

Feasibility of developing a stock assessment model for Main Hawaiian Islands Yellowfin Tuna Fishery

Part Two

John Sibert*

Joint Institute of Marine and Atmospheric Research
University of Hawai'i at Manoa
Honolulu, HI 96822 U.S.A.

February 5, 2016

Abstract

Single population models with simplified model structure were developed to test the feasibility of developing a stock assessment model for the Main Hawaiian Islands yellowfin tuna fishery. These models are capable of estimating critical reference points such as maximum sustainable yield (MSY) and fishing mortality at MSY. Biomass trends between 1952 and 2012 estimated by using different model configurations differ in general level, but are qualitatively consistent across models. All models estimate a period of high biomass between 1970 and 1990, including periods where the biomass exceeds the equilibrium biomass or “carrying capacity”. These models are promising starting points for development of a full-featured stock assessment model.

*sibert@hawaii.edu

1 Introduction

A previous evaluation of the feasibility of developing a stock assessment model for the Main Hawaiian Islands (MHI) yellowfin tuna (YFT) fishery concluded that such a model is feasible, but that estimation of fishery management reference points is difficult (Sibert, 2015). The ambiguity of this conclusion is unsatisfying, and further research was undertaken to develop more practical alternative models. The 2015 model represented the dynamics of two coupled tuna populations with immigration, emigration, and fishing and required estimation of approximately 15 parameters. Here I report results of evaluating single population models with simplified dynamics and fewer parameters.

2 Methods

The data used in this analysis are the annual catch data from five gear types fishing within 200 nm of the Main Hawaiian Islands (Sibert, 2015).

The basic model is a state-space implementation of the Schaefer biomass dynamics model (Schaefer, 1954). The principle model assumptions are:

1. The dynamics of the population of YFT in the MHI follows a simple Schaefer model.
2. Fishing mortality is represented by a random walk (Nielsen and Berg, 2014).
3. The local dynamics are “forced” by assuming that the local abundance is approximately proportional to some “index” population.

The basic model was implemented with two different parameter substitutions in an attempt to find parameter combinations that are more reliably estimated. Indexing was implemented flexibly to demonstrate the effects of omitting the index altogether.

Model estimates of yellowfin biomass by MULTIFAN-CL (MFCL) from the most recent Western Central Pacific Fisheries Commission stock assessment (Davies et al, 2014) provide a convenient choice of biomass indices. The MHI straddle the boundary between MFCL regions 2 and 4. Region 2 is arguably more similar ecologically to the MHI than the more equatorial region 4. The YFT population in region 4 is much larger and exhibits a greater level

Table 3.1: Model estimates from four different model configurations using the default prior on r . Model complexity, expressed in number of parameters estimated (n) increases from left to right. Long dashes (—) indicate parameters not estimated. $-\log L$ is the negative log likelihood (the smaller the number, the better the fit); $|G|_{max}$ is the curvature of the likelihood at the its apparent minimum (values greater than 0.01 indicate non-convergence); other variables are defined in Table A.1.

Index Parameterization Designation	None		MFCL 2	
	\tilde{Y} $F_{\tilde{Y}}$	B_1 d	\tilde{Y} $F_{\tilde{Y}}$	B_1 d
	A	B	C	D
n	4	5	5	6
$-\log L$	-237.238	-237.968	-247.175	-243.343
$ G _{max}$	0.0016409	33.1289	3.51082e-05	3.77653
B_1	—	1184.2	—	2802.3
d	—	9.6674	—	2.6348
\tilde{Y}	1147.5	1199.3	1288.7	1032.6
$F_{\tilde{Y}}$	0.82239	0.20952	0.1668	0.2797
r	1.6448	0.41904	0.3336	0.5594
K	2790.8	11448	15452	7383.5
σ_P	0.37416	0.36757	0.2743	0.2649
σ_Y	0.41693	0.43062	0.46924	0.47614
Q	—	—	0.04321	0.016535

of depletion than the population in region 2. Estimated biomass trends from MFCL region 2 were used as the abundance index for most model feasibility evaluations.

Complete details of model structure are presented in Appendix A.

