CHAPTER 1: MODEL STRUCTURE AND FORMULATION

1.0 BACKGROUND – THE ICES MSVPA APPROACH

The Multispecies Virtual Population Analysis (MSVPA) approach was developed within International Council for the Exploration of the Seas (ICES) as a multispecies extension of cohort analysis or virtual population analysis (VPA). The basic approach was initially described by Pope (1979) and Helgason and Gislason (1979) and later modified and described in Gislason and Helgason (1985). The approach can be viewed essentially as a series of single-species virtual population analysis (SSVPA) models that are linked by a simple feeding model to calculate natural mortality rates. The system of linked single-species models is run iteratively until the predation mortality (M2) rates converge. The basic model is therefore performed in two primary iteration loops. First, all single-species VPAs are run to calculate population size at all ages for predators and prey, then predation mortality rates are calculated for all age classes of each species based upon the simple feeding model. The single-species VPAs are run again using the calculated M2 rates, and this iteration is repeated until convergence (reviewed in Magnusson, 1995). The single-species VPAs for the ICES model employ the basic catch equation and VPA approach as described in Gulland (1983) using input values for terminal fishery mortality rates (F) that are generally derived from single-species assessments.

Predator diets, and therefore prey consumption and predation mortality, are driven by feeding selectivity parameters that are assumed constant for a given predator-prey combination. Actual values of selectivity indices may be derived from a simplified feeding model. In the original formulation of the model, these indices were not well defined and the choice of selectivity parameters was arbitrary. The MSVPA approach is therefore implemented by including diet information and an additional iteration loop to solve for appropriate values of the selectivity indices. Diet data must be available for all predators and age classes in a particular year of the time series. To solve for the selectivities in the year where diet data are available, it is necessary to know the abundance (and biomass) of all prey in that year. A third iteration loop is therefore imposed where the MSVPA calculations are performed with arbitrary starting values for selectivity parameters, then the selectivities are solved for based upon diet information, and the iteration loops are repeated with the derived selectivity values until convergence. It is assumed that selectivity values are constant through time and independent of prey abundance.

The MSVPA formulation gives rise to a type-II functional feeding (Holling, 1965) response between prey abundance and predation rates. This is consistent with the interpretation that feeding selectivities are independent of prey abundance. In the case of active “switching”, where more abundant prey items are preferentially consumed and therefore selection is a function of prey abundance, a sigmoid type-III functional response would occur. While it may be desirable to explore a type-III feeding response, the solutions of the MSVPA equations become non-unique under this formulation at even moderate predation mortality rates (Hilden, 1988).

The standard MSVPA approach has been applied extensively by the ICES working group in the North Sea ecosystem. The main conclusions, as summarized in Pope (1991), are that natural mortality rates are high and variable from year to year and that predation mortality may significantly impact recruitment. In addition, changes in mesh size to increase the abundance of

older, larger fish, may result in higher predation rates and lower fishery yields. The MSVPA approach has also recently been applied to the Georges Bank fish community (Tsou and Collie, 2001) with a slightly modified expression for size selectivity and to the groundfish community of the eastern Bering Sea (Livingston and Juardo-Molina, 2000).

1.1 FORMULATION OF THE EXPANDED MSVPA (MSVPA-X)

The expanded MSVPA (MSVPA-X) approach described here builds upon the framework of the standard MSVPA by incorporating a variety of SSVPA approaches including a "tuned" VPA, modification of the consumption model, introducing a weak Type III functional feeding response, formalizing the derivation of selectivity parameters from diet data, altering the size-selectivity model, and including predators without age-structured assessment data. These additions allow a clearer definition of the input parameters used to model diets and consumption rates and improve the MSVPA equations to reflect processes controlling feeding and predation rates.

1.1.1 Single-species VPA formulation

Implementation of multiple SSVPA models allows greater flexibility in model construction to address particular data availability and the most appropriate assessment approach for each modeled species. Several forms of SSVPA are implemented in the MSVPA-X program. Some of these were included specifically to match previous assessment approaches for species considered in this application. However, for this application, all species use the XSA method.

