

Incorporating stochasticity in the study of exploited fish population dynamics: implications for the study of post-recruitment harvest strategies

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Key results

1. Spawning stock biomass is higher when harvest occurs post-spawning than when harvest occurs pre- or concurrent with spawning events.
2. The benefit to spawning stock biomass of post-recruitment harvest is diminished when high variance in the age-specific harvest rates are incorporated into the modeling framework.
3. Stochasticity in age-dependent harvest rates can lead to unexpected dynamics, and the effects of inclusion of stochastic parameters in models of exploited fish stocks warrants further investigation.

Keywords: hybrid model, fisheries, temporal, stochastic, Bluefin tuna

Reply for reviewer comments for MBS-D-15-00227

Elizabeth Council

Reviewer #1's comments were fully implemented in the revised draft.

Reviewer #2's comments were nearly fully implemented in the revised draft with the following exceptions:

The reviewer suggested that equations (10) and (17) be condensed. While the form for these equations is identical, their usage and interpretation are slightly different, and it is my opinion that they remain as they are so that readers may see the fully-explicit form for each within the context of their usage and derivation. The reviewer also suggesting switching the order or presentation of R and g with the presentation of SSB , $W(a)$, and $m(a)$. I disagree with this suggestion, as the formulation for SSB , $W(a)$, and $m(a)$ are required for a correct formulation for R and g to be presented as they were used during the simulation phase. I believe the current presentation of methods is clearly stated and provides the best framework for future researchers to easily modify and adapt the methods presented.

I found that both reviewer's comments were very helpful and constructive and appreciate the contribution that each reviewer made to improve the draft. I believe this revised draft is substantially improved over the original.

Please also note my organization affiliation update noted on the first page of the revised draft.

Abstract:

Previous work has shown that an effective method of maintaining spawning stock biomass (SSB), the biomass of fish that are reproductively mature, within an exploited stock is to regulate harvest so that maximum fishing mortality rates occur after peak spawning during the year. This is known as post-recruitment harvest. The goal of this work is to examine if the advantages of post-recruitment harvest hold when reported stochasticity in the age and time distribution of harvest rates, known as selectivity, is considered. A hybrid dynamical systems model, one in which both continuous-time and discrete-time processes operate simultaneously, was derived, and recursive solutions were found. Results from other studies indicating the benefit of post-recruitment harvest were verified using this hybrid model when selectivity was considered fixed. Simulations were repeated including variance in selectivity using a Markov Chain Monte Carlo (MCMC) procedure. Results show that the benefits of post-recruitment harvest to the preservation of SSB were considerably less advantageous when each age class was assumed to be subject to annual stochastic selectivity. Furthermore, the stochastic scenarios gave estimates of SSB that were lower than their fixed selectivity analogs, indicating that the benefits of theoretical post-recruitment harvest may be diminished to some extent when stochasticity plays a large role in the dynamics.

Introduction

Spawning events in exploited fish stocks are strongly reliant upon seasonal environmental triggers, and consequently, mature fish spawn at distinct times within the year (Lutcavage et al. 1999; Musick 1999; Arnasson et al. 2000; Block et al. 2001; Bonfil et al. 2005; Kurita et al. 2006; Murura and Motos 2006; Mukai et al. 2007; Bushnell et al. 2010; Tu et al. 2012; Tseng et al. 2013; Claydon et al. 2014; Leaf and Friedland 2014). Moreover, fishing mortality rates are not fixed at a constant rate across the year, as many fishery management organizations implement seasonal closures of fisheries in an effort to preserve stock sustainability (Roy 1998; van Poorten and Post 2005; Perea et al. 2011; Lin et al. 2013).

Some fully age structured models have been developed to include time-dependent harvest mortality in a unified framework to either simulate spawning stock biomass (SSB) of a fishery over time or to examine the effects of density-dependent recruitment dynamics (Ault and Olson 1996; Xiao 1997, 2002; Politikos et al. 2012). Previous work has shown that fisheries that control harvest so that the maximum rate of fishing mortality occurs post recruitment, after peak spawning period, support greater biomass and abundance of mature fish within the stock than those that harvest before peak recruitment (Politikos et al. 2012). Results from previous work supports the notion that the pre-recruitment phase, the time within the year before peak spawning rates occur, plays a crucial role in the preservation of SSB of exploited fish stocks. These models have adapted work from Sanchez (1978), which modifies the McKendrick-von Foerster partial differential equation (McKendrick 1926; von Foerster 1959; Kot 2001) to include a time-dependent switching function that controls the susceptibility of the population to fishing mortality with respect to time. In fisheries literature, this function is known as the selectivity of a fishery. Though selectivity is more frequently used to describe the susceptibility by age to

fishing mortality (Crone et al. 2013), it will be used to describe the proportion of fishing mortality prescribed by age and time in this work. Kot (2001) provides an explicit solution to the Sanchez model when maternity rates are only age-dependent, and Ault and Olson (1996) and Politikos (et al. 2012) provide a thorough examination of the Sanchez model with time-dependent birth function. However, because fish are either fully selected or not selected with respect to time, models that utilize the Sanchez (1978) base model do not incorporate intermediate levels of selection throughout the year, a scenario that may more accurately represent the time-distribution of the fishing mortality rates for many exploited stocks.

Additionally, most fully age structured models with explicit time dependence in fisheries do not incorporate stochasticity in the age-component of selectivity, despite very large variance in the age component of selectivity reported across multiple stocks (Stewart and Hamel 2010; ALBWG 2011; ICCAT 2012; Davies et al. 2011). The combined effects of the within-year temporal pattern of harvest rates in the context of uncertainty surrounding age-dependent selectivity are not well understood, despite the importance of understanding these dynamics for both fishery management and ecological purposes (Pfister 1997; Wood and Austin 2009).

Drawing inspiration from the main result in Politikos et al. (2012), namely that post-recruitment harvest is preferable to pre- or concurrent recruitment harvest with respect to the preservation of spawning stock biomass, this work has three objectives:

- (1) Determine if the main result from Politikos (et al. 2012) and others can be reproduced using a different but analogous modeling framework applied to a different stock in which harvest rates are modeled using a continuous time probability density function in lieu of a switching function.

- (2) Determine if these results hold when variance in the age component of selectivity from assessment reports are incorporated.
- (3) Qualify the effects of stochastic variation in age-specific selection and determine if the incorporation of stochasticity into a fully age structured model provides new insight into the effects of time-dependent harvest strategies relative to temporal recruitment patterns.