3 Results

Fitting results are summarized in Table 3.1. Both the indexed and non-indexed configurations of the \tilde{Y} $F_{\tilde{Y}}$ parameterization appear to converge to a meaningful solution with $|G|_{max} < 0.01$ whereas the B_1 d parameterizations appear not to have converged. Non-indexed models can be considered

“nested” within indexed models with the parameter Q constrained to be zero. A likelihood ratio test is therefore appropriate to test the effect of including the abundance index in converged $\tilde{Y} F_{\tilde{Y}}$ models. The change in negative log likelihood from -237.238 to -247.175 with one degree of freedom is a statistically significant change with $P < 0.005$.

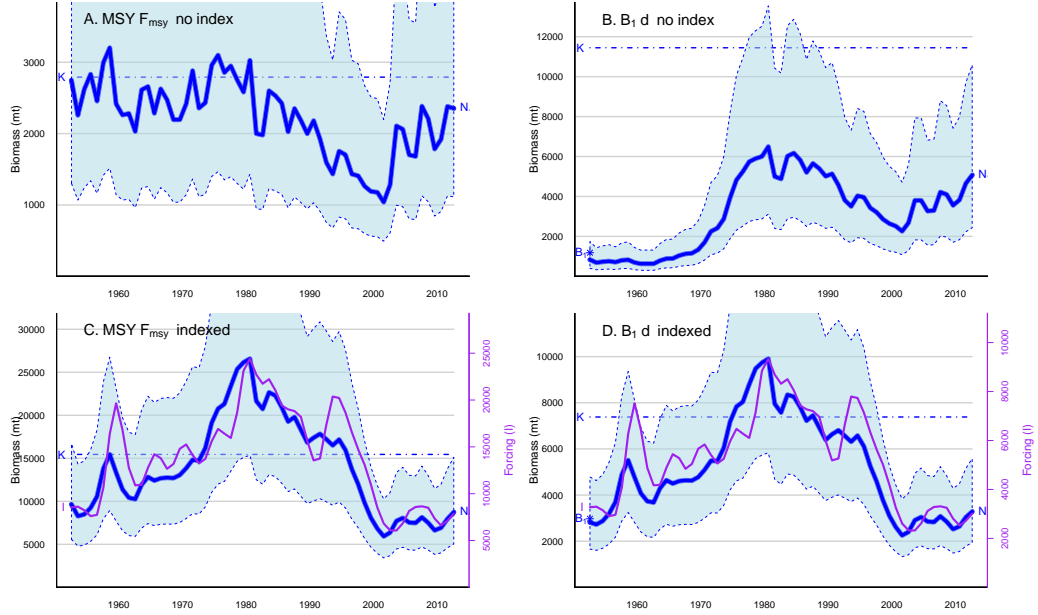


Figure 3.1: Estimated biomass trends for the model configurations indicated in the upper left of each panel. Blue lines indicate the estimated biomass in metric tons (mt). The purple line indicates the estimated biomass index using MFCL region 2 biomass as the index of abundance. The light blue shaded areas represent the process error as $\pm 2\sigma_P$. The equilibrium biomass K is indicated by the blue dot-dash line. Note that the scale of the ordinate is different in each panel.

Estimated biomass trends for the four models are shown in Figure 3.1. All four models, including the non-indexed models, predict a large decrease in biomass between 1975 and 2000. The estimated biomass decrease mimics the MFCL region 2 biomass trend in the indexed models, and the indexed models amplify the decrease. The predicted biomass in the both $\tilde{Y} F_{\tilde{Y}}$ models and the indexed $B_1 d$ model exceeds the equilibrium biomass in the 1970s.

There is an approximate five-fold difference in estimated population size between the indexed and non-indexed $\tilde{Y} F_{\tilde{Y}}$ models. The indexed model estimates a larger and slower growing stock than the non-indexed model as indicated by estimated values of r and K .

