**THE IMPACT OF BIAS IN LENGTH FREQUENCY DATA
ON AN AGE-STRUCTURED FISHERIES
STOCK ASSESSMENT MODEL**

by:

Eliza C. Heery

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements
for the degree of

Master in Science
In
Fisheries and Wildlife Sciences

James M. Berkson
Brian R. Murphy
Michael H. Prager

April 25, 2007
Blacksburg, Virginia

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(ABSTRACT)

Statistical age-structured models are widely used in fisheries stock assessment.
These models have been become increasingly complex over recent decades, allowing
them to incorporate a larger variety of fisheries data. These typically include information
regarding annual fishery yields, indices of abundance and catch composition data, which
reflect the distribution of ages in the harvested population each year. In some fisheries,
age composition can be determined annually through the examination of annuli on hard
parts, such as otoliths or scales. These methods are, however, costly, time consuming
and require a relatively high level of expertise on the part of data collectors.
Alternatively, length frequency distributions within the annual catch are relatively simple
and inexpensive to acquire, and can be employed to extrapolate age structure given that
some information regarding age length relationships in the population is known. This
type of data is therefore critical for many age-structured fisheries models.

Length frequency data are compiled from length measurements of a sub-sample
of the commercial catch. Even when they derive from a relatively large sample size,
however, these data depend on a number of biological, economic and logistical factors.
In some fisheries, for example, larger, more valuable fish may be separated from the
overall catch and sold quickly, before port samplers have chance to gather sub-samples
(Burns et al. 1983). This can reduce the relative frequency of large individuals in length

frequency data. Alternatively, fish may become stratified in holding bins or storage containers according to size, due to their slippery texture and body shape (Hilborn and Walters 1992). With smaller, shorter individuals falling to the bottom where they are less likely to be picked up and measured, length frequency data may contain a disproportionately high frequency of large fish.

This study used simulations to examine the impact of these two types of bias in length frequency data on a statistical age-structured model. The model, which was similar to those used in stock assessments for black sea bass (*Centropristis striata*) and gag (*Mycteroperca microlepis*) in the southeastern United States, produced erroneous population estimates when given biased data. Length frequency data that contained too many small fish caused stock status estimates to became overly pessimistic, indicating that populations were more heavily depleted than was actually the case. This type of bias supported overly conservative management measures, which posed an unnecessary cost to fishermen. Conversely, when the data included too many large fish, estimates of stock status were overly optimistic, and supported management actions that did not effectively protect the stock from overfishing. These results indicate that the quantity of length frequency data alone does not protect against bias when using complex age-structured models. The likelihood and magnitude of bias in these must also be examined in order to determine whether results are likely to be biased. For a given fishery, it is therefore critical that potential sources of bias in length frequency data be thoroughly inspected, and that the modeling approach used to assess the stock be appropriate based on the availability and accuracy of the data.

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Introduction

Length frequency data play an important role in marine fisheries stock assessment models, particularly in age-structured techniques, where they are frequently employed as auxiliary information during the model fitting process. Length frequency distributions are compiled from measurements of sub-sampled individuals in the catch or from fishery-independent surveys, and are relatively inexpensive to collect. There are a number of biological, economic and logistical factors, however, that can cause length frequency data to contain nonrandom errors. When applied to age-structured models during the assessment process, such errors may have a considerable effect on estimates of a population's dynamics and status. This study explores the role of length frequency data in age-structured fisheries stock assessment models. After presenting the collection processes and general use of length compositions, it reviews the development of age-structured models in fisheries and explores current statistical age-structured analyses in greater depth. Possible sources of bias in length frequency data are also considered and their potential impact on statistical age-structured models and biological reference points for management is then discussed.

Length frequency data in marine fisheries

Length measurements provide one of the most common forms of data for fisheries research, as they are relatively simple and inexpensive to collect (Quinn and Deriso 1999). There are several standardized measurements of fish length, including the total

length (TL), fork length (FL) and standard length (SL) (Sparre and Venema 1998). Length data are sorted into bins of a specified interval to produce length compositions, or length frequency distributions, for each fishery, year, or gear type (Figure 2.1).

For the purposes of stock assessment, length measurements may be compiled from several different sources. Fishery-dependent length frequency data are those derived from sub-samples of the total catch and assumed to reflect the distribution of lengths among fish that are selected by the fishing gears. Length compositions from biological field surveys are a form of fishery-independent data, and may also be used as auxiliary information for stock assessments.

Length frequency distributions serve several purposes in stock assessment. Shifts in length composition of a fished population over time often reflect trends in the intensity of harvest (Hilborn and Walters 1992). These trends can be examined qualitatively to provide general and preliminary information on the dynamics of a stock (Asila & Ogari 1988; Froese and Binohlan 2003). Basic quantitative techniques can also be applied to length frequency data to produce an initial evaluation of stock status (Froese and Binohlan 2000). For example, Beverton and Holt (1956) used mean measured sizes to estimate fishing mortality rates, and this method was subsequently expanded by Ault and Ehrhardt (1991). When more thorough assessment methods are possible, however, length compositions can be used in conjunction with several other forms of data to generate quantitative indicators for management.

Length composition data can be used directly as inputs for size-structured stock assessment models. These techniques are often complex and computationally difficult, however, particularly in calculations relating to growth (Quinn and Deriso 1999). Age-

structured models, which require the conversion of lengths to age data, are therefore more commonly used. (Sparre and Venema 1998). The relationship between age and length has been thoroughly studied for this reason, and is presented below.

Age length relationships

Length and age are correlated throughout the life of individual fish due to the fact that fish growth is indeterminate. Growth models, which were first developed by Putter (1920), are thus a useful foundation for quantitative comparisons of length and age. Fish growth is most commonly modeled according to an equation put forth by von Bertalanffy (1934). The model expresses length (L) as a function of age (t) (Gulland 1983):

$$L(t) = L_\infty \left[1 - e^{-\kappa(t-t0)}\right]$$

(1.1)

where L_∞ represents the maximum length, or the asymptotic length and κ is the growth coefficient, which determines how quickly the individual reaches maximum length. t_0 is the age of the individual when its theoretcial length is zero. The von Bertalanffy growth model is based on the observation that an individual's growth rate decreases with age (Quinn and Deriso 1999) and has been shown to fit observed data for most fish relatively well (Sparre and Venema 1998).

Estimation of the parameters, κ, t_0 and L_∞, can be carried out in a number of different ways when age data and length compositions are available. Methods have been presented by von Bertalanffy (1934), Ford (1933) Gulland and Holt (1959) and Chapman (1961). An age length key, which expresses the percentage or fractional age-frequency distribution for each length class of a stock, may then be derived from the parameterized model. Age validation is critical, however, to ensure that the estimated age length

relationship is accurate (Beamish and McFarlane 1983). Variations in growth within a

single species over time and across its range require that age length keys be generated

periodically for each geographically defined population. In some fisheries, the

relationship is reexamined annually, as yearly or seasonal variations in fishing methods

and data collection may influence growth as well (Sparre and Venema 1998).

Since it is not always possible to determine the age of fish experimentally,

mathematical and graphical approaches have also been developed that break down length

compositions into separate age groups, or cohorts. Some of the earliest graphical

methods for converting length compositions to ages were presented by Harding (1949)

and Tanaka (1956) and separated modes within the length composition of the entire

population as a series of normal distributions. Similarly, a method developed by

Bhattacharya (1967) was based on the linear relationship between successive points, or

frequencies on the normal curve for each cohort:

$$ln \, (f_i \, / \, f_{i+1}) \; = \; a \; - \; b \, l_i \qquad\qquad (1.2)$$

where l_i is the length of group i and f_i represents the frequency of l_i. By plotting $ln(f_i/f_{i+1})$ against l_i, one could identify modes in the length frequency distribution as points

that fell in a straight line. Estimates of the parameters a and b could then be derived from

the linear relationship and used to estimate the mean (μ) and variance (σ^2) for that age-

class:

$$\mu = d/2 + a/b \qquad\qquad (1.3)$$

$$\sigma = 1/b - d^2/b^2 \qquad\qquad (1.4)$$

where d is the width of the length interval (Bhattacharya 1967). This method was

adapted by Pauly and Caddy (1985) for analyses with the use of calculators.

A number of more complex mathematical approaches for length frequency

analysis (LFA) can also be used to develop age length keys when age data are limited.

Modes in the length composition have been identified through a maximum likelihood

approach (Hasselblad 1966; MacDonald and Pitcher 1979). Alternatively, based on

given information for the smallest and largest modes, Schnute and Fournier (1980) used a

modified version of the von Bertalanffy curve to determine the position of each age

group. Furthermore, length compositions can be analyzed through a "smoothing"

technique, by which observed frequencies were compared to a running average of 5

previous points (Pauly and David 1981). This method is the basis for the Visual Basic

program ELEFAN. A more thorough discussion of the different approaches for length

frequency analysis is available from MacDonald (1987).

Age-structured population models

When age compositions can be effectively derived from length frequency data,

they enable the use of age-structured stock assessment models. These models reconstruct

the dynamics of fish populations over time, and produce estimates of mortality and

abundance that reflect the status of the stock and its response to fishing pressure. As

such, they are useful for the assessment of marine fish stocks and have been developed

extensively for the purposes of fisheries management.

Perhaps the earliest work on age-structured population dynamics was that of

Soviet scientists in the early 1900s, who estimated the average age composition of

sturgeon (*Acipenser fulvescens*) from multiple years of age and catch data (Ricker 1971).

A similar method was used many years later by Fry (1949) for populations of lake trout

(*Salvelinus namaycush*), and incorporated annual age composition data rather than averages over the time series (Megrey 1989). Fry (1949) modeled each cohort as a "virtual population," in that it experienced no natural mortality, and was estimated for each year through a back-calculation procedure known as virtual population analysis (VPA) (Quinn and Deriso 1999). Fry's approach was later expanded to include a natural mortality term by Beverton and Holt (1954) and Paloheimo (1958).

Building on these developments, Gulland (1965) incorporated the catch equation from Baranov (1918) into a VPA for Arctic cod (*Gadus morhua*). Gulland's method was based on the following equations (Gulland 1965):

$$C_a = N_a * (F_a / F_a + M) * (1 - e^{-(F_a + M)})$$ (1.5)

$$N_{a+1} = N_a \, e^{-(F_a + M)}$$ (1.6)

where, for each year, N_a is the population at age, F_a is the fishing mortality rate at age and M is the natural mortality rate. Back-calculation of the equations began with the terminal abundance, or the population size of the oldest cohort. By assuming values for the natural mortality and the oldest cohort's fishing mortality rate, terminal abundance could be calculated through the catch equation as N_a. This value was then used to back-calculate abundance across progressively younger cohorts (Gulland 1965).

Gulland (1965) was able to obtain estimates of F_a for each previous year by substituting N_a into the previous year's catch equation. A similar approach presented by Murphy (1965) compared catches from two successive years for the same cohort. Ratios of the catch, defined as in the above formula, were compiled to produce a system of equations that was density-independent (Murphy 1965). In both methods, the catch equations had to be solved in iterations, which was computationally arduous.

Furthermore, with no analytical solution for F_a, it is difficult to examine the impact of initial values for mortality on the results of the models. For these reasons, Pope (1972) developed a simplified method for VPA called cohort analysis, which used an approximation to solve for F_a. The approximation made the assumption that catch, as it was defined by Gulland (1965), occured half-way through the year for every cohort. The approximate formula and the resulting equation for F_a are as follows (Pope 1972):

$$N_a = C_a \, e^{(M/2)} + N_{a+1} \, e^{(M)}$$
(1.7)

$$F_a = ln(N_a \, / \, N_{a+1}) - M$$
(1.8)

Pope's method was very similar to VPA in that the abundance and, consequently, the fishing mortality rate, were estimated through a back-calculation. N_a and F_a estimates were shown to be less sensitive to initial values for fishing mortality as the back-calculation proceeded (Pope 1972). Cohort analysis was thus established as a relatively robust tool for considering past trends in age-structured populations (Quinn and Deriso 1999). The model was, however, highly sensitive to chosen values for the natural mortality (Agger et al. 1973; Sims 1984; Sampson 1988; Hilden 1988; Lapointe et al. 1989). It also assumed that catch-at-age data were without error, which was not always practical. Erroneous catch data were shown to have a considerable affect on the model's results (Ulltang 1977; Sims 1982b; Rivard 1989).

Although back-calculations had the notable advantage of producing progressively smaller errors, forward analysis of age structured populations was also possible (Murphy 1965; Sims 1982a). Forward-calculating techniques also assumed available catch-at-age data without error. The forward calculation for abundance-at-age was performed through the following equation:

$$N_a = N_r \, e^{-(a-r)M} - \sum C_x \, e^{-[a-(x+1/2)]M} \qquad (1.9)$$

This formulation assumed that fishing and natural mortality rates were constant for each

time step (Quinn and Deriso 1999). According to the term $(x + \frac{1}{2})$, catch was

incorporated at the halfway point of each year. A subsequent approach from Hearn et al.

(1987) allowed for catch at different times throughout each annual time step.

Although forward and back-calculating techniques were originally based on

catch-at-age data alone, a number of "tuning" methods have been applied to VPA in

order to incorporate auxiliary information. Many of the methods require *ad hoc*

algorithms that have no formal statistical basis (Patterson and Kirkwood 1995). One such

approach, which has been applied extensively to incorporate information on the fishing

effort, was presented by Laurec and Shepherd (1983). The Laurec-Shepherd method can

be used to generate estimates of fishing mortality rates for incomplete cohorts at the end

of a time series (Laurec and Shepherd 1983). It utilizes a catchability coefficient (q),

which is the ratio of fishing mortality to effort (Darby and Flatman 1994):

$$q_{y,a} = F_{y,a} / E_y \qquad (1.10)$$

Tuning of the model is carried out in iterations. For each time step, catchability-at-age is

assumed constant and is estimated as the geometric mean of q_a over prior years. The

estimates are then multiplied by effort to derive fishing mortality rates across each cohort

in the final year. Terminal fishing mortality is assumed to be proportional to the average

F of younger age-classes. Values for the terminal F are determined and then used for the

next iteration until a stable solution is found (Laurec and Shepherd 1983; Darby and

Flatman 1994). The Laurec-Shepherd method has been shown to perform effectively

with simulated data and has been applied widely (Pope and Shepherd 1985). There has

been very little work, however, to justify or validate the technique theoretically (Quinn and Deriso 1999).

A number of more formal statistical tuning methods have been developed concurrently to these iterative procedures. Some of the earliest statistical techniques used a least-squares approach to estimate the terminal fishing mortality (Parks 1976; Doubleday 1981). These techniques were expanded upon by Gavaris (1988), who presented an adaptive framework for virtual population analysis in a computer program called ADAPT. The method assumes that there is error only in auxiliary CPUE data, which are required as indices of abundance (I'). The indices are related linearly to back-calculated estimates of abundance in the model (Gavaris 1988):

$$I'_{i,a,x} = q_{0,i,a} + q_{1,i,a}\ N_{a,x} + \varepsilon \qquad (1.11)$$

where i represents the index, x is the survey year, and q_0 and q_1 are the calibration coefficients. Values for the calibration coefficients are determined by minimizing a weighted sum of squares term based on the above equation (Gavaris 1988). Terminal fishing mortality can also be estimated in this process, but is often derived indirectly or in iterations by assuming a structure for its distribution (Quinn and Deriso 1999).

While ADAPT has been modified and enhanced for specific applications in fisheries (Conser and Powers 1989; Conser 1993), it maintains the assumption that catch data are without error. Statistical catch-at-age methods, developed by Fournier and Archibald (1982) and Deriso et al. (1985), incorporated additional sources of data and allowed for observed error in the catch-at-age. In order to reduce the number of parameters, these models used a separability assumption, which defined fishing mortality

through two components: an age-dependent coefficient for gear selectivity and a time-dependent exploitation fraction (Doubleday 1976; Pope and Shepherd 1982):

$$F_{ay} = S_a \; q \; E_y \qquad (1.12)$$

The selectivity, S_a, catchability coefficient (q_a) and exploitation level, E_y, could be substituted directly for fishing mortality in the catch equation. They could then be estimated with the use of fishing effort data, thus eliminating the need to determine fishing mortality rates for each cohort, and reducing the number of parameters considerably (Pope and Shepherd 1982).

The generalized mathematical models presented by Fournier and Archibald (1982) and Deriso et al. (1985) were more flexible than previous approaches in terms of the number of parameters they could incoporate (Megrey 1989). These included values for the population abundance by age and year, the annual recruitment and the catchability, which defined the proportional relationship of fishing mortality to fishing intensity, or effort. Model parameters for the annual fishing intensity were defined either by annual rates of fishing mortality (Deriso et al. 1985) or annual deviations from an overall mean F (Fournier and Archibald 1982). Gear selectivity could also be incorporated, through selectivity parameters for each age or parameters that described the selectivity trend across all age classes (Fournier and Archibald 1982).

The flexibility of statistical age-structured models was advantageous in that it allowed for a variety of different forms of data and error structures to be used in the fitting process. And yet, with greater flexibility came the risk of over-parameterization relative to the information provided by data available from the fishery. With too many specified parameters and insufficient data, the models converged poorly or produced

unrealistic estimates (Megrey 1989). Fournier and Archibald (1982), for example, were unable to get stable parameter estimates when they used separate selectivity parameters for each age group. Only upon reducing the number of selectivity parameters did the model converge to produce stable estimates defining the selectivity trend in the expected population (Megrey 1989).

The statistical methods employed by Fournier and Archibald (1982) and Deriso et al. (1985) have several advantages. In addition to their increased flexibility, statistical age-structured models allow for parameters to be estimated with confidence intervals and can be combined with a Bayesian framework to account for high levels of uncertainty (Fournier et al. 1998). The generality of these models also allows fisheries biologists to explore those forms of error and data that constitute the "best" model structure for a given fishery. By comparing the objective function of the proposed model structure with that of another model in iterations, the analyst can select a method most appropriate for the stock of interest (Megrey 1989).

The development of high-speed computing resources has enabled more complex statistical techniques to become commonplace in fisheries stock assessment (Megrey 1989). One of the most widely used computing tools called Stock Synthesis was presented by Methot (1989, 1990) and adapted earlier statistical age-structured techniques of Fournier and Archibald (1982), Deriso et al. (1985) and others. Stock Synthesis provides several advantages for fisheries stock assessment. The program is capable of incorporating large amounts of data and a variety of different data types, and allows for a highly flexible model structure (Helu et al. 2000). And yet, erroneous model assumptions and input data have been shown to influence Stock Synthesis estimates

considerably (Sinclair et al. 1991; Bence et al. 1993; Sampson 1993; Chen 1996; Hightower 1996; Crone and Sampson 1998; Sampson and Yin 1998; Chen 2003; Yin and Sampson 2004). In addition, the model performs best when a long time series of data are available (Yin and Sampson 2004) and when an appropriate error structure is assigned to each data set (Bence et al. 1993; Sampson and Yin 1998; Helu et al. 2000).

As software packages and the statistical age-structured models they employ grow ever more advanced, there are ongoing questions regarding the level of complexity that is actually useful for stock assessments (Ludwig and Walters 1985, Richards and Schnute 1998, Cotter et al. 2004). Statistical age-structured models are currently applied in fisheries to estimate hundreds of parameters and determine quantitative indicators for management. Based on a range of different sources of data from multiple gear types, collection sources and time periods, the behavior of these parameters can be unidentifiable and unpredictable at times, requiring that additional model constraints or data be supplied.

Statistical age-structured models in fisheries stock assessment

Statistical age-structured models are used in stock assessments for a range of different species, including pelagic tunas (Fournier et al. 1990; Fournier et al. 1998; Hampton and Fournier 2001), groundfish (Helser et al. 2002; Dorn et al. 2003) several anadromous fish (Gibson and Myers 2003; Savereide and Quinn 2004) and others. Although their structure varies widely, these methods reconstruct the demographic history of a population based on observed trends in the catch composition and harvest. Through forward projection, statistical age-structured models simulate a population

through time based on a number of biological and harvest-related parameters. The

model's parameters are then altered systematically until expected data match those

observed in the fishery.

Statistical age-structured models typically calculate and project expected

populations forward through time based on a series of common equations, many of which

are derived from earlier age-structured techniques. The separability assumption is

applied to compute fishing mortality from an age-dependent coefficient for gear

selectivity and a time-dependent exploitation fraction (Doubleday 1976; Pope and

Shepherd 1982). The total mortality is calculated as the sum of the fishing mortality and

natural mortality in each age class annually.

The von Bertalanffy growth model is commonly used to estimate the mean

length-at-age in statistical catch-at-age models. From these estimates, weight-at-age is

then derived through the weight-length power relationship:

$$W = a\,L^b \tag{1.13}$$

where a is the scaling constant and b is the allometric growth parameter.

Similar to earlier forward calculations of annual population size and catch,

numbers-at-age and catch-at-age are often determined through exponential decay

calculations and the Baranov catch equation. The exponential decay of cohorts predicts

the population in each age class based on the survival in each cohort from the previous

year:

$$N_{a,y} = N_{a-1,\,y-1}\ e^{-(F_{a-1,\,y-1} + M)} \tag{1.14}$$

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where $F_{a-1,y-1}$ is the fishing mortality rate in the previous year and cohort, and M is the

constant natural mortality rate. The Baranov catch equation estimates catch-at-age as a

function of the population size, fishing mortality and total mortality rate:

$$C_{a,y} = (F_{a,y} / Z_{a,y})\, N_{a,y}\, (1 - e^{-Z_{a,y}})$$

where $Z_{a,y}$ is the total mortality-at-age in year y. $\hspace{4cm}$ (1.15)

Recruitment is commonly modeled according to methods put forth by Beverton

and Holt (1957). The Beverton-Holt recruitment model is a hyperbolic function relating

recruitment to spawning stock. In is most basic form, the model states:

$$R = aS / b + S \hspace{4cm} (1.16)$$

where R is the number of recruits entering the population. S is the spawning stock, a is

the maximum number of recruits produced and b is the spawning stock needed to produce

a recruitment of $a/2$ (Hilborn and Walters 1992). The Beverton-Holt relationship is

density-dependent, with recruitment approaching an asymptote as the spawning stock

size increases and reduces the availability of resources necessary for larval and juvenile

survival (Gulland 1983).

A re-parameterized stock Beverton-Holt equation was presented by Francis

(1992) such that the function's parameters became more biologically relevant. By

assuming that the virgin (unfished) population has attained a stable age distribution, the

stock-recruitment relationship can be redefined according to a curve steepness parameter,

h, and virgin recruitment, R_0, and biomass, B_0. The Beverton-Holt equation is then

defined as:

$$R = S / \alpha + \beta S \hspace{4cm} (1.17)$$

where $\alpha = B_0(1–h) / 4hR_0$ and $\beta = 5h–1 / 4hR_0$. These calculations can also be carried out

using the calculated spawner biomass per recruit rather than the virgin biomass (Francis

1992).

Recruitment is also affected by the maturity and fecundity of the stock. The

number of cohorts contributing to reproduction is determined by the age of sexual

maturity. Similarly, variations in the fecundity across age classes will affect the relative

contribution of each sexually mature cohort to recruitment. These factors are

incorporated into estimates of spawning stock biomass (SSB) by relating ages of maturity

and fecundity rates to the age composition of the stock. These estimates are then used

interchangeably with spawning stock size (S) in equations 1.16 and 1.17 to compute

values for the recruitment for given year.

Biological benchmarks and stock status indicators – Statistical age-structured models are

often used to estimate several biological benchmarks, which provide the basis for

fisheries management in the United States (Rose and Cowan 2003). These benchmarks

are based on the theoretical relationship between the long term fishing mortality rate (F)

and sustainable fishery yield (Y), which follows a dome-shaped trend as the level of F

increases (Graham 1935; Schaefer 1954, 1957). The relationship reaches an equilibrium

at the dome's peak, where the yield is at its maximum value and the rate of change in Y is

equal to zero. This point is defined as the maximum sustainable yield (MSY), as it

represents the largest yield that can be sustained over an indefinite period of time,

without inhibiting the renewability of the fishery resource (Caddy and Mahon 1995). The

fishing mortality rate that produces this maximum yield is denoted F_{MSY}. Similarly, B_{MSY}

is the spawner biomass that produces MSY when fishing levels remain at F_{MSY} (Gulland and Boerema 1973; Sissenwine and Shepherd 1987; Goodyear 1993).

Although the theoretical relationship that was originally used to define MSY, F_{MSY} and B_{MSY} omitted age structure, similar terms can be estimated for age-structured populations through a yield per recruit analysis (Thompson and Bell 1934; Beverton and Holt 1957). Analyses of the yield per recruit incorporate information from the stock-recruitment relationship to estimate the yield potential of a stock. In the Beverton-Holt yield per recruit model, all members of a cohort are assumed to enter the fishery (become vulnerable to fishing) at the same age (t_c), following "knife-edge selectivity" (Beverton and Holt 1957). The fishing mortality rate is also assumed to remain constant across all age classes greater than t_c (Quinn and Deriso 1999). Year class abundance is thus defined by the exponential decay equation:

$$N(t) = \begin{cases} Re^{-M(t-t_r)} & \text{for } t < t_c \\ Re^{-M(t_c-t_r)}e^{-Z(t-t_c)} & \text{for } t \geq t_c \end{cases} \qquad (1.18)$$

where t_r is the age of new recruits to the population, R is the recruitment, or abundance in the youngest cohort, M is the natural mortality rate and Z is the total mortality rate, computed as the sum of M and F (Quinn and Deriso 1999). By assuming that fishery yield is proportional to the population abundance, the rate of increase in yield per recruit as F increases can be calculated as:

$$Y(t) = \int_{t_c}^{t} FN(x)W(x)dx = FRe^{-M(t_c-t_r)}\int_{t_c}^{t} e^{-Z(x-t_c)}W(x)dx \qquad (1.19)$$

where $W(x)$ is the average weight in each age class (Quinn and Deriso 1999). The maximum yield per recruit is computed as the point at which the derivative of $Y(t)$ is

equal to zero. F_{max} is defined as the fishing mortality rate that produces the maximum

yield per recruit value (Caddy and Mahon 1995). This term is greater than F_{MSY} in most

cases (Quinn and Deriso 1999), and several more conservative benchmarks have been

developed for the Beverton-Holt model, since F_{max} led to over-harvesting in some

fisheries (Gulland and Boerema 1973; Anthony 1982; Doubleday et al. 1984).

