3. BIOLOGICAL INFORMATION

The California Sheephead is a protogynous (female to male) sequential hermaphrodite (Warner 1973; Warner 1975) found near-shore along the Pacific Coast of California and Mexico and into the Gulf of Mexico (Miller and Lea 1972). Sheephead are generalist carnivores (Cowen 1983) and feed on species such as mussels (Robles and Robb 1993) and red sea urchins (*Strongylocentrotuys franciscanus*) (Tegner and Dayton 1981; Cowen 1983) and may play an important role in regulating the density of their prey (Cowen 1983; Hobson and Chess 1986; Robles 1987; Robles and Robb 1993).

3.1 Age and Natural Mortality: Two studies used observed patterns of age structure to estimate (annual) natural mortality in California Sheephead by assuming age- and sex-independent mortality. Warner (1975) estimated the annual survival at Catalina Island, California and Guadalupe Island, Mexico to be approximately 0.7 while Cowen (1990) estimated annual survivorship in 5 different populations ranging from 0.577 at Guadalupe Island, Mexico to 0.745 at San Nicolas Island, California (see Table 3.1, Figure 1.1). Since the relationship between mortality rate and survivorship is given by $S=e^{-M}$ (where M is annual natural mortality rate and S is annual survival), we use M=0.35 as the baseline natural mortality and conduct sensitivity analyses on natural mortality by allowing the parameter to vary ranging from 0.05 to 0.5 in our assessment. The oldest fish ever reported was 53 years old (Fitch 1974). However, size at age data based on dorsal spines found fish that were at most 21 years old (Cowen 1990). Therefore we used the 53-year-old fish to set a realistic lower bound on mortality. Based on Hoenig (1983), this corresponds with a constant mortality of 0.07 approximately. Thus we use 0.05 as a lower bound for our sensitivity analyses. The upper bound was determined by the populations with the lowest observed survival (see Table 3.1).

3.2 Growth: The precise growth patterns as well as size and age distributions of Sheephead in the wild appear to vary slightly among sites and over time (Warner 1973; Warner 1975; Cowen 1990; DeMartini et al. 1994). The largest individual ever observed was 91 cm (Miller and Lea 1972). DeMartini et al. (1994) found the relationship (R^2=0.92 p<0.0001 N=61) between total length (in inches) L_T and wet body weight W (in grams) to be

$$\ln W=\ln 0.688 + 2.723 \ln L_T \tag{3.1}$$

We used the following relationship from the Recreational Fisheries Information Network (RecFIN) database to convert total length (L_T) in cm to fork length (L_F) in cm

$$L_F = -1.4564+1.094 L_T \tag{3.2}$$

For our model, we used the power relationship in Equation 3.1 and the length conversion from Equation 3.2 to calculate the expected relationship (Figure 3.1) between fork length in centimeters L_F and body weight in kilograms W

$W = aL_F^b$ where a=0.000026935 and b=2.857   (3.3)

Using linear regression, we found the relationship between standard length and total length for California Sheephead using individual lengths from the Central California Spearfishing Tournament database (CenCAL, N=100). We excluded one data point because it reported the biologically impossible situation where total length was less than standard length. This gave the relationship between standard length in cm L_s and total length in cm L_T

$L_T = 0.604 + 1.207\ L_s$ (3.4)

We used the size at age data (converted into fork length using Equations 3.2 and 3.4) for Catalina Island, California published in Warner (1973) for our baseline estimates and size at age data from Cowen (1990) for sensitivity analyses on these parameters. Because we did not have any age data from the fisheries or surveys, we fixed the growth parameters within any single run of the model rather than allow them to be estimated. However, we performed sensitivity analyses on these growth parameters as described in greater detail below.