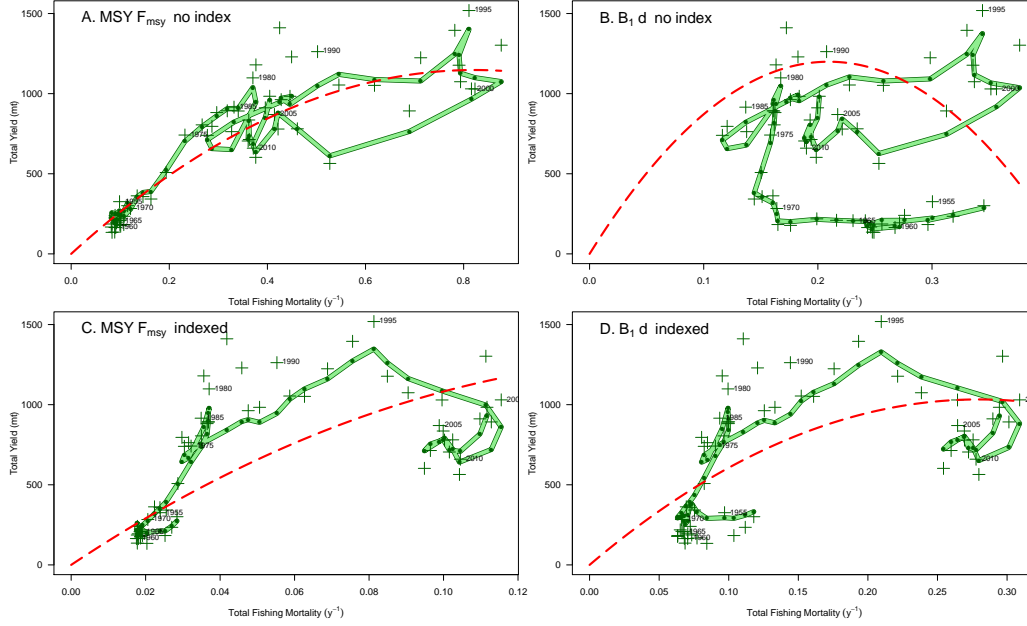


Figure 3.2: Catch plotted against fishing mortality (production curves) for the model configurations indicated in the upper left of each panel. The green line and dark green dots are estimated catch plotted against fishing mortality. The green + symbols are the observed catch annotated with the year. The dashed red line is the theoretical equilibrium yield. Note that the scale of the abscissa is different in each panel.

Production curves for the four models are shown in Figure 3.2. The peaks of the production curves are near the highest observed catches in the two non-indexed models and occur within the range of the estimated fishing mortality. In contrast, the peak of the production curve for the indexed models are greater than the highest observed catches and greater than the highest estimated fishing mortality. Catches exceed the production curve between the mid 1970s through the mid 1990s and drop below the production curve after 2000.

Table 3.2: Model estimates from four different model configurations omitting the prior on r . Model complexity, expressed in number of parameters estimated (n) increases from left to right. Long dashes (—) indicate parameters not estimated. $-\log L$ is the negative log likelihood (the smaller the number, the better the fit); $|G|_{max}$ is the curvature of the likelihood at the its apparent minimum (values greater than 0.01 indicate non-convergence); other variables are defined in Table A.1.

Index	None		MFCL 2	
Parameterization	\tilde{Y}	$F_{\tilde{Y}}$	\tilde{Y}	$F_{\tilde{Y}}$
Designation	A	B	C	D
n	4	5	5	6
$-\log L$	-284.898	-236.212	-246.302	-242.176
$ G _{max}$	2.45563	151.693	1.24795e-05	39.9125
B_1	—	1540.2	—	—
d	—	12.567	—	—
\tilde{Y}	—	1274.9	1579.3	—
$F_{\tilde{Y}}$	—	0.13174	0.1293	—
r	—	0.26347	0.25859	—
K	—	19355	24430	—
σ_P	—	0.35682	0.27044	—
σ_Y	—	0.43481	0.47162	—
Q	—	—	0.073752	—

Table 3.2 summarizes the effects of omitting the Bayesian prior on the growth rate parameter, r . Only one model configuration, $\tilde{Y} F_{\tilde{Y}}$, converged to a solution with $|G|_{max} < 0.01$. The negative log likelihood is slightly higher than the same model configuration using the default prior, suggesting poorer agreement to the data. The estimated population dynamics indicates a larger and slower growing population.