      Shepherd (1982) presented an approach that incorporated a spawner biomass per

recruit analysis into the yield per recruit procedure to estimate the benchmarks MSY,

F_{MSY} and B_{MSY}. The spawner biomass per recruit model determined the rate at which

recruits produce spawners as a function of the fishing mortality rate (Shepherd 1982).

Shepherd (1982) used a replacement line, computed from the spawner biomass per recruit

at all possible values of *F*, to define the survivorship needed to replace the spawning

stock (Sissenwine and Shepherd 1987). By comparing this line with the stock-

recruitment relationship estimated for the population, an equilibrium point could be

determined, providing values for MSY, F_{MSY} and B_{MSY} (Shepherd 1982). Shepherd's

(1982) approach can be applied in statistical age-structured models, with equilibrium

points estimated either through derivative calculations or approximation techniques, in

which per recruit calculations are made for a range of *F* values (Sissenwine and Shepherd

1987; Mace and Sissenwine 1993).

      The benchmarks computed through yield per recruit and spawner biomass per

recruit analyses are essential for fisheries management, as they provide key information

on the status of fish stocks and necessary management actions. In accordance with the

Magnuson Stevens Fisheries Management and Conservation Act of 1976 (MSFMCA),

F_{MSY} and B_{MSY} estimates are used to specify an MSY control rule when available

(Restrepo et al. 1998). Control rules are quantitative functions that describe how fishing

levels should change in relation to spawning stock biomass (Katsukawa 2004). They

represent planned harvest strategies that are anticipated to result in yields close to MSY

over the long term. While federal law encourages fisheries managers to select control

rules that are consistent with the management techniques and characteristics of each

fishery (Restrepo and Powers 1999), Restrepo et al. (1998) recommended the following

form be used as a precautionary default control rule:

$$F(B) = \frac{F_{MSY} B}{cB_{MSY}} \qquad \text{for all } B \leq cB_{MSY} \qquad (1.20)$$

$$F(B) = F_{MSY} \qquad \text{for all } B > cB_{MSY} \qquad (1.21)$$

where B the spawning stock biomass and $F(B)$ is the fishing mortality rate that should

occur at B. The factor c in these equations reflects the extent to which the stock is

expected to fluctuate naturally above and below B_{MSY} if fishing is held at F_{MSY} over time

(Restrepo et al. 1998). Since these fluctuations should depend on the level of mortality

that occurs naturally in the stock, c is often defined based on the survival rate after

natural mortality (M), or 1-M. Federal management guidelines require, however, that the

term be no less than ½, and c is therefore specified as ½ when this value is greater than 1-

M (Restrepo et al. 1998).

Control rules are important because they provide definitions for two key

thresholds, or limits, for fisheries management. The maximum fishing mortality

threshold (MFMT) is the fishing level necessary to maintain a stock within a safe range,

and is equivalent to $F(B)$ in equations 1.20 and 1.21. Similarly, the minimum spawning

stock threshold (MSST) is the spawning stock biomass that is needed to produce long

term average yields close to MSY, and is defined in the above control rule as cB_{MSY} (Restrepo et al. 1998). These limits provide the criteria for determining the status of marine fish stocks. When a stock is fished at a rate that exceeds MFMT, it is said to be undergoing "overfishing." When its spawning stock biomass is estimated to fall below MSST, the stock is identified as "overfished" (Restrepo et al. 1998). In both cases, fisheries managers must respond accordingly by enacting more stringent fishing restrictions or constructing a rebuilding plan that aims at rebuilding the population above B_{MSY} (MSFMCA 1976; Powers 1999). In order for fish stocks to be adequately protected and for the objectives of fisheries management to be achieved, the accuracy of these estimates is therefore critical (Rose and Cowan 2003).

Observed data – Statistical age-structured models typically use either a least squares (Doubleday 1976; Deriso et al. 1985; Kimura 1989) or a maximum likelihood method (Fournier and Archibald 1982; Methot 1989) to fit expected data to those observed in the fishery. Although these two estimation techniques often assume distinct error structures for the data, they can both be used to fit data with lognormal or multinomal error structures (Kimura 1990). Methot (1990) presented multinomial error structure as the preferred form, as it most appropriately represented variation in catch-at-age estimates. This was supported further by results from Crone and Sampson (1998), which showed that multinomial error more closely followed variation in catch-at-age data for Oregon groundfish than a lognormally distributed error structure.

Three forms of data are generally used in the fitting process: landed catch (or removals), abundance indices and catch composition. In a study that compared the

relative importance of various forms of fisheries data to model estimates, Shepherd (1984) ranked recorded landings among the most informative for population assessments. Landed catch data can be produced from log books or from surveys of the catch (Williams 1977). Unless they are adjusted to account for discarding or sampling error, fishery landings used in age-structured models are assumed to represent the total biomass of fish harvested.

Indices of abundance were characterized by Deriso et al. (1985) as a critical form of data for population biomass estimates. They are most commonly available in the form of catch-per-unit-effort (CPUE) data (Gavaris 1980), but can also be computed from mark-recapture information (Seber 1982), trawl surveys (Doubleday and Rivard 1981), acoustic surveys (Johannesson and Mitson 1983) or other sources. Expected abundance indices are mathematically defined as a fixed proportion of the total annual abundance in the expected population:

$$I_t = q\, B_t$$
(1.22)

where I_t is the annual abundance index, B_t is the expected biomass and q is the catchability coefficient.

Catch composition information reflects age- or length-structure within the harvested population for each year. Unlike earlier ad hoc methods, statistical age-structured models can incorporate any combination of age composition and length frequency data from fishery-dependent and independent sources (Hilborn et al. 2001). Nonrandom errors in these data, particularly in length frequency data, may cause considerable bias and imprecision in statistical age-structured model results. Potential sources of systematic error in length compositions are examined in the following section.

Sources of bias in length frequency data

In a statistical context, bias is defined as the difference between the expected value of a statistic and the value of a population parameter (Kotz and Johnson 1982). For example, suppose a statistic Z is used to estimate a parameter λ. The expectation of Z is represented as:

$$E_\lambda(Z) = \lambda + b(\lambda) \tag{1.23}$$

where the quantity $b(\lambda)$ is the bias of the statistic Z. Bias is thus defined mathematically by the following equation:

$$b(\lambda) = E_\lambda(Z) - \lambda \tag{1.24}$$

When $b(\lambda) = 0$, the statistic Z, is an unbiased estimator of λ (Kotz and Johnson 1982).

Although samples inevitably contain some level of random error, bias is a result of systematic error, or consistent variations from the true values of the population. Systematic error can occur when the selection or measurement of samples is nonrandom. The impact of length frequency data that are affected by systematic error on age-structured fisheries stock assessments is unclear, as it has not been previously explored. This study will therefore examine the affect of biased length frequencies on the parameters and outputs of a statistical age-structured model.

Several aspects of the data collection process in fisheries can result in systemic error within length frequency data. Hilborn and Walters (1992) identify three main issues affecting the random collection of length data to be gear selectivity, changes in a population's size distribution, and problems with subsampling of catch (Hilborn and Walters 1992). These issues are discussed below.

Gear selectivity

As a sampling mechanism, fishing gear is inherently size selective. This is partly due to the morphological characteristics of fish in different size and age classes. For example, longlines target fish with a gape large enough to bite a specific hook size. A net selects for larger fish unable to escape through the dimensions of its mesh.

Selectivity in fishing also originates from the simple fact that fish are mobile. Larger fish that are capable of swimming faster will be less likely to succumb to active gears, such as trawls and purse seines. Behavioral differences between age and size groups of a mobile species can lead to further variations in selectivity across size classes. For example, some age groups may occupy specific areas or microhabitats where they come in contact with a gear type more readily.

Methods to identify and account for gear selectivity have traditionally been based on the principle of geometric similarity, a concept developed by Baranov in 1948 (Hovgård and Lassen 2000). The principle states that the selectivity of different gears is equal when the gears have the same ratio of fish size to mesh size. Writing selectivity(s) as a function of mesh size(m) and fish size or length (z), Baranov concluded:

$$s(z , m) = s(kz , km)$$ (1.25)

where k is any constant (Hovgård and Lassen 2000). This function affectively normalizes the proportional relationship of (z/m) across different gears with the constant k. Baranov used selection curves to illustrate the principle of geometric similarity (Hovgård and Lassen 2000). Depending on the biological characteristics of a fish species and the selective processes that occur when gear is operated, the shape of this normalized

selection curve can be described by a number of statistical distributions (Lewy et al. 2004).

In a sampling program intended to gather representative information on an entire population of fish, issues of gear selectivity that are not adequately accounted for could result in systematic errors in the length-frequency data. Fisheries data used in stock assessments, however, are generally derived from harvest information, which is limited to a size range of fish that is often intentionally selected for by a particular gear type. Length samples are thus expected to represent the length-frequency distribution of selectively caught fish, and not that of the entire population. Because gear selectivity can change over time and can be accounted for in assessments to model the dynamics of harvest (see Chapter 2), it is not considered in this study as a potential source of length frequency bias.

Changes in size distribution

Changes in a population's size distribution across spatial and temporal scales can also affect the way fish lengths in samples relate to actual frequencies in the population. Variation in the lengths of individuals across a geographic area can result from changes in habitat specialization throughout a species' life cycle (Polis 1984; Werner and Gilliam 1984). Many reef fish, for example, begin their life in nursery areas, but move to other locations as juveniles and adults. For other marine fish, especially pelagic long distance swimmers, the spatial range of size frequencies not only varies according to phases in the life cycle, but also seasonally, as adults may migrate to spawning or foraging sites at different times of the year.

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A sample of individuals collected at any given location and time will reflect these inherent variations in the population's size distribution (Methven and Schneider 1998; Gauthier and Rose 2005). For example, samples of reef fish collected mostly from fore-reef areas will suggest the population has higher frequencies of larger fish than is actually the case. A survey conducted in the foraging areas of some pelagic fish during spawning season may reveal a length distribution that only includes small fish that have not yet reached sexual maturity. Systematic errors may thus result from nonrandom sampling or fishing at any one location and season (Hilborn and Walters 1992; Pecquerie et al. 2004). Errors such as these, however, are likely to be less common than those relating to subsampling of fisheries landings.

Representative sampling

The length composition of fishery-dependent data is often estimated by subsampling the overall catch. There are several ways in which problematic subsampling can inaccurately report length composition in catch data. These biases can arise as a result of nonrandom sample selection on the part of the data collector, limited or inconsistent access to fisheries catch, or poor sampling design.

Data collectors, even when well trained and experienced, may unintentionally introduce bias into length frequency data. Some samplers may be drawn to larger fish because of their importance to anglers, producing length frequency data that are skewed towards larger animals. If the data collector seeks a sample of fish from each size class rather than a random sample, the resulting distribution will likely be disproportionate and not reflect the true distribution of the landings.

Biased subsampling may also result if the samples available to data collectors are limited or nonrandom. This may occur when fishermen are uncooperative, only allowing their landings to be sampled at certain times of the year or when a specific size class has been caught. In some fisheries, length frequencies may also be affected by the practice of discarding larger or smaller fish at sea. Unreported discarding can introduce considerable bias into fisheries data (Saila 1983; Sampson 1994), and can occur as a result of a variety of factors. For example, size limits or catch regulations may give fishermen incentive to discard fish of an illegal or restricted size class. On the other hand, highgrading is the process by which fishermen discard smaller, less valuable fish in order to make their overall catch more marketable (Saila 1983). The length frequency data resulting from either of these examples might accurately reflect the size distribution in the landed catch, but not in the entire population that has died as a result of fishing.

The data collected from subsampling are affected by both gear selectivity and variation of size distributions across spatial and temporal scales (Lewy et al. 2004). They become unrepresentative when they are collected in a nonrandom or poorly designed manner. For example, while a fishing event may yield fish of varying length, the different sizes may become stratified as holds or containers are moved about. A data collector measuring random fish from the top of the container may therefore record data with a higher frequency of large fish than in the fished population. Similarly, schooling fish often congregate in groups of similar size and are harvested with gears that capture entire schooling groups at once. If not random, subsampling of these kinds of fishing activities may result in bias towards one size class or another, since catch will often consist of many fish of the same length.

Possible impacts of biased length compositions on assessment models

The impact of erroneous data on statistical age-structured models has been considered in several studies. Schweigert (1998) found that discrepancies in stock trends predicted by an age-structured model and an escapement model for Prince Rupert herring were likely due to bias in the data rather than model misspecification. Limited fall catch-at-age data and possible biases in the spawn index resulted in overestimates of stock abundance from the age-structured model (Schweigert 1998). Similarly, Gavaris and Van Eeckhaute (1998) applied a diagnostic model to investigate possible systematic errors in catch data for Georges Bank haddock. Their findings suggested that nonrandom errors may have resulted in over- and underestimates of population size during certain periods in the model (Gavaris and Van Eeckhaute 1998).

Several studies have examined the effect of sample size and aging error on model estimates and have noted considerable bias in estimates due to these issues (Lai and Gunderson 1987, Bradford 1991). In addition, estimates of sustained yield, which are important for the purposes of fisheries management and policy, were dramatically affected by aging bias and imprecision in a simulation study by Coggins and Quinn (1998).

And yet, while previous studies have considered how statistical age-structured models are affected by bias in other forms of fisheries data, the impact of nonrandom error in length compositions has not been thoroughly examined. Biased length frequency distributions may be anticipated to affect statistical age-structured models in a number of ways. Most notably, the von Bertalanffy parameters detailing the age length relationship

may be most closely related to expected length compositions, and may therefore change

to minimize the difference between observed and expected length frequency data. The

distribution of age within expected catch would likely shift as well based on the age-

composition reflected in observed length frequencies. Also, the parameters for gear

selectivity, which affect the proportion of the population size-at-age that is subjected to

fishing, might change to maintain an estimated population size consistent with those

found in presumably nonbiased abundance indices. Finally, biased age distributions in

the expected population caused by erroneous length frequencies could affect the stock-

recruitment relationship, as annual recruitment would need to be generated from a

proportionally smaller or larger spawning stock, depending on the direction of bias in the

population's age structure. Since yield per recruit analyses used to generate estimates of

MSY, B_{MSY} and F_{MSY} depend heavily on stock-recruitment parameters, estimates for

management benchmarks and relative stock status indicators may also be affected.

These are some of the possible effects of biased length frequency distributions on

statistical age-structured model estimates. A thorough analysis of nonrandom errors in

length compositions is necessary, however, to more definitively identify both the ways in

which.h model estimates are affected and the forms of biased length compositions that

are most problematic for statistical age-structured stock assessments.

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Summary

Length frequency data are an important component of fisheries stock assessment models. However, due to gear selectivity, changes in length distributions, and problems with subsampling, collecting and compiling non-biased information on length can be difficult. While biases may exist in length frequency data for many fisheries, their impact on stock assessments is unclear, and may be substantial. As fisheries models grow more complex and continue to applied in fisheries management, it is important that the potential impact of these biases be identified and considered more thoroughly. Further study of the role of length compositions and the effects of biased length frequency data on forward-projecting age-structured stock assessment methods is therefore critical.

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CHAPTER 2 – THE IMPACT OF BIASED LENGTH FREQUENCY DATA ON MARINE FISHERIES STOCK ASSESSMENT

Abstract

Statistical age-structured models are widely used in fisheries stock assessment, and require several forms of fisheries data. One critical form of data required for many age-structured models comes from length measurements, which are compiled to derive the length frequency distribution across all samples. Although these data are a crucial source of information for many age-structured models, length frequencies may be biased due to a number of biological, economic and logistical factors. In this study, a simulation approach was used to examine the impact of biased length frequency data on statistical age-structured models. Length frequency distributions were first generated without sampling error and used to fit the assessment model. Sampling error was then incorporated to generate data containing two different forms of bias, and model results from these data were compared with those from original "base" runs of the assessment model.

Biases in length frequency data were shown to have a considerable impact on several key indicators of stock status. Data containing too many large fish had the greatest impact on stock status estimates, particularly for long-lived species, and supported regulatory policies that were insufficient to protect stocks from overfishing. For depleted populations, on the other hand, length frequencies that contained too many small fish supported rebuilding plans that did not effectively rebuild stocks. The accuracy of length frequency data is thus an important factor for and should be thoroughly considered in the context of fisheries sampling and for stock assessment model selection.

Introduction

Statistical age-structured models are widely used in fisheries to evaluate the dynamics of harvested fish populations and provide critical information to fisheries managers regarding the status of marine fish stocks (Megrey 1989). Arising from several deterministic age-structured modeling techniques (Fry 1949; Gulland 1965; Murphy 1965; Pope 1972), these models have been developed extensively over recent decades (Doubleday 1976; Paloheimo 1980; Fournier and Archibald 1982; Pope and Shepherd 1982; Dupont 1983; Deriso et al. 1985; Methot 1989). Statistical age-structured models essentially reconstruct the demographic history of a population based on observed trends in total harvest and composition of the catch (Megrey 1989). To do this, they incorporate a range of datasets that may include fishery landings, which specify the total harvested biomass annually, indices of abundance such as the catch-per-unit-effort (CPUE), and catch composition data that reflect the distribution of ages in the harvested population (Williams 1977; Gavaris 1980; Shepherd 1984).

In some fisheries, the age composition for a sub-sample of the catch can be determined directly through the examination of annuli on hard parts, such as otoliths or scales (Hilborn and Walters 1992). However, these methods are time consuming, expensive and require a relatively high level of expertise on the part of data collectors. Because otoliths and other hard parts develop rings as a result of seasonal environmental changes, age composition data can also be particularly difficult to acquire in tropical and sub-tropical environments (Gulland 1983).

Conversely, length measurements provide one of the most common forms of data for fisheries monitoring, as they are relatively simple and inexpensive to collect (Quinn

and Deriso 1999). Since length and age are correlated throughout the life of individual fish, growth models relating length to age can thus be used to extrapolate a population's age structure from length frequency data (Kimura 1977). In such cases, length frequency data may thus have a considerable influence on estimates of stocks status that are generated in age-structured stock assessments and central to the formulation of fisheries policies.

Length frequency data, which are acquired by compiling recorded lengths from sub-samples of the overall catch, are ideally collected onboard fishing vessels by independent observers. More commonly, however, these data are instead gathered by port samplers, who intercept fishing vessels as they return from sea (Burns et al. 1983; OSB 2000). Given to the high cost of observer programs, length frequencies collected through port sampling constitute a significant portion of the available catch composition information in some fisheries. And yet, it is unclear whether this sampling approach captures the true distribution of lengths in the catch accurately.

Zwanenberg and Smith (1983) found inconsistencies in observer and port-sampled length frequency data for Canadian finfish. They described several events that could alter length frequency distributions of the catch between the time fish are captured and the time they are measured by port agents (Zwanenberg and Smith 1983). For example, certain size classes may be discarded at sea due to economic or regulatory factors, and thus be excluded from length frequency data collected at ports. Highgrading, the process by which fishermen discard smaller fish in order to make their overall catch more marketable, has been recorded in several fisheries (Pikitch et al. 1988; Evans et al. 1994; Sampson 1994; Breeze 1998; Dewees 1998; Stratoudakis et al. 1998). In some

cases, less valuable fish may also be discarded due to a lack of hull space in fishing vessels (Hall et al. 2000). Moreover, when minimum size limits are implemented as a management tool, fishermen may throw back smaller fish in order to comply with fishing regulations (Hilborn and Walters 1992).

Length composition data may also be influenced by onboard sorting and storage procedures. Burns et al. (1983) described the practice of culling in several fisheries in the northeastern United States, during which fishermen separate harvested fish into size groups based on their market price. The number of "culls", or market categories, changes over time depending on the scarcity or abundance of the stock (Burns et al. 1983). Burns et al. (1983) stated that "it is necessary to sample each market category in order to obtain representative length frequencies." This is only possible, however, when the number of culls is continuously well monitored. Size groups often vary on an annual or seasonal basis, but can also change in a less predictable fashion, due to fluctuations in the market price per pound for a given stock (Burns et al. 1983). Unless these changes are quickly recognized and incorporated into sampling protocol, the actual distribution of lengths in the catch may differ from that in the data.

Several biological factors can affect length frequency data. Hilborn and Walter (1992) suggested that fish can become stratified based on size when stored onboard fishing vessels due to their "slimy and slippery" texture. Also, many fish species tend to school in groups of similar size. The mean length of schools harvested at various locations and times may therefore differ. Since this can affect the manner in which size groups are stored, sampling efforts must be entirely random and incorporate adequate

sampling intensity in order to capture the true spatial and temporal variability of lengths in the catch.

These factors may affect a variety of fisheries, and introduce systematic errors into length frequency data. As the primary source of information reflecting the age composition of stocks in some age-structured stock assessments, length frequency data have a considerable impact on estimates of stock status, which are critical for fisheries management. The objective of this study was to identify the impact of biased length frequency data on a statistical age-structured model. Using a simulation approach, the analysis compared estimates of stock status produced from two types of erroneous length frequency data to estimates generated without nonrandom errors. In order to identify the extent to which bias affected assessments for populations with contrasting biological characteristics, simulations were based on three separate sets of life history parameters. By examining the ways in which systemic errors influenced assessment model results, this analysis evaluated which types of bias were most problematic for stock status estimates and identified the potential consequences of biased length frequencies on fisheries management and policy development.

Scenarios of bias

In a statistical context, bias is defined as the difference between the expected value of a statistic and the value of a population parameter (Kotz and Johnson 1982). For example, suppose a statistic Z is used to estimate a parameter λ. The expectation of Z is represented as:

$$E_\lambda(Z) = \lambda + b(\lambda)$$

(2.1)

where the quantity $b(\lambda)$ is the bias of the statistic Z. Bias is thus defined mathematically

by the following equation:

$$b(\lambda) = E_{\lambda}(Z) - \lambda \qquad\qquad (2.2)$$

When $b(\lambda) = 0$, the statistic Z, is an unbiased estimator of λ (Kotz and Johnson 1982).

Although samples inevitably contain some level of random error, bias is a result

of systematic errors, or consistent variations from the true values of the population.

Systematic errors can be introduced into length frequency data as a result of several

biological, economic and logistical factors. This analysis focused on two such factors,

which are described below and summarized in Table 2.1.

Scenario A: High value fish – Although the price per pound of catch varies between

species and over time, larger, heavier fish may have a higher market value than smaller

individuals. Length and weight are closely related in most fish species (Hilborn and

Walters 1992), and catch from the upper range of length classes in a population thus

provides the highest profits for fishermen in most cases. For example, warsaw grouper

(*Epinephelus nigritus*) caught along the southeastern United States sold for an average of

$2.32 / lb in 2004 (NOEP 2006), making the largest recorded specimens (up to 580 lbs)

worth over $1000 each (Froese and Pauly 2003). These larger individuals may be sold

quickly by fishermen trying to recover their operating costs and profit from their catch,

and may be sent to market before they can be sampled by data collectors.

Length composition data that exclude the largest, most valuable specimens would

be expected to contain a negative bias, with a higher relative frequency of small

individuals than was actually harvested. The length frequency distribution therefore would shift to the left (Figure 2.1).

This type of scenario was described by Burns et al. (1983) for several major fisheries in the northeastern United States. They noted that larger, more marketable size groups from the sorted, or "culled" catch were boxed and shipped immediately, often before the catch had been surveyed by port samplers. The unpacking of shipment boxed was economically inhibiting and objectionable to dealers, and larger fish were regularly excluded from the data for this reason (Burns et al 1983).

Scenario B: Shuffled bins – Since the cost of operating a fishing vessel and traveling to fishing sites can be quite high, it is often more economically advantageous for fishermen to make fewer trips of a longer duration and store harvested fish onboard while at sea. Large bins containing the catch can shift as boats remain at fishing sites or travel to other locations. Because of their slippery texture and body shape, fish may become stratified in holding bins according to size, with smaller, shorter individuals falling to the bottom where they are less likely to be picked up and measured (Hilborn and Walters 1992). Length frequency data resulting from this scenario may become positively biased, exhibiting a higher frequency of large individuals than was actually present in overall catch. This anticipated trend is shown in Figure 2.1, and shifts further to the right as the intensity of stratification within containers and, consequently, the probability of sampling large fish increases.

This type of bias may occur as a result of several factors. For example, Gunderson (1993) stated that "there is usually a tendency for samplers to take the largest

fish first in the process of sorting the catch," which may enhance the sample size of length measurements for larger individuals. Higher frequencies of large fish may occur in the data if larger culls of fish are more accessible to port samplers due to the manner by which they are loaded and unloaded from vessels (Zwanenberg and Smith 1983). Additionally, a similar trend might result from highgrading or discarding of fish below minimum size limits (Hilborn and Walters 1992).

Simulated populations

Although this was a simulation study, our goal was to ground simulations in reality so that the results were both relevant to current matters in fisheries sampling and stock assessment and applicable to the management of real world fish stocks. We sought to identify the impact of biased length frequency data on estimates of stock status of three different populations with contrasting life history characteristics. Life history parameters were selected from various serranid species in the Western Central Atlantic to generate simulated populations with differing lifespans, lengths, weights, maturation times, and sex ratios. While these populations therefore were simulated to reflect actual fish stocks in the southeastern United States, they were not true representations of populations for a specific species.

By selecting case-study species from the same biological family (Serranidae), it was possible to apply a consistent model structure in age-structured assessments for each simulated populations. Serranids share a number of biological attributes. They tend to grow relatively slowly, and, as protogynous hermaphrodites, typically change sex from male to female at some point during the life cycle (Wyanksi et al. 2001; McGovern et al.

2002, 2005). Females are thought to undergo sexual transition only after they are

reproductively mature and have spawned at least once (Carpenter 2002). Most serranids

are also demersal, and several species of this family are harvested with similar gear types

in multi-species fisheries the southeastern United States.

The life history parameters used in this study were all taken from species within

Serranidae, but were selected so that simulated populations contrasted in their age

structure, length and weight, reproduction and response to fishing. This allowed for

comparisons of the effects of biased length frequency data given differing life history

strategies in the stock. The life history characteristics of each simulated species are

described below.

Species 1: BSB – Simulations of the first species were based on the life history

parameters of black sea bass (*Centropristis striata*), a relatively short-lived and fast-

growing serranid of commercial importance in the southeastern United States.

McGovern et al. (2002) reported a maximum age of 10 years in *C. striata* collected

between Cape Hatteras, North Carolina and Fort Pierce, Florida, with most between 1 and

5 years of age. The annual natural mortality rate for all age-classes was estimated at

0.298 by McGovern et al. (2002) and the maximum size recorded in their study was 660

mm in total length (TL), or 3.6 kg (McGovern et al. 2002).

Adult black sea bass are generally found in depths of 20-60 m (Vaughan et al.