We found the best-fit estimates of growth parameters by minimizing the sum of squared deviations between the predicted and observed size at age (Hilborn and Mangel 1997). We compared the ability of four different methods of fitting the growth parameters k and L_{inf} to predict the observed growth data. We first used a Ford Plot (Quinn and Deriso 1999) with an unconstrained L_{inf} and found the growth parameter k and asymptotic size L_{inf} that best fit the data. Second, we used a Ford Plot but constrained L_{inf} to be the maximum observed size of 91 cm and only fit the growth rate k. Both of these approaches lead to a good fit between the predicted change in size between ages and the observed size at age data (SS_1=18.68 and SS_2=19.15). Third, we fit the growth rate k using the Schnute (1981) parameterization of the von Bertalanffy growth equation with an estimated L_{inf} using t_1=1, L_1=12.92 and t_2=13, L_2=52.60 cm fork length (the smallest and largest ages for which a mean size at age was given in Warner (1975) data). Finally, we fit the Schnute (1981) parameterization with the asymptotic size L_{inf} set to maximum observed size. The estimated mean size at age predicted from the best-fit growth parameters using the third and fourth approach did not fit the data well (SS_3=1988.71 and SS_4=1687.07). The Ford plot with an unconstrained asymptotic size (predicting the size at time t+1 from time t) gave the best fit to the observed size at age data and thus we used these estimates of the growth parameters in the baseline version of the model (k=0.068, L_{inf}=83.86 cm, Figure 3.2). Although this gave a smaller asymptotic size than the maximum size ever reported, it was a better fit with the observed size at age data and is consistent with the maximum length of fish observed in the fisheries (see Section 4). Because Synthesis uses the Schnute parameterization of the von Bertalanffy growth equation (Schnute 1981; Methot 2000), we used the parameters t_1=1 (years), L_1=12.92 (cm fork length), t_2=13 (years), L_2=52.60 (cm fork length) and k=0.068 as the baseline values in our model (Figure 3.2). We also used the same method to find growth parameters for the other populations for which we had data (Warner 1975; Cowen 1990) and used each set of growth parameters (given in Table 3.1, Figure 3.3) in a separate run

of the model as a sensitivity analysis on size at age. We also used the error bars in the mean size at age data given in Warner (1975) to estimate a coefficient of variation in size. The small sample sizes (N=2 to 12 for each age class) led to a very high estimate for coefficient of variation of growth per age class (CV=0.3) so we used this value as an upper bound for the Synthesis model and allowed the model to estimate the coefficient of variation at age (CV_1 and CV_2).

3.3 Distribution and Abundance: Sheephead are found from Monterey Bay to the Gulf of California (see Figure 1.1) but are uncommon north of the Point of Conception and are much less common in the Gulf of California than along the Pacific Coast (Miller and Lea 1972). In the Channel Islands, densities of 1475-1525 individuals of all sizes per hectare have been observed (Davis and Anderson 1989) while Cowen (1985) reports densities ranging from 16-290 adult fish per hectare.

3.4 Dispersal: Tagged adult Sheephead were usually caught again on the same reef (DeMartini et al. 1994), showed little movement (Davis and Anderson 1989) and a high rate of recapture (71%, 36 of 51 individuals) (DeMartini et al. 1994). Although weak population structure has been found between southern California and Baja California, Mexico (Waples and Rosenblatt 1987), the genetic structure is consistent with frequent dispersal among populations, probably at the early life stages although adults may disperse short distances through deep water. Bernardi et al. (2003) found no genetic structure between populations of Sheephead both when comparing Pacific and Gulf of California populations and when comparing California with Mexican populations along the Pacific coast (F_{ST}=0) (Bernardi et al. 2003). Thus, there appears to be high levels of gene flow between populations of Sheephead, at least for evolutionary time scales (Bernardi et al. 2003).