The XSA (Shepherd, 1999) is a tuned VPA method that provides solutions for mortality rates in incomplete cohorts based upon multiple fishery-dependent and -independent abundance indices. The approach is related to the ADAPT VPA currently applied in many ASMFC single-species stock assessments. However, the ADAPT method requires extensive model building and minimization routines, resulting in a thorough statistical treatment that generally requires considerable analytical expertise and judgments of input parameters to develop the most appropriate model. While XSA does not reflect the full statistical approach of ADAPT methodology and does not require as intensive computational or model-building demands, it retains a similar theoretical basis and provides similar results. The XSA approach is therefore preferred within the MSVPA-X framework because it provides an SSVPA assessment tuned to external abundance indices that is relatively simple to execute.

The MSVPA-X implementation of XSA is identical to that described in Darby and Flatman (1994). The XSA approach includes a method described as "shrinkage to the mean F" to constrain estimates of fishery mortality rate in terminal age classes and years of the catch matrix. In general, applications not incorporating shrinkage result in unconstrained estimates of F in the last years and ages of the assessment and prevent convergence of the model. Estimates of terminal fishing mortality rates may be sensitive to values of shrinkage parameters, and the model estimates of F for a range of these parameters should be explored when implementing the XSA approach. Individual parameter descriptions are included below. For more details, please see Darby and Flatman (1994).

CV for Shrinkage Mean: This parameter controls the weighting applied to the shrinkage mean F. Large values result in lower weighting of the mean and therefore less constraint of terminal F values to the time series average F.

Number of Years for the Shrinkage Mean: In the last year of the catch matrix, estimates of F on each age class are constrained by the average F calculated over the previous N years of the assessment as determined by this parameter value.

Number of Ages for the Shrinkage Mean: In the terminal age class of each year of the catch matrix, the estimate of F on the last true age class is constrained by the average F over the previous N age classes as determined by this parameter value.

Downweight Early Years: In the calculation of shrinkage means and terminal F estimates, early years of the catch matrix are "downweighted" on the assumption that catchabilities and average F estimates in recent years are more similar to those of the terminal years. It is highly recommended that downweighting be applied when shrinkage is employed.

Select Weighting Method: Linear, Bisquare, and Tricubic downweighting can be applied in increasing order of the strength of the downweighting function. In the tricubic downweighting, early years of the time series have the least influence on estimates of terminal F.

1.1.2 Predator Consumption Model

Predation mortalities in the ICES MSVPA approach are calculated based upon a simplified feeding model developed directly from the approach described by Andersen and Ursin (1977) formulated as discrete expressions standardized to a duration of one year. Total food consumption rates in biomass for a given predator species and age class is expressed as a simple ratio of total predator weight:

$$(1.1) \qquad R_{ia} = v_{ia} w_{ia}$$

where v_{ia} is a constant ratio (biomass prey / biomass body weight) and w_{ia} is predator body weight. This constant ratio therefore does not reflect effects of food availability on feeding rates or temperature effects on predator metabolism.

In reality, food consumption rates in fish can vary strongly, particularly between seasons as a function of food availability, changing temperatures, and metabolic demands. To account for these processes, a somewhat more detailed consumption model was implemented using the Elliot and Persson (1978) evacuation rate approach within the MSVPA-X equations and including a modified functional relationship between food availability and predator consumption rates.

The daily ration, R, calculated in equation 1.1 is replaced with the consumption rate (in biomass) for predator *i*, age class *a*. Total consumption in year, *y,* for a predator during a given season, *s*, is then:

$$(1.2)\quad C_{ys}^{ia} = 24E_s^{ia} \cdot \overline{SC_s^{ia}} \cdot D_s \cdot w_{ys}^{ia} \cdot \overline{N_{ys}^{ia}},$$

where SC_s is the mean stomach contents weight relative to predator body weight in a season, D_s is the number of days in the season, w_{ys} is the average weight-at-age for the predator species, and N_{ys} is the abundance of the predator age class during the time interval. The evacuation rate (hr^{-1}) is given as:

$$(1.3)\quad E_s^{ia} = \alpha_{ia} \exp(\beta_{ia} \cdot temp_s),$$

with *temp* equal to seasonal temperature (°C) and α and β are fitted parameters based upon laboratory feeding experiments, field studies, or other sources (Elliot and Persson 1978, Durbin *et al.* 1983). The evacuation rate (1.3) reflects the temperature dependent metabolic rates of the predator, and requires that the MSVPA-X equations be seasonally resolved. Whereas the mean stomach contents weight reflects both the size of the predator and encounter rates with suitable prey items. The evacuation rate approach for calculating predator consumption was previously implemented within MSVPA by Tsou and Collie (2001).