1995), and form aggregations over reefs, wrecks and other rocky substrates. They spawn

from March through May along the US Atlantic coast (Wenner et al. 1986), but a second

spawning period from September through November has also been recorded in some

areas (McGovern et al. 2002). Females have been shown to reach sexual maturity between age 0-3 (100 -180 mm), and cohorts are estimated to be 50% mature by 0-1 years of age. McGovern et al. (2002) identified males in all sampled age classes of black sea bass, however most were greater than 220 mm and 4 years of age or older. Specimens undergoing sexual transition were between 160 and 259 mm, or 2 and 4 years of age (McGovern et al. 2002). Previous assessments for black sea bass along the southeastern United States have incorporated a logistic curve to represent both the proportion of females that are sexually mature-at-age and the proportion of males expected in each age class (SEDAR2 2005).

Species 2: GAG – Simulated populations of the second species were most closely representative of gag (*Mycteroperca microlepis*). Gag is one of the most commonly caught groupers in the southeastern United States (Chapman et al. 1999). Adults are found at depths of 5-150 m (Froese and Pauly 2006) and up to 70 km from shore (Bullock and Smith 1991), although more typically near inshore reefs and shelf-break habitats (Hood and Schlieder 1992). While specimens up to 31 years of age have been recorded in the Gulf of Mexico, Harris and Collins (2000) reported a maximum age of 26 among gag collected along the US Atlantic coast. These specimens are thought to range from 215 to 1300 mm in length and weigh up to 32.74 kg (SEDAR10 2006).

Sexual maturity in female gag occurs between ages 3 – 7, and 50% of females are thought to be mature by age 3, or 648 mm (SEDAR10 2006). The sex ratio in gag stocks shifts over time (Chapman et al. 1999). Recent estimates suggest that 50% of gag are male at 10.5 years of age and a length of 1025 mm (McGovern et al. 1998). Natural

mortality for the Atlantic coast stock has been estimated between 0.14 – 0.16 (SEDAR10 2006).

Species 3: WSW – The life history characteristics of simulation species 3 were similar to those recorded for warsaw grouper (*Epinephelus nigritus*). Warsaw grouper live up to 41 years (Manooch and Mason 1987), grow up to 2300 mm in length (Heemstra and Randall 1993) and have a low natural mortality rate (SEDAR4 2004). Data for this species are quite limited, however, and when life history parameters were not available from data, populations for species 3 were therefore simulated using life history traits that contrasted most drastically from species 1 and 2.

Species 3 differed from actual warsaw grouper populations in the following ways. First, very little information is known regarding female maturation in warsaw grouper, and simulated populations for species 3 were based on arbitrary definitions of the logistic maturation parameters, η_m and m_{50}. The age at 50% maturity was calculated for females as the mean age when fish reached half of their maximum length (SEDAR4 2004). Female maturation was arbitrarily assumed to occur over a 10 year period surrounding this value. This was consistent with the approach used to specify these values for warsaw grouper in the stock assessment report for the South Atlantic deepwater snapper-grouper complex (SEDAR4 2004). Given that they were not based on experimental evidence, however, female maturation in species 3 probably do not reflect that in real populations of warsaw grouper.

Second, a similar definition was used to specify logistic sex ratio parameters. The sex ratio curve was also based on the maximum length, as the age at which 50% of the

population was male was set equal to the mean age at 75% of the maximum length

(SEDAR4 2004). Sexual transition was assumed to occur over a 20 year period

surrounding this point (Table 2.4). These were, again, consistent with the approach used

in SEDAR 4 (2004).

Finally, coefficients of variation (CV) of the lengths in each age class were not

available for warsaw grouper, unlike the first two species. The primary study on age and

growth for warsaw grouper was conducted by Manooch and Mason (1987), who

estimated the maximum length (L_∞) and von Bertalanffy growth coefficient (k) from 124

specimens caught in the recreational headboat fishery along southeastern United States.

Maximum length was estimated at 2394 mm, while the von Bertalanffy growth

coefficient was reported to be approximately 0.0544 (Manooch and Mason 1987).

Neither original data nor confidence intervals were provided with these estimates,

however. CV values were therefore defined here as a cumulative function of the growth

rate across age classes. This is described in further detail in the Methods section below.

<center>Stock status and rebuilding</center>

Black sea bass, gag and warsaw grouper inhabit federally managed regions of the

Atlantic coast (SEDAR4 2004; SEDAR2 2005; SEDAR10 2006). As such, they are

managed in accordance with the Magnuson Stevens Fishery Conservation and

Management Act (MSFCMA), the primary federal legislation pertaining to marine

fisheries. The national standards and technical guidelines set forth by MSFCMA require

that fisheries management be based on several key biological benchmarks when

available. These benchmarks are based on the theoretical relationship between the

fishing mortality rate (F) and fishery yield (Y), which follows a dome-shaped trend as the level of F increases (Graham 1935; Schaefer 1954, 1957). The relationship reaches an equilibrium at the dome's peak, where the yield is at its maximum value and the rate of change in Y is equal to zero. This point is defined as the maximum sustainable yield (MSY), as it represents the largest yield that can be sustained over an indefinite period of time, without inhibiting the renewability of the fishery resource (Caddy and Mahon 1995). The fishing mortality rate that produces equilibrium yield is denoted F_{MSY}, and is important in fisheries management as a threshold, or limit for the exploitation rate. Similarly, B_{MSY} is the spawner biomass that produces MSY when fishing levels remain at F_{MSY}. A harvested population that falls below this theoretical biomass value is expected to produce low fishery yields (Gulland and Boerema 1973; Sissenwine and Shepherd 1987; Goodyear 1993).

In accordance with MSFMCA, managers use MSY control rules to define the status of fish stocks (Restrepo et al. 1998). Through these control rules, two thresholds are estimated: the maximum fishing mortality threshold (MFMT) and the minimum spawning stock threshold (MSST). A stock is said to be undergoing *overfishing* when the fishing mortality rate affecting it exceeds MFMT. Similarly, an *overfished* stock is one that has a spawning stock biomass less than the estimated value for MSMT (Powers 1999).

MSFMCA requires that regulatory steps be taken to prevent overfishing and reduce fishing levels if stock assessment estimates indicate that overfishing is occurring (Powers 1999; Rose and Cowan 2003). When a population is identified as overfished, fisheries managers must also develop a plan to rebuild the stock to B_{MSY} within some

specified time period (Powers 1999). In order to support the establishment of rebuilding plans, biologists frequently develop a series of recovery trajectories, which define the recovery process quantitatively under various regulatory alternatives (Ianelli and Hastie 2000; Kruse et al. 2000; Mori et al. 2001; Caddy and Agnew 2003; Powers 2003; Dulvy et al. 2005; Nowlis 2005). This is done by projecting the population that is estimated in an assessment model forward through time based on a range of different fishing mortality rates. Projected populations are then compared with estimates for B_{MSY} to determine that effectiveness of each policy in rebuilding the stock within the required time horizon (Restrepo et al. 1998; Powers 1996; Darcy and Matlock 1999).

Statistical age-structured models are often used to estimate stock status and produce population rebuilding trajectories. As noted above however, these models may be greatly affected by length frequency data that contain nonrandom error. Biased length frequency data may cause estimates of stock abundance and equilibrium yield to deviate from real values, and may therefore be greatly detrimental to the accuracy of stock status estimates and recovery projections. As the basis for fisheries management, these estimates could hinder the effectiveness of management actions and rebuilding plans if erroneous. It is therefore critical that the impact of biased length frequency data be examined thoroughly and that careful consideration be given to the potential consequences of these biases on fisheries management.

Methods

Simulation was used to examine the effects of biased length frequency data on a statistical age-structured model, as it enabled comparisons of known population values

with estimates affected by bias. The analysis consisted of three main components: a

simulation model, an age-structured stock assessment model and a projection model. In

the simulation, 100 age-structured populations were generated for each of the three case-

study species, based on two different trends for the annual fishing mortality rate.

Simulated fisheries data for each of these 100 populations were then computed and the

two different scenarios of bias were incorporated into the length frequencies. These

datasets were then used in the stock assessment model to estimate several biological and

harvest-related parameters. Relative indicators of stock status were computed from the

assessment model estimates, recorded and provided to the projection model, along with

estimated parameters and the expected stock abundance from the last year of the time

series. These results were used to project the expected populations from each biased data

set forward through time under five different regulatory alternatives.

Simulation model

Simulated populations – The simulation model was constructed in the statistical

programming language R (R Foundation for Statistical Computing 2005). For each of the

three case-study species, it projected 100 age-structured populations over a 40 year

period based on two alternative trajectories of fishing effort (E_y). In the first trajectory,

the effort level increased linearly over the first half of the time series from 100 to 500

annual fishing days, and then decreased to 100 annual fishing days by year 40. The

opposite occurred in the second trajectory, with fishing effort decreasing from 500 to 100

annual fishing days from year 1-20 and increasing from 100 to 500 in year 21-40 (Figure

2.2). These alternative trajectories were simulated in order to later distinguish between

the impact of biased length frequency data on population estimates from that of the
specific trajectory in the data.

A catchability coefficient (q) specific to each case-study species (Table 2.2, 2.3,
2.4) was then multiplied by annual effort to produce a time series of fishing mortality
rates (F_y) (Quinn and Deriso 1999):

$$F_y = E_y q \qquad (2.3)$$

Experimental estimates of q were not available from the literature. Catchability
coefficients were instead extrapolated based on annual harvest rates estimated in stock
assessments (SEDAR4 2004; SEDAR2 2005; SEDAR10 2006). The value for q was
computed as the ratio of the average fishing mortality rate ($\hat{F}_y$), which was derived from
estimates of harvest ($\hat{H}_y$) through a negative logarithmic relationship [$\hat{F}_y = -\ln(1-\hat{H}_y)$]
(Haddon 2001), to the average of E_y for all years in simulation model. Since the data for
warsaw grouper were not sufficient to generate estimates of the annual harvest rate
(SEDAR4 2004), the catchability coefficient for the simulated WSW species was based
on estimates for snowy grouper (*Epinephelus niveatus*), which is caught in association
with warsaw grouper and shares similar life history traits (SEDAR4 2004).

This approach was used to compute annual fishing mortality for different
populations because it provided a consistent definition for the two different trajectories
while allowing for the harvest rate to differ between species, which was expected based
on actual catch records from each fishery (SEDAR4 2004; SEDAR2 2005; SEDAR10
2006). When used to project simulated populations forward through the time series, the
two trajectories of fishing effort produced 100 "recovering" populations for each species

that decreased and then increased beyond year 20, and 100 "declining" populations for each species, which increased and then decreased with time.

A single matrix of 100 sets of random uniform error variants ($0.5 \leq X \leq 1.5$) was then multiplied by the annual fishing mortality rate under both trajectories for each species to represent stochasticity in the harvest process. This range of errors was consistent with the most recent assessment for black sea bass in the southeastern United States, which incorporated uniform variants between 0.5 and 1.5 into stochastic rebuilding projections for the stock (SEDAR2 2005). By using the same random variants across all species and trajectories, differences in the results of the assessment model could be attributed to bias in length frequency data alone, rather than variations in the stochastic error imposed on each population.

For every species and trajectory, annual fishing mortality (F_y) was multiplied by a species-specific vector of fishing gear selectivity (s_a) to compute the fishing mortality rate ($F_{a,y}$) (Quinn and Deriso 1999):

$$F_{a,y} = s_a F_y \qquad (2.4)$$

Since black sea bass, gag and warsaw grouper are all harvested by hook-and-line gears (SEDAR4 2004; SEDAR2 2005; SEDAR10 2006), gear selectivity was modeled to reflect the proportion of fish retained by hook-and-line when caught. The simulation model used a logistic equation (Hasting and Peacock 1975) to calculate the selectivity-at-age (Quinn and Deriso 1999):

$$s_a = \frac{1}{1 + e^{-\eta(a - a_{50})}} \qquad (2.5)$$

where η defined the slope of the logistic curve and a_{50} represented the age at which 50% of fish were selected by fishing gears. This was consistent with selectivity functions used to represent hook-and-line landings in the SEDAR assessments for black sea bass (SEDAR2 2005) and gag (SEDAR10 2006). Gear selectivity was not modeled for the simulated WSW species due to limitations in the data (SEDAR4 2004), but was assumed in this study to resemble that of the other two case-study species.

The average length for each age class was computed using the von Bertalanffy (1934) growth equation, which was held constant over time. The equation computed length-at-age based on species-specific values for the maximum number of age classes and for the parameters L_∞ (the maximum length), k (the growth coefficient) and a_0 (the hypothetical age at zero length) (von Bertalanffy 1934):

$$L_a = L_\infty (1 - e^{-k(a-a_0)}) \tag{2.6}$$

A length-weight power function was used to derive weight-at-age from the average length in each age class based on a scaling constant (w_1), and an allometric growth parameter (w_2) (Quinn and Deriso 1999; Haddon 2001). The power function was transformed to produce the following equation (SEDAR2 2005):

$$w_a = e^{w_1 + w_2 \log(L_a)} \tag{2.7}$$

Female maturity and the proportion of males in each age class were both modeled using the logistic equation (Hasting and Peacock 1975), which is presented above for gear selectivity. The logistic equation for female maturity (m_a) was defined by the slope parameter η_m and the location parameter m_{50}, the age at which 50% of females are mature. Similarly, the proportion of males-at-age (p_a) was defined by η_p and the age at which 50% of fish are male (p_{50}) (SEDAR2 2005).

Population abundance was calculated using a series of exponential decay equations, which originate from several early works in age-structured population dynamics (Fry 1949; Gulland 1965; Murphy 1965; Pope 1972). The equations define abundance of age a in a given year ($N_{y,a}$) as the number of survivors from age a-1 in the previous year. Terminal abundance ($N_{A,y}$), or the number of fish in the oldest age class, is defined as the sum of the previous year's survivors from the oldest two age classes (Quinn and Deriso 1999; Haddon 2001):

$$N_a = N_{a-1,y-1}e^{-Z_{a-1,y-1}} \tag{2.8}$$

$$N_A = N_{A-1,y-1}e^{-Z_{A-1,y-1}} + N_{A,y-1}e^{-Z_{A,y-1}} \tag{2.9}$$

where $Z_{a,y}$ is the total mortality rate for age a in year y, and is equal to the sum of the fishing mortality rate, $F_{a,y}$, and a constant natural mortality rate, M (Quinne and Deriso 1999).

A vector of population abundance in year 1 was required to initialize the simulation, and was computed based on the virgin stock structure. Virgin stock size in age 1 was set equal to the virgin recruitment parameter, R_0, which represented the recruitment level before the population was subjected to fishing pressure ($f = 0$). The value of R_0 was taken from the assessment for black sea bass (SEDAR2 2005) and applied arbitrarily to all species, since the actual recruitment level for the virgin stock of most fish populations is unknown (Quinn and Deriso 1999). The virgin stock structure was then computed from the exponential decay of R_0 from natural mortality (M) only. Terminal abundance was calculated from a quotient function of survivorship in the two oldest age classes (Quinn and Deriso 1999):

$$\tag{2.12}$$

$$N_{1,0} = R_0$$

$$N_{a,0} = N_{a-1,0}e^{-M} \tag{2.10}$$

$$N_{A,0} = N_{A-1,0}\frac{e^{-M}}{1-e^{-M}} \tag{2.11}$$

The virgin stock was then subjected to fishing mortality (from year 1) and projected forward over 500 years according to equations 2.8-2.9 in order to achieve a stable age structure. This vector was then employed as the initial abundance in year 1 of the simulation.

Once abundance-at-age ($N_{a,y}$) had been simulated for each year, annual spawner biomass (B_y) was computed as the total biomass of mature females and males in the population.

$$B_y = \sum w_a \left(N_{a,y}m_a[1-p_a]\right) + \left(N_{a,y}p_a\right) \tag{2.13}$$

where m_a is the proportion of females that are sexually mature and p_a is the proportion of males in each age class. The term, w_a, represents the average weight-at-age computed from equation 2.7. A reparameterized Beverton-Holt stock-recruitment function was then used to calculate annual recruitment from the spawner biomass B_y (Beverton and Holt 1957, Francis 1992):

$$R_y = \frac{0.8R_0 h B_{y-1}}{0.2R_0\varphi_0(1-h) + (h-0.2)B_{y-1}} \tag{2.14}$$

where R_0 is the virgin recruitment, h is the steepness parameter for the stock-recruit curve and φ_0 is the spawner biomass per recruit of the virgin stock. While values for R_0 and h were provided to the simulation model (Table 2.6, 2.7, 2.8), φ_0 was computed based on virgin stock abundance, in a similar way to B_y (Francis 1992, Quinn and Deriso 1999):

$$\varphi_0 = \sum w_a \left(N_{a,0}m_a[1-p_a]\right) + \left(N_{a,0}p_a\right) \tag{2.15}$$

Due to differences in the parameters w_a and w_b, the average weights for simulated

populations of warsaw grouper (WSW) were generally larger than those simulated for

black sea bass (BSB). Spawner biomass per recruit for WSW was larger as a result,

which caused the stock-recruit curve for this species to reach its asymptote more

gradually. In other words, a progressively larger spawner biomass was required to

produce the same number of recruits as the value of φ_0 increased.

Abundance-at-age was also used to calculate the annual number of fish caught

from each age class. Catch of age a fish for each year in the time series ($C_{a,y}$) was

determined according to the Baranov catch equation (Baranov 1918):

$$C_{a,y} = N_{a,y}(1 - e^{-Za,y})F_{a,y}/Z_{a,y} \tag{2.16}$$

where $F_{a,y}$ is the fishing mortality rate and $Z_{a,y}$ is the total mortality rate for age a in year

y. $N_{a,y}$ and $C_{a,y}$ were then used to formulate three different forms of "observed" data for

each simulated population. These computations are described below.

Simulated data – Three forms of data were generated from each simulated population:

landings, indices of abundance and annual length compositions. These data are typical of

those collected for stock assessments of these species. Landings were calculated as the

total annual weight of the simulated catch:

$$L_y = \sum C_{a,y} w_a \tag{2.17}$$

Catch-per-unit-effort (CPUE) from a hypothetical fishery-independent survey was

used to represent abundance indices, and were computed as a constant portion ($\dot{q}$) of the

population abundance that was selected for by survey gears (SEDAR2 2005):

$$CPUE_y = \dot{q} \sum N_{a,y} \dot{s}_a \tag{2.18}$$

Both the catchability coefficient, $\dot{q}$, and selectivity-at-age vector, $\dot{s}_a$, used to calculate

CPUE were specific to survey gears, and were defined separately from q and s_a based on

experimental information from the Marine Resources Monitoring Assessment and

Prediction Program (MARMAP), a fishery-independent survey in the southeastern United

States.

An age length key, defined as the probability of age a fish falling within length

bin l ($\rho_{a,l}$), was used to compute length composition data for all years in the time series

(Kimura 1977). Calculations for $\rho_{a,l}$ were based on the assumption that the lengths for

each age class were normally distributed, and therefore required values for the standard

deviation of length-at-age (σ_a). For black sea bass and gag, the coefficient of variation

(CV_a) for lengths in each age class had been estimated in previous stock assessments

(SEDAR2 2005; SEDAR6 2007). This was converted into σ_a values by multiplying each

CV_a by the average length-at-age.

For warsaw grouper, however, neither coefficients of variation or standard

deviations for the length-at-age were available from previous studies. Simulation values

for σ_a were instead determined arbitrarily for simulated WSW stocks, as a cumulative

function of the growth rate (ΔL). This required the implicit assumption that a higher

growth rate coincided with a higher variance of lengths in a given age class. As age

increased, the growth rate, defined as the derivative of the von Bertalanffy growth

function, decreased:

$$\Delta L_a = dL_a / da = e^{-\kappa(a - a_0)} \tag{2.19}$$

In other words, the annual change in length of younger fish is greater than that of older fish. Based on the assumption that the growth rate and the variance of lengths coincide, variation in length would be expected to accumulate as fish age, but at a progressively slower rate. The standard deviation σ_a was thus computed as the cumulative sum of the growth rate multiplied by a constant (c):

$$\sigma_a = \sum_{i=1}^{a} \Delta L_a c \tag{2.20}$$

For all three species, the probability of length-at-age was then determined according to a normal probability density function (Kimura 1977):

$$\rho_{a,i} = \frac{e^{-\left[(l_i - L_a)^2 / 2\sigma_a^2\right]}}{\sqrt{2\pi\sigma_a}} \tag{2.21}$$

where l_i was defined by the midpoint of length bin i. For every year, the relative frequency of age a fish caught within each length bin was determined as the product of $\rho_{a,l}$ and $C_{a,y}$ divided by the total annual catch ($\sum C_y$) (Kimura 1977):

$$P_{y,i} = \frac{\rho_{a,i} C_{a,y}}{\sum C_y} \tag{2.22}$$

The relative frequencies for each length bin were then summed across all age classes and then standardized to generate simulated length composition data (SEDAR2 2005):

$$LF_y = \frac{\sum_{i=1}^{} P_{y,i}}{\sum_y \sum_{i=1}^{} P_{y,i}} \tag{2.23}$$

Incorporating bias into length frequency data – Systematic errors resulting from two different scenarios (Table 2.1) were incorporated mathematically into simulated data.

For scenario A (High-value fish), the probability of data collectors selecting and measuring fish from each length class was modeled by an inverse logistic function (1 – logistic probability distribution). This probability decreased with increasing length, since the immediate sale of larger fish made them less available to samplers. Levels of bias for scenario A were intensified by shifting the logistic selectivity curve further to the left. This was done by modifying the logistic location parameter, which was defined as L_{MAX}, 75% L_{MAX}, 65% L_{MAX} and 55% L_{MAX}. The probability distribution was then multiplied by the simulated catch-at-length in each year of the time series. The resulting matrix was converted to relative frequencies, which were provided to the objective function as the observed length composition data (Figure 2.1).

Similarly, a logistic function was used to model the probability of samplers selecting and measuring fish from each length class during scenario B (Shuffled bins). In this case, the probability increased with increasing length, as larger fish were assumed to remain at the top of storage bins during transport, where they were more easily accessible and visible to samplers. The level of bias was increased by adjusting the logistic location parameter from 15% L_{MAX}, 25% L_{MAX}, 35% L_{MAX} to 45% L_{MAX}. The probability distribution was again multiplied by the annual catch-at-length for each simulated population and converted to relative length frequencies (Figure 2.1).

<center>Assessment model</center>

Estimated parameters – A forward-projecting statistical age-structured assessment model was constructed to estimate model parameters and biological reference points from the data generated for each set of simulated populations. The assessment model used the

same functional relationships that were employed during the simulation, and was based on the model structure of the SEDAR stock assessments for black sea bass and gag (SEDAR2 2005; SEDAR10 2006). The parameters for female maturity, the proportion male-at-age and the natural mortality were assumed known. Estimated parameters included the virgin recruitment (R_0), stock-recruitment curve steepness (h), maximum length (L_∞), growth coefficient (k), hypothetical age at zero length (a_0), slope of the selectivity curve (η), and age at which 50% of fish were retained by fishing gear (a_{50}). Annual fishing mortality rates were also estimated in the assessment model. Each of the parameter values used in the simulation was multiplied by a random variant from a lognormal distribution with a mean of 0 and a standard deviation equal to 0.5 in order to generate the initial guesses for the assessment model.

Estimated landings, abundance indices and length compositions were then compared to those "observed" in the simulated fishery using a negative log-likelihood function (Hasting and Peacock 1975). Landings and abundance indices were assumed to follow lognormal distributions with the likelihood function (SEDAR 2):

$$L = \left[\log(\hat{X} + 0.001) - \log(X + 0.001)\right]^2 / 2CV^2 \qquad (2.24)$$

where X is the observed data set and $\hat{X}$ is the expected data. In the absence of estimates for the coefficient of variation (CV), this term computed across time from simulated data. The CV was calculated as the standard deviation of the observed data divided by the mean annual value observed. A multinomial log-likelihood function was used for length frequency data (SEDAR 2):

$$L = -\sum n_y \sum (P + 0.001)\log(\hat{P} + 0.001) \qquad (2.25)$$

where P is the observed length frequency distribution, $\hat{P}$ is the expected distribution and

n_y is the total annual sample size of length measurements, which was set arbitrarily as a

0.1% of the catch in each age class. The combined negative log-likelihood functions for

the three data sets were minimized using the R command optim(). The method of Byrd et

al. (1995) was specified as an argument of optim(), and allowed for box constraints to be

placed around the assessment model's parameters.

Relative indicators of stock status – Based on the estimated population from the

optimization process, the assessment model performed a yield per recruit analysis

(Beverton and Holt 1957; Shepherd 1982) to estimate the biological benchmarks MSY,

F_{MSY} and B_{MSY}. The analysis followed Shepherd's (1982) method, and incorporated a

spawner biomass per recruit model, determining the rate at which recruits produced

spawners as a function of the fishing mortality rate. The total mortality in each age class

($\dot{Z}_a$) was first calculated over a range of instantaneous fishing mortality rates ($\dot{F}$)

according to the following equation (SEDAR2 2005):

$$\dot{Z}_a = (\dot{F}s_a) + M \tag{2.26}$$

where s_a is the proportion of age a individuals that are selected by fishing gear and M is

the natural mortality rate. The spawner biomass per recruit (*SBR*) was computed for each

$\dot{F}$ following the same steps presented in Equations 2.3 through 2.15, but with the natural

mortality term M replaced by $\dot{Z}_a$ (Shepherd 1982), such that:

$$\dot{N}_a = \prod_{i=1}^{a} e^{-\dot{Z}_a} \tag{2.27}$$

$$\dot{N}_A = \frac{\prod\limits_{i=1}^{a} e^{-\dot{Z}_{A-1}}}{\left(1 - \prod\limits_{i=1}^{a} e^{-\dot{Z}_A}\right)} \tag{2.28}$$

$$SBR = \sum \dot{N}_a \left[m_a (1 - p_a) + p_a \right] w \tag{2.29}$$

The vectors m_a, p_a and w_a were those computed previously for the proportion of mature females, proportion male and average weight in each age class. Based on the calculations of ($\dot{N}_a$) at each level of $\dot{F}$, yield per recruit (YPR) was calculated based on the following equation (Quinn and Deriso 1999):

$$YPR = \sum w_a \left(\dot{N}_a \frac{\dot{fs}_a}{\dot{Z}_a} (1 - e^{-\dot{Z}_a}) \right) \tag{2.30}$$

Following these calculations, the equilibrium recruitment ($\dot{R}$), equilibrium yield ($\dot{Y}$) and equilibrium spawner biomass ($\dot{B}$) were determined for each level of $\dot{f}$ (SEDAR2 2005):

$$\dot{R} = \frac{R_0}{SBR(5h-1)} \cdot SBR4h - SBR(1-h) \tag{2.31}$$

$$\dot{Y} = \dot{R} \cdot YPR \tag{2.32}$$

$$\dot{B} = \dot{R} \cdot SBR \tag{2.33}$$

where R_0 and h represented the virgin recruitment and stock-recruitment steepness parameter estimated by the assessment model. The maximum sustainable yield (MSY) was computed as the maximum value of $\dot{Y}$ across all levels of $\dot{F}$. F_{MSY}, the fishing mortality rate required to produce MSY, was determined from the $\dot{F}$ value at equilibrium at which $\dot{Y}$ reached a maximum. The $\dot{B}$ value coinciding with the maximum $\dot{Y}$ was used to define the B_{MSY}, the spawner biomass anticipated to produce MSY if F were

maintained at F_{MSY}. Equilibrium values were compared with fishing mortality rates and spawner biomass levels estimated by the assessment model for each year in the time series to generate the relative indicators of stock status, F_y / F_{MSY} and B_y / B_{MSY} (SEDAR2 2005).