3.5 Recruitment: Recruitment patterns are temporally and seasonally variable (Cowen 1985; Cowen 1985; Cowen 1991). Sheephead have a pelagic larval stage prior to recruitment in shallow waters. Although the pelagic larval duration ranges from 37-78 days, the size at settlement varies little (range 12.7-16 mm and mean 13.5 mm) and growth after settlement is not affected by age at settlement (Cowen 1991). A comparison of 9 years of recruitment data found that recruitment patterns (based on field transects as well as age structure data) are highly variable but can be related to oceanographic data and proximity to other populations that may supply larva (Cowen 1985). Cowen (1985) also found a positive relationship between adult density and recruitment, but did not report any other evidence of density-dependence. Sheephead larval availability depends on season and peaks July to October and larva are found mainly nearshore (Cowen 1985).

3.6 Maturity and Sex Change: California Sheephead individuals have been observed to mature at about 4 years of age and with a mean standard length of 20 cm (Warner 1975) although individual variation as well as differences among populations exist (Cowen 1990). Sex change occurs at approximately 30 cm standard length at an age of 7-8 years although it can occur at standard lengths as low as 18 cm and ages as young as 4 years (Warner 1975; Cowen 1990). The degree to which sex change is determined by endogenous versus exogenous cues is not known. However, sex change appears to

depend on size rather than age and the size at sex change is consistent with predictions of the size-advantage model (Cowen 1990). Populations with higher growth rates and higher survival also have larger sizes at sex change and sex ratio seemed to affect population patterns of sex change as well (Cowen 1990). Warner (1975) reports the frequency of immature individuals, mature females and mature males at Catalina Island, California. We used these data to find the L_{50} (length at which the proportion mature or male is 50%) for maturity and sex change. We then fit these data to a logistic function estimating the slope parameter that minimized the sum of squared deviations between the predicted and observed proportion of mature individuals and the proportion of mature individuals that are female for use in the model. We used the parameters based on the Catalina Island data for our baseline model and use the other maturity and sex change parameters for sensitivity analyses (see Table 3.1, Figure 3.4).

3.7 Fecundity: Reproduction occurs June through early October, while sex change occurs during the winter months (Warner 1975; Cowen 1990). Females appear to spawn multiple times during the reproductive season. DeMartini et al. (1994) estimated that females spawn approximately 86 times per year (about every 1.3 days) and calculated the batch fecundity of females to be 5755 eggs per spawning event, but found no significant relationship between the number of eggs released per kilogram of body weight and total female body weight (an average of 15 eggs per gram of body weight or 15,000 eggs per kg, DeMartini et al. 1994). From these data, we estimate both the total egg production of a female based on her weight (Figure 3.5 dashed line) as well as the annual total egg production per kilogram of female body weight (batch fecundity per kg and number of patches per year, Figure 3.6 dashed line).

Warner (1975) found that the ovary weight (O_W in grams) of females scaled with standard length (L in cm) according to

$$O_W = 0.00131 \, L^{2.95} \tag{3.4}$$

Warner (1975) also found that on average females have 5377 yolky oocytes per gram of female gonad. Thus it is also possible to estimate the total and mass-specific egg production from Warner (1975) and the weight-length relationship given in Equation 3.3 (Figures 3.5 and 3.6). The difference in the exponents between Equation 3.3 and 3.4 imply that a weak increase in mass-specific egg production is predicted (Figure 3.6). However, in the weight and size range in which individuals are actually expected to be female, the relationship is nearly linear. Furthermore, one set of data measured the number of eggs being spawned while the other counted the number of oocytes in the gonad. These lead to slightly different estimates of total egg production. However, the general functional form is basically the same (Figures 3.5 and 3.6). Since the number of eggs actually spawned by females is a better estimate of total egg production, we used the DeMartini at al.(1994) based estimates of fecundity for our baseline version of the model. However, we explored the effect of the lower oocyte production from Warner (1975) as one of our sensitivity analyses.

Nothing is known about fertilization rates or sperm production in California Sheephead.

At high fishing mortality, the potential for sperm limitation exists since fishing may remove large males preferentially (Alonzo and Mangel 2004). However in Sheephead, large males may experience sperm competition from smaller males (Adreani et al. In Press) and thus sperm production may be high in this species (Birkhead and Møller 1998) making the species less prone to sperm limitation.