Target Species

The stock of interest for this work is western Atlantic Bluefin tuna (*Thunnus thynnus*), also known as the Gulf of Mexico (GOM) stock of Atlantic Bluefin tuna (ICCAT 2012). Bluefin tuna are highly-prized both commercially and recreationally, and the Gulf of Mexico stock supports a multi-billion dollar international fishing industry (Collete et al. 2011). Additionally, this stock has a distinct spawning period with peak in early to middle June, but the majority of spawning activity occurs within approximately three months from early April until late June (Aranda et al. 2013). The availability of a recent stock assessment report containing estimates of the necessary recruitment, harvest, and aging data required to define the parameters of a temporally and fully age structured model makes the western stock of Atlantic Bluefin tuna a suitable species to use as a case study to parameterize this work.

Methods

A multi-step procedure was developed to carry out this investigation. First, a fully age-structured pulsed hybrid dynamical systems model was specified, and explicit cohort-based solutions were identified. Such a model incorporates both continuous-time and discrete-time dynamics into a single modeling framework with output from the discrete process regularly “pulsed” into the system (Bainov and Simeonov 1989). Second, a stochastic parameterization of

the model was specified using data extracted from the 2012 ICCAT (International Commission for the Conservation of Atlantic Tunas) stock assessment report on Atlantic Bluefin tuna and other published works. Thirdly, three test cases, corresponding to fishing mortality rates that peak pre-recruitment, concurrent with recruitment, and post-recruitment were tested with and without annual stochasticity in the selection parameters, and 30 replicates were produced for each scenario using Markov Chain Monte Carlo (MCMC) simulations (Diaconis 2009), with both simulations incorporating stochasticity in annual peak harvest times. Numerical convergence was confirmed by running the simulations out 500 years, though only the first 200 years are reported, as simulations that were longer did not show appreciable change in estimates of biomass or abundance. Lastly, within-year equilibrium SSB was extracted to examine how these within-year patterns differ between the two simulated cases when the age-component of selectivity was considered a pseudo-random stochastic effect with variance equal to reported variance from the Report of the 2012 Atlantic Bluefin Tuna Assessment (ICCAT 2012) (stochastic simulation) and when it is considered fixed and equal to the mean value of selectivity from the assessment report (partially stochastic simulation).

A Note on Model Choice

The model utilized for this work is a pulsed hybrid dynamical systems model (also known as a semi-discrete or a semi-continuous model) (Bainov and Simeonov 1989). These models belong to a class of dynamical systems models in which both discrete-time and continuous-time processes are incorporated into a single modeling framework, with the output from the discrete process “pulsed” into the system at user-specified times. Hybrid models have recently been used in numerous biological and ecological modeling applications since their original introduction to fishery science by Beverton and Holt (1957) (Zhang et al. 2003, Shosh

and Pugliese 2004, Singh and Nisbet 2007, Pachevsky et al. 2008). Readers interested in better acquainting themselves with this class of models and their applications in biology should consult Maillaret and Lemesle (2009), and those interested in a more rigorous mathematical treatment of hybrid models should consult Webb (1985) and Bainov and Simeonov (1989).

The primary benefit of using a hybrid model for this project in lieu of a discrete-time model, as is more commonly used in fisheries literature, comes from the hybrid model's unique ability to incorporate continuous-time harvest processes without requiring the use of a continuous-time continuous-age partial differential equation (PDE) that may not have a readily-identifiable analytic solution and may also be difficult to numerically analyze. As shown below, the hybrid model for these simulations has an explicit recursive set of solutions, making it somewhat unique for a non-autonomous fully age-structured nonlinear dynamical systems model.

Model Construction and Parameterization

Here, w gives the maximum age class, τ_{max} gives the maximum number of years for which the simulation runs, a represents the index corresponding to age, t represents the index used for within-year time, and τ is the index for among-year time. Movement of individuals up age classes occurs annually with age classes defined in one year steps. Recruitment and mortality for age-1 fish occurs at monthly discrete times within the year, and within-year mortality for ages greater than 1 is a continuous-time process. The time step size for the discrete process of age-1 fish production was chosen so that this process reasonably well approximates a continuous recruitment process, which would require the introduction of a PDE if explicitly modeled. Additionally, a monthly time step gives an easily-understood intuition for the process of recruitment, as it occurs at fixed and easily-defined intervals. For ages, $a = 2, \dots, w$, within-

year time, specified by t on the interval $0 \leq t \leq 1$ and between-year time steps $\tau = 1, 2, \dots, \tau_{max}$, the age-class population abundance, $N(a, t, \tau)$, is governed by a simple separable non-autonomous ordinary differential equation (ODE).

$$\frac{dN}{dt}(a, t, \tau) = -z(a, t)N(a, t, \tau) \quad (1)$$

where $z(a, t)$ is the total instantaneous annual mortality rate for the population, equal to the sum of the natural and fishing mortality rates. For any fixed value of a , it is assumed that $z(a, t)$ is an integrable function with respect to both a and t with finite values over $0 < t < 1$. Aging is controlled by an initial condition (2), so that at the beginning of each simulation year, survivors from the previous age class at the end of the previous year are transferred to the beginning of the subsequent year and age class, with $k(a)$ the given initial distribution of the population.

$$N(a, 0, \tau) = \begin{cases} k(a) & \tau = 1 \\ N(a-1, 1, \tau-1) & \tau > 1 \end{cases} \quad (2)$$

Equation (1), together with (2), can be solved to give (3) for $a = 2, \dots, w$.

$$N(a, t, \tau) = N(a, 0, \tau) \exp\left(-\int_0^t z(a, x)dx\right) \quad (3)$$

The recruit population, $N(1, t, \tau)$, is controlled by a discrete-time process. For a fixed value of $\Delta t \leq 1$ and positive integer, n , such that $n\Delta t = 1$, the population of recruits, defined as fish age 1, is controlled by a discrete process, where $\Lambda(t, \tau)$ is the number of recruits produced by the spawning population at time t and year τ . Mortality and recruitment for year-1 fish is a discrete-time process with mortality rate equal to $z(1, t)$. Equation (4) gives the recruit population abundance with $N(1, 0, \tau) = 0$.

$$N(1, t + \Delta t, \tau) = \Lambda(t, \tau) + N(1, t, \tau)(1 - z(1, t)\Delta t) \quad (4)$$

For age classes 2 and older, recursivity, which is defined as the dependence of the current year and age class abundance, $N(a, t, \tau)$, on the previous year class abundance at the end of the

previous year, $N(a - 1, 1, \tau - 1)$, from the initial condition (2) can be eliminated by treating each age class as a cohort produced at year τ . Namely, given the abundance of a cohort that survives their first year at year τ , given by $N(1, 1, \tau)$, $N(a, t, \tau + a)$ can be calculated directly in one computational step. To see this, for simplicity, assume that $\tau > 1$. For $\tau = 1$, the same result applies with $k(a)$ substituted accordingly. To remove the recursivity, first, note that:

$$N(a, t, \tau) = N(a - 1, 1, \tau - 1) \exp\left(-\int_0^t z(a, x) dx\right) \quad (5)$$