4 Discussion

The consistent predictions of high biomass in the 1970s followed by a persistent decrease in biomass through 2000 in the non-indexed models is evidence

that the catch data provide information on the relative abundance of YFT in the MHI. The dependency of absolute biomass estimates on an abundance index is characteristic of production models (*references*) and is cause for caution in drawing fishery management conclusions from these tentative results.

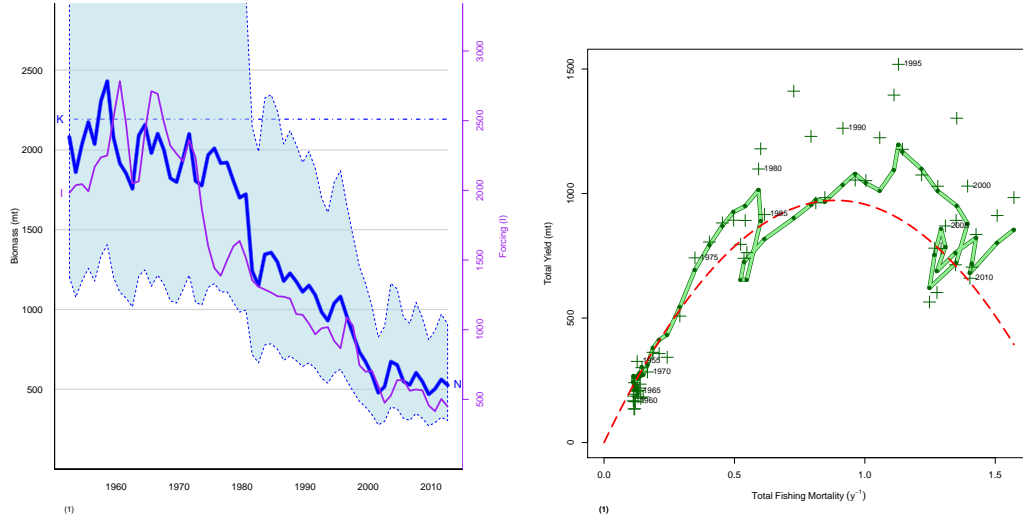


Figure 4.1: Estimated biomass trend and production curve from the $\tilde{Y} F_{\tilde{Y}}$ model indexed to MULTIFAN-CL region 4. See Figures 3.1 and 3.2 for legends.

The choice of index populations makes a large difference in fishery management conclusions. Figure 4.1 shows the biomass trend and production curve for the MHI population indexed to the MFCL region 4 biomass estimates. This choice of index would lead to completely different fishery management conclusions. An alternative to selecting MFCL region biomass estimates as population indexes would be to use biomass estimates and predictions from the SEAPODYM model (Senina et al, 2008) as an index of MHI biomass.

Using the output of one model in another model is sometimes known as “off-line” coupling, and is used in SEAPODYM to couple ecosystem models to tuna population dynamics. This approach is also sometimes disdained as “piecemeal” modeling because the variance structure is not usually propagated from one model to the next. Such propagation may be possible but was not examined.

Both MULTIFAN-CL and SEAPODYM predict age and size structure of tuna stocks. There are some size data for the MHI YFT landings that could be incorporated into an age-structured model. No work was undertaken to develop age-structured models.

The use of a random walk to represent fishing mortality (F) is a unique feature of the model presented here. This approach avoids the problem of attempting to contrive an objective measure of fishing effort along with a time-varying catchability coefficient on which some estimate of F could be based. The random walk provides a convenient measure of F that enables the logistic model to estimate population dynamics parameters from catch data alone.

The imposition of Bayesian priors on Schaefer model growth parameters is often considered essential (*references*). Both the $\tilde{Y} F_{\tilde{Y}}$ and $B_1 d$ parameterizations avoid the problem of estimating K and r simultaneously. The use of a prior on r would appear to offer no benefit to the $\tilde{Y} F_{\tilde{Y}}$ models, but seems to assist the $B_1 d$ models. The great disadvantages of priors are the difficulty of finding suitable values and the unwanted risk of introducing bias into the resulting estimates.