<div align="center">Projection model</div>

Although not all populations were estimated to be below B_{MSY}, the projection model generated recovery trajectories for all estimates from the assessment to ensure that comparisons of results for each bias scenario were comprehensive. The structure of the projection model was identical to the simulation and assessment, consisting of the same functional relationships and model parameters. Initial abundance was taken from year 40 of the expected abundance-at-age matrix computed during the assessment and projected forward based on the corresponding set of estimated life history parameters. Projected populations were expressed in terms of spawner biomass and compared with estimated values of B_{MSY} from the assessment, which was used as the stock rebuilding target (Restrepo et al. 1998). For each projection, recovery time was therefore computed as the number of years it took the population's spawner biomass to surpass B_{MSY}.

The time necessary to rebuild a fished population depends on its reproductive capacity and stock status. Since black sea bass, gag and warsaw grouper exhibit contrasting life history characteristics, the time horizon most appropriate for each species was expected to differ considerably. All populations were therefore projected over a 40 year period, which was considerably greater than the time anticipated for each of the case-study species to recover, given the moderate fishing levels.

Fishing mortality rate – Five different management alternatives were used to project estimated populations forward through time (Table 2.5). These were based on fishing mortality rates used in recovery projections for black sea bass and gag in the Western Central Atlantic (SEDAR2 2005; SEDAR10 2006). In alternative 1, the fishing mortality rate was maintained at the estimated level from year 40 of the assessment model. The fishing mortality rate under alternative 2 was equal to the expected fishing mortality rate at MSY (F_{MSY}). Alternatives 3, 4 and 5 employed fishing mortality rates that were 85%, 75% and 65% of the estimated value for F_{MSY} (Table 2.5).

Stochasticity – Stochasticity was incorporated into the fishing mortality rates for each management alternative and as multiplicative, random uniform error ($0.5 \leq x \leq 1.5$). As mentioned previously, these values were adopted from a recent assessment that employed uniform variants within this range to incorporate stochasticity into projected fishing mortality rates for black sea bass (SEDAR2 2005). Recovery projections from assessments for both black sea bass and gag also incorporated a lognormal error term into projected annual recruitment. Multiplicative lognormal errors, with a mean of 0 and a standard deviation calculated from the annual estimated recruitment in the original assessment (SEDAR2 2005; SEDAR10 2006), were thus incorporated into projection model for this analysis as well.

For each set of estimates, 1000 bootstraps were then computed with stochasticity in annual recruitment and fishing mortality to produce a range of biomass projections (SEDAR2 2005; SEDAR10 2006). The mean, median, standard deviation and 95%

confidence interval were calculated for the projected biomass in each year of the time series and compared for each form of bias and species. Recovery times based on both B_{MSY} and MSST were also recorded from bootstrapped biomass projections and summarized for all 100 estimated populations of a given species, population trajectory and bias type.

Results

When high value, large fish are sold before they can be sampled, the resulting bias in length frequency data creates two, interesting effects. Firstly, the population appears to be overfished and undergoing overfishing more often than is actually the case. This would support more conservative management policies, which ultimately affect fishermen with a reduced catch. Secondly, when rebuilding is necessary, the biased data cause the population to appear to recover more quickly than it would in actuality. As a result, the population would be declared rebuilt before it should be, which could liberalize regulations before it is appropriate.

In contrast, when smaller fish are shuffled to the bottom of bins, making them less accessible to samplers, the opposite trends occur. First, the population appears to be overfished and undergoing overfishing less often than is actually the case. Policies resulting from this form of bias would thus allow for unsustainable fishing and continued depletion of fish stocks. Second, when rebuilding is necessary, the biased data cause populations in the projection model to recover more slowly than they would in actuality. This supports overly conservative rebuilding policies, which would ensure the population reaches a rebuilt status, but at an unnecessary cost to the fishermen.

These results occurred due to changes in the estimated parameter values for several different functional relationships in the assessment model. These parameters and their response to biased length frequency data are discussed in further detail in the sections that follow. Since the simulated populations in this study were not representative of real stocks or trajectories, the abbreviations BSB, GAG and WSW are used here instead of species names to discuss the results for Species 1, 2 and 3. The bias in assessment model estimates under each scenario is discussed in terms of percent deviations, or the difference between estimated and simulation parameter values, expressed as a percentage of the simulation value. Since the variances of parameter estimates for trajectories 1 and 2 were quite similar, only combined results for recovering and declining populations are presented in the results. Median percent deviations from each trajectory, and for the combined trajectories for each species, are provided in Table 2.9.

<div align="center">Growth</div>

The average length in each age class of an expected model population depended on three parameters: the maximum length (L_∞), the growth coefficient (k) and the age at length zero (a_0) (see Equation 2.6). In base runs of the assessment model, when bias was excluded from length frequency data, these parameters were estimated to be within 6% of their simulated value for all three case study species, although estimates for BSB exhibited the greatest variance (Table 2.9). Growth parameters estimated from biased data deviated considerably from these initial base estimates, however.

Scenario A – In response to Scenario A, the average size of older fish in expected model populations decreased. This was due to reduced estimates for the maximum (asymptotic) length, L_∞ (Figure 2.3). Underestimates of L_∞ were most extreme for WSW, deviating from the simulation L_∞ value by a median of -19.15% under bias level 2. The maximum length parameter (L_∞) was also underestimated for GAG and BSB, with median deviations of -9.37% and -1.39% under the highest intensity of bias.

At the same time, estimates for the growth coefficient, k, increased for all three species under Scenario A, causing young fish in expected populations to reach their maximum size more rapidly (Figure 2.3). Estimates of k exceeded simulation values by a median of 31.66% for WSW, and 1.00% for BSB. The growth coefficient was particularly large in assessment model estimates for GAG, with an estimated median value of 0.354 (approximately 46.12% greater than the simulated value of k). The hypothetical age at zero length for this simulated species was also grossly overestimated, by a median of 103.24% (Table 2.9). This increased the length of age 1 fish in expected populations for GAG. It should be noted that the simulated values for both the growth coefficient and the age at zero length were much higher for GAG than for the other two species (Table 2.2, 2.3, 2.4), and greater deviations in the estimated values of k and a_0 may thus have been required to modify its the growth curve.

These trends were translated into assessment model estimates for the average weight-at-age, since weight and length were related by a fixed power function in the assessment (Figure 2.4). Decreased estimates for the weight of older fish caused a considerable decrease in both the spawner biomass and the spawner biomass per recruit, particularly for WSW.

Scenario B – Under Scenario B, growth curves shifted so that young fish had a higher average expected length. This occurred due to overestimates for the growth coefficient, k, which defined the rate at which the length-at-age curve reached its asymptote, L_∞. Overestimates in k were most extreme for WSW, and exceeded the simulation value for k by more than 200% (Table 2.9). For GAG, the growth coefficient was overestimated by a median of 108.33%, while estimates of k for BSB deviated above the simulation value by a median of 57.51%. Higher k values caused cohorts to grow more rapidly, and increased the average length of fish during their earliest years of development (Figure 2.3).

Overestimates in k were coupled with decreases in the estimated value of a_0, the hypothetical age at zero length. As a result, cohorts started off at a smaller initial length. Underestimates in a_0 were particularly extreme for GAG, as the growth coefficient for this species was already higher than that for the BSB and WSW. Since k was already large, small decreases in this parameter had less of an impact on the average length in early age classes. The age at zero length was therefore underestimated for GAG with a median percent deviation of -388.13%, causing the expected length of age 1 fish to decrease. For BSB, underestimates in a_0 were more minor, and deviated below the simulation value by a median of 2.80%. The theoretical age at zero length, a_0, had a median percent deviation of -2.37% for WSW (Table 2.9).

The values determined by the assessment model for the maximum length parameter, L_∞, varied considerably in Scenario B, but tended to be negatively biased. Median maximum length estimates for BSB were 6.87% lower than the simulation value,

while the parameter was underestimated by a median of 4.95% for GAG. The most

notable deviations in L_∞ were exhibited by expected populations for WSW, and fell below

the corresponding simulation value by a median of 24.51% (Table 2.9). These decreases

in the maximum length were unexpected, and reduced the overall height of the growth

curve (Figure 2.3). Although this minimized the number of extremely large fish in the

expected population, it also caused cohorts to remain at a steady average length as they

aged. This uniformity in lengths across age classes meant that the average size of young-

and medium-aged fish, which made up the majority of the overall annual catch, was

comparable to that of older fish. Lower L_∞ estimates therefore allowed expected length

frequency data to shift towards larger length bins without overly augmenting the relative

frequency in the far right tail of the distribution.

Selectivity

The proportion of each age class retained by fishing gears was computed based on

estimates of the slope parameter (η) and the age at 50% selectivity (a_{50}) (see Equation

2.5). Although base estimates for these parameters deviated by less than 4% for all three

species, estimated values of a_{50} varied most for BSB and GAG. This was likely due to

differences in the age of maturation for each simulated species, a vector that was held

taken from the simulation and held constant in the assessment model. Females in BSB

simulations, for example, reached sexual maturity several years before they were

subjected to fishing, while GAG females matured around the time they entered the

fishery. For these two simulated species, changes in the estimated gear selectivity

therefore had a relatively minor effect on the annual spawning stock biomass in the

population. On the other hand, juveniles in WSW simulations were fished for several years before maturing and contributing to reproduction. For this simulated species, modifications to the gear selectivity thus resulted in more drastic changes to the spawning stock size (Figure 2.5).

Although selectivity parameters tended to fluctuate more dramatically for BSB and GAG, a_{50} estimates for all three simulated species were particularly affected by both scenarios A and B. The impact of biased length frequency data on estimates of gear selectivity are discussed in the following sections.

Scenario A – The higher frequency of small fish in the data for Scenario A caused the estimated age at 50% selectivity to decrease, shifting the selectivity curve towards younger fish (Figure 2.6). Estimates of this parameter did not change dramatically under Scenario A (Table 2.9). However, for GAG, a_{50}, was underestimated by a median of 10.73% in order to shift the gear selection curve to the left. Fish in the expected population therefore entered the fishery at an earlier age, causing the expected catch-at-age curve for GAG to shift slightly toward younger fish (Figure 2.12). Changes in the selectivity-at-age were less extreme for WSW (Figure 2.6). The catch-at-age distribution for this simulated species was instead adjusted through shifts in the expected population abundance (discussed below).

Scenario B – Estimates of a_{50} increased in the assessment model due to bias from Scenario B. This occurred for all three simulated species. The expected age at 50% selectivity was overestimated, and median estimates deviated above the simulated a_{50}

value for BSB by 36.37%, and for WSW by 4.29%. Median estimated values of a_{50} increased most dramatically for GAG, exceeding simulated values by 82.73% (Table 2.9). This reduced the impact of fishing in younger age classes, allowed more fish to survive into adulthood (Figure 2.6).

<u>Fishing mortality rate</u>

Expected populations in the assessment model were projected forward through time based on annual estimates of the fishing mortality rate (F_y). In base runs of the assessment model, F_y estimates were most variable for BSB and tended to be slightly overestimated (Table 2.9). However, these larger estimates of F_y typically coincided with slight overestimates in the selectivity parameter, a_{50}, which minimized the overall impact of high annual fishing mortalities on the expected population.

For all three species, estimates of the annual fishing mortality rate deviated more dramatically from simulated values as a result of bias from scenarios A and B. These deviations were most extreme when the parameters for gear selectivity were estimated very close to base values. Since a_{50} tended to fluctuate most dramatically for BSB, the fishing mortality rates generated by the assessment model for this simulated species were less affected by biased length frequency data than those for GAG and WSW (Table 2.9).

Scenario A – Under Scenario A, estimates for the annual fishing mortality rate fluctuated considerably, but tended to increase. Estimates of F_y exceeded corresponding simulation values by up to 32.31% for WSW (Figure 2.7). This increased the mortality rate in each age class for this simulation species, so that fewer fish survived from one year to the next.

Consequently, population abundance in older age classes effectively decreased in relation to that in the simulation model.

Scenario A did not greatly affect estimates of F_y for GAG or BSB. The median annual fishing mortality rate was overestimated by a median of 1.72% for GAG and 8.54% for BSB, which was comparable to base estimate of F_y for this species. Since low a_{50} estimates increased the relative mortality rate among young age classes in GAG and reduced the expected abundance of older fish, changes in the annual fishing mortality rate for this species therefore may not have been necessary to fit expected length frequencies to biased "observed" data.

Scenario B – Annual fishing mortality rates decreased when length frequency data contained a higher frequency of large fish. Unlike in the previous scenario, F_y estimates for all three species decreased under Scenario B. Average annual fishing mortalities were underestimated by a median of 17.52% for BSB and 60.46% for WSW (Figure 2.7). The survival rate for each species was therefore higher as cohorts in the expected population moved from one age class to the next. With a greater number of young and medium aged fish surviving over time, the expected abundance of older fish in the population increased.

Estimates of the annual fishing mortality rate for GAG were quite close to simulated values under Scenario B. For this simulated species, F_y fluctuated considerably, but was estimated with a median percent deviation of 0.03% in relation to simulation values. This variation in the annual fishing mortality rate coincided with gross overestimates in the age at 50% selectivity for GAG (Table 2.9). Large values for a_{50}

increased the survival rate of young fish in expected GAG populations, and had a

comparable affect to the smaller F_y estimates that were generated by the assessment

model for the other two simulation species under Scenario B.

Recruitment

Two stock-recruitment parameters were estimated directly in the assessment

model: the virgin recruitment (R_0) and the curve steepness (h). While the asymptote of

the stock-recruit curve was defined by R_0, the curve's slope depended both on the

steepness parameter and on the spawner biomass per recruit (φ_0). Spawner biomass per

recruit was calculated internally by the assessment model based on simulated values for

m and p (maturity and sex ratio), and on expected values for the virgin stock structure and

w_a, the weight-at-age (Equation 2.15). This term determined the rate at which the stock-

recruit curve reached its asymptote. Lower values of φ_0 caused the stock-recruit curve

became more gradual, reducing the number of recruits that were produced at each level of

spawner biomass. The opposite was true for larger φ_0 values, which increased the slope

of the curve and raised the computed recruitment level relative to the total biomass of

spawners in the population (Figure 2.8). Although φ_0 was not adjusted statistically

during the optimization process like estimated parameters, changes in the average

expected length-at-age, which was related to weight through a fixed power-function in

the assessment model, caused the spawner biomass per recruit term to shift.

In base runs of the assessment model, the values computed for the spawner

biomass per recruit were typically within 2% of simulated values (Table 2.9). Variability

in the calculated value of φ_0 was greatest in simulated species with a large number of age

classes. Similarly, base estimates of R_0 and h fell within 3% of simulated values. And yet, scenarios A and B caused the expected stock-recruit relationship in the assessment model to shift considerably, affecting both estimates of R_0 and h, and internally computed values for the spawner biomass per recruit.

Scenario A – Scenario A caused annual recruitment in the assessment model to become overestimated (Figure 2.10). This raised the expected population abundance in younger age classes, and thus increased the number of younger, small fish included in the annual expected catch. Overestimates in annual recruitment were largely due to low values computed for the spawner biomass per recruit (Figure 2.9). Since the average size of older fish decreased under Scenario A as a result of low estimates of L_∞, φ_0 tended to be underestimated, and the expected stock-recruit curves for each species therefore became steeper (Figure 2.10). For WSW, spawner biomass per recruit was estimated below simulation values by a median of 21.88% in Scenario A. Similarly, median estimates for φ_0 fellow below simulation values by a median of 5.52% for GAG and 2.46% for BSB (Table 2.9).

Annual recruitment was also increased in the assessment model as a result of changes in the estimated parameters for virgin recruitment and curve steepness. Scenario A caused R_0 estimates to increase slightly, with median deviations of 0.62% for BSB, 5.62% for GAG and 2.36% for WSW. Deviations in the virgin recruitment tended to be less dramatic for WSW, as recruitment for this simulated species tended to be computed from the slope region of the stock-recruit curve and was thus less affected by alterations to the asymptote, R_0 (Figure 2.8). Recruitment for WSW was instead increased as a

result of large estimates for the estimated steepness parameter, h, the median values of

which exceeded the corresponding simulation value by a median of 13.04%.

Although recruitment in expected GAG populations was computed from in

between the slope and asymptotic regions of the stock-recruit curve (Figure 2.8), the

curve steepness parameter was not overestimated for this simulated species. Instead, the

median h estimate for GAG decreased as a result of bias from Scenario A by 3.73%.

This apparently did not diminish the impact of bias from Scenario A on the expected

stock-recruitment relationship for this species, however. Even with low estimates of h,

Scenario A produced consistent overestimates in the annual expected recruitment for all

model populations (Figure 2.10).

Scenario B – Under Scenario B, expected annual recruitment in the assessment model

decreased (Figure 2.11), reducing the abundance of young fish in expected model

populations. Since length was overestimated in young and medium age classes, φ_0 values

tended to be positively biased in assessment model runs for Scenario B. Spawner

biomass per recruit was overestimated, with median deviations of 22.90% for BSB and

41.53% for GAG. Median deviations in φ_0 were less extreme for WSW, and exceeded

the corresponding simulation value by 10.53% (Table 2.9, Figure 2.9). Increases in the

estimated value of φ_0 caused the slope of the stock-recruitment curve to become more

gradual, producing fewer recruits at low to moderate spawner biomass levels (Figure

2.11).

The virgin recruitment parameter also decreased, further diminishing the annual

recruitment estimated from the expected spawner biomass in each year of the assessment

model.   The virgin recruitment (R_0) was underestimated for expected populations of

BSB, with a median bias of -13.80%. The estimated values for the asymptotic

recruitment, R_0, changed most dramatically in this simulation species, since recruitment

for BSB was computed from the asymptotic region of the stock-recruit curve and was

therefore most influenced by estimates for this parameter (Figure 2.8). Recruitment for

GAG and WSW, on the other hand, was computed from the slope and middle regions of

the curve (Figure 2.8), and deviations in R_0 estimates for these simulated species were

less consistent, falling both above and below simulated values. For WSW, R_0 was

underestimated by 1.80% in median estimates, while the median estimate of this

parameter for GAG was 1.94% above of the coinciding simulation value (Table 2.9).

Consistent underestimates in the steepness parameter of the stock-recruit curve

were also observed under Scenario B. Median estimates of h deviated below simulated

values for BSB by 30.05% and below those for GAG by 36.84%. Steepness, h, was most

dramatically underestimated for expected populations of WSW, with median deviations

of 39.39% (Table 2.10).

Population age structure

Based on the estimated values of the parameters described above, abundance- and

catch-at-age were estimated annually for each expected model population (see Equations

2.10-2.12 and Equation 2.16). In base runs of the assessment model, the age-structure of

expected populations mimicked that of simulated stocks quite closely. Abundance-at-age

and catch-at-age were altered, however, during assessment model runs for Scenarios A

and B, in order to minimize the difference between expected length frequencies generated by the model and biased length frequency data from the simulation.

Scenario A – In order to increase the frequency of small fish in estimated length frequency data, the relative number of young individuals in the catch was increased in the assessment model under Scenario A as a result of two factors (Figure 2.12). Firstly, the annual recruitment increased, so that a larger number of small fish were introduced into the each estimated model population in every year of the time series. Secondly, mortality across younger age classes increased, either as a result of higher estimates for the annual fishing mortality rate or underestimates in the selectivity parameter a_{50}. As a result, a larger number of young fish were estimated to be captured by fishing gears annually, increasing the relative frequency of small fish in the catch.

The cumulative impact of these factors on the age-structure of estimated model populations for each species is illustrated in Figure 2.12. Since overestimates in recruitment were most dramatic for WSW, the population abundance for this species exhibited the greatest deviations from simulated abundance values. This increased the perceived relative frequency of young, smaller fish in the estimates for this stock, allowing for a superlative fit to "observed" length frequencies from Scenario A. On the other hand, recruitment was only minimally overestimated in estimated populations of BSB, and expected length compositions were fit to observed data only when the selectivity-at-age was also decreased, enhancing the relative rate at which young fish were harvested.

Scenario B – Under Scenario B, the relative number of older fish in the expected catch increased in order to augment the frequency of large fish in the data (Figure 2.12). This occurred due to underestimates in the annual recruitment, which reduced the number of young fish in the expected model population. At the same time, population abundance was disproportionately high across medium and older age classes, as fishing mortality rates were concurrently underestimated in each year of the time series under Scenario B, increasing the survival of cohorts as they aged. The age-distribution in the expected populations generated by the assessment model for this scenario are presented in Figure 2.12.

<div align="center">Indicators of stock status</div>

In each run of the assessment model, MSY, F_{MSY} and B_{MSY} were computed based on each of the estimated parameter values described above. Base estimates for these biological reference points were within 7% of simulated values in all cases, although estimated values for F_{MSY} exhibited the greatest variance (Table 2.10). Similarly, relative indicators of stock status generated during base runs of the assessment model deviated from simulation values by no more than 4% (Table 2.10).

Scenario A – The maximum sustainable yield was estimated with a relative high level of accuracy during assessment model runs for Scenario A (Table 2.10). For all three species, MSY estimates fluctuated both above and below simulated values by less than 5%.

The fishing mortality rate expected to produce MSY (F_{MSY}) and the minimum fishing mortality threshold (MFMT) were estimated with high variance under Scenario A, but tended to be slightly overestimated for GAG and BSB when compared with simulation values (Table 2.10). At the same time, the fishing mortality rate in the last year of the time series was also overestimated, causing the ratio of $F_{current}$/MFMT to increase slightly in most cases (Table 2.10, Figure 2.13). Larger estimates for $F_{current}$/MFMT indicated that fishing was occurring at high levels in relation to that which was sustainable. For WSW, F_{MSY} was overestimated with a median bias of 31.82% and MFMT was overestimated by a median of 20.70%. However, this coincided with substantial overestimates in annual fishing mortality rates in the assessment model (median bias of 32.31%). Consequently, the relative fishing mortality rate for this species also increased. The estimates of $F_{current}$/MFMT produced under Scenario A were therefore overly pessimistic for all three simulation species (Figure 2.13).

B_{MSY} and MSST (equal to ½ B_{MSY}) were consistently underestimated in the assessment model under the first scenario. Estimates of B_{MSY} and MSST decreased from simulated values by a median of 3.03% for BSB, 5.49% for GAG and 30.48% for WSW (Table 2.10). This was due to decreases in the spawner biomass per recruit curve computed at each level of fishing mortality in the yield per recruit analysis. The low values calculated for MSST resulted in underestimates for the relative spawner biomass ($B_{current}$/MSST), which suggested that the stock was more heavily depleted than was actually the case. The extent to which stock status was underestimated under Scenario A is presented in Table 2.10.

Deviations in relative indicators were particularly extreme for expected populations of WSW (Table 2.10, Figure 2.13). Even at low levels of bias, the annual spawner biomass for this species was inaccurately estimated below the minimum target threshold on several occasions (Table 2.10). The relative fishing mortality rate for this simulated species was also estimated to be particularly high, and frequently indicated that fishing had surpassed sustainable levels (Figure 2.13). In other words, Scenario A produced overly pessimistic estimates of stock status. This type of bias may therefore support regulatory actions that are adequately precautionary from a conservation standpoint, but that present an unnecessary cost for fishermen.

Scenario B – Yield per recruit curves computed by the assessment model for Scenario B were highly variable, and fluctuated both above and below simulated values from the YPR analysis, particularly at higher levels of fishing mortality. Consequently, the maximum sustainable yield was estimated with a high variance for all three simulation species. This made it difficult to draw definitive conclusions regarding the impact of bias from Scenario B on this particular biological reference point. Based on median estimates for each species, MSY appeared to be at least slightly overestimated in the majority of assessment model runs. For BSB, median estimates for MSY were 8.38% greater than simulated MSY values. Median MSY estimates for GAG exceeded simulated values estimates by 10.19%. The maximum sustainable yield was slightly underestimated for WSW under Scenario A (Table 2.10).

The fishing mortality rate expected to result in MSY varied substantially under Scenario B as well. F_{MSY} was overestimated, with median percent deviations of 16.37%

for BSB and by 39.13% for GAG. On the other hand, median estimates of F_{MSY} tended

to be negatively biased for model populations of WSW, and deviated below simulated

values by a median of 49.43% (Table 2.10).

The spawning stock biomass produced at MSY was consistently overestimated in

assessment model runs for the second scenario. The most dramatic overestimates in this

reference point were those computed for GAG, which exceeded simulated values with a

median deviation of 66.40%. Less drastic overestimates in B_{MSY} were observed for BSB,

with a median percent deviation of 39.06%. For WSW, B_{MSY} was overestimated with a

median deviation of 34.52% (Table 2.10).

Although the value of B_{MSY} increased as a result of Scenario B, this was

accompanied by large overestimates in the annual spawner biomass. The relative

spawning stock biomass was therefore consistently larger in assessment model runs for

this scenario than in original simulated populations (Table 2.10, Figure 2.14), indicating

that the stock was more abundant than was actually the case. Similarly, F_{MSY} estimates

for each simulation species, regardless of whether they were over- or underestimated,

were offset by analogous deviations in the estimated annual fishing mortality rate.

Relative fishing mortality thus was underestimated with increasing levels of bias,

suggesting that fishing was lower than in actuality (Figure 2.14). In other words,

Scenario B produced overly optimistic estimates of stock status. This kind of bias might

therefore result in management measures that do not adequately protect stocks from

overfishing.