For $a = 2$ in (5) above and noting that $N(2, 0, \tau) = N(1, 1, \tau - 1)$:

$$N(2, t, \tau) = N(2, 0, \tau) \exp\left(-\int_0^t z(2, x) dx\right) \quad (6)$$

Iterating forward by age and τ from (6), evaluated at $t = 1$:

$$N(3, t, \tau + 1) = N(2, 0, \tau) \exp\left(-\int_0^1 z(2, t) dt\right) \exp\left(-\int_0^t z(3, x) dx\right) \quad (7)$$

Repeating up to $N(a, t, \tau + a)$ and noting that

$\exp\left(-\sum_{i=2}^{a-1} \left[\int_0^1 z(i, x) dx\right]\right) = \prod_{i=2}^{a-1} \exp\left(-\left[\int_0^1 z(i, x) dx\right]\right)$, equation (8) arises.

$$N(a, t, \tau + a) = N(2, 0, \tau) \exp\left(-\sum_{i=2}^{a-1} \left[\int_0^1 z(i, x) dx\right]\right) \exp\left(-\int_0^t z(a, x) dx\right) \quad (8)$$

Equation (8) relies only on the function $z(a, t)$ and the value of $N(2, 0, \tau) = N(1, 1, \tau - 1)$.

Parameterization

Mortality

Mortality rates, $z(a, t)$, are equal to the sum of natural mortality rates, $M(a)$, and fishing mortality rates, $F(a, t)$. It is assumed that natural mortality rates are not time-dependent.

Recruitment, $\Lambda(t, \tau)$, is the product of a stock-recruitment relationship, relating the spawning stock biomass to the number of recruits produced, and a continuous-time function controlling the magnitude of the spawning event at time t and year τ . Parameterization of these three terms,

$M(a)$, $F(a, t)$, and $\Lambda(t, \tau)$, follows.

The instantaneous annual fishing mortality rate at age a and time t , $F(a, t)$ (equation (9)), is the product of three components: δ , a constant equal to the ratio of F , the estimated mean annual fishing mortality rate, to F_{MSY} , the fishing mortality rate that produces a theoretical maximum sustainable yield (MSY); Q , the annual fishing mortality rate calculated by the stock assessment procedure; and the selectivity of the fishery, $Sel(a, t)$, a function controlling the susceptibility of fish age a to the fishery at time t . Age-dependent natural mortality rates were provided by the of the 2012 Atlantic Bluefin Tuna Assessment (ICCAT 2012) and are plotted in Figure 1.

$$F(a, t) = \delta Q Sel(a, t) \quad (9)$$

Selectivity

Selectivity, $Sel(a, t)$, is the product of the proportion of fishing mortality prescribed to age class a , $p(a)$, with a continuous-time function, $h(t)$, controlling the proportion of fishing mortality prescribed to the whole population at time t . Specifically, $h(t)$ is the proportion of the fishing mortality to which the stock is susceptible at time t . The values, $p(a)$, will be the primary focus of investigation in this work. A parameter, $\varepsilon_{p(a)}$, drawn from a normal distribution with mean zero and standard deviation $\sigma_{p(a)}$ that is added to $p(a)$, will serve as the stochastic component of $p(a)$. The function, $h^*(t)$, is a skewed normal distribution, where l is a scaling factor controlling the width of the distribution, ξ is the mean time of harvest within the year in units of t , and $\hat{\alpha}$ is the skewness. This formulation comes from Azzalini (1985), whose formulation for the skew normal distribution includes the standard normal probability density function, $\phi(x)$, and its corresponding cumulative distribution function, $\Phi(x)$, giving an intuitive and compact formulation for the skew normal distribution. To represent imperfect peak harvest rates within the year, skewness of the peak time of harvest, $\hat{\alpha}$, is allowed to slightly vary from

year to year by adding a stochastic variation term, $\varepsilon_{\hat{\alpha}}$, drawn from a normal distribution with mean zero standard deviation equal to $\sigma_{\hat{\alpha}}$. H is a constant equal to the integral of (10) over $0 \leq t \leq 1$.

$$h^*(t) = \frac{2}{l} \phi\left(\frac{t-\xi}{l}\right) \Phi\left((\hat{\alpha} + \varepsilon_{\hat{\alpha}})\left(\frac{t-\xi}{l}\right)\right) \quad (10)$$

with $\Phi(x) = \frac{1}{2}\left[1 + \operatorname{erf}\left(\frac{x}{\sqrt{2}}\right)\right]$ and $\phi(y) = \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{y^2}{2}\right)$.

$h(t)$ is given by scaling (10) by a constant, H , so that $0 \leq h(t) \leq 1$. The scaling of (10) is necessary so that $0 \leq h(t) \leq 1$, and $\int_0^1 h(t) dt = 1$.

Hence,

$$h(t) = H^{-1} \left[\frac{2}{l} \phi\left(\frac{t-\xi}{l}\right) \Phi\left((\hat{\alpha} + \varepsilon_{\hat{\alpha}})\left(\frac{t-\xi}{l}\right)\right) \right] \quad (11)$$

Selectivity is given by (12).

$$\operatorname{Sel}(a, t) = (p(a) + \varepsilon_{p(a)})h(t) \quad (12)$$

The parameter $\hat{\alpha}$ is the parameter that controls the peak of the harvest season. When $\hat{\alpha} = 0$, the peak of (11) occurs at $t = \xi$. When $\hat{\alpha} < 0$, the peak of (11) shifts to the left, and when $\hat{\alpha} > 0$, the peak of (11) shifts to the right.

Recruitment

Recruitment, $\Lambda(t, \tau)$, at time t and year τ is the product of a Beverton-Holt stock-recruitment relationship, $R(t, \tau)$, (Beverton and Holt 1957), that relates the spawning stock biomass to the number of year-1 fish produced by the stock; and a continuous-time function, $g(t)$, controlling the proportion of the spawning stock that spawns at time t . Construction of the stock-recruitment relationship first requires a calculation of spawning stock biomass, SSB. This requires a maturity function, $m(a)$, the proportion of the stock that is mature at age a (see Figure 1), and a weight-at-age function, $W(a)$. Weight-at-age is given by the von Bertalanffy (LVB)

generalized weight-at-age relationship where \widehat{W} is a dimensionless scalar controlling body mass per unit length growth; K is the rate of increase in length with age; a_0 is the age when a fish would have length zero ($a_0 < 0$); and s is a dimensionless scalar controlling body mass from length growth.

$$W(a) = \widehat{W} [L_\infty (1 - \exp(-K(a - a_0)))]^3 \quad (13)$$

SSB, denoted $S(t, \tau)$, is the sum over all age classes of the product of maturity, weight-at-age, and abundance and is given by (14).