The recreational catch of yellowfin tuna in the MHI is thought to be quite large, approximately the same order of magnitude as the commercial catch *references*. The lack of readily available accurate estimates of the recreational catch of YFT makes development of a credible assessment model very difficult. No attempts were made to evaluate the effects of this deficiency on estimated model parameters.

5 Conclusions

1. Yellowfin catch data from fleets operating in the Main Hawaiian Islands waters are sufficiently informative to estimate relative biomass trends.
2. An index of abundance is required to estimate absolute biomass, but absolute estimates are sensitive to the choice of index population.
3. Representing trends in fishing mortality as a random walk is a convenient and effective approach to accounting for the removal of biomass from the fish population.
4. Bayesian prior on r are difficult to assign and probably not required.

Acknowledgements. This work was funded by the Western Pacific Regional Fisheries Management Council. I thank the Council for its generous support and Council Staff Paul Dalzell and Eric Kingma for encouraging me to actually take on this challenging project and for their on-going collaboration. Thanks to David Fournier for suggesting the “ $B_1 d$ ” parameterization of the Schaefer model, to David Itano for sharing insights into the small-boat fisheries in Hawaii, to Reginald Kokubun of the Hawaii Division of Aquatic Resources for supplying catch report data from the HDAR commercial fisheries data base, to Keith Bigelow and Karen Sender of NOAA Pacific Island Fisheries Science Center for supplying logbook reporting data and weight-frequency data from the PIFSC data base. Thanks also to John Hampton of the Secretariat of the Pacific Community, Oceanic Fisheries Programme, for making available MULTIFAN-CL output files from the latest Western and Central Pacific Fisheries Commission yellowfin tuna stock assessment, and to Nick Davies for sharing R scripts and advice on interpreting those files.

References

- Carruthers, T. and M. McAllister. 2011. Computing prior probability distributions for the intrinsic rate of increase for atlantic tuna and billfish using demographic methods. *Collect. Vol. Sci. Pap. ICCAT*, 66(5): 2202-2205.
- Davies, N., S. Harley, J. Hampton, S. McKechnie. 2014. Stock assessment of yellowfin tuna in the western and central pacific ocean. WCPFC-SC10-2014/SA-WP-04.
- Fournier, D. A., H.J. Skaug, J. Ancheta, J. Sibert, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen. 2012. AD Model Builder: using automatic differentiation for for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27, 233249.
- Nielsen, A., C. Berg. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. *Fisheries Research* 158:96-101.
- Murray, J. D. 1993. *Mathematical biology*. Second Edition. Springer-Verlag. 767pp.
- Quinn, T, R. Deriso. 1999. *Quantitative fish dynamics*. Oxford University Press, New York.
- Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *IATTC Bull.* 1(2):27-56.
- Senina, I., J. Sibert, P. Lehodey 2008. Parameter estimation for basin-scale ecosystem linked population models of large pelagic predators: Application to skip-

- jack tuna. *Prog. Oceanogr.* 78:319-335.
- Sibert, J. R. 2015. Feasibility of developing a stock assessment model for Main Hawaiian Islands Yellowfin Tuna Fishery. 119th Meeting of the Scientific and Statistical Committee. Document 7.A.1(1)Rev 1.
- Skaug, H., Fournier, D., 2006. Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. *Computational Statistics & Data Analysis* 51, 699709.
- Wells, D., J. Rooker, D. Itano. 2012. Nursery origin of yellowfin tuna in the Hawaiian Islands. *Mar. Ecol. Prog. Ser.* 461:187-196.

A Model development

State-space models separate variability in the biological processes in the system (transition model) from errors in observing features of interest in the system (observation model).

Transition Model $T(\alpha_{t-1})$. The general form of the transition model is

$$\alpha_t = T(\alpha_{t-1}) + \eta_t \quad (\text{A.1})$$

where α_t is the state at time t and the function T embodies the dynamics mediating the development of the state at time t from the state at the previous time with random process error, η_t .

Stock dynamics follow the classic Schaefer differential equation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - FN \quad (\text{A.2})$$

where N is the biomass of YFT in the MHI, r is the logistic growth rate per year, K is the asymptotic biomass, and F is the total fishing mortality per year in the MHI.