<div align="center">Projections</div>

Estimated populations from base runs of the assessment model were projected

forward under each of the five regulatory alternatives listed in Table 2.5. For BSB and

GAG populations that had a "recovering" trajectory, base estimates of the spawner

biomass in year 40 were not typically below MSST. A larger percentage of "declining"

WSW populations were identified as depleted in base runs of the assessment model,

however, as they fell below estimated values of B_{MSY} in the final year of the time series.

For all three simulation species, "declining" trajectories tended to be depleted more

frequently than those with a "recovering" trend. Table 2.9 presents the percentage of

"declining" populations, as well as total populations, that were estimated below MSST.

While recovery projections would normally be completed for fish stocks identified as

depleted, projections were computed for all simulated populations in this analysis in

order to gain more comprehensive information on the response of each stock to various

fishing rates over time.

None of the simulated populations for BSB or GAG were below MSST in the last

year of the simulation, nor were they estimated below this threshold in base runs of the

assessment model. On the other hand, 90% of declining WSW populations and 8% of

recovering WSW populations were depleted in year 40 of the simulation. In base runs of

the assessment model, 88% of declining populations and 8% of recovering populations

for this species were estimated to be below MSST. While none of the regulatory

alternatives rebuilt depleted WSW populations above the target of B_{MSY} within the 10

year time horizon, alternatives 2 through 5 produced steady increasing trends in spawner

biomass. The average recovery time of "declining" populations for this species under

alternative 5 was 21.64 years, compared with 26.50 years under alternative 4 and 33.72 years under alternative 3 (Table 2.11).

Scenario A – Since biased length frequency data for Scenario A caused the assessment model to underestimate annual spawner biomass, the population projections in this scenario were initialized at a lower starting biomass. When projected forward into the future, however, spawner biomass increased *more* rapidly over time (Figure 2.15). This was due to greater productivity in expected model populations under Scenario A, which generated more recruits at each spawner biomass level.

Scenario A caused the estimated recovery time for projected WSW populations to decrease (Table 2.12). Under the most conservative regulatory alternative (alternative 5), projected populations were estimated to exceed the rebuilding target within an average of 18.77 years, approximately 2 to 5 years earlier than in base projections (Figure 2.15). This was caused solely by increases in the estimated productivity of the stock, as Scenario A also reduced estimates of the initial spawner biomass dramatically (by a median of 107.65%). Although recovery times under the other regulatory alternatives also decreased (Table 2.11), alternative 5 continued to provide the best rebuilding strategy for estimated WSW stocks.

Bias from Scenario A caused projected populations for all three simulation species to rebuild more rapidly than they would in actuality under each regulatory alternative (Table 2.11). Thus, policies that would likely be deemed appropriate by managers based on these projections would not necessarily allow actual populations to fully rebuild before they were again exposed to high fishing mortality rates. When

populations are in fact depleted, long-term management strategies that ensue from this form of bias may therefore be ineffective in establishing and maintaining a sustainable stock size.

Scenario B – Scenario B caused annual estimates of spawner biomass in the assessment model to be biased upwards. Projections for all three species under this scenario were therefore initialized at a higher starting biomass (Figure 2.16). At the same time, each level of spawner biomass was expected to produce fewer recruits, as this scenario estimated a less productive stock-recruitment relationship. Consequently, projected populations responded more gradually to reductions in fishing mortality, and required more time to recover above minimum target thresholds (Figure 2.16).

Since estimated populations in the assessment model had a higher overall biomass under Scenario B, fewer populations were estimated to be below MSST in the last year of the time series. For WSW, the percentage of "declining" stocks that were below the minimum threshold in the last year decreased from 90% to 39%. None of the populations estimated for BSB or GAG were depleted below sustainable levels in this scenario (Table 2.11).

Populations identified as depleted in Scenario B recovered more slowly than simulated populations under each regulatory alternative (Figure 2.16). Under alternative 5, the average recovery time for "declining" WSW stocks increased from 21.64 years to 29.53 years on average. Projected populations for this simulation species were estimated to recover within an average of 31.93 years under alternative 4 and within 34.06 years

under alternative 3, roughly 4 to 12 years after simulated populations surpassed B_{MSY} (Table 2.11).

Scenario B produced initial estimates of stock status suggesting that populations are overfished and undergoing overfishing less often than is actually the case. Policies formulated based on these results would tend to allow fishermen to harvest the stock at a higher level than is sustainable. Since Scenario B reduced the number of populations that were estimated to be below MSST, managers would be less likely to develop rebuilding plans for depleted stocks that are affected by this form of bias. When rebuilding projections are performed, however, they would likely reflect an overly gradual and prolonged recovery process. Recovery projections under Scenario B would therefore favor a more precautionary rebuilding strategy that ensures protection of the stock, but negatively impacts fishermen who are dependent on the resource.

Discussion

For the purposes of fisheries management, the extent to which each scenario of bias affected policy depended on whether the stock was healthy or depleted. If the population was well above minimum target thresholds in the simulation, estimates of stock status did not tend to indicate that management action was necessary, even under the highest levels of bias for each scenario. Biased length frequency data were therefore not terribly problematic for healthy stocks. On the other hand, if a population was heavily fished or depleted, biased data posed a much larger threat for fisheries management. Since relative indicators of stock status were either under- or overestimated as a result of each scenario, erroneous length frequencies tended to support

inappropriate management actions when populations were close to their minimum threshold.

The trajectory and status of the three simulated fish stocks in this study was not representative of that in the actual populations of black sea bass, gag or warsaw grouper in the southeastern U.S. Assessments were recently conducted for two of these species. Assessment results for gag and black sea bas bass indicated that both stocks were undergoing overfishing in the Southeast. While only black sea bass was determined to be overfished, the spawning stock biomass of gag in 2005 was estimated only slightly above B_{MSY} (SEDAR2 2005; SEDAR10 2006). Both stocks were therefore within close proximity to their minimum target threshold, and management actions affecting them could consequently be affected if length frequency data are biased.

Not all types of bias in these data have the same impact on age-structured stock assessments and consequent policies. In the present study, length composition data that contained an excessive frequency of large fish were shown to cause the largest deviations in estimates of stock status (Table 2.11). Underestimates in the relative fishing mortality rate coupled with overestimates in the relative spawning stock biomass indicated that the stock was much more abundant and less heavily fished than it was in actuality. As a result, the percentage of populations identified as overfished was 10-13% too low. Management actions resulting from this type of bias might be less stringent than necessary, and were therefore problematic from a conservation standpoint. This was particularly the case for longer-lived species. As with other simulation species, depleted WSW stocks were less likely to be identified as overfished under Scenario B, but also required a longer time to recover, due to their low productivity and slow growth, if

management actions failed to maintain their populations above the minimum target threshold.

Although current stock status estimates were less significantly affected by underreporting of large fish, this type of bias may be of critical importance for rebuilding plans that attempt to reestablish depleted populations. Scenario A caused the biomass projections to increase more rapidly under each proposed level of fishing mortality (Alternatives 1-5), supporting policies that would likely have been inadequate to rebuild the population within the specified time horizon. These results were accentuated in projections for WSW, which were declared to be overfished 74% less often under Scenario A. This type of bias may therefore be particularly problematic for regulatory efforts aimed at rebuilding longer-lived species.

Each type of bias may occur in a variety of fisheries, as they can result from a number of different factors, including culling (Burns et al. 1983), spatial heterogeneity in the stock (Zwanenberg and Smith 1983), the shuffling of catch containers (Hilborn and Walters 1992), or, simply, a tendency among port samplers to measure the largest fish (Gunderson 1993). In addition, one of the most problematic factors influencing fisheries data is unreported discarding. Highgrading, the process by which fishermen discard smaller fish in order to make their overall catch more marketable, has been reported in a number of fisheries (Pikitch et al. 1988; Evans et al. 1994; Sampson 1994; Breeze 1998; Dewees 1998; Stratoudakis et al. 1998). Biased data that result from highgrading may impact stock assessment in a similar fashion to the simulated data for Scenario B in this study. It is therefore important that sampling programs be reviewed to ensure that they provide accurate length frequency data, particularly when there may be instances of

highgrading in the fishery. It is also critical that each of the factors influencing the data

be carefully considered when selecting an appropriate model for stock assessment.

<u>Reevaluating model structure and complexity</u>

The process of identifying a modeling approach that is most appropriate for the

assessment of a given fish stock depends on several factors, including the goal of the

assessment, the life history characteristics of the species and the data that are available

from the fishery. While these factors are important, and may often support the use of

more simplistic modeling strategies, fisheries stock assessment models have tended to

increase in their level of complexity over recent decades (Schnute and Richards 2002).

More complex models allow for the incorporation of additional types of data, however,

they have frequently been criticized (Cotter et al. 2004). Having fewer data observations

in relation to the number of fitted parameters decreases the degrees of freedom for model

estimates, and therefore reduces the precision and predictive power of assessment results

(Walters and Martell 2002). They also incorporate additional assumptions regarding the

dynamics of the stock (Hilborn 2002), which may or may not be justified (Kelly and

Codling 2006).

 The model used in this study was constructed based on an age-structured

assessment for black sea bass in the southeastern United States (SEDAR5 2005). The

catch-at-age model in the black sea bass assessment was fairly complex, incorporating

228 different parameters with 30 years of data (SEDAR2 2005). Due to limitations in the

aging information that was available for this species, age composition data were deemed

unreliable for the purposes of stock assessment and were therefore excluded from the

model. Age-structure in the stock was instead extrapolated based on length frequency distributions in the annual catch (SEDAR2 2005).

The results of this study suggest that simply having a large sample size of length frequency data is not sufficient on its own to warrant a complex model structure. The likelihood and magnitude of bias in length frequency data must also be examined in order to determine whether they should be included in stock assessments. There are a number of less complex modeling approaches that do not require length frequencies and may be favorable when the quality of these data is poor or uncertain. For example, production models define the population based on the total annual biomass, and typically require only catch data and abundance indices to generate estimates of stock status (Zhang et al. 1991; Prager 1994; Prager 1995; Prager 2002). These models are particularly effective when abundance indices are accurate and informative (Ludwig 1989), and when the variability in annual recruitment is relatively low (Quinn and Deriso 1999). It should be noted that a production model applied in conjunction with the catch-at-age model for black sea bass was relatively consistent in the population trends it predicted (SEDAR2 2005).

Another alternative to fully age-structured approaches are delay-difference models (Deriso 1980), which describe annual biomass based on the sum of surviving biomass from the previous year, the growth and the biomass of recruits in each year. This model incorporates information regarding the stock-recruitment relationship, natural morality and growth, but does not require length frequency data (Quinn and Deriso 1999).

Controlling potential sources of error

When length frequency data are abundant and reliable, a fully age-structured method may in fact be the most appropriate technique for assessing a stock. In order to ensure that the quality and quantity of length frequency data is sufficient for this type of modeling approach, several goals and standards should be incorporated into fisheries sampling programs. Firstly, when at all possible, these data should be collected by onboard observers as fish are harvested and brought onto fishing vessels. Length frequency distributions compiled by observers would be much less likely to contain bias caused by culling, discarding or size-stratification in storage containers.

Since significant increases in observer coverage may not be plausible in many fisheries due to the associated cost, port sampling programs should also be designed to account for any factors that alter the length frequency distribution in the catch between the time fish are harvested and measured. For example, in order to ensure that random samples are collected from all size groups in the catch, culling should be consistently well monitored, particularly in fisheries for which there are large seasonal, annual or unpredictable changes in the market value of each size class. Randomized tests on the spatial variability of fish lengths within hulls and storage containers should also be conducted regularly to ensure that the data are representative of true length compositions in the harvested population.

The effectiveness of port sampling is often reliant upon the discretion and consent of fishermen and dealers (Burns et al. 1983). Although it may be economically advantageous to sell large fish immediately, the management actions resulting from data that contain fewer large fish may be overly stringent, protecting the stock at an

unnecessary cost to resource users. It is therefore critical that all data be made available

to port agents. At the same time, port sampling programs must be designed with the

economic interests of fishermen and dealers in mind, and pose as little impedance to

regular business activities as possible. This may require employing a larger team of data

collectors at each port, who can work simultaneously to sample landed catch in a manner

that is quick and efficient.

Finally, incentives and opportunities should be developed for fishermen to

become involved in the data collection process, as this could potentially improve the

quality and quantity of fisheries data, as well as improve communication between

fishermen and data collectors. Alternative data collection programs that emphasize

fishermen participation have proven beneficial in several fisheries (Starr et al. 1997;

Ticheler et al. 1998; Shephard et al. 2006). Similar pilot programs have been established

in the Southeast as part of the Cooperative Research Program (CRP) program, but could

be more broadly implemented given sufficient monetary and logistical support.

<u>Future research</u>

Perhaps the primary objective of future work on this subject should be to identify

fisheries in which length frequency data may be biased and determine how this might

influence the effectiveness of policies that are currently in place. Simulation results from

this study suggest that biased length frequencies have a considerable impact on age-

structured estimates of stock status. And yet, for most marine fish stocks, the extent to

which length frequency data are affected by systematic sampling errors remains unclear.

For fisheries that are assessed and managed through the use of age-structured stock

assessment models, it is especially critical that potential sources of bias in these data be recognized. Although this will likely require a thorough examination of the sampling design in a given fishery, systematic errors might also be recognized using a quantitative diagnostic approach similar to that of Gavaris and Van Eeckhaute (1998), or by comparing observer and port sampled length frequency data sets when available (Zwanenberg and Smith 1983).

There are several remaining questions regarding the impact of biased length frequency data on fisheries stock assessment. The response of stock status indicators to biased data would likely change under a different model structure. For example, selectivity parameter estimates for longer-lived species may have fluctuated more dramatically if the logistic parameters defining the proportion of mature females in each age class had been estimated rather than fixed as known constants in the model. Perhaps stock status estimates would have responded even more drastically to biased length frequency data had the parameters for growth been excluded from the statistical estimation process and instead been held constant in the model. There are a variety of parameters that could be included and excluded from the statistical fitting process. Future work examining the importance of model structure and the response of estimates to biased length frequencies might consider the following questions: When length frequency data are biased, are there certain parameters that are best to set as known constants? And as the level of bias intensifies, at what point are erroneous estimates for these parameters more detrimental to the model's results than less accurate, fixed values?

Secondly, this analysis did not incorporate stochastic error into landings data or abundance indices, as variability in these data was attributed solely to stochasticity in the

annual fishing mortality rate. Error was excluded from these data in order to ensure that the effect of biased length frequencies could be clearly identified. Although the variability in landings and abundance indices was therefore probably quite low, larger, more realistic variances may act as a confounding factor for the effects described here. It would be useful to understand the response of stock status indicators to biased length frequency as the level of stochastic variation in landings and abundance indices progressively increases across a more realistic range, as this may be more consistent with real fisheries data.

Summary and Conclusions

In this study, bias in length frequency data was shown to have a considerable impact on several key indicators of stock status, which are central to the formulation of fisheries policy in the United States. Biased length composition data were particularly problematic for populations that were heavily fished or depleted, as the estimates they produced tended to support management actions that were inappropriate. Data containing too many large fish were shown to have the greatest impact on stock status estimates, particularly for long-lived species, and supported regulatory policies that were insufficient in their ability to protect stocks from overfishing. At the same time, however, when the data for overfished populations contained too many small fish, projections tended to support rebuilding plans that did not rebuild stocks within the specified time horizon. These types of bias may affect the length frequency data for a variety of different fisheries, and it is important that they be considered in fisheries sampling designs. Furthermore, when length frequencies are suspected to contain

inaccuracies, stock assessments may be more effective by applying more simplistic

fisheries models that exclude these data.

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Table 2.1: Two scenarios of systematic error were considered in this study. Bias anticipated to result from each scenario was incorporated into simulated length frequency data using logistic probability functions (described on pp 24-25).

Scenario		Description
A	High value fish removed	Larger, more marketable individuals are sold before a sampling.
B	Shuffled bins	Smaller fish are shuffled to the bottom of bins or containers during transport.

Table 2.2: Life history parameters used to simulate populations for BSB, the species that most closely represented black sea bass. Parameters are categorized into groups relating to mortality and survival, length, weight, female maturity and the proportion male.

Species 1: BSB

Parameter		Value	Source
Mortality & Survival –			
Natural mortality rate	M:	0.3	(SEDAR2 2005)
Maximum age	A:	10 years	(McGovern et al. 2002)
Catchability coefficient	q:	0.001718	*Extrapolated from exploitation rates (SEDAR2 2005)*
Length –			
Maximum length	L_∞:	544.5 mm	(SEDAR2 2005)
Growth coefficient	k:	0.16	(SEDAR2 2005)
Age at zero length	a_0:	1.16 years	(SEDAR2 2005)
Weight –			
Scaling constant	w_1:	16.952	(SEDAR2 2005)
Allometric growth parameter	w_2:	2.794	(SEDAR2 2005)
Female maturity –			
Age range	η_m:	age 0 – 2	(McGovern et al. 2002)
Age at 50% female maturity	m_{50}:	age 1	(McGovern et al. 2002)
Proportion male –			
Age range	η_P:	age 3 – 7	(McGovern et al. 2002)
Age at 50% male	p_{50}:	age 5	(McGovern et al. 2002)

Table 2.3: Life history parameters used to simulate populations for GAG, the species that most closely represented gag. Parameters are categorized into groups relating to mortality and survival, length, weight, female maturity and the proportion male.

Species 2: GAG			
Parameter		**Value**	**Source**
Mortality & Survival –			
Natural mortality rate	*M:*	0.16	(SEDAR10 2006)
Maximum age	*A:*	30 years	(Harris & Collins 2000)
Catchability coefficient	*q:*	0.000772	*Extrapolated from exploitation rates (SEDAR10 2006)*
Length –			
Maximum length	L_∞:	1051 mm	(SEDAR10 2006)
Growth coefficient	*k:*	0.24	(SEDAR10 2006)
Age at zero length	a_0:	0.48 years	(SEDAR10 2006)
Weight –			
Scaling constant	w_1:	-17.843	(SEDAR10 2006)
Allometric growth parameter	w_2:	2.943	(SEDAR10 2006)
Female maturity –			
Age range	η_m:	age 2 – 4	(SEDAR10 2006)
Age at 50% female maturity	m_{50}:	age 3	(SEDAR10 2006)
Proportion male –			
Age range	η_P:	age 7 – 15	(McGovern et al. 1998)
Age at 50% male	p_{50}:	age 11	(McGovern et al. 1998)

Table 2.4: Life history parameters used to simulate populations for WSW. This simulated species was similar to warsaw grouper, but also had several arbitrarily specified parameters that contrasted most extremely with those for BSB and GAG. Parameters are categorized into groups relating to mortality and survival, length, weight, female maturity and the proportion male.

Species 3: WSW			
Parameter		Value	Source
Mortality & Survival –			
Natural mortality rate	M:	0.1	(SEDAR4 2004)
Maximum age	A:	41 years	(Manooch & Mason 1987)
Catchability coefficient	q:	0.000491	*Extrapolated from exploitation rates for snowy*
Length –			
Maximum length	L_∞:	2394 mm	(SEDAR4 2004)
Growth coefficient	k:	0.0544	(SEDAR4 2004)
Age at zero length	a_0:	3.616 years	(SEDAR4 2004)
Weight –			
Scaling constant	w_1:	-10.772	(SEDAR4 2004)
Allometric growth parameter	w_2:	2.9797	(SEDAR4 2004)
Female maturity –			
Age range	η_m:	age 6 – 12	(SEDAR4 2004)
Age at 50% female maturity	m_{50}:	age 9	*a when La = 50%L_∞*
Proportion male –			
Age range	η_p:	age 15 – 30	(SEDAR4 2004)
Age at 50% male	p_{50}:	age 22	*a when La = 75%L_∞*

Table 2.5: The five regulatory alternatives applied constantly to populations as they were projected into the future. Ideal regulatory alternatives were those that rebuilt depleted populations above B_{MSY} within 10 years or within closest subsequent possible time horizon.

REGULATORY ALTERNATIVES	FISHING MORTALITY RATE
Alternative 1	$F = f_{40}$
Alternative 2	$F = F_{MSY}$
Alternative 3	$F = 85\% \ F_{MSY}$
Alternative 4	$F = 75\% \ F_{MSY}$
Alternative 5	$F = 65\% \ F_{MSY}$

Table 2.6: Parameter and biological reference point estimates for BSB from base runs of the assessment model, in which length frequency data were unbiased. Simulated values are presented along with the median and quartiles (25% and 75% quantiles) for each estimate.

Species 1: BSB			Simulation value	Base estimates	
				median	(1st quantile, 3rd quantile)
Growth	Maximum length	L_∞	544.5	561.0	(555.5, 570.5)
	Growth coefficient	k	0.16	0.1508	(0.1455, 0.1536)
	Age at zero length	a_0	-1.16	-1.136	(-1.143, -1.133)
Mortality	Fishing mortality rate	f_y	0.2631	0.2764	(0.2714, 0.2794)
	Selectivity slope parameter	η	5	5.005	(5.003, 5.005)
	Age at 50% selectivity	a_{50}	3	3.108	(3.070, 3.138)
Recruitment	Virgin recruitment	R_0	10000000	9879970	(9835459, 9965516)
	Stock-recruit curve steepness	h	0.6	0.6202	(0.6120, 0.6310)
	Spawner biomass per recruit	φ	1.315	1.302	(1.299, 1.307)
Reference Points	Maximum sustainable yield	MSY	$8.627*10^5$	$8.616*10^5$	$(8.588*10^5, 8.628*10^5)$
	Fishing mortality rate at MSY	F_{MSY}	0.3055	0.3270	(0.3185, 0.3380)
	Spawner biomass at MSY	B_{MSY}	$4.643*10^6$	$4.499*10^6$	$(4.455*10^6, 4.582*10^6)$

Table 2.7: Parameter and biological reference point estimates for GAG from base runs of the assessment model, in which length frequency data were unbiased. Simulated values are presented along with the median and quartiles (25% and 75% quantiles) for each estimate.

Species 2: GAG			Simulation value	Base estimates	
				median	(1st quantile, 3rd quantile)
Growth	Maximum length	L_∞	1051	1052	(1052, 1053)
	Growth coefficient	k	0.24	0.2388	(0.2381, 0.2402)
	Age at zero length	a_0	-0.48	-0.4784	(-0.4795, -0.4708)
Mortality	Fishing mortality rate	f_y	0.1182	0.1167	(0.1117, 0.1199)
	Selectivity slope parameter	η	5	5.001	(5.001, 5.002)
	Age at 50% selectivity	a_{50}	3	3.019	(3.014, 3.025)
Recruitment	Virgin recruitment	R_0	10000000	9997645	(9941801, 10016324)
	Stock-recruit curve steepness	h	0.6	0.6012	(0.6005, 0.6071)
	Spawner biomass per recruit	φ	42.56	42.52	(42.51, 42.54)
Reference Points	Maximum sustainable yield	MSY	$1.632*10^7$	$1.631*10^7$	$(1.630*10^7, 1.633*10^7)$
	Fishing mortality rate at MSY	F_{MSY}	0.1265	0.1270	(0.1270, 0.1290)
	Spawner biomass at MSY	B_{MSY}	$1.459*10^8$	$1.456*10^8$	$(1.441*10^8, 1.461*10^8)$

Table 2.8: Parameter and biological reference point estimates for WSW from base runs of the assessment model, in which length frequency data were unbiased. Simulated values are presented along with the median and quartiles (25% and 75% quantiles) for each estimate.

Species 3: WSW			Simulation value	Base estimates	
				median	*(1st quantile, 3rd quantile)*
Growth	*Maximum length*	L_∞	2394	2370	(2359, 2380)
	Growth coefficient	k	0.0544	0.5512	(0.5478, 0.5541)
	Age at zero length	a_0	-3.616	-3.616	(-3.616, -3.615)
Mortality	*Fishing mortality rate*	f_y	0.07519	0.07424	(0.07101, 0.07620)
	Selectivity slope parameter	η	5	5.000	(5.000, 5.001)
	Age at 50% selectivity	a_{50}	3	3.003	(2.999, 3.006)
Recruitment	*Virgin recruitment*	R_0	10000000	10000000	(9986000, 10030000)
	Stock-recruit curve steepness	h	0.6	0.6021	(0.5996, 0.6042)
	Spawner biomass per recruit	φ	370082	365395	(363326, 367551)
Reference Points	*Maximum sustainable yield*	MSY	$6.862*10^{10}$	$6.843*10^{10}$	$(6.798*10^{10}, 6.873*10^{10})$
	Fishing mortality rate at MSY	F_{MSY}	0.0440	0.0445	(0.0440, 0.0450)
	Spawner biomass at MSY	B_{MSY}	$1.269*10^{12}$	$1.244*10^{12}$	$(1.233*10^{12}, 1.257*10^{12})$

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Table 2.9: Median percent deviations of parameter estimates for all three simulated species under Scenario A, when simulated length compositions contained a disproportionately high frequency of small fish, and Scenario B, when simulated length compositions contained a disproportionately high frequency of large fish.

| | | | Species 1: BSB | | | | | Species 2: GAG | | | | | Species 3: WSW | | | | |
| | | | | Scenario A | | Scenario B | | | Scenario A | | Scenario B | | | Scenario A | | Scenario B | |
Parameter		Trajectory	BASE	Level 1	Level 2	Level 1	Level 2	BASE	Level 1	Level 2	Level 1	Level 2	BASE	Level 1	Level 2	Level 1	Level 2
Growth	L_∞	traj. 1	3.03	2.47	-1.25	-7.11	-7.62	0.14	-1.00	-9.47	-2.42	-4.97	-1.01	-4.98	-17.56	-24.44	-25.83
		traj. 2	3.13	2.47	-1.58	-7.06	-6.19	0.13	-1.01	-9.26	-2.63	-4.84	-0.59	-9.18	-20.81	-17.17	-22.30
		combined	3.11	2.47	-1.39	-7.10	-6.87	0.13	-1.00	-9.37	-2.55	-4.95	-0.87	-7.15	-19.15	-21.67	-24.51
	k	traj. 1	-5.75	-5.04	0.71	29.87	61.98	-0.51	3.92	46.66	13.34	108.33	1.32	6.43	27.91	124.02	277.20
		traj. 2	-6.03	-5.12	1.44	29.10	52.97	-0.64	4.03	45.64	14.35	108.33	0.75	13.42	36.92	56.74	206.15
		combined	-6.03	-5.10	1.00	29.49	57.51	-0.63	4.00	46.12	13.99	108.33	1.13	9.68	31.66	99.12	263.00
	a_0	traj. 1	2.04	1.96	2.36	-10.97	-2.76	0.33	9.44	102.16	-129.30	-385.25	0.01	-0.04	-0.47	-1.05	-0.61
		traj. 2	1.48	1.98	2.14	-11.02	-2.88	0.95	9.75	104.15	-116.08	-440.31	0.06	0.09	0.10	-20.48	-11.37
		combined	1.60	1.97	2.22	-10.97	-2.80	0.89	9.61	103.24	-122.64	-388.13	0.02	0.00	-0.23	-5.13	-2.37
Selectivity & Mortality	η	traj. 1	0.09	0.09	0.06	1.01	0.19	0.02	0.00	0.10	2.34	2.51	0.01	0.01	0.02	0.04	0.03
		traj. 2	0.09	0.08	0.06	1.03	0.20	0.02	0.00	0.25	2.02	2.25	0.01	0.01	0.00	1.12	0.57
		combined	0.09	0.09	0.06	1.02	0.20	0.02	0.00	0.20	2.19	2.44	0.01	0.01	0.01	0.23	0.14
	a_{50}	traj. 1	3.60	3.20	2.72	26.04	34.95	0.63	-1.26	-11.51	23.03	82.58	0.11	0.12	0.59	3.44	2.48
		traj. 2	3.37	3.11	2.46	27.29	38.00	0.64	-1.36	-10.34	23.45	83.04	0.18	0.02	-0.10	49.13	15.38
		combined	3.38	3.18	2.64	26.47	36.37	0.64	-1.30	-10.73	23.10	82.73	0.15	0.07	0.28	12.42	4.29
	F_y	traj. 1	8.16	7.78	8.83	-1.61	-18.92	0.63	-0.56	1.13	-5.01	0.75	1.22	5.65	28.06	-38.40	-61.45
		traj. 2	7.69	7.67	8.20	-1.25	-16.36	0.65	-0.60	2.29	-5.44	-2.64	0.75	11.00	36.12	-27.50	-59.11
		combined	7.78	7.75	8.54	-1.41	-17.52	0.65	-0.57	1.72	-5.18	0.03	1.09	8.43	32.31	-35.52	-60.46
Recruitment	R_0	traj. 1	-1.20	-0.75	0.61	-6.13	-14.17	-0.02	0.43	6.26	-3.59	1.80	0.01	0.21	0.90	-3.81	-5.38
		traj. 2	-0.59	-0.72	0.63	-6.70	-13.34	0.03	0.34	4.84	-3.25	6.24	-0.22	2.31	7.70	-1.55	19.54
		combined	-0.66	-0.74	0.62	-6.45	-13.80	0.02	0.37	5.62	-3.50	1.94	-0.05	0.62	2.36	-2.54	-1.80
	h	traj. 1	3.37	2.95	1.25	-19.33	-27.86	0.20	-0.60	-5.08	-7.55	-36.63	0.36	1.71	8.52	-26.72	-38.47
		traj. 2	2.90	3.06	1.83	-21.09	-32.05	0.16	-0.47	-2.24	-12.71	-46.10	0.55	5.16	15.17	-31.35	-50.00
		combined	2.93	3.02	1.57	-20.44	-29.85	0.17	-0.52	-3.73	-10.09	-37.00	0.36	3.58	13.04	-28.95	-47.35
	φ_0	traj. 1	-2.12	-1.78	-2.42	8.86	23.41	-0.08	-0.34	-4.99	1.36	39.70	-1.14	-6.05	-22.57	-7.54	8.18
		traj. 2	-1.35	-1.93	-2.49	7.92	22.42	-0.09	-0.38	-5.98	1.93	59.67	-1.03	-9.14	-21.56	-0.13	49.18
		combined	-1.44	-1.84	-2.46	8.27	22.90	-0.08	-0.36	-5.52	1.72	41.53	-1.10	-7.98	-21.88	-3.88	10.53

Table 2.10: Median percent deviations of estimated biological reference points, current stock status measures, minimum thresholds and relative indicators of stock status for all three simulated species under Scenario A, when simulated length compositions contained a disproportionately high frequency of small fish, and Scenario B, when simulated length compositions contained a disproportionately high frequency of large fish.

| | | Species 1: BSB | | | | | Species 2: GAG | | | | | Species 3: WSW | | | | |
| | | | Scenario A | | Scenario B | | | Scenario A | | Scenario B | | | Scenario A | | Scenario B | |
		BASE	Level 1	Level 2	Level 1	Level 2	BASE	Level 1	Level 2	Level 1	Level 2	BASE	Level 1	Level 2	Level 1	Level 2
Benchmarks																
MSY	*traj. 1*	-0.13	-0.12	-0.22	3.61	11.80	-0.01	-0.04	-0.76	5.70	10.85	-0.28	-1.51	-3.55	-2.34	2.00
	traj. 2	0.03	0.07	0.12	0.02	1.97	-0.01	0.07	0.76	1.54	-4.62	-0.31	0.68	4.81	-10.21	-7.78
	combined	0.01	-0.05	0.00	1.72	8.38	-0.01	0.04	-0.07	4.07	10.19	-0.29	-0.33	0.25	-6.97	-5.12
F_{MSY}	*traj. 1*	7.04	6.46	6.71	17.84	26.10	0.40	-0.40	-1.19	22.33	41.50	1.14	4.55	22.73	-18.18	-32.95
	traj. 2	6.14	7.04	7.77	11.54	8.92	0.40	0.00	3.56	9.49	-1.58	1.14	12.50	36.36	-26.70	-59.09
	combined	6.38	6.71	7.36	14.24	16.37	0.40	0.00	1.19	15.61	39.13	1.14	7.95	31.82	-22.73	-49.43
B_{MSY}	*traj. 1*	-3.11	-2.52	-2.82	18.14	38.09	-0.21	-0.20	-3.93	4.36	65.16	-1.94	-7.85	-29.09	1.77	27.69
	traj. 2	-2.03	-2.87	-3.07	17.79	40.88	-0.23	-0.42	-6.38	7.12	101.86	-1.79	-13.29	-31.28	13.73	90.97
	combined	-2.24	-2.65	-3.03	17.84	39.06	-0.22	-0.37	-5.49	6.50	66.40	-1.86	-11.03	-30.48	7.35	34.52
Current stock estimates																
F_{cur}	*traj. 1*	10.56	10.15	11.08	-6.71	-26.69	0.71	-0.56	2.15	-7.55	-3.49	1.42	6.78	32.85	-41.42	-63.05
	traj. 2	6.17	6.31	6.48	2.61	-8.22	0.64	-0.61	1.10	-4.04	3.88	1.04	12.75	38.98	-30.83	-60.61
	combined	6.85	9.19	8.53	-1.17	-17.53	0.65	-0.58	1.53	-5.57	-3.09	1.25	10.20	35.38	-37.58	-62.04
B_{cur}	*traj. 1*	-4.53	-4.23	-4.84	32.37	79.18	-0.37	0.02	-6.19	19.16	83.42	-1.97	-9.05	-33.27	51.44	117.74
	traj. 2	-2.87	-2.98	-3.27	19.90	48.68	-0.39	0.11	-4.61	13.61	61.20	-1.22	-16.41	-38.55	42.12	121.25
	combined	-3.20	-4.04	-4.06	26.71	66.04	-0.38	0.07	-5.34	17.44	81.69	-1.64	-12.79	-35.71	47.87	118.83
Limit reference points																
$MFMT$	*traj. 1*	7.04	6.46	6.71	17.84	26.10	0.40	-0.40	-1.19	22.33	41.50	1.31	3.84	16.84	12.05	2.02
	traj. 2	6.14	7.04	7.77	11.54	8.92	0.40	0.00	3.56	9.49	-13.04	1.14	11.36	29.78	-23.28	-59.09
	combined	6.38	6.71	7.36	14.24	16.37	0.40	0.00	1.19	15.61	39.13	1.29	6.62	20.70	-15.17	-52.27
$MSST$	*traj. 1*	-3.11	-2.52	-2.82	18.14	38.09	-0.21	-0.20	-3.93	4.36	65.16	-1.94	-7.85	-29.09	1.77	27.69
	traj. 2	-2.03	-2.87	-3.07	17.79	40.88	-0.23	-0.42	-6.38	7.12	101.86	-1.79	-13.29	-31.28	13.73	90.97
	combined	-2.24	-2.65	-3.03	17.84	39.06	-0.22	-0.37	-5.49	6.50	66.40	-1.86	-11.03	-30.48	7.35	34.52
Relative indicators of stock status																
$F_{cur}/MFMT$	*traj. 1*	3.41	2.89	3.31	-20.18	-41.23	0.03	-0.26	3.13	-23.47	-29.91	-0.25	1.66	11.94	-46.78	-63.56
	traj. 2	-0.48	-0.73	-0.74	-8.35	-15.54	0.10	-0.51	-2.06	-11.95	5.65	-0.46	1.23	4.91	-8.76	-6.13
	combined	0.31	2.07	0.86	-13.78	-33.30	0.07	-0.47	0.88	-17.78	-27.47	-0.35	1.57	7.42	-24.04	-20.89
$B_{cur}/MSST$	*traj. 1*	-1.78	-1.55	-1.67	12.59	29.95	0.02	0.26	-2.30	20.14	24.71	0.20	-0.84	-5.40	48.67	71.33
	traj. 2	-0.71	-0.27	-0.40	1.95	6.04	-0.09	0.49	1.63	9.60	-7.63	0.60	-3.05	-10.49	26.13	19.60
	combined	-0.84	-1.24	-0.95	7.71	19.76	-0.07	0.42	-0.44	16.36	21.66	0.39	-1.59	-6.98	40.94	53.69

Table 2.11: Projection model estimates for base populations and stocks estimated for Scenario A and B. The first two columns shows the percentage of populations with "declining" stocks and all stocks that were estimated to be below the minimum threshold, MSST, in year 40 of the assessment model. In subsequent columns, the recovery time for "declining" populations under each regulatory alternative is presented. Standard deviations that are larger than the coinciding mean recovery time occurred in cases where the majority of projected populations were initialized above MSST.

		% of *declining* stocks < MSST	% of *all* stocks < MSST	Recovery Time				
				Alternative 1	Alternative 2	Alternative 3	Alternative 4	Alternative 5
BASE	*BSB*	0%	0%	25.9 ± 16.5 yrs	18.3 ± 7.1 yrs	3.1 ± 2.9 yrs	0.8 ± 1.0 yrs	0.6 ± 0.7 yrs
	GAG	0%	0%	22.3 ± 18.4 yrs	17.9 ± 9.0 yrs	1.7 ± 2.6 yrs	0.6 ± 1.2 yrs	0.4 ± 0.8 yrs
	WSW	88%	48%	38.0 ± 7.5 yrs	38.3 ± 6.6 yrs	36.9 ± 7.6 yrs	33.5 ± 8.2 yrs	30.0 ± 8.6 yrs
Scenario A	*BSB*	0%	0%	26.0 ± 15.4 yrs	18.6 ± 7.1 yrs	3.2 ± 3.2 yrs	0.8 ± 1.1 yrs	0.6 ± 0.7 yrs
	GAG	0%	0%	28.9 ± 15.0 yrs	18.6 ± 9.7 yrs	2.7 ± 3.6 yrs	1.2 ± 1.8 yrs	0.9 ± 1.3 yrs
	WSW	96%	84.5%	39.7 ± 2.5 yrs	39.5 ± 2.7 yrs	35.8 ± 5.3 yrs	31.3 ± 6.8 yrs	27.7 ± 7.6 yrs
Scenario B	*BSB*	0%	0%	2.2 ± 7.3 yrs	10.6 ± 6.8 yrs	0.9 ± 2.0 yrs	0.0 ± 0.0 yrs	0.0 ± 0.0 yrs
	GAG	0%	0%	10.7 ± 15.2 yrs	10.7 ± 10.6 yrs	2.9 ± 7.3 yrs	1.7 ± 5.3 yrs	1.3 ± 4.3 yrs
	WSW	39%	24%	35.4 ± 11.7 yrs	36.0 ± 9.8 yrs	34.1 ± 11.9 yrs	31.9 ± 12.9 yrs	29.5 ± 13.6 yrs

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Figure 2.1: Simulated length frequency distributions for all three species for Scenario A (left column) and Scenario B (right column). Histograms of the original, unbiased length composition data are overlayed with biased length frequencies. Dashed lines represent lower levels of bias while dotted lines represent more intense biases in the data.

Scenario A   **Scenario B**
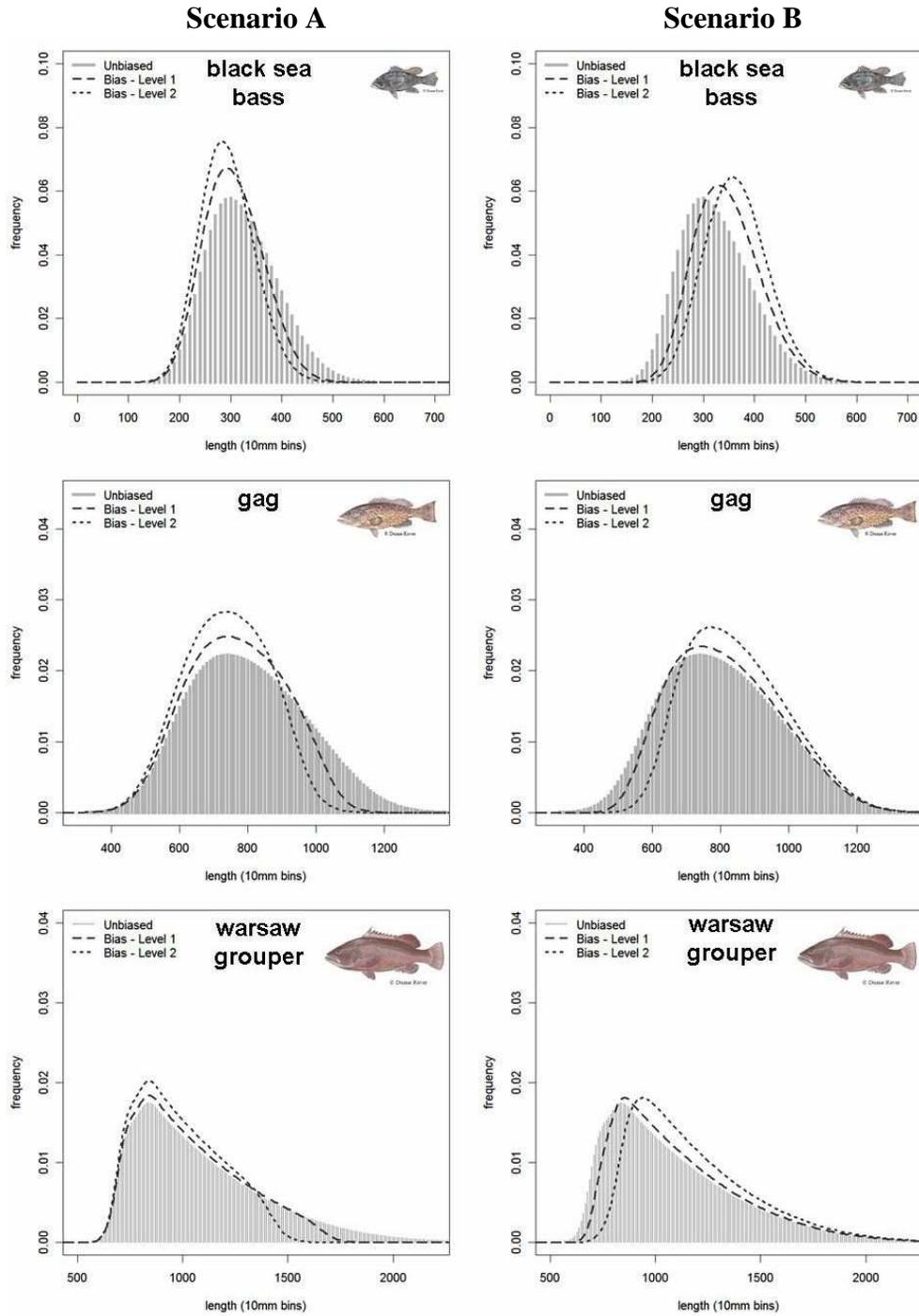
Figure 2.2: Trajectories of fishing mortality rates used to simulate declining (top) and recovering (bottom) populations forward across the time series. Dark, thicker grey lines represent annual fishing mortalities before stochasticity errors have been incorporated. Light grey lines represent stochastic trajectories of fishing mortality, and were computed from the same matrix of uniform errors.

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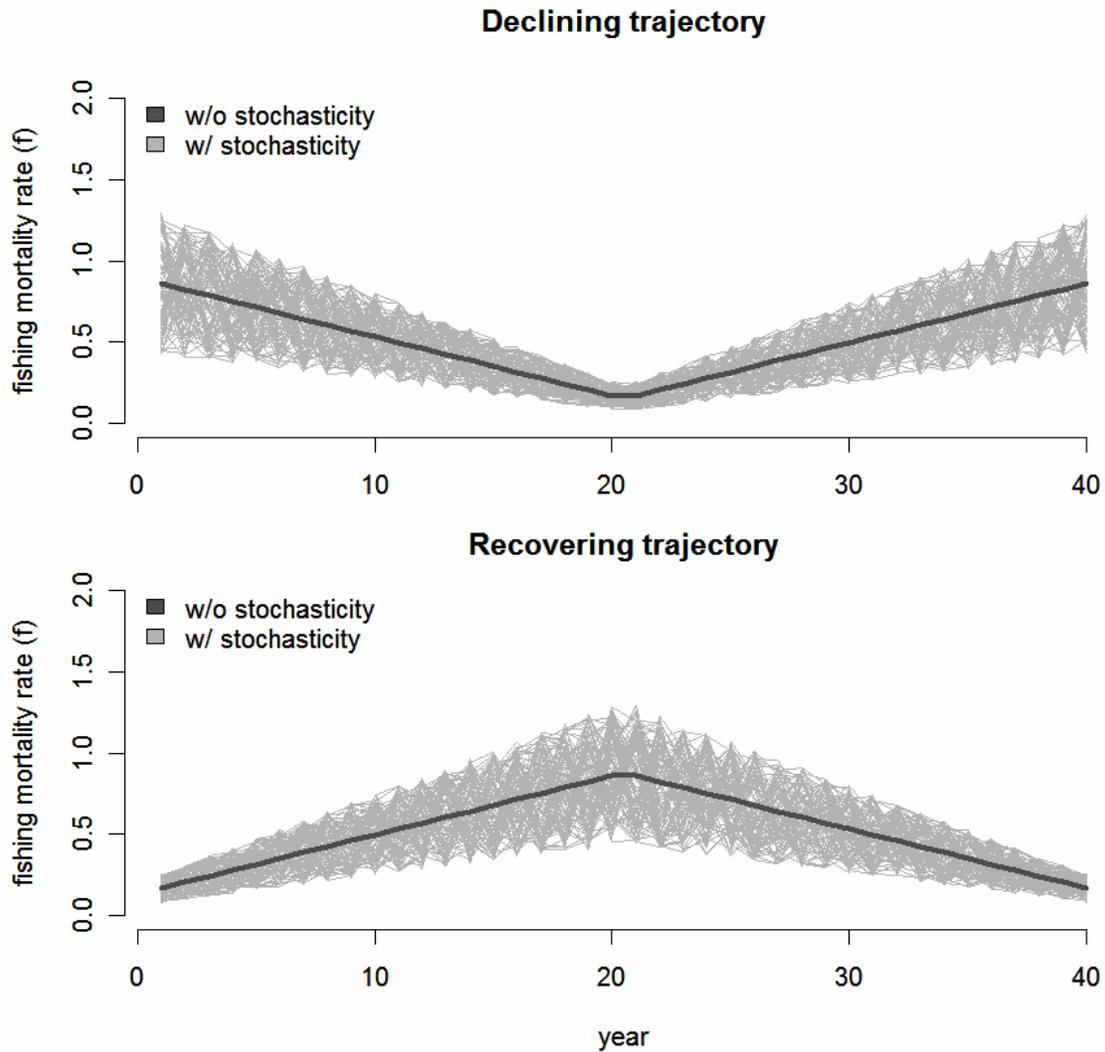
Figure 2.3: Growth curves estimates for each species under scenarios A and B. a) The estimated growth curve under Scenario A decreased in height due to underestimates in the maximum length parameter, L. This reduced the average length of medium and older fish. b) The growth coefficient was dramatically overestimated in Scenario B, causing the growth curve to become steeper. As a result, fish in expected model populations reached a large size early on in their development.

Length-at-age

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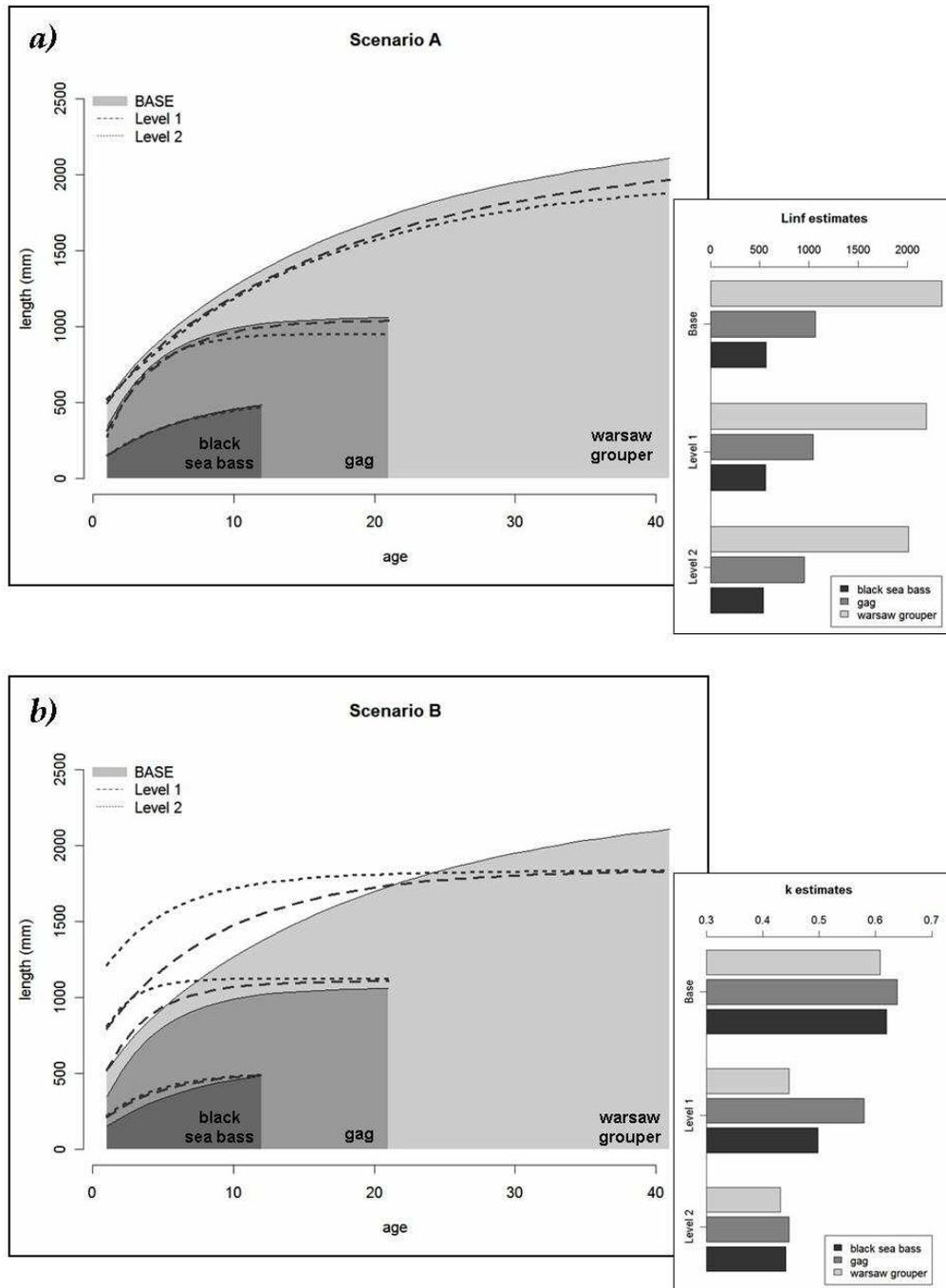
Figure 2.4: Average weight-at-age estimated by the model under scenarios A and B. a) The average weight of older fish decreased in Scenario A. b) In Scenario B, the average weight of younger fish in expected model populations increased.

Weight-at-age

122
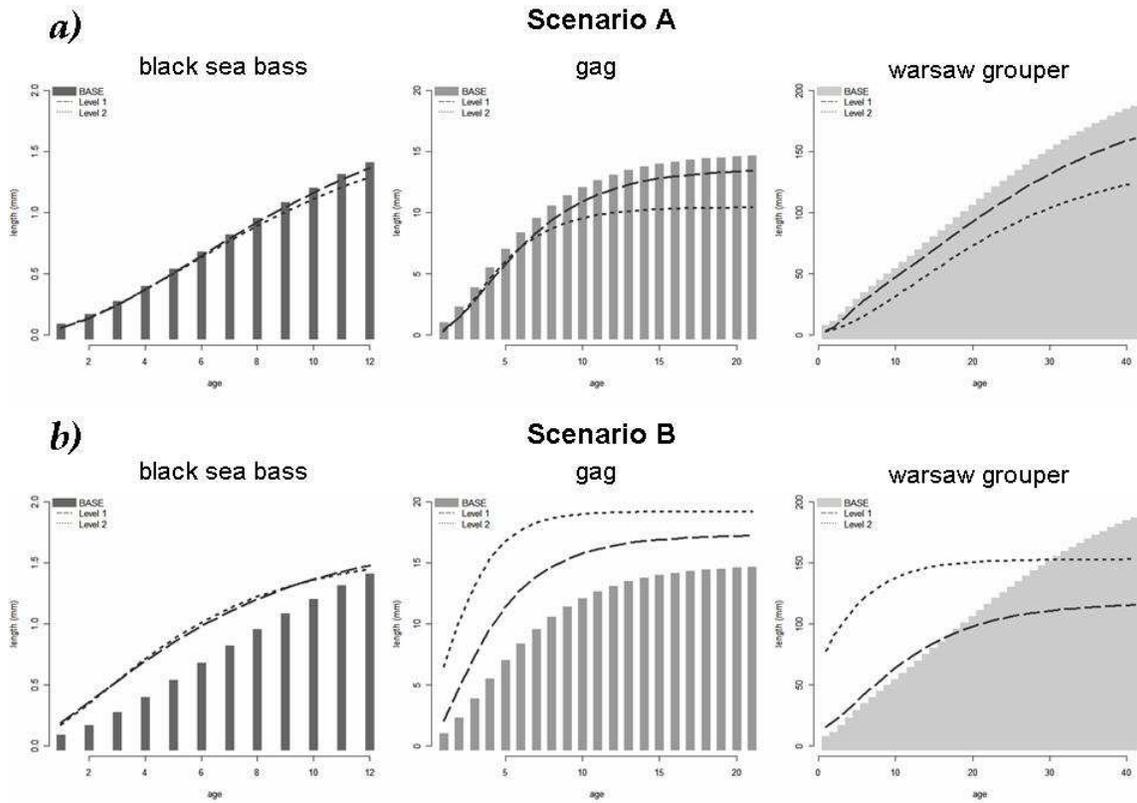
Figure 2.5: The simulated proportion of females in each age class that were sexually mature is represented here for each species in light grey bars. These proportions were held as known, fixed vectors in the assessment model and differed in their relationship to gear selectivity. The simulated gear selectivity-at-age is represented in the graphs below for each species by the dark lines.