$$S(t, \tau) = \sum_{a=1}^w m(a)W(a)N(a, t, \tau) \quad (14)$$

The recruitment function, $R(t, \tau)$, is a Beverton-Holt stock-recruitment relationship (Beverton and Holt 1957) with α and β strictly positive constants such that α/β gives the maximum number of recruits producible with infinitely large spawning stock biomass, and α is the rate of increase in recruitment when the spawning stock biomass is near zero. α is commonly referred to as the initial slope of the recruitment function in fishery literature. It should be remembered that recruitment occurs on a monthly basis, as age-1 fish are produced on monthly intervals.

$$R(t, \tau) = \frac{\alpha S(t, \tau)}{1 + \beta S(t, \tau)} \quad (15)$$

The number of recruits produced at time t and year τ is given by the product of $R(t, \tau)$ and the proportion of the stock that spawns at time t , $g(t)$.

$$\Lambda(t, \tau) = R(t, \tau)g(t) \quad (16)$$

The function, $g^*(t)$, is a skewed normal distribution of similar form as $h^*(t)$, where j is a scaling factor, q is the mean spawning time in units of t , and r is the skewness. Again, scaling of $g^*(t)$ by $G = \int_0^1 g^*(t)dt$ gives:

$$g(t) = G^{-1} \left[\left(\frac{2}{j} \right) \phi \left(\frac{t-q}{j} \right) \Phi \left(r \frac{t-q}{j} \right) \right] \quad (17)$$

with $\Phi(x) = \frac{1}{2} \left[1 + \operatorname{erf} \left(\frac{x}{\sqrt{2}} \right) \right]$ and $\phi(y) = \frac{1}{\sqrt{2\pi}} \exp \left(-\frac{y^2}{2} \right)$.

Simulations

Three simulated harvest timing scenarios were simulated: pre-recruitment, concurrent with recruitment, and post-recruitment. Each of these scenarios were simulated twice, once with deterministic selectivity and once with stochastic selectivity which allows $p(a)$ to vary stochastically from year to year. The first harvest timing scenario is one in which harvest is assumed to occur pre-recruitment with peak in early April ($\hat{\alpha} = -1$). The second is one in which peak harvest is assumed to occur concurrent with recruitment with peak in mid-June ($\hat{\alpha} = 0$). The third harvest scenario is one in which peak harvesting occurs post-recruitment in early August ($\hat{\alpha} = 1$). Peak spawning is assumed to occur mid-June ($r = 0$), matching available data on the western stock of Atlantic Bluefin tunas (ICCAT 2012). Two types of stochasticity were simulated for each harvest scenario. The first assumes that $\varepsilon_{p(a)}$ is zero, and $\varepsilon_{\hat{\alpha}}$ is chosen from a truncated normal distribution with mean and variance from reported data. This value is truncated in the sense that $\varepsilon_{\hat{\alpha}}$ is chosen so that $\varepsilon_{\hat{\alpha}} > 0$. This simulation assumes that stochasticity only exists in the skewness of the time component of selectivity, and that the age components of selectivity are fixed. This case will be referred to as the “fixed selectivity” case. The second assumes that both $\varepsilon_{\hat{\alpha}}$ and $\varepsilon_{p(a)}$ are strictly positive. This simulation represents the case when stochasticity exists in the skewness and the age-components of the selectivity function. This case will be referred to as the “stochastic selectivity” case when discussed below. In both cases, $\varepsilon_{\hat{\alpha}}$ is allowed to vary. This was done to include some level of uncertainty about the true time of peak harvest rates in each simulation, as peak harvest rates vary slightly year-to-year even under the tightest regulatory regimes (ICCAT 2012). See Figures 2 and 3.

Recruitment parameters, α and β , were calculated using reference case data from Butterworth (et al. 2003) using steepness of 0.6. It should be noted that the interpretation of α and β are slightly different in this work than as reported in Butterworth (et al. 2003), but easily transformed given a straightforward algebraic conversion.

30 simulations were run for each combination of harvest timing scenario and stochasticity assumption, for a total of 180 simulations. For each simulation, convergence was confirmed numerically, and simulations were run for 200 years (approximately 20 generations). Longer run times failed to produce statistically different estimates of within-year SSB. Convergence plots are shown in supplemental materials Figures S1 through S6.

Initial conditions, $k(a)$, were randomly chosen from a normal distribution with mean equal to 100,000 and standard deviation equal to 100. Equilibrium within-year SSB was extracted from the year 200 simulation. All simulations, plots, and analyses were run in MATLAB v2014b. The parameters used to perform the simulations are given in Table 1. The simulation procedure is summarized in Table 2.

Results

The fixed selectivity model did replicate the primary result from Politikos (et al. 2012). Namely, post-recruitment harvesting strategies produced greater spawning stock biomass than pre- or concurrent recruitment harvest strategies. Additionally, the SSB reported in the ICCAT 2012 assessment matches the output of these simulations nicely with the estimate of SSB being approximately equal to $1.8e8 - 2.0e8$ kilograms (ICCAT 2012), a range which contains the output SSB from the fixed selectivity post-recruitment harvest scenario (see Figure 4). Additionally, the fixed selectivity results indicate that post-recruitment harvest has a strong effect on biomass retention with estimates of SSB in the $1.7e8 - 2.0e8$ kilogram range, and

concurrent or pre-recruitment harvest producing estimates of SSB in the $0.3e8 - 0.4e8$ kilogram range.

The stochastic runs produced quite different distributions of biomass data than the fixed selectivity simulations, with the magnitude of the benefit in retention of SSB greatly masked by the stochasticity of the estimated SSB. Namely, while post-recruitment harvest is still beneficial in the retention of biomass in the spawning stock, but the magnitude of the difference between simulations where harvest occurs post-recruitment and those that occur concurrent to or pre-recruitment is much smaller with the average within-year SSB under post-recruitment harvest equal to $6.0e7$ kilograms and average within-year SSB under pre-recruitment harvest equal to $3.8e7$ kilograms (Figure 4).

Discussion

In both the fixed and stochastic selectivity simulations, the main result from Politikos (et al. 2012), namely that post-recruitment harvest strategies are beneficial as a management strategy to sustain spawning stock biomass, was confirmed when applied to the western Atlantic stock of Bluefin tuna using the hybrid modeling approach. However, the magnitude of this benefit becomes much less apparent when among-year variation in the selectivity of the fishery is considered. Additionally, interannual variation in the age component of selectivity may lead to a stock with a lower SSB than one in which selectivity is considered fixed across years. Consequently, these results indicate that the ability to detect any benefit of post-harvest recruitment on SSB may become difficult as more variance from recruitment, growth, and/or egg production is included. Alternatively, these results may indicate that stochasticity in the timing and age distribution of spawning within the population itself may reduce the benefits of post-recruitment harvesting strategies on the retention of SSB in an exploited fish stock. This second

view requires significantly more investigation both from ecological modelers and fishery scientists.