The state space transition equation for the single population model is developed by solving A.2 analytically from one time to the next (see Appendix B).

$$N_t = \frac{K(r - \bar{F}_t)}{\frac{K(r - \bar{F}_t)}{N_{t-\Delta t}} e^{-\Delta t(r - \bar{F}_t)} - r e^{-\Delta t(r - \bar{F}_t)} - r} \cdot e^{\eta_t}; \quad \eta_t \sim N(0, \sigma_N^2) \quad (\text{A.3})$$

where \bar{F}_t is the total fishing mortality, i. e.,

$$\bar{F}_t = \sum_{g=1}^n F_{g,t-\Delta t}.$$

and $\eta_t \sim N(0, \sigma_N)$ is a process error expressing variability in population dynamics.

Fishing mortality is treated as a random walk. The logarithm of fishing mortality is assumed to follow a random walk with normal increments, as suggested by Berg and Nielsen (2014).

$$\log F_{g,t} = \log F_{g,t-1} + \xi_t; \quad \xi_t \sim N(0, \sigma_F^2) \quad (\text{A.4})$$

where σ_F^2 is a process error expressing the year to year variability in fishing mortality.

The indexed abundance model assumes that the biomass of YFT in the MHI is approximately proportional to the biomass of an “index” population.

$$\log N_t - \log(Q \cdot I_t) = \omega_t; \quad \omega_t \sim N(0, \sigma_I^2) \quad (\text{A.5})$$

where I_t is the size of the index population at time t , Q is the estimated ratio of the MHI population size to the index population, and σ_I^2 is a process error representing the difference between the MHI biomass and the abundance index.

All process errors are assumed to have the same distribution $N(0, \sigma_P^2)$; σ_N, σ_F , and σ_I are assumed to be equal and estimated as a global process error with variance σ_P^2 .

The logistic parameters r and K are notoriously difficult to estimate accurately. Two different alternative parameter substitutions were tested. In the first alternative, MSY (\tilde{Y}) and fishing mortality at MSY ($F_{\tilde{Y}}$) were estimated directly and substituted in A.3 as $r = 2F_{\tilde{Y}}$ and $K = \frac{4\tilde{Y}}{r}$. In the second alternative, the initial population size B_1 and a proportionality constant d are estimated directly and substituted in A.3 as $K = d \cdot B_1$.

Carruthers and McAllister (2011) recommend use of Bayesian priors for the logistic growth parameter r in equation (A.2). They suggest $\tilde{r} = 0.486$ with a standard deviation of $\sigma_r = 0.046$ and coefficient of variation of $\text{cv} = 0.094$ for Atlantic YFT. A lognormal prior on r was implemented with $\tilde{r} = 0.486$ and $\sigma_r = 0.8$.

$$\log r - \log \tilde{r} = \rho; \quad \rho \sim N(0, \sigma_r^2) \quad (\text{A.6})$$

which is a fairly “loose” constraint on the estimate of r . ρ becomes a component of the likelihood (equation A.10).

Observation Model, $O(\alpha)$. The general form of the observation model is

$$x_t = O(\alpha_t) + \varepsilon_t \quad (\text{A.7})$$

where the function O describes the measurement process with error ε in observing the population.

Predicted catch, $\hat{C}_{g,t}$, for each gear is the product of estimated fishing mortality and the total biomass.

$$\hat{C}_{g,t} = F_{g,t} \cdot \left(\frac{N_{t-\Delta t} + N_t}{2} \right) \cdot e^{\varepsilon_t} \quad (\text{A.8})$$

Table A.1: Complete list of estimated parameters for two alternative parameterizations of the state-space single population Schaefer model. Values of non-estimated model variables, e.g., K , are computed by parameter substitution formulas.

\tilde{Y}	$F_{\tilde{Y}}$	B_1	d	Definition
$F_{\tilde{Y}}$				Fishing mortality at maximum sustainable yield
\tilde{Y}				Maximum sustainable yield
		r		Instantaneous growth rate
		B_1		Biomass at time of first observation
		d		Constant of proportionality; $B_1 = Q \cdot K$
Q	Q			Abundance index proportionality constant
σ_P	σ_P			Global process error SD; $\sigma_P = \sigma_N = \sigma_F = \sigma_Q$
σ_Y	σ_Y			Observation error SD
p_0	p_0			Proportion of zero catch observations; fixed at $p_0 = 0.15738$
\tilde{r}	\tilde{r}			An <i>a priori</i> assumed value for r fixed at $\tilde{r} = 0.486$ (Carruthers and McAllister, 2011)
σ_r	σ_r			Assumed standard deviation of r around its prior; fixed at $\sigma_r = 0.8$.

where the total biomass is the average biomass over the time step (Quinn and Deriso, 1999), and ε_t is a “zero-inflated” log normal likelihood given by

$$\log \varepsilon_t = \begin{cases} C_{g,t} > 0 : & (1 - p_0) \cdot \left(\log \frac{1}{\sqrt{2\pi\sigma_Y^2}} - \left(\frac{\log C_{g,t} - \log \hat{C}_{g,t}}{\sigma_Y} \right)^2 \right) \\ C_{g,t} = 0 : & p_0 \cdot \log \frac{1}{\sqrt{2\pi\sigma_Y^2}} \end{cases} \quad (\text{A.9})$$

where σ_Y is the observation error and p_0 is the proportion of observed catch observations equal to zero. This proportion may be estimated or fixed at a constant value. For current analysis, it is fixed at $p_0 = 0.15738$ as computed from the data.

Estimation. The model states, N_t and F_{gt} , are assumed to be random effects (Skaug and Fournier, 2006). Model parameters are estimated by max-

imizing the joint likelihood of the random effects and the observations.

$$L(\theta, \alpha, x) = \prod_{t=2}^m [\phi(\alpha_t - T(\alpha_{t-1}), \Sigma_\eta)] \cdot \prod_{t=1}^m [\phi(x_t - O(\alpha_t), \Sigma_\varepsilon)] \cdot \rho \quad (\text{A.10})$$

Here, m is the number of time steps in the catch time series and θ is a vector of model parameters (Table A.1). The model is implemented in ADMB-RE (Fournier et al, 2012). The actual number of parameters to be estimated depends on the model configuration, specified by phase flags in the input file. All computer code, data files, and draft reports in support of this analysis can be found at Github: <https://github.com/johnrsibert/XSSA.git>.

B Integrating Schaefer Models

The widely used Schaefer (1954) fisheries stock assessment model is a simple extension of the logistic population model with a term added to represent removals from the population due to fishing.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - FN = N\left(r - F - \frac{r}{K}N\right) \quad (\text{B.1})$$

where N is the population size, r is the instantaneous growth rate (t^{-1}), K is the asymptotic population size in the same units as N , and F is the instantaneous rate of removal due to fishing (t^{-1}). Equation (B.1) reduces to the logistic model if F is assumed to be zero. Logistic models are usually integrated numerically with “explicit” finite difference methods to compute an approximation of the value of N at some (future) time. Such approximations are often unstable for values of r large relative to the time step used in the finite difference solution. Statistical procedure depending on numerical function minimizers, i.e, models built using ADMB, TMB and BUGS, do not perform well in the face of numerical instabilities in solving differential equations. The accuracy, speed, and use of computing resources of estimation methods involving logistic models are greatly improved analytical solutions can be used in preference to finite difference approximations.

B.1 Single population

The integral of the logistic differential equation can be found in several places; Murray (1993), Quinn and Deriso (1999). Numerous mathematics tutorials are available on the World Wide Web that use integration of the logistic differential equation as an exercise to illustrate the technique of integration by partial fractions. The same procedure can be applied to the Schaefer differential equation. Equation (B.1) is rearranged and variables separated to become

$$\frac{K}{N(K(r - F) - rN)} dN = dt. \quad (\text{B.2})$$

The fraction in the left hand side can be factored into two parts,

$$\frac{K}{N(K(r - F) - rN)} = \frac{A}{N} + \frac{B}{(K(r - F) - rN)}. \quad (\text{B.3})$$

A and B are constants that can be found by solving $K = A(K(r - f) - rn)) + BN$ setting $N = K$ and $N = 0$; $A = \frac{1}{r-F}$ and $B = 1 + \frac{F}{r-F}$. The desired integral becomes

$$\begin{aligned} \int \frac{K}{N(K(r - F) - rN)} dN &= \int dt \\ \int \frac{A}{N} dN + \int \frac{B}{K(r - F) - rN} dN &= \int dt \\ \frac{1}{r - F} \int \frac{1}{N} dN + \left(1 + \frac{F}{r - F}\right) \int \frac{1}{K(r - F) - rN} dN &= \int dt \\ \frac{1}{r - F} \log |N| + \frac{1}{r} \left(1 + \frac{F}{r - F}\right) \log |K(r - f) - rN| + \log C &= t \\ \log |N| - \log |K(r - F) - rN| + \log C &= t(r - F) \\ \frac{|N|}{|K(r - F) - rN|} \cdot C &= e^{t(r-F)} \\ \frac{|K(r - F) - rN|}{C|N|} &= e^{-t(r-F)} \end{aligned}$$

where C is the constant of integration. Setting $|N| = N_t$, the population size at time t , yields

$$N_t = \frac{K(r - F)}{C e^{-t(r-F)} + r} \quad (\text{B.4})$$

A formula suitable for computing population size at successive time steps can be found by setting $N_t = N_{t-\Delta t}$ at time $t = t - \Delta t$ in equation (B.4). The integration constant becomes

$$C = \left(\frac{K(r - f)}{N_{t-\Delta t}} - r \right) e^{(t-\Delta t)(r-F)}, \quad (\text{B.5})$$

and finally

$$N_t = \frac{K(r - F)}{\frac{K(r-F)}{N_{t-\Delta t}} e^{-\Delta t(r-F)} - r e^{-\Delta t(r-F)} - r} \quad (\text{B.6})$$

Further simplification of this equation may be possible, but I have not found it. In any case, equation (B.6) is the only general solution of the Schaefer ODE that I have seen, and it appears to work well in numerical applications.

B.2 Two populations with exchange

The motivation for the two population Schaefer model with exchange is developed fully elsewhere.

The basic equations can be written

$$\frac{dN_{1,1}}{dt} = N_{1,1} \left(r - F - T_{12} - 2(1-q) \frac{r}{K} N_{2,1} - \frac{r}{K} N_{1,1} \right) \quad (\text{B.7})$$

$$\frac{dN_{2,1}}{dt} = N_{2,1} \left(r - F - T_{12} - 2q \frac{r}{K} N_{1,1} - \frac{r}{K} N_{2,1} \right) + T_{21} \quad (\text{B.8})$$

where $N_{1,1}$ is the biomass of fish originating in region 1 and residing in region 1, and $N_{2,1}$ is the biomass of fish originating in region 2 but residing in region 1. The parameters r , K and F are unchanged from equation (B.1), and T_{12} is the emigration rate from region 1 (t^{-1}), T_{21} is the rate of immigration of biomass from region 2 to region 1 in units of biomass per time, and q ($0 < q < 1$) partitions the mortality caused by “competition” between the two subpopulations. Substitute

$$Z_1 = F + T_{12} + 2(1-q) \frac{r}{K} N_{2,1} \quad (\text{B.9})$$

$$Z_2 = F + T_{12} + 2q \frac{r}{K} N_{1,1} \quad (\text{B.10})$$

into equations (B.7) and (B.8) respectively to produce model equations in a similar form to equation (B.1)

$$\frac{dN_{1,1}}{dt} = N_{1,1} \left(r - Z_1 - \frac{r}{K} N_{1,1} \right) \quad (\text{B.11})$$

$$\frac{dN_{2,1}}{dt} = N_{2,1} \left(r - Z_2 - \frac{r}{K} N_{2,1} \right) + T_{21}. \quad (\text{B.12})$$

Equation (B.11) can be integrated in the same manner as equation (B.1) to yield

$$N_{1,1t} = \frac{K(r - Z_1)}{C_1 e^{-t(r - Z_1)} + r}. \quad (\text{B.13})$$

An equivalent integral for equation (B.12), possibly by completing the square and solving the resulting quadratic, and a means to simultaneously solve for C_1 and C_2 are required to achieve a complete solution to the two population model differential equations.