Selectivity and Female Maturity

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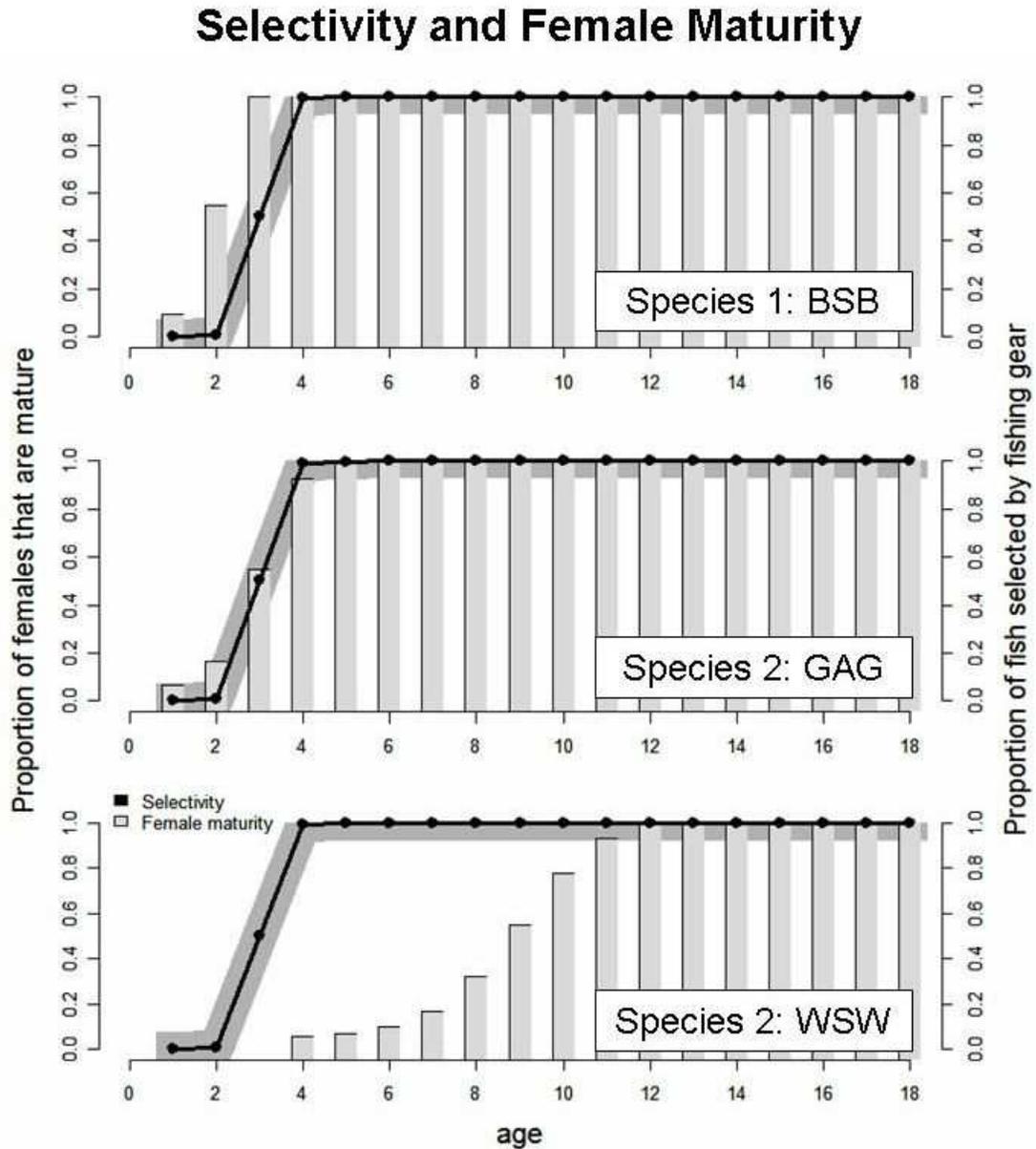
Figure 2.6: Estimated gear selectivity-at-age for each species under scenarios A and B. a) Scenario A caused very little change in the estimated parameters for gear selectivity. b) Scenario B produced overestimates of the selectivity parameter a_{50}, which shifted the selection curve towards older fish.
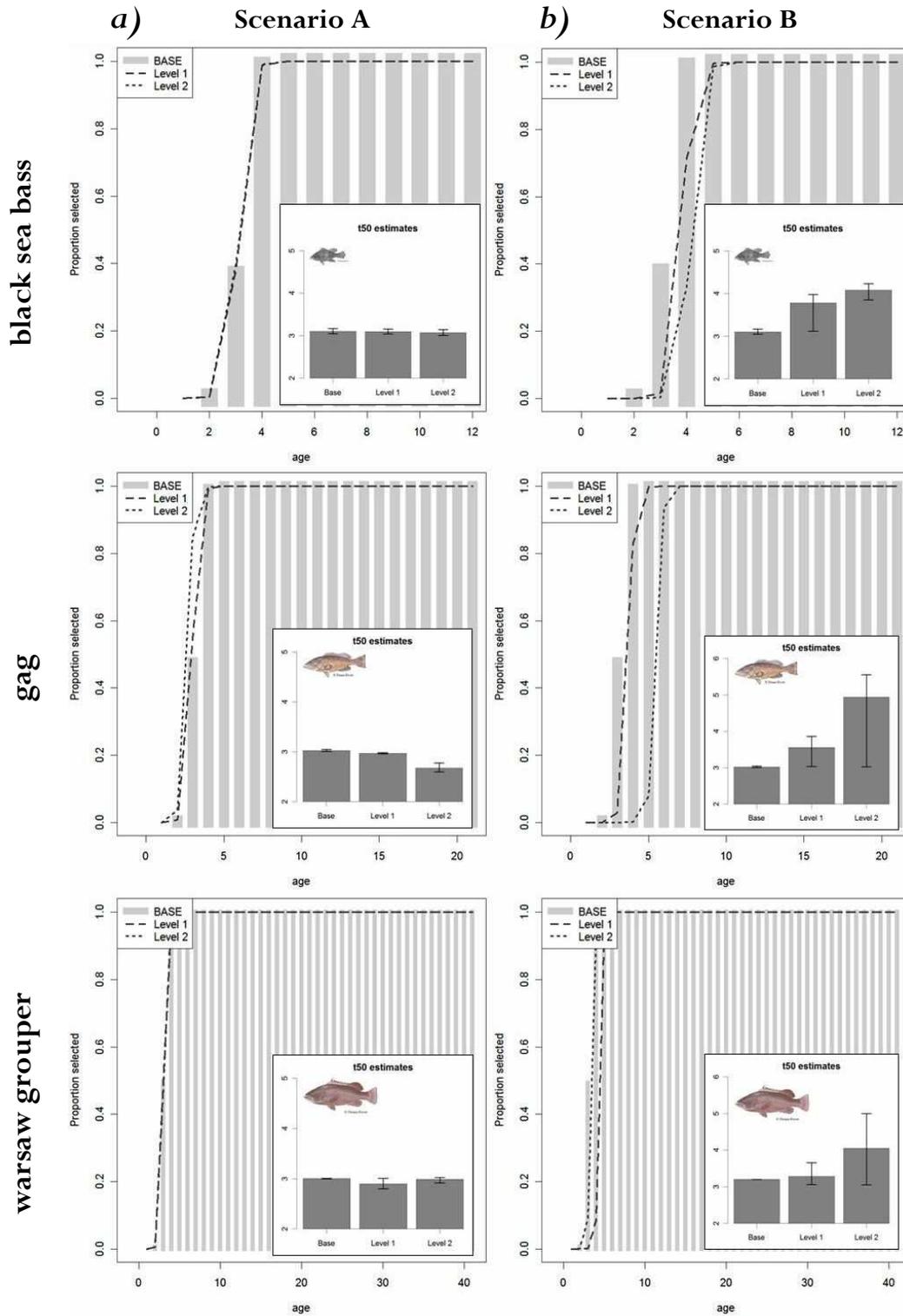
Figure 2.7: Estimated annual fishing mortality rates for all three case study species. a) Fishing mortalities for WSW tended to increase slightly under Scenario A, but did not shift for GAG or BSB. b) In Scenario B, fishing mortalities tended to decrease, particularly for WSW. Median simulated values are represented by dashed dark gray lines.
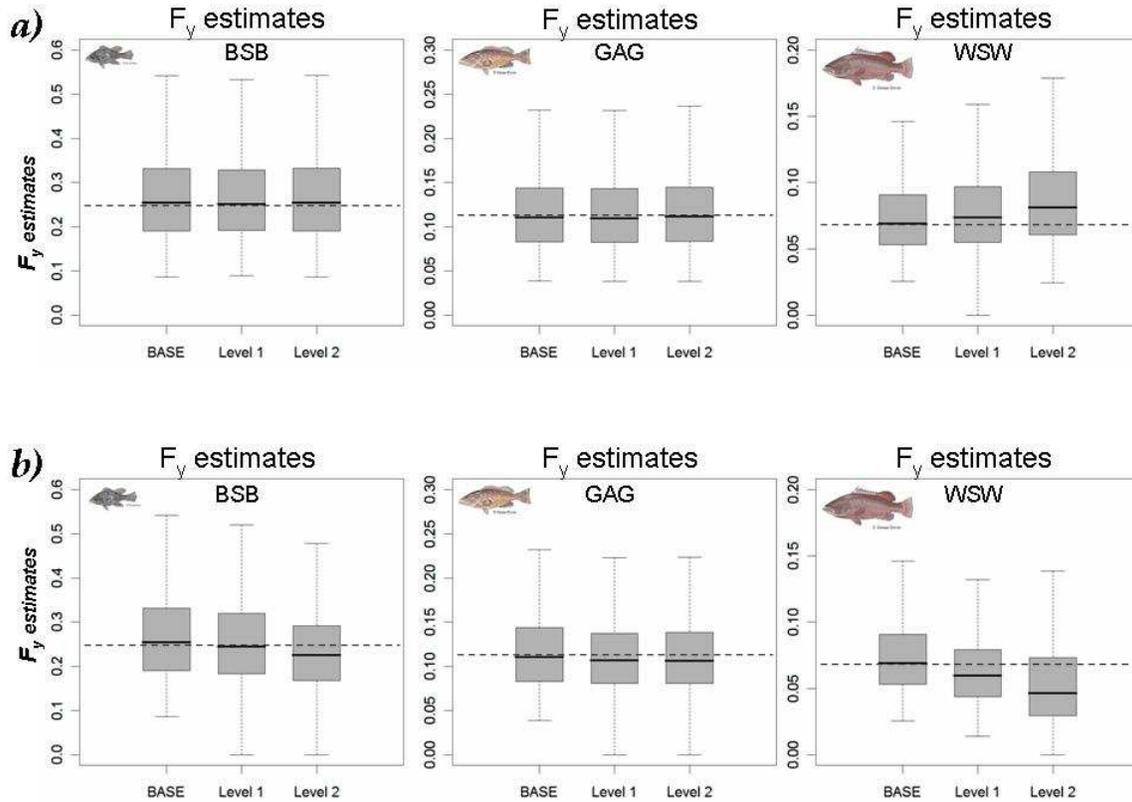
Figure 2.8: Stock-recruit curves for three different levels of spawner biomass per recruit. Longer-lived species with a higher SPR would have a more gradual stock-recruit curve (represented by the darker green line). Recruitment for such a species would consequently be computed from the slope region of the curve. On the other hand, the stock-recruit curve for shorter-lived species with a lower SPR would be steeper (represented by the light green line). Annual recruitment for this species would typically be calculated from the asymptotic region of the curve.

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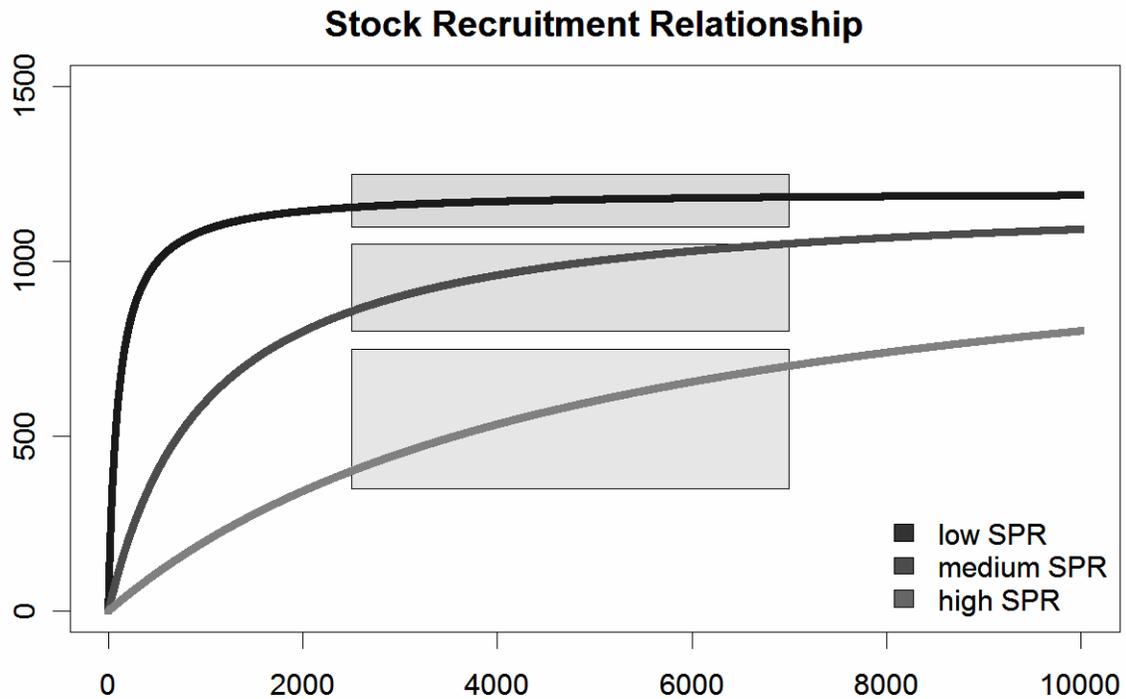
Figure 2.9: Spawner biomass per recruit and spawning stock biomass under each scenario. Scenario A (top) caused spawner biomass and spawner biomass per recruit to decrease, particularly for WSW. This was due to the decreases in both the average weight and the expected abundance of older fish. Conversely, Scenario B (bottom) caused increases in the spawner biomass and spawner biomass per recruit, as the average weight and abundance of older fish increased under this scenario.
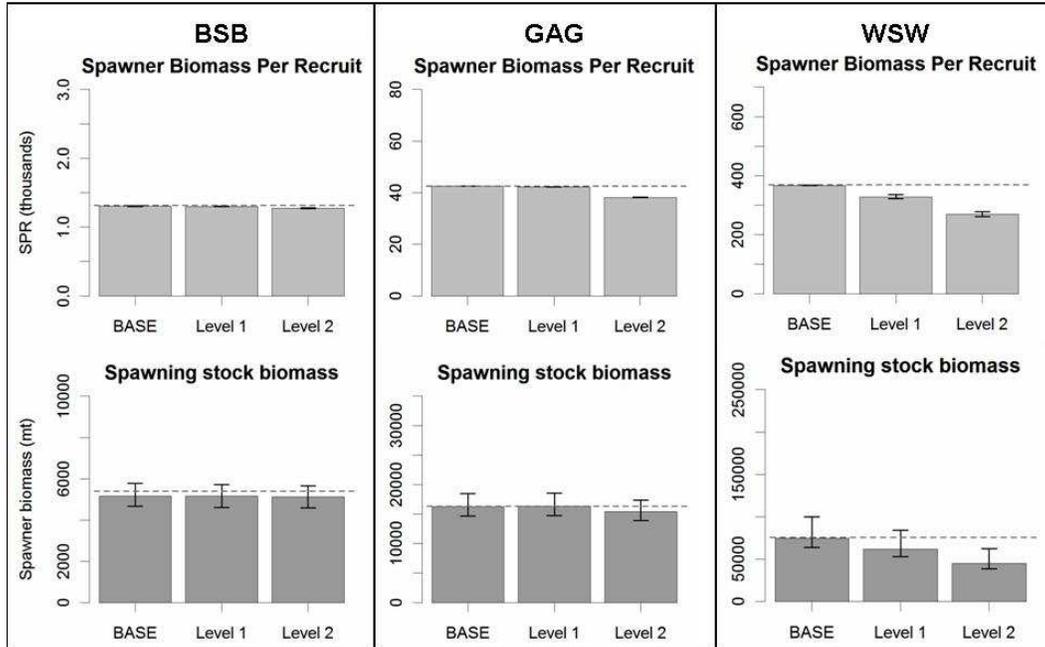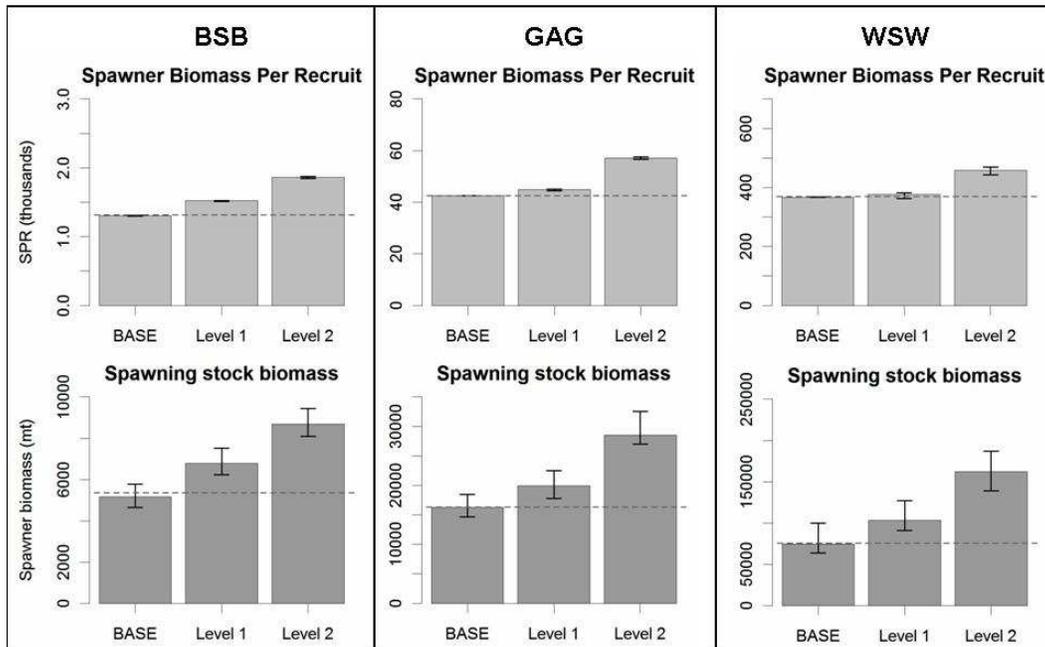
Figure 2.10: Expected stock-recruit curve and median annual recruitment under Scenario A. Scenario A caused very little change in the stock-recruit relationship for BSB (top), but caused the average recruitment relative to spawner biomass in GAG and WSW to increase (middle and bottom).
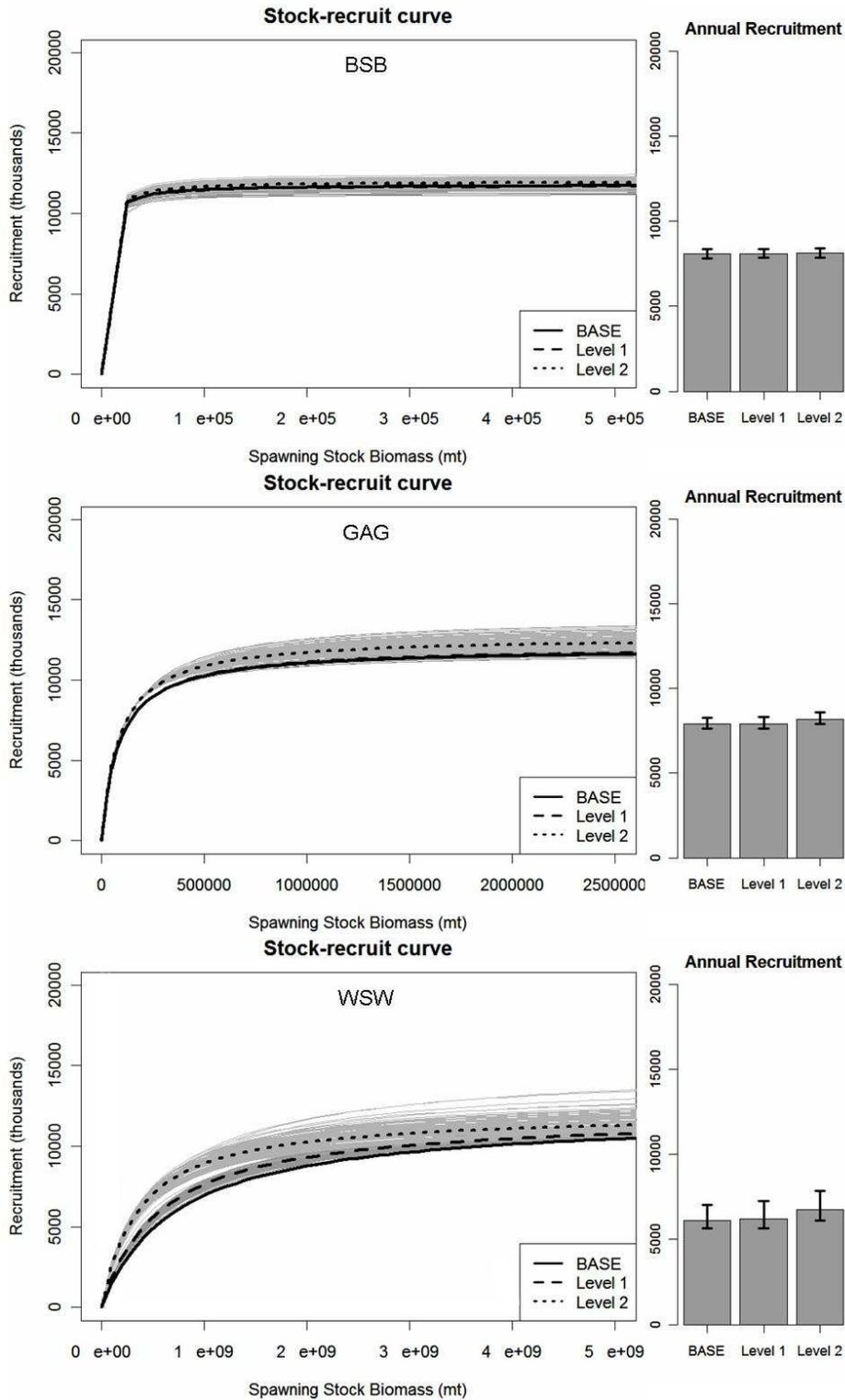
Figure 2.11: Expected stock-recruit curve and median annual recruitment under Scenario B. Scenario B caused annual recruitment to decrease for all three simulation species. This occurred due to decreases in the spawner biomass per recruit and the estimated curve steepness parameter.

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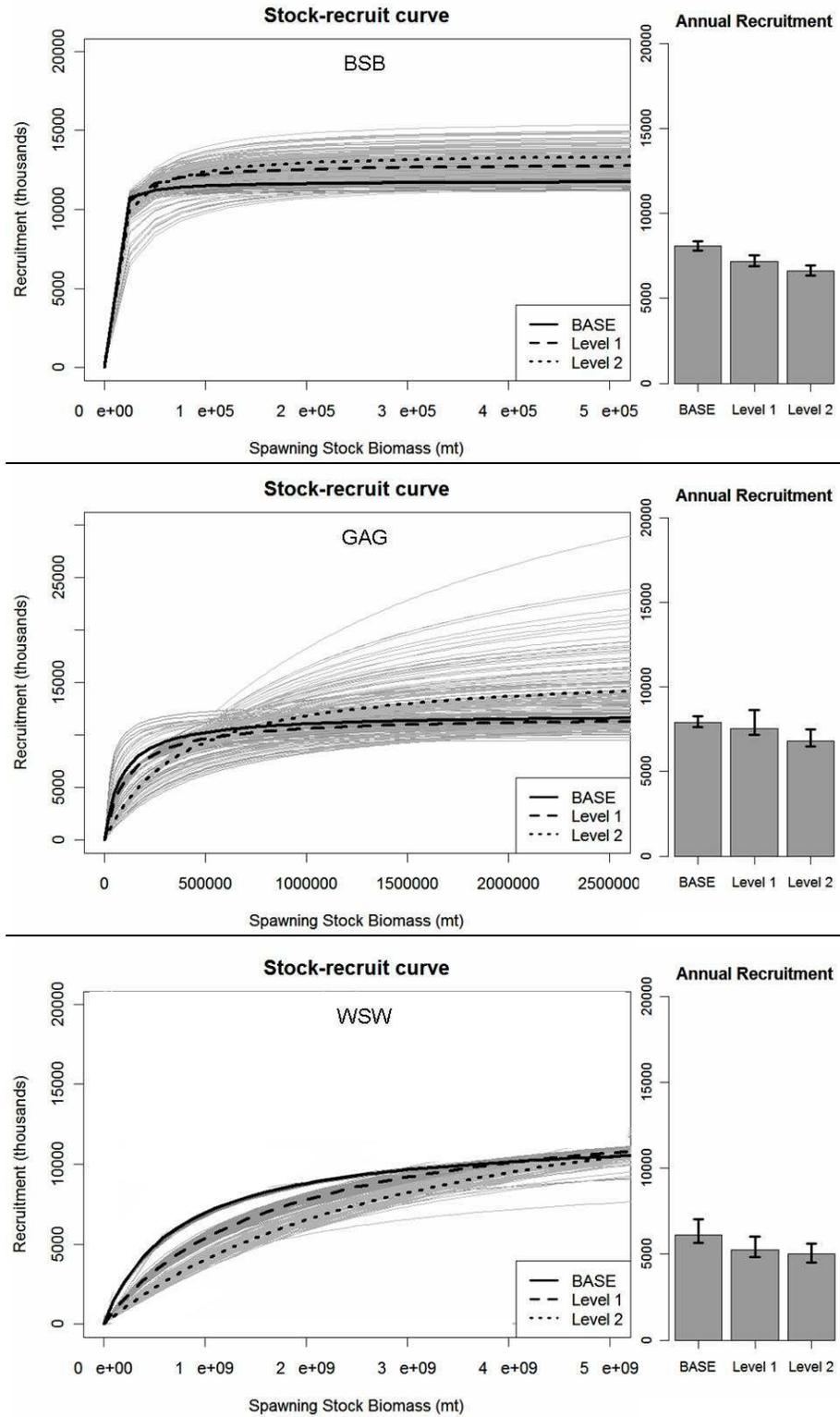
Figure 2.12: Median abundance-at-age (darker curves) and catch-at-age (lighter curves) under Scenarios A & B. Scenario A (top) caused the abundance of young fish to be slightly overestimated, producing a coinciding in increase in the height of catch-at-age curve. Scenario B (bottom) caused the abundance of young fish to decrease, but allowed also fewer old fish survived into older age classes, causing the catch-at-age curve to decrease in height.
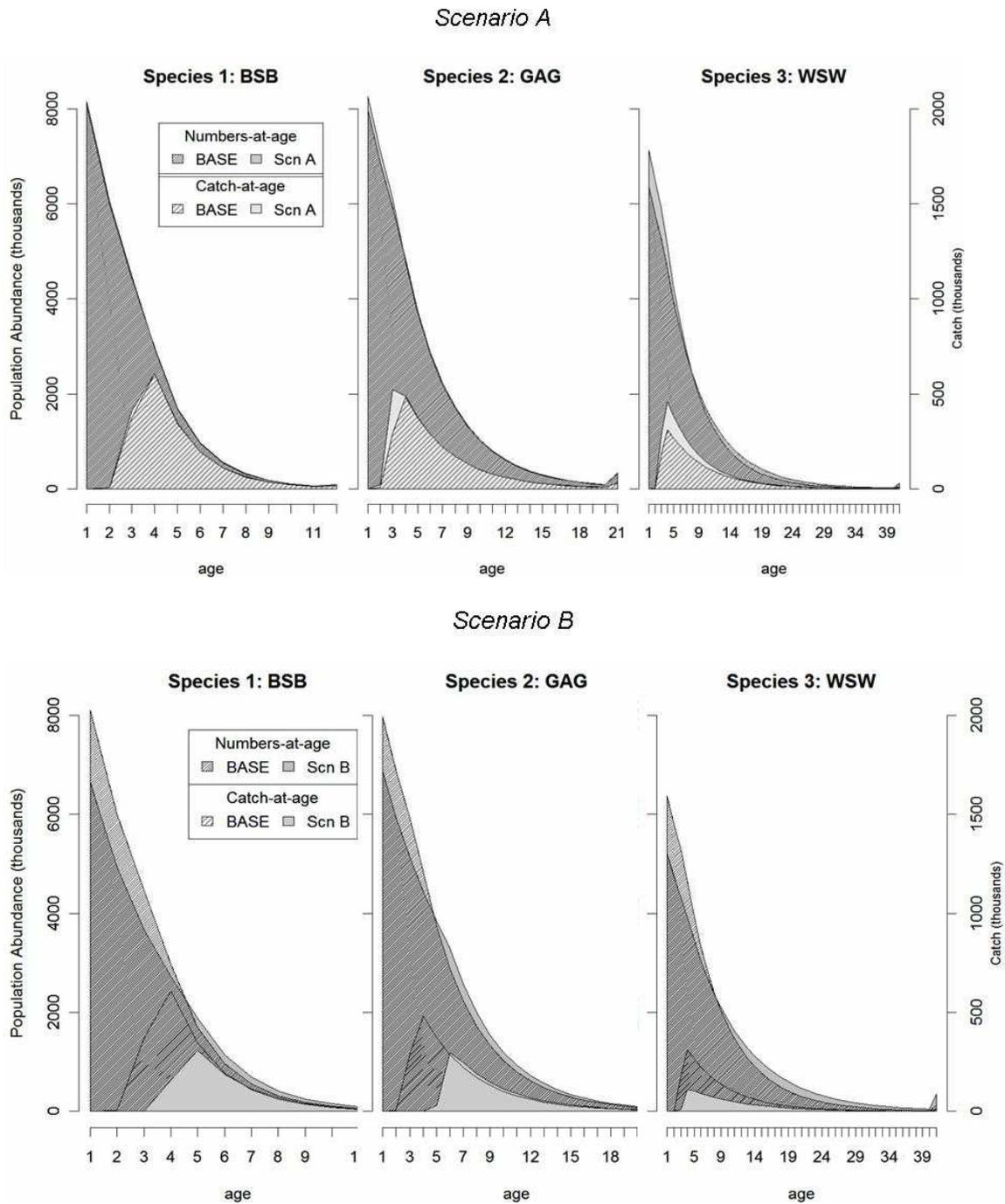
Figure 2.13: Relative indicators of stock status under Scenario A for all three simulation species. Scenario A generally caused relative fishing mortality to increase and relative spawning stock biomass to decrease. This trend was most evident in model runs for WSW (bottom).

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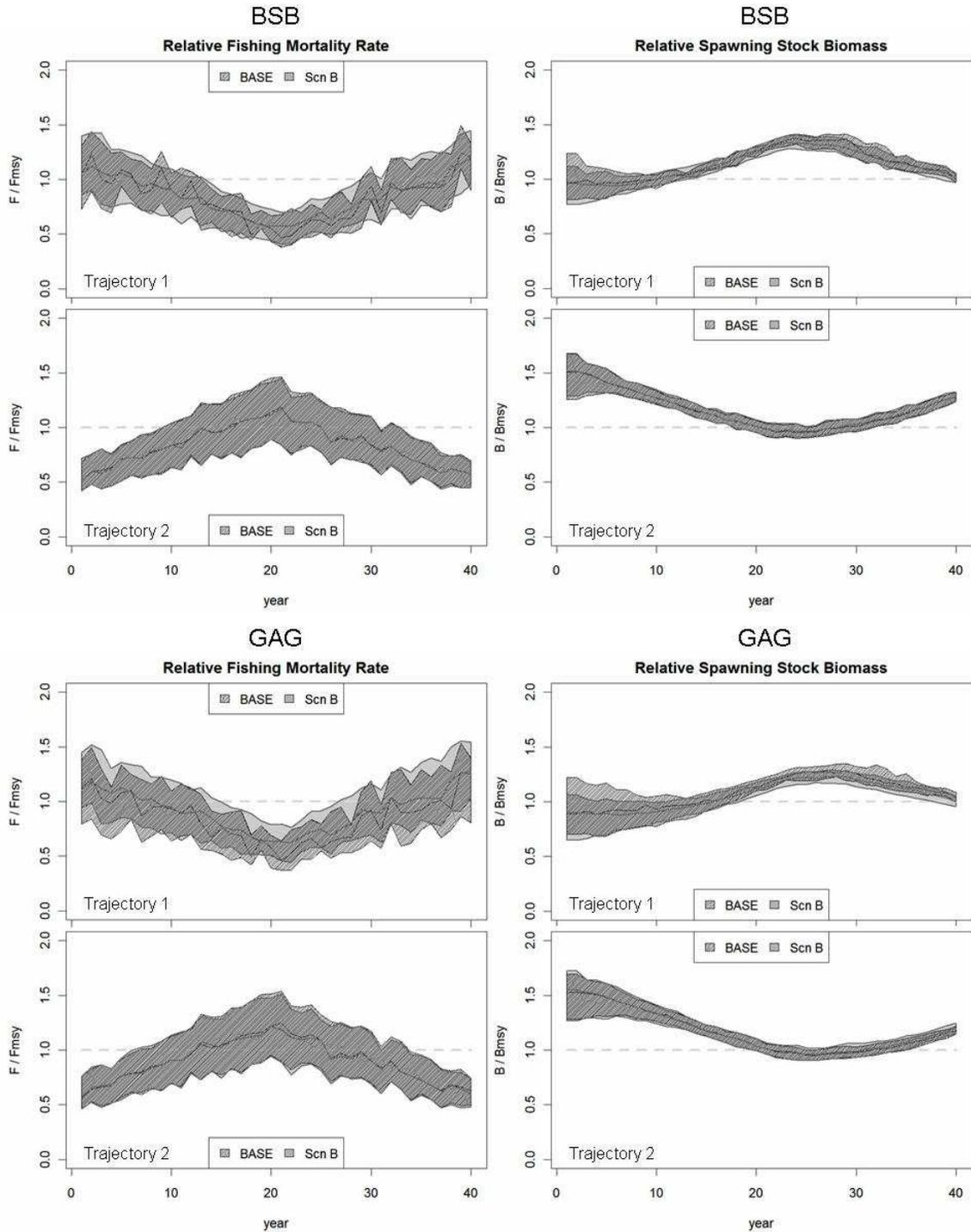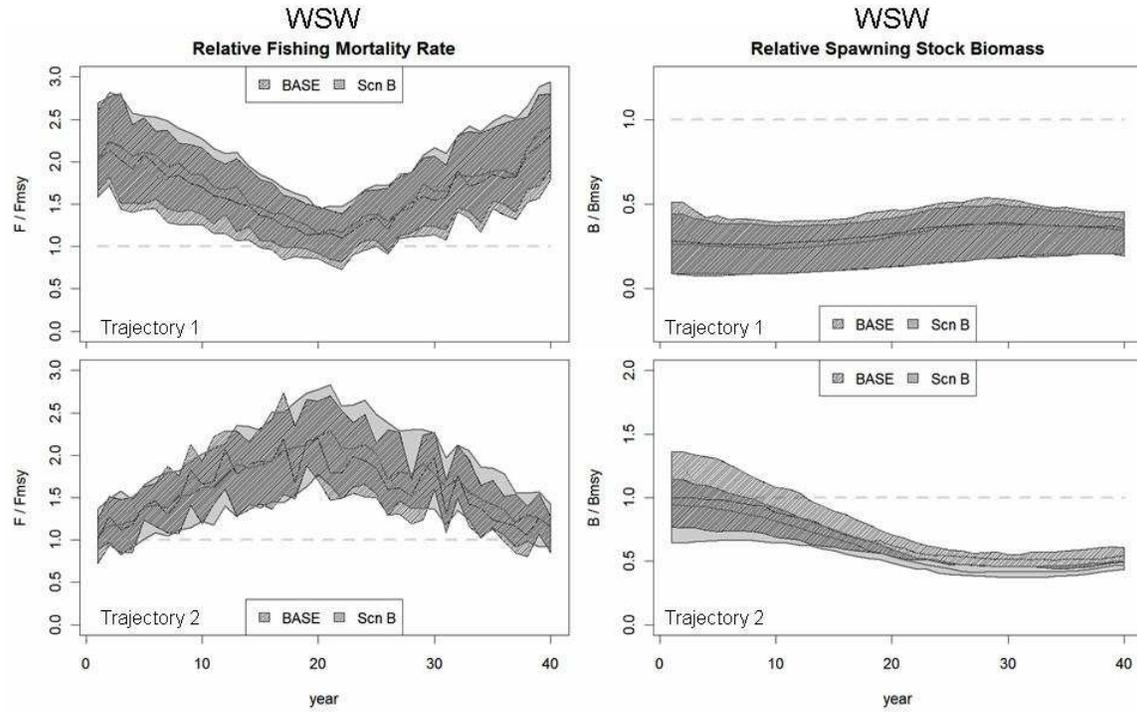
Figure 2.14: Relative indicators of stock status under Scenario B for all three simulation species. Scenario B caused relative fishing mortality to decrease and relative spawning stock biomass to increase.
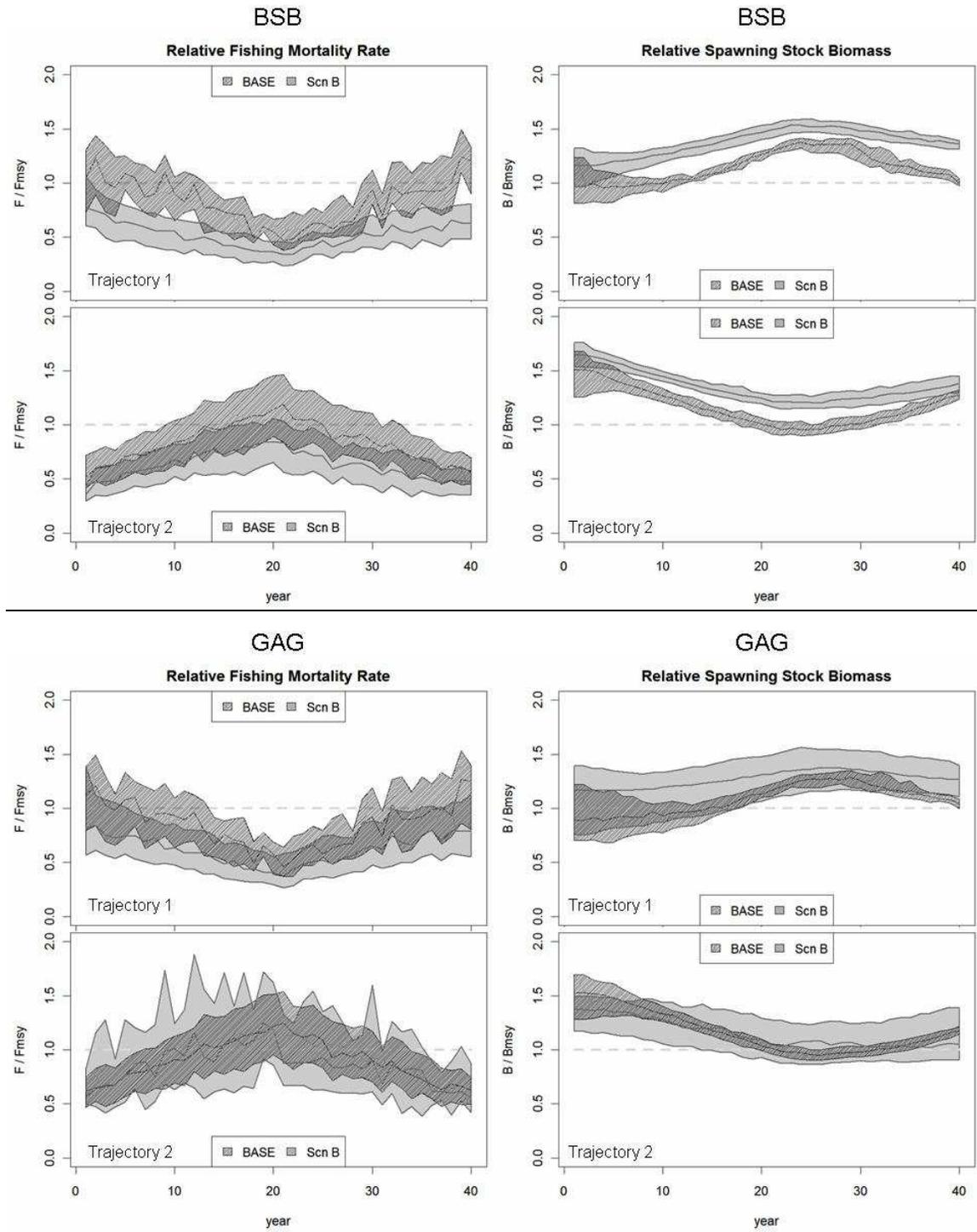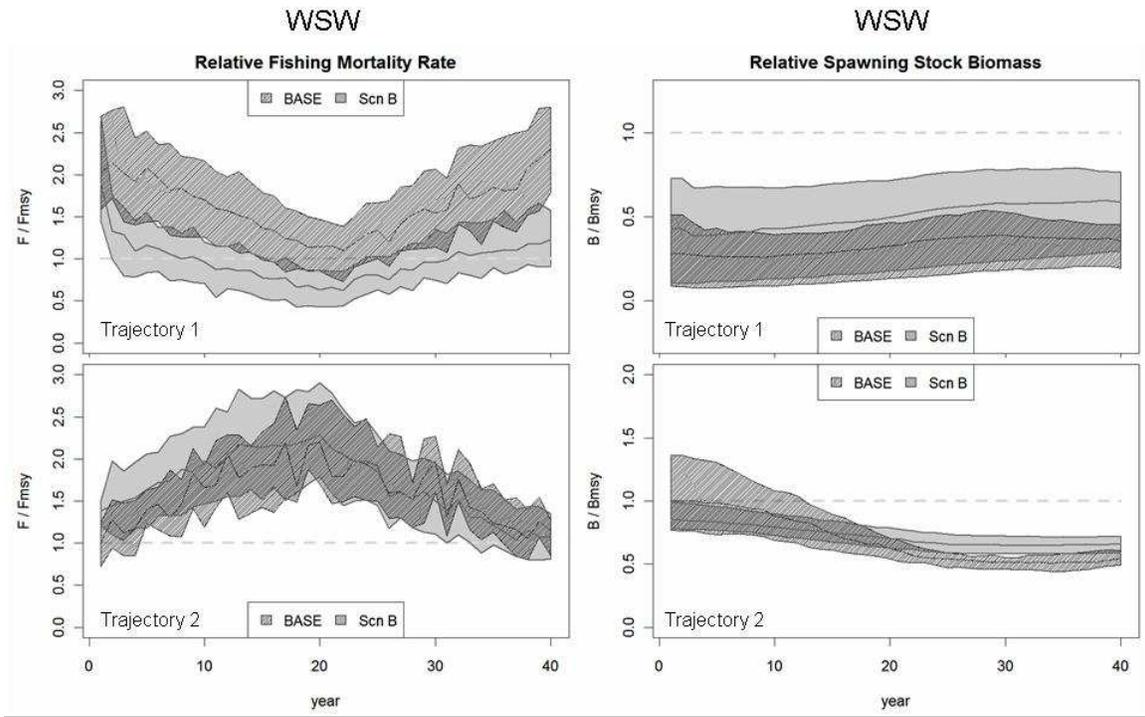
Figure 2.15: Recovery of depleted WSW under Scenario A for each of regulatory alternatives 2-5. As a result of Scenario A, projected biomass tended to be smaller than it was in actuality, but increased more rapidly as in response to changes in fishing pressure. Similar, but less dramatic trends were observed for BSB and GAG projections.

**Projected Relative Spawning Stock Biomass**
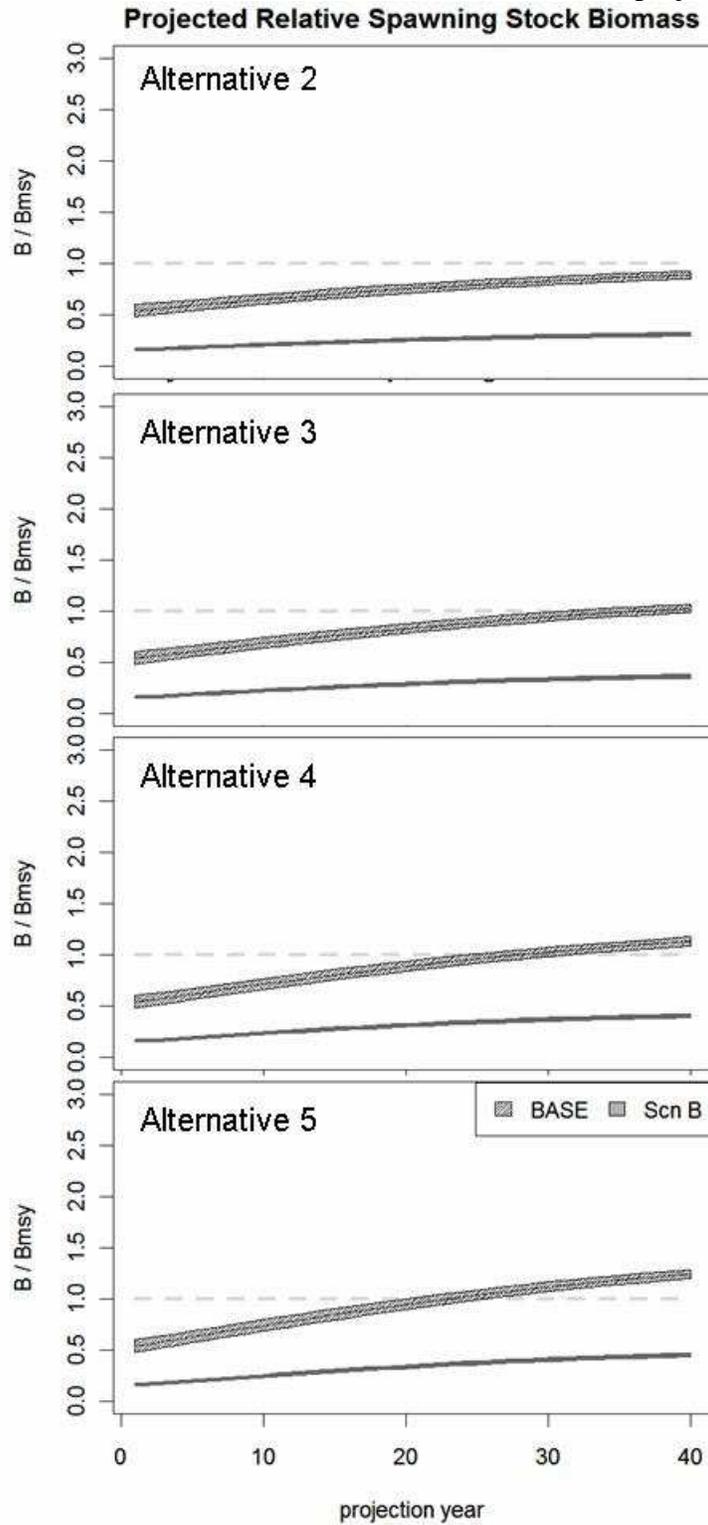
Figure 2.16: Recovery of depleted WSW under Scenario B for each of regulatory alternatives 2-5. As a result of Scenario B, projected biomass tended to be larger than it was in actuality, but increased more slowly as in response to changes in fishing pressure. Similar, but less dramatic trends were observed for BSB and GAG projections.

Projected Relative Spawning Stock Biomass
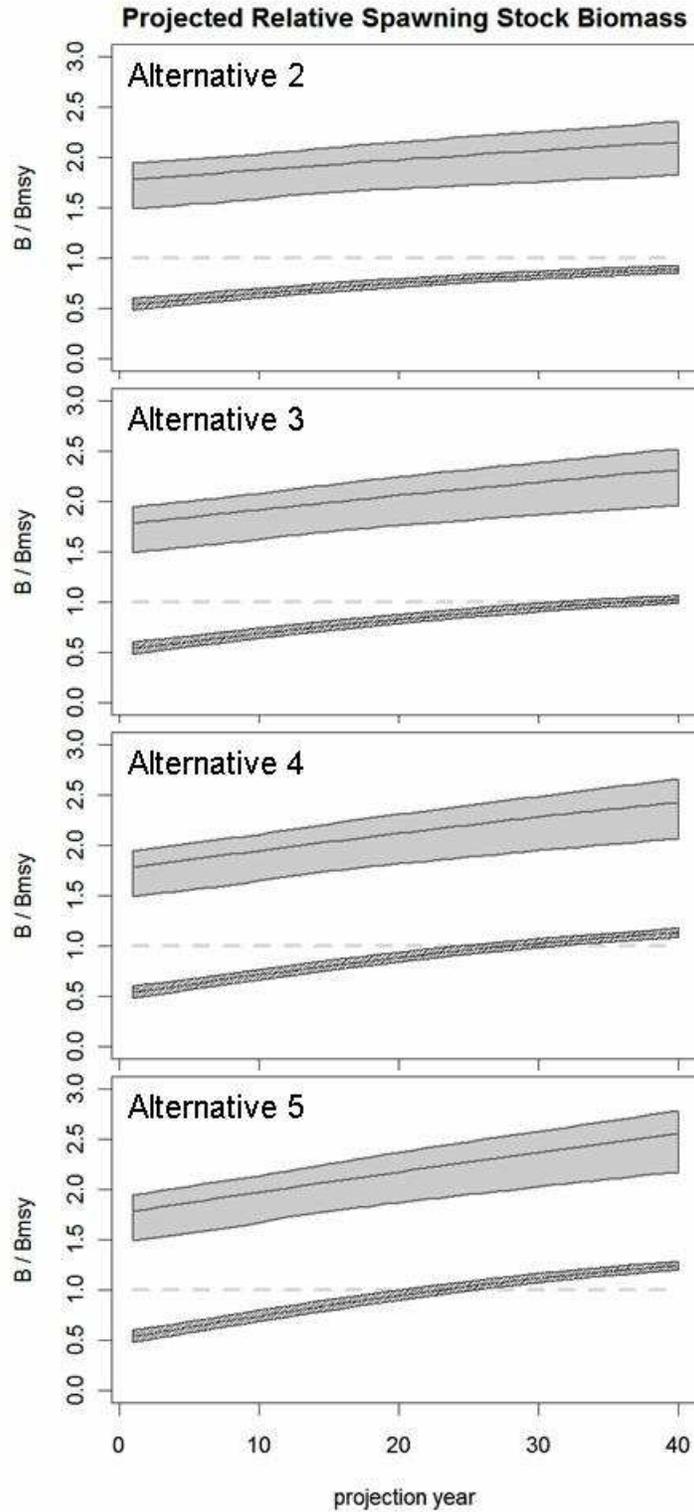
VITA

Eliza Heery, the daughter of Loretta Lowrey and Shepherd Heery, was born in Berkeley, California in 1983. She grew up in the San Francisco Bay Area and attended Marin Academy High School in San Rafael, California, while working at the California Academy of Sciences in San Francisco. Eliza began college at the University of Miami in Florida as a Marine Science and Biology major. As a sophomore, she participated in the East/West Marine Biology Program through Northeastern University and then worked as an intern in the Marine Science Department at Chulalongkorn University in Bangkok, Thailand. She completed her Bachelors degree in Biology at Emory University in Atlanta, Georgia, before entering the Fisheries and Wildlife graduate program at Virginia Tech in 2004. Eliza defended her Master's thesis on April 25, 2007.