Outside of the direct application to the study of within-year SSB patterns, these results imply that ignoring reported stochasticity in theoretical models of exploited stocks may significantly bias results. This is especially true of exploited fish stocks, since many of these stocks, particularly those with fast generation times, show very large variation in annual estimates of recruitment and selectivity at age (ICCAT 2012; Kurita et al 2006; Lief and Friedland 2014;Perea et al. 2011). Stocks with lower annual variance in estimated parameters may be better choices for theoretical models that do not incorporate variance in parameterization. In most cases of exploited marine stocks, interannual variance in recruitment and selectivity is typically fairly high with reported standard deviations close to, equal to, and sometimes in excess of the reported means. This high reported variance stems from the difficulty in eliminating uncertainty from available data for assessments. Given this, it is difficult to be certain that the mean of these estimates represents the true value of recruitment or selectivity in the stock. Thus, theoretical ecologists interested in parameterizing models designed to emulate exploited fish stocks should carefully consider not only the mean of these parameter estimates but also the spread and breadth of the data itself when attempting to draw meaningful ecological conclusions.

Finally, these results support previous work that implies that incorporation of parameter stochasticity in fully-age structured models of exploited stocks can lead to interesting and unexpected outcomes. The stochasticity in selectivity, when included into the modeling framework, produced estimates of SSB that were an order of magnitude less and with far less spread than expected given the high variance in the selectivity parameters. One might expect that the stochastic model may have produced data around the fixed selectivity estimate of SSB. This

was not the case, indicating that interannual variance in the distribution of harvest mortality rates across age classes may be a crucial dynamic of an exploited fish stock that warrants further ecological investigation.

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1 Table 1

<i>Parameter</i>	<i>Description</i>	<i>Simulated Values</i>	<i>Source (where applicable)</i>
w	Maximum age simulated	16	ICCAT 2012
τ_{max}	Number of year steps simulated	200	
$m(a)$	Proportion of fish that are mature at age (a) (see Figure 1)		ICCAT 2012
α	Initial slope for recruitment function	0.0553	
σ_{α}	Standard deviation for stochasticity in α	0.01	
β	Rate of increase in recruitment	9.0253e-6	
σ_{β}	Standard deviation for stochasticity in β	1e-6	
j	Scaling factor for $g(t)$	0.33	
q	Mean time t of spawning	0.5	
w_N	Expected terminal age population	16	ICCAT 2012
$M(a)$	Computed rate of natural mortality at age (see Figure 1)		ICCAT 2012
$Sel(a, t)$	Selectivity at age a and time t (see Figure 2)		ICCAT 2012
L_{∞}	Maximum length	320.5	ICCAT 2012
K	Growth rate	0.1035	ICCAT 2012
a_0	Age at length zero	-0.7034	ICCAT 2012
F	Fishing mortality rate	0.1	ICCAT 2012
α_W	Length-Weight conversion scalar	0.001	ICCAT 2012
β_W	Length-Weight conversion exponent	2.4	ICCAT 2012
L	Age at which 50% of population is susceptible to the fishery	4.5	ICCAT 2012
l	Scaling factor for skewed normal distribution of selectivity function	0.33	
ξ	Mean of time component of selectivity function	0.5	
$\hat{\alpha}$	Skewness of time component of selectivity	-1, 0, 1	
$\sigma_{\hat{\alpha}}$	Standard deviation for stochasticity in $\hat{\alpha}$	0.1	
r	Skewness of time component of recruitment	0	
η	Scalar adjustment for weight at length	0.001	
δ	Ratio of F to F_{MSY}	1	ICCAT 2010

B_0	Calculated virgin recruit biomass (biomass of recruits in unharvested stock)	5.54e8	Butterworth et al. 2003
R_0	Calculated virgin recruitment (number of recruits in unharvested stock)	5.106e6	Butterworth et al. 2003

2

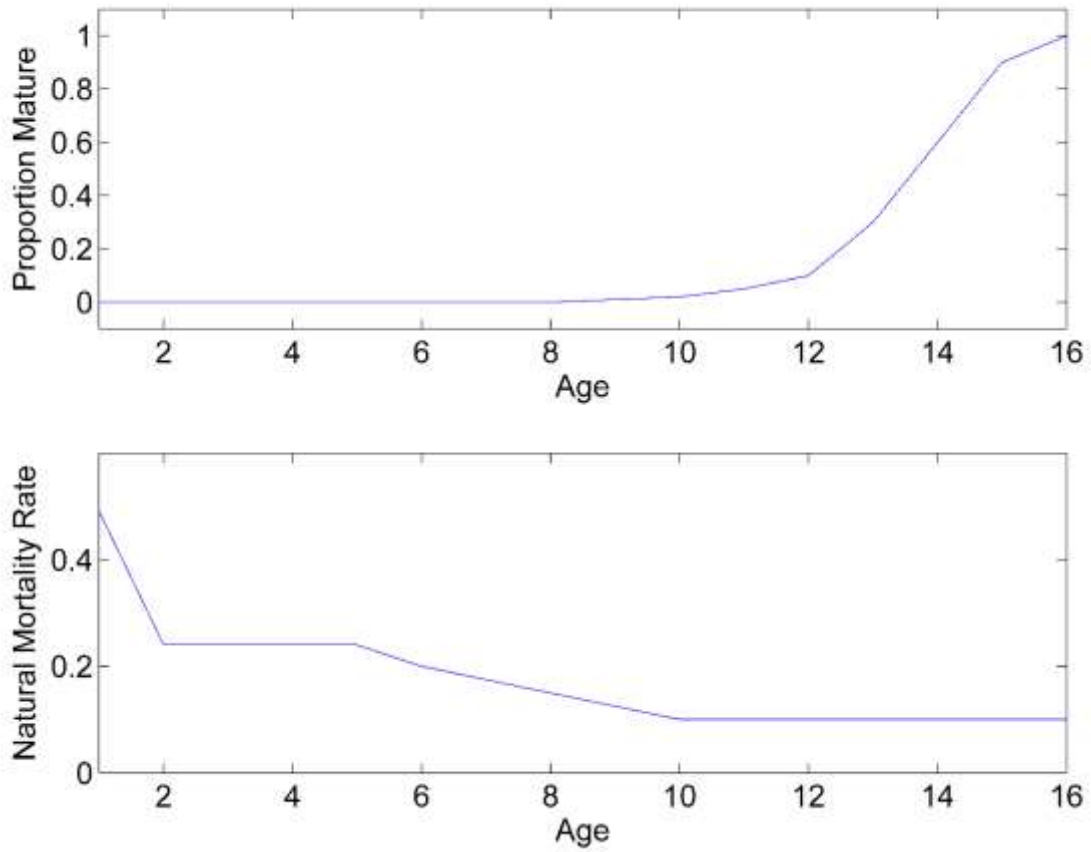
3

4 Table 2

Simulation Procedure Step	Description
1	Set fixed parameters.
2	Select initial conditions, $k(a)$.
3	Begin simulation year.
4	Select \hat{a} and associated error, $\varepsilon_{\hat{a}}$.
5	Set selectivity by age, $p(a)$, and associated error $\varepsilon_{p(a)}$ (If $p(a) + \varepsilon_{p(a)} < 0$, reselect $\varepsilon_{p(a)}$).
6	Set δ and associated error, ε_{δ} .
7	Compute $N(a, t, \tau)$ for ages 2+.
8	Set α and β together with associated errors, ε_{α} and ε_{β} .
9	Calculate $\Lambda(t, \tau)$ and $N(1, t, \tau)$.
10	End simulation year and set initial condition for the subsequent year using (3).
11	Repeat steps 4-10 for 200 years.
12	Repeat steps 3-11 for 30 replicates.

5

6 Figure 1



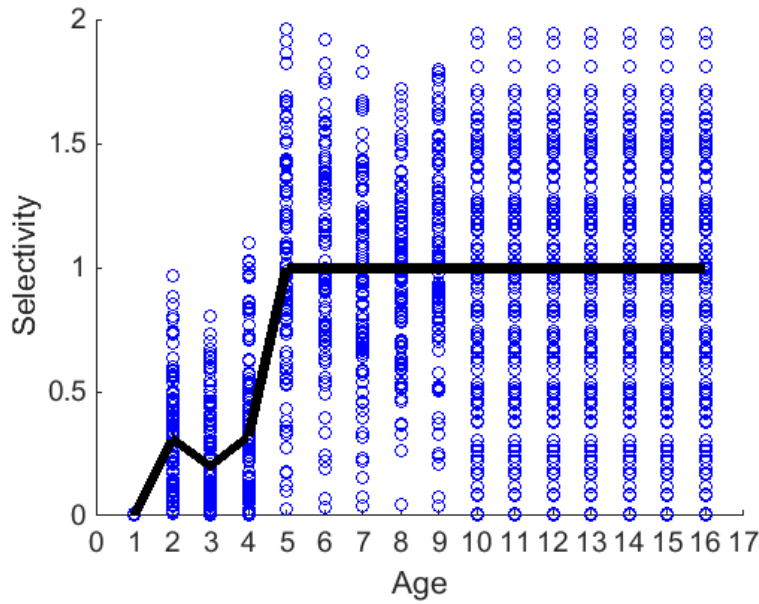
7

8 Figure 1: Plots of reported maturity schedule (top graph) and annual natural mortality rates

9 (bottom graph).

10

11 Figure 2

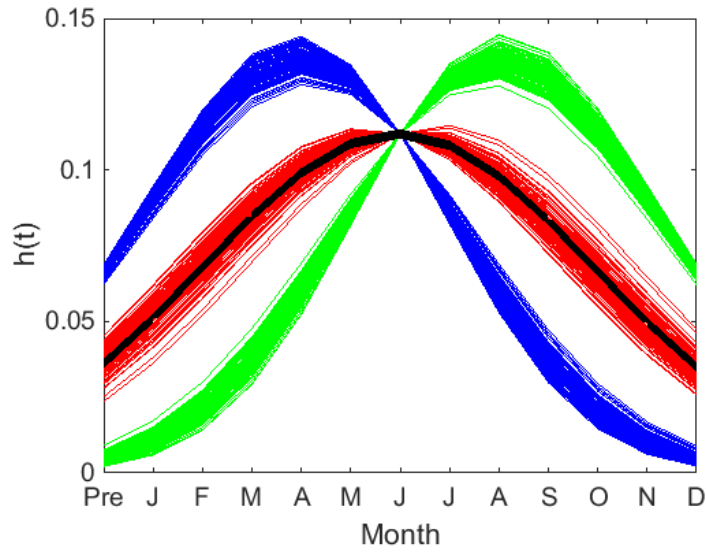


12

13 Figure 2: Subsample of tested selectivity values. Blue dots represent a random subsample of 100
14 tested values of selectivity per age. Each blue dot was selected from a normal distribution with
15 mean equal to the average selectivity value and standard deviation equal to the square root of the
16 reported variance in selectivity by age. The black line gives the mean selectivity reported by the
17 stock assessment report and represents the values tested in the deterministic model simulations.

18

19 Figure 3

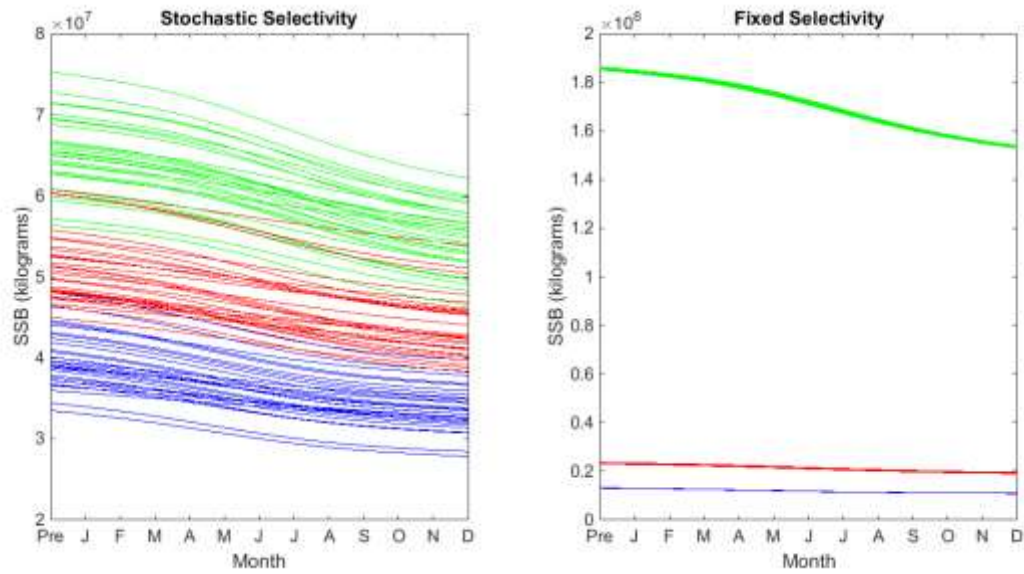


20

21 Figure 3: Subsample of testing functions $h(t)$. Blue lines represent pre-recruitment harvest. Red
22 lines give concurrent recruitment harvest, and green lines give post-recruitment harvest. The
23 black line is the time component of recruitment, $g(t)$.

24

25 Figure 4

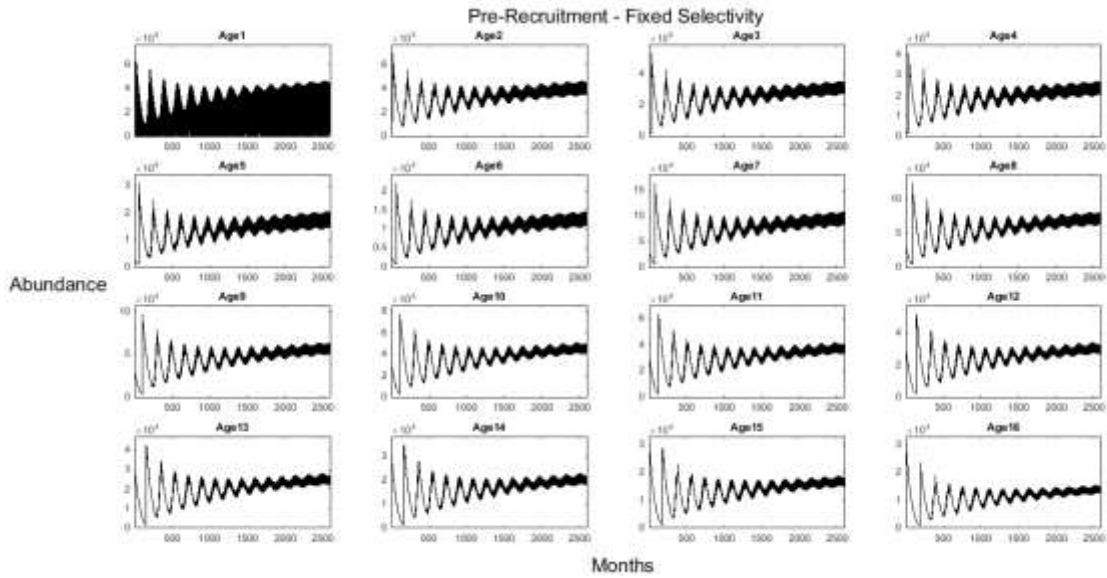


26

27 Figure 4: Left plot shows within-year estimates of SSB at equilibrium by month under stochastic
28 selectivity. Right plot shows within-year estimates of SSB at equilibrium by month under
29 deterministic selectivity. Green lines are post-recruitment runs. Red lines are concurrent
30 selectivity runs, and blue lines are pre-recruitment runs.

31 SUPPLEMENTAL PLOTS – CONVERGENCE PLOTS

32 Figure S1

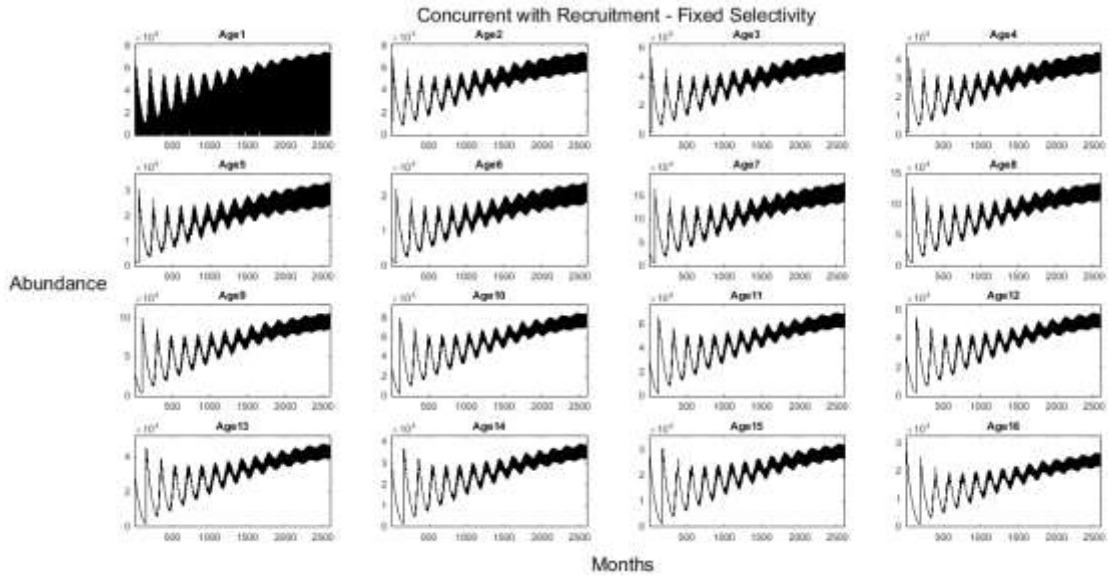


33

34 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
35 corresponding to blue lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)} \equiv 0$.

36

37 Figure S2

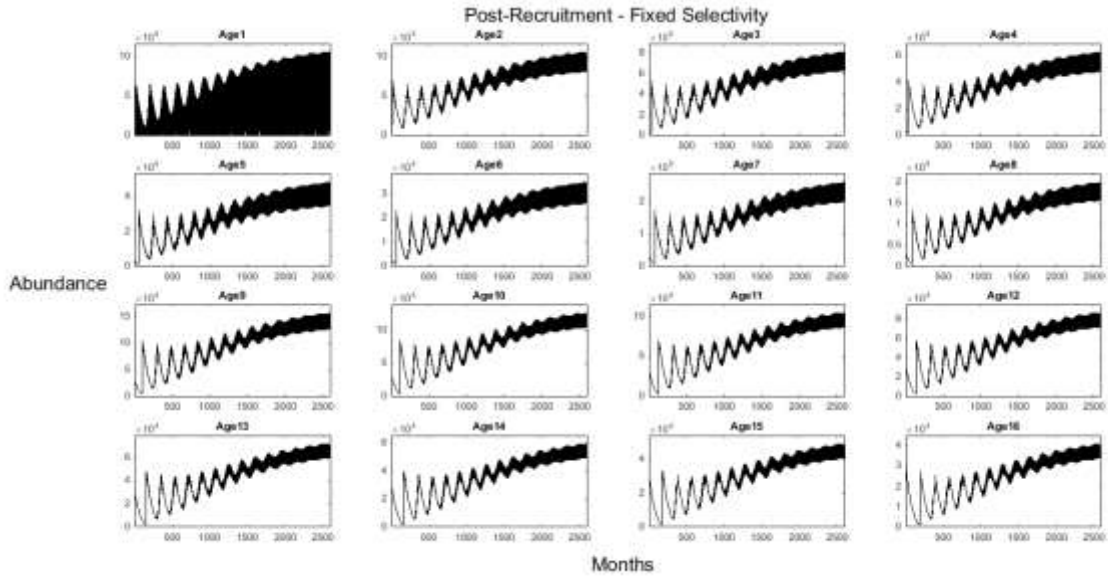


38

39 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
40 corresponding to red lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)} \equiv 0$.

41

42 Figure S3

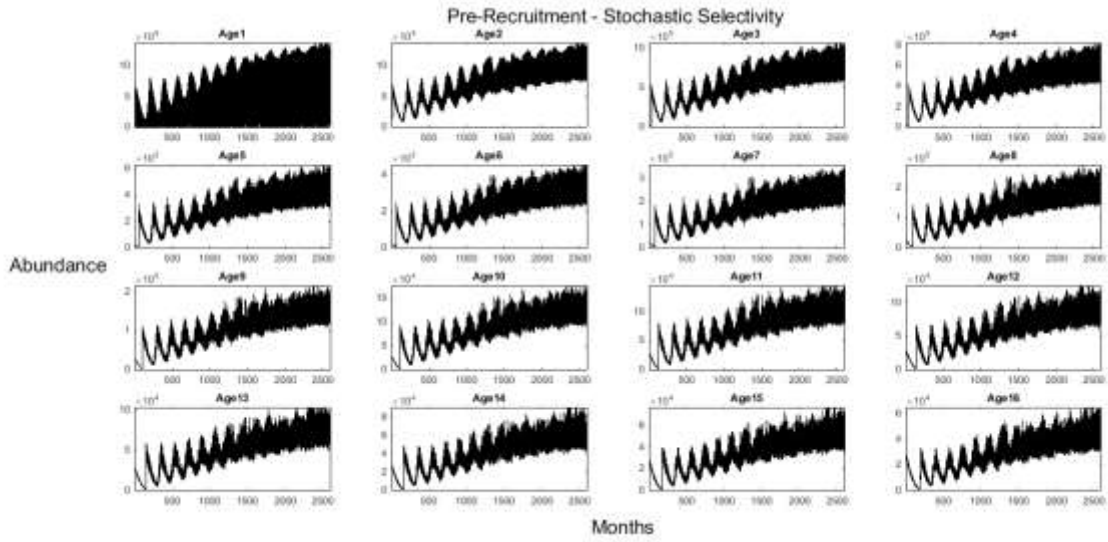


43

44 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
45 corresponding to green lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)} \equiv 0$.

46

47 Figure S4

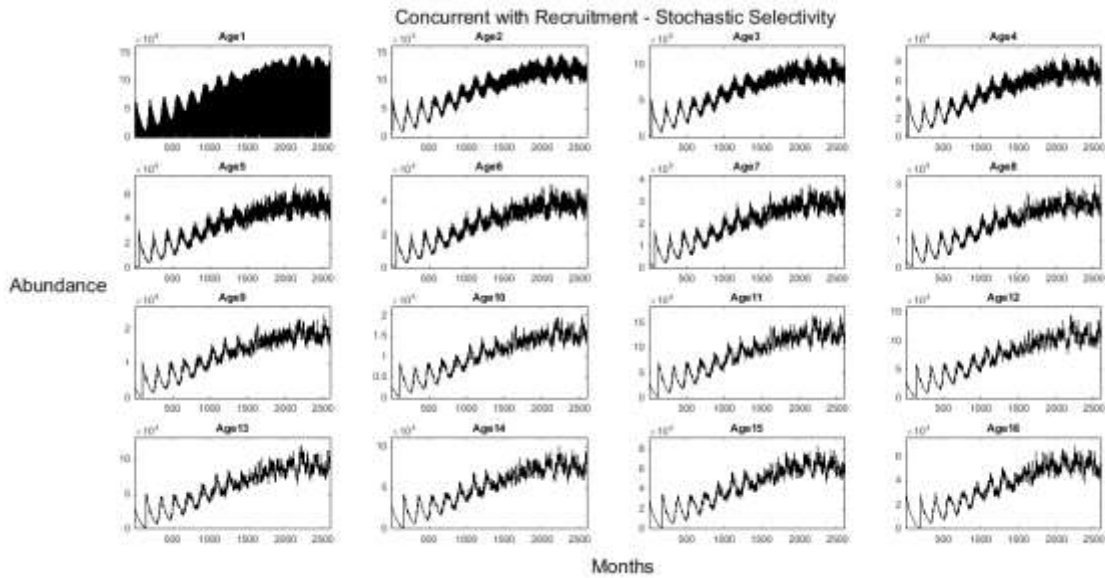


48

49 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
50 corresponding to blue lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)}$ are
51 assumed to be drawn from a truncated normal distribution so that $\varepsilon_{p(a)} > 0$.

52

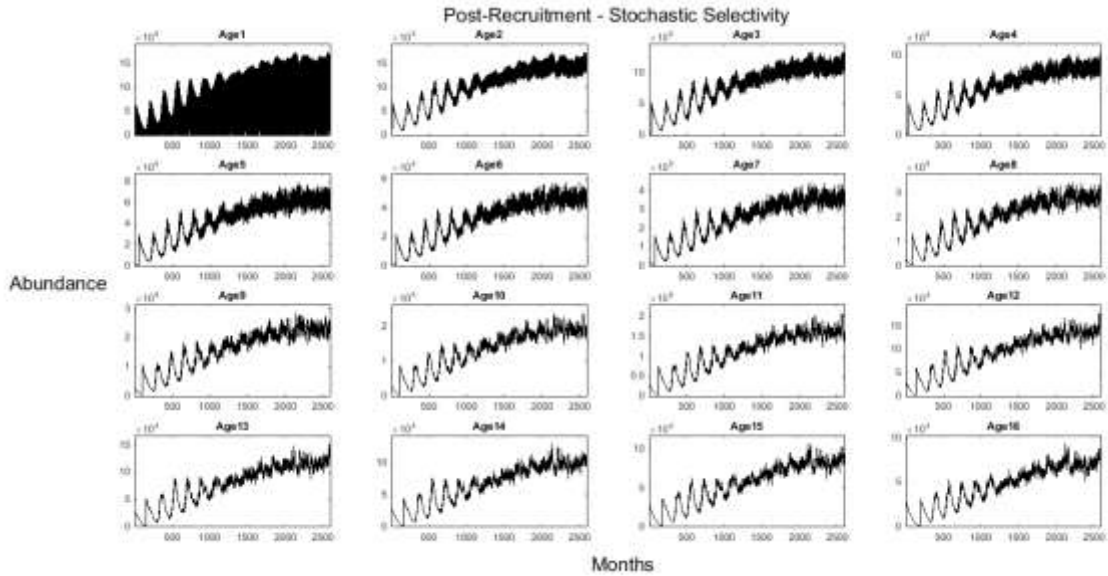
53 Figure S5



54

55 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
56 corresponding to red lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)}$ are
57 assumed to be drawn from a truncated normal distribution so that $\varepsilon_{p(a)} > 0$.
58

59 Figure S6



60

61 Figure shows abundance over 2000 months for all 30 simulated runs for pre-recruitment harvest,
62 corresponding to green lines in Figure 3, and fixed selectivity assumptions, where $\varepsilon_{p(a)}$ are
63 assumed to be drawn from a truncated normal distribution so that $\varepsilon_{p(a)} > 0$.
64