the growth rate,  $\varepsilon_g$  is the normally distributed uncertainty term for the growth rate,  $L_\infty$  is the asymptotic size in cm,  $W(a)$  is at age in kg, and  $c$  and  $d$  are the length-to weight multipliers. In the weight equation and all subsequent equations, length-at-age is suppressed to age. In both models, mortality is autocorrelated and varies annually, where  $\rho$  is the autocorrelation parameter and  $\varepsilon_m$  is uncertainty

$$M(t+1) = \rho M(t) + \sqrt{1 - \rho^2} \varepsilon_m.$$
(5.2)

We assume that sex does not affect growth, so we used the same size-based fishery calculations for both models. Fishing selectivity for fishery  $i$ ,  $\theta_i$  (Figure 5.2 Methot 2000), is a length-based, four-parameter double logistic where  $\beta_1$  is the steepness

parameter

$$\theta_i(a) = \text{pr}\{\text{capture}\}_i = \frac{T_i}{(1 + \exp(-\beta_{1_i}(L - \beta_{2_i}))) (1 + \exp(\beta_{3_i}(L - \beta_{4_i})))} \text{ where } i = 1, 2, \dots, n \quad (5.3)$$

of the ascending side,  $\beta_2$ , in our case, a length, is the midpoint of the ascending side,  $\beta_3$  is the steepness parameter of the descending side,  $\beta_4$  is the midpoint of the descending side, also a length in cm, and  $T_i$  is the scaling factor (Methot 2000). We specify two different hypothetical fisheries with different  $\theta_i$  and effort,  $E_i$ , for each fishery, loosely based on size composition of landings from the data. Total fishing mortality,  $F$ , for each size-at-age is

$$F(a) = \sum E_i \theta_i(a). \quad (5.4)$$

We calculated annual catch,  $C_i$ , for each fishery,  $i$ , for the single-sex and sex-changing models whose total populations are represented interchangeably as  $N(a, t)$  in equation 5.5 with observation error,  $\varepsilon_f$ .

$$C_i(t) = \sum_a N_i(a, t) (1 - \exp(M(t) - F(a))) \frac{E_i \theta_i}{(M(t)) + F(a)} \varepsilon_f \quad (5.5)$$

**5.2 Creating the Single-Sex and Two-Sex Models:** Because Sheephead are protogynous sequential hermaphrodites, fecundity estimates in the form of egg production must include not only the proportion of the female population becoming mature, but also the loss of females as mature females become male. We chose to capture this in two ways: 1) as a single-sex model where the entire population is female and the fecundity for each age class is determined by the proportion of the age class that is reproductive as females and 2) as a sex-changing model where the fecundity for each age class is determined simply by the number of females that are mature and the number of females is reduced as females become male. In the sex-changing model, all individuals recruited to the population as females, and became mature with a probability at each length-at-age, then became male with a different probability at each length-at-age, (Figure 5.3)

$$p_m(a) = \frac{1}{1 + \exp(r(L - L_{50_m}))} \quad (5.6)$$

represented by  $p_f(a)$  in an equation similar to Equation. 5.6, with  $r$  determining the rate of maturity between lengths and  $L_{50_m}$  is the length at which half the length class is mature. Because population size is represented in the single-sex approximation as only female, a single equation had to encapsulate maturity and the switch from male to female. We adjusted the probability of maturity based on the conditional between becoming male given that an individual is a mature female (Equation 5.7).

$$p_s(a) = p_m(a) p_f(a) \quad (5.7)$$

Since a portion of the mature females transition to males, the total proportion of mature females in the cohort declines independently, resulting in a decrease in the number of individuals who can produce eggs for that cohort (Figure 5.4).

We determine the number of eggs produced,  $\varphi$  (Equation 5.8), from a relationship

$$\begin{aligned}\varphi(a)_{\text{sex changing}} &= \sigma N_{\text{female}}(a,t) p_m(a) W(a) \\ \varphi(a)_{\text{single sex}} &= \sigma N(a,t) p_s(a) W(a)\end{aligned}\quad (5.8)$$

between body weight,  $W(a)$ , and fecundity where  $\sigma$  is the eggs/kg multiplier. We calculate the total number of eggs for the age class by multiplying the estimated number of eggs produced by the size of the age class,  $N(a,t)$ , and the proportion of the age class that is mature or producing eggs. We use the Beverton-Holt recruitment (Mace and Doonan 1988; Dorn 2002) where total recruitment is given by equation 5.9 and  $h$  is the steepness parameter,  $\varphi$  is the total number of eggs produced used in place of spawning stock biomass,  $R_0$  is virgin recruitment, and  $\phi_0$  is the measure of virgin eggs per recruit and  $\varepsilon_r$  is process uncertainty in recruitment:

$$\begin{aligned}N_{\text{female}}(1,t+1) &= \frac{0.8R_0h \sum_a \varphi(a)_{\text{sex changing}}}{0.2\phi_0R_0(1-h) + (h-0.2) \sum_a \varphi(a)_{\text{sex changing}}} \varepsilon_r \\ N(1,t+1) &= \frac{0.8R_0h \sum_a \varphi(a)_{\text{single sex}}}{0.2\phi_0R_0(1-h) + (h-0.2) \sum_a \varphi(a)_{\text{single sex}}} \varepsilon_r\end{aligned}\quad (5.9)$$

We use an age-structure model to generate population dynamics. In the sex-changing model, males and females must maintain separate population dynamics, with individuals within each age class leaving the female population with a certain probability to join the male population (Equation 5.10a). The single-sex model (Equation 5.10b) uses a single population

$$N_{\text{female}}(a+1,t+1) = \exp(-M(t) - F(a)) \left( N_{\text{female}}(a,t) p_f(a) \right) \quad (5.10a)$$

$$N_{\text{male}}(a+1,t+1) = \exp(-M(t) - F(a)) \left( N_{\text{male}}(a,t) + N_{\text{female}}(a,t) (1 - p_f(a)) \right) \quad (5.10b)$$

$$N(a+1,t+1) = \exp(-M(t) - F(a)) N(a,t)$$

to represent both the male and female populations.

Both models produced identical results without stochasticity (Figure 5.5) and identical long-term averages with stochasticity in population size as well as catch yields. Combining sex change and maturity into a single fecundity equation did not change the population dynamics, as long as the order of maturity, sex change, reproduction, and mortality were correct.