1.1.3 Functional Feeding Response

The standard MSVPA formulation assumes that predator feeding rates are independent of prey availability, resulting in a Holling type II predator-prey feeding response (Magnusson, 1995). Type II feeding responses result in depensatory dynamics in predation mortality rates. The estimated predation mortality rate on a given prey item will increase exponentially at low prey biomasses, thus creating a "predation pit" that can result in unrealistic model dynamics such as prey extinction due to predation. In contrast, type III functional responses are compensatory in nature in that the feeding rate on a particular prey item will decline at low prey abundances, and hence predation mortality pressure is released. To avoid the unrealistic dynamics resulting from the type II feeding relationship, the MSVPA-X implements a weak type III feeding response by modifying the consumption equation (Equation 1.2) to incorporate a logarithmic relationship between food availability (measured as total suitable prey biomass) and the amount of prey consumed by a predator.

Given an average stomach contents across years for predator *i*, age class *a*, in season *s*, $\overline{SC_s^{ia}}$, as an input to the model, the stomach contents corrected for food availability in a given year, *y*, is calculated as:

$$(1.4)\quad SC_{ys}^{ia} = \overline{SC_s^{ia}} + \log\left(\frac{SB_{ys}^{ia}}{\overline{SB_s^{ia}}}\right) \bullet \overline{SC_s^{ia}}$$

where SB is the total suitable biomass available to the predator. The proportional stomach content weight calculated by equation 1.4 is substituted for the average value in equation 1.2 to calculate total consumption for a predator age, year, and season. The corrected stomach contents are further constrained to be > 10% of the input average value and less than three times the input

value. These constraints avoid unrealistically small or large predator feeding rates in very extreme cases. The resulting consumption rate as a function of food availability is shown in Figure D.1.

In Figure D.1, the suitable biomass of a particular prey type is varied across a broad range while that of other prey types is held constant. The standard type II feeding response model results in an asymptote of total consumption with increasing prey biomass. In contrast, the model including a correction for food availability results in increasing predator consumption with increasing prey biomass and reduced consumption at lower prey availability relative to the standard model. The resulting predation mortality rates as a function of food availability are shown in Figure D.2.

Through most of the range of prey biomass, the two approaches result in similar predation mortality rates. However, at low prey biomasses, the standard type II model results in exponentially increasing predation mortality. The alternative model has a slower rate of increasing predation mortality, and there is a point at which predation mortality declines with further decreases in prey biomass. This approach avoids the depensatory dynamics that can result in unrealistic model predictions under the standard model.

1.1.4 Feeding Selectivity Parameters

To calculate the composition of prey, a feeding model is employed that includes a "suitability index" for a given prey species, *j*, and age class, *b*, for predator species, *i*, and age class, *a*:

$$(1.5) \qquad S_{jb}^{ia} = O_j^i \cdot A_j^i \cdot B_{jb}^{ia},$$

where O is a spatial overlap index, A is a measure of "general vulnerability", and B reflects size selection (Gislason and Helgason, 1985). Each of these terms ranges between 0 and 1. In the initial formulation of the approach, the general vulnerability index was given a somewhat arbitrary definition and was taken to reflect vertical overlap between predator and prey species. The spatial overlap index was likewise developed to express the proportion of predator and prey populations that overlapped horizontally and interact with one another. However, in the original formulation these terms are not explicitly defined and were often chosen in an *ad hoc* manner. Therefore, the approach has relied upon the presence of extensive diet information for at least one year to "tune" the selectivity parameters. The MSVPA-X model more explicitly defines the parameters entering the basic selectivity equation rather than relying on the somewhat circular approach of back-calculating selectivities through an additional iteration incorporating diet information that may not be available for all species and age classes.

1.1.4.1 Spatial Overlap (O)

Williamson (1993) separated the predation components into what he termed "density risk" and "prey vulnerability". Density risk reflects the relative encounter rate of predators and prey driven by spatial overlap, while prey vulnerability reflects the combined probabilities of attack, capture, and ingestion. Density risk is expressed as a product of predator abundance and a spatial overlap

index. In this case, a similarity index is calculated based upon the relative abundance of predators and prey in defined areas within the model's spatial domain:

$$(1.6) \quad O_{ij} = 1 - 0.5\sum_{z}\left|p_{iz} - p_{jz}\right|,$$

where $p_{.z}$ is the abundance of each predator or prey in each of z spatial cells. The index ranges between 0 and 1. The spatial overlap index between predator and prey types can be calculated based upon available data across a relevant level of spatial resolution and scope. Likewise, because there are seasonal differences in spatial distribution, the spatial overlap value can be seasonally resolved in the MSVPA-X implementation. Spatial overlap indices should be developed on a seasonal basis across the entire range of the model area. Potential sources of data include fishery-independent surveys, tagging studies, and fishery landings data.

1.1.4.2 Type Preference (A)

The MSVPA-X follows the general approach of the standard MSVPA and resolves feeding selectivity into two components reflecting "type" and "size" selection. However, the model follows the definitions of Chesson's (1983) electivity index in parameterizing these as opposed to the *ad hoc* definitions used in the original implementation of the MSVPA. Chesson's index is a relative index ranging from 0 to 1 that reflects the probability of selection of food type i given the presence of m food types in the environment:

$$(1.7) \quad P_i = \frac{\alpha_i n_i}{\sum_{j=1}^{m} n_j},$$

where n is the abundance of a given prey type in the environment. The selectivity index, α_i, is the amount of food type in the diet relative to the amount in the environment scaled so that the sum of all α_i is 1. This index expresses the expected diet composition of the predator if all prey were equally available in the environment (Chesson, 1983) and is calculated as:

$$(1.8) \quad \alpha_i = \frac{r_i / n_i}{\sum_{j=1}^{m} r_j / n_j}.$$

Under a case of random selection (no preference), $\alpha_i = 1/m$ This is equivalent to the selectivities form solved for in the final iteration loop of the standard MSVPA, which combines spatial overlap and size selection into a single index.

The MSVPA-X model resolves feeding selectivity, and resulting indices, into two components of type and size selection. Type selection reflects preference for a particular species relative to all others based upon ease of capture, energy content, or other factors that result in a preferred prey type. Size selection reflects primarily capture and ingestion probabilities and is a function of relative prey to predator length as opposed to weight in the standard MSVPA equations. This

formulation explicitly assumes that type selection is independent of prey size. This is consistent with several examples in the literature that suggest consistent type selection for a range of prey sizes. For example, in juvenile bluefish, fish prey were preferred over shrimp prey across a range of sizes for each type (Juanes *et al.*, 2001). To reflect changing type preferences across predator ontogeny, type selection is entered for each predator age class in the MSVPA-X implementation.

1.1.4.3 Deriving Ranked Type Preferences

Type selection is entered as a proportional rank index to further reduce the data demands. Thus, for each prey type (or species), a preference rank is assigned for a given predator age class. If a prey species is not consumed by that predator age class, then it is given a rank of zero. The proportional inverse rank is calculated as:

$$(1.9) \qquad A_i = \frac{m - r_i}{\sum_{j=1}^{m} r_j},$$

where m is the number of prey species and r_i is the preference rank for each species. The resulting proportional index is equivalent to the expected diet composition for the predator given equal prey abundances and equal prey sizes. If there is no type selection, then all prey species are given equal, tied ranks.

Developing prey type selection rankings requires reviewing available diet information for each predator. Ideally, diet studies would be available over a broad geographic area and encompass the same temporal resolution (seasons) and scale (duration) of the model runs. A suggested empirical approach for developing these input parameters from available data is as follows:

Step 1: Obtain all raw diet data and information on the scales and sampling methods of the individual studies.

Step 2: Weight individual studies by length of time series, geographical coverage, and the number of samples. Also, diet studies in which the abundance of a single prey item dominates should be examined closely. Assigning a weighting factor for spatial, temporal, and sample size differences will attempt to account for local abundance issues associated with the particular diet study.

Step 3: Generate an average seasonal diet matrix over temporal and spatial range of model to separate effect of differences in abundance.

Step 4: Develop a relative abundance/biomass matrix by season for all prey species. This would aid both when considering the influence of abundance of prey affecting selectivity and testing the difference between generalist feeding and choice of prey type.

Step 5: Calculate a electivity matrix based on diet and abundance information to develop prey type ranking.

1.1.4.4 Size Preference (B)

The final component of the feeding selectivity relationship is size selectivity. Again, this is framed in terms of Chesson's index such that the size selection parameters across the size range of the prey sum to 1 and the selection parameter for a certain sized prey, *l*, reflects the proportion of the predator's diet that would be comprised of prey items of that size independent of type selectivity and relative abundance. The original equation from the ICES MSVPA for size selectivity does not follow this formulation and instead uses a weight ratio to determine selection for a particular prey item. The vast majority of the feeding literature indicates that the relative length of the prey is the more pertinent measure, presumably due to factors such as gape width limitations and, relative swimming speed. For example, predator-prey length ratios had a significant effect on prey capture probabilities for juvenile bluefish (Scharf *et al.*, 1998). In general, this effect results in a dome-shaped relationship between predator-prey length ratios and the capture success and is often reflected as a unimodal distribution of prey in the diets.

To effectively model this pattern, the MSVPA-X model takes a similar approach to that described in Tsou and Collie (2001) by using a flexible unimodal function to describe the relationship between prey size and the proportion of the prey in the diet. However, the MSVPA-X model uses the incomplete beta integral. The form of this function is more consistent with the formulation of Chesson's selectivity index as it integrates to 1 over the domain of predator to prey ratios being considered. The size selection index for a prey of a particular size thus corresponds to the predicted proportion of prey of that size in the predator's diet.

The beta integral is given as:

$$(1.10) \quad B(\alpha,\beta) = \int_0^1 t^{\alpha-1}(1-t)^{\beta-1}dt$$

and this is related to the incomplete beta integral as:

$$(1.11)\, I(z;\alpha,\beta) = \int_0^z t^{\alpha-1}(1-t)^{\beta-1}dt / B(\alpha,\beta)\,.$$

The size selection coefficient over some size range between $x_{\min}$ and $x_{\max}$ is calculated as:

$$(1.12) \quad S(\alpha,\beta) = I(x_{\max};\alpha,\beta) - I(x_{\min};\alpha,\beta)\,.$$

In this case, *x* is the prey to predator length ratio. The incomplete beta function can be fit to data on the length distribution of fish prey in stomach data by maximum likelihood estimation and goodness of fit assessed with chi-square tests to derive values for the coefficients α and β. This assumes that length distribution of prey in the diet reflects selection rather than availability, which may be a reasonable assumption in data sets of broad spatial and temporal scope. Example size selection curves for different age ranges of a fish predator using the beta function are shown in Figure D.3.

To develop size selectivity parameters, the following procedure is suggested:

Step 1: Compile data for relative length-frequency of prey items in diet by species.

Step 2: These studies should be weighted on the length of study (number of years), area covered, and number of samples to obtain average picture of prey length consumed.

Step 3: Based upon these weighted average curves, fit the beta integral to available data to derive parameters for input into the model. An Excel spreadsheet function is provided with the program distribution to allow fitting of these parameters based upon available data.

1.1.4.5 Biomass Predators

One potential limitation of the previous application is that all predator species must be explicitly modeled within the standard MSVPA and must therefore have age-structured catch data and meet other assumptions of the model. While there is a capability to include "other prey" that do not correspond to these assumptions, there is no mechanism to incorporate removals by other predators for which only biomass or abundance information is available. Examples of such sources include fish species where age-structured models are unavailable or inappropriate and for species such as birds and marine mammals for which age-structured models are typically impractical. An approach to incorporate "biomass predators" that may have significant predatory impacts has been implemented in the model to overcome this limitation. These predator populations are not explicitly modeled; however, biomass and feeding information are incorporated to calculate the predation mortality rates due to these predators on explicitly modeled prey species.

Inputs for biomass predators include total predator biomass across the time frame of the model, the proportion of the predator biomass in user specified size intervals, consumption parameters, mean stomach contents, and spatial overlap and type preference parameters similar to those for standard species. In addition, one must specify the size selectivity parameters (equation 1.10; α and β) and the size range of the predator. Size selection by other predators is implemented in a similar manner to that for other prey. Size selectivity for a particular sized prey is integrated across the size range for a given size class of biomass predator:

$$(1.13)\quad S = \int_{l\min}^{l\max} S(x/l;\alpha,\beta)dl\ .$$

Where l is the predator length, x is the prey length, and the function in the integral is the size selectivity function (equation 1.12). This is essentially an average value for the selectivity parameter over the range of the predator size class. Aside from this modification, the biomass predators are treated identically to other species when calculating suitable prey biomass, consumption rates, and diets.

1.2 CALCULATION OF PREDATION MORTALITY RATE (M2)

In addition to standard prey, an additional prey type is included in the MSVPA formulation to account for other fish prey and system biomass that is available to the predator species. As with

explicitly included fish prey (i.e., menhaden), selectivity for "other prey" is calculated using equation 1.5. However, the size selection must be calculated based upon an input size distribution for the other prey biomass. The size-selectivity function is then integrated over the size range of the other prey:

$$(1.14)\quad S_x^{ia} = O_x^i \cdot A_x^i \int B_x^{ia} \cdot BM(l)_x \, dl \,.$$

The total food available for a given predator species and age class, or "suitable biomass" is expressed as:

$$(1.15)\quad SB^{ia} = \sum_x S_x^{ia} B_x + \sum_j \sum_b S_{jb}^{ia} \cdot w_{jb} \cdot \overline{N_{jb}} \,,$$

and,

$$SB_{jb}^{ia} = A_j^{ia} \cdot B_{jb}^{ia} \cdot O_j^{ia} \cdot w_{jb} \cdot \overline{N_{jb}}$$

which is the weighted sum of biomass, B_x, across all "other prey" types, and the sum of prey biomass ($w_{jb} * N_{jb}$) across all prey species, j, and age classes, b. It is important to note that the relevant abundance is the average number of prey available during the time interval given as:

$$(1.16)\quad \overline{N_{jb}} = N(0)_{jb} \cdot \frac{\exp(-\alpha Z) - \exp(-\beta Z)}{(\beta - \alpha) Z} \,,$$

where α and β are the beginning and end of the time period being considered expressed as a proportion of a year.

The biomass of a particular prey consumed by a predator is the product of total consumption by the predator and the proportion of total suitable biomass represented by that prey type:

$$(1.17)\quad P_{jb}^{ia} = \frac{SB_{jb}^{ia}}{S^{ia}} \cdot C^{ia} \,,$$

and, the predation mortality rate due to the predator is the ratio of these removals to the average abundance of the prey during the time interval:

$$(1.18)\quad M2_{jb}^{ia} = \frac{P_{jb}^{ia}}{w_{jb} \overline{N_{jb}}} \,.$$

Total predation mortality rate for a given prey species and age class is finally the sum across all predators:

$$(1.19) \quad M2_{jb} = \sum_i \sum_a M2_{jb}^{ia} .$$

The model is initiated with user-entered, fixed values of M2 for each species. The SSVPAs are run and M2 values are calculated using the equations above based upon calculated biomasses and selectivity parameter inputs. The M2 values are then used in successive iterations of the model which are repeated until the M2 values do not change appreciably between iterations. The iteration loop implemented in the MSVPA-X application is shown in D.4.

1.3 MULTISPECIES FORECAST MODEL

MSVPA-X includes a forecast model that allows exploring potential effects of management scenarios. The forecast model includes the feeding response and consumption equations used in the historical model. A given application of a forecast model is based upon a reference MSVPA-X implemented in the project file. The forecast model is built upon the basic age-structured population model:

$$(1.20) \quad N_{t+1} = N_t \exp[-(F + M1 + M2)],$$

Population biomass is then simply:

$$(1.21) \quad B_t = N_t w_t$$

where w_t is the weight of an individual at time t. Thus, given an initial population size (N_0), fishing mortality rate (F), and other natural mortality rate (M1) it is necessary to calculate both individual weight at time t and M2 to project the population forward.

As shown previously, predation mortality rate is a function of prey selection, predator biomass, predator weight, and prey abundance. However, to calculate M2 for a given season using the standard MSVPA-X equations, one must know the average prey and predator biomass during the season, which require estimates for the total mortality rate (Z), and hence M2, experienced during the season. The projection model is resolved to a daily time step to avoid this problem.

At each daily time step in a given season, the size and weight of predators and prey species are calculated from input growth parameters. These terms are used to calculate feeding selectivity parameters, and the total suitable prey biomass for the daily time step is calculated based upon biomasses at the beginning of the day. Predator consumption is modeled as in the historical MSVPA-X approach. The correction for food availability is relative to the historical time series average of total suitable prey biomass from a reference MSVPA-X run.

The amount of each prey type consumed is then converted into a daily mortality rate from the total biomass consumed. This is accomplished first by converting biomass consumed to numbers consumed by dividing by prey weight. The predation mortality rate during the daily time step is then solved iteratively for total mortality, Z, using a solution of the standard catch equation:

$$(1.22)\ \frac{C}{N} = \frac{M2}{Z}(1 - \exp(-Z)),$$

where N is prey abundance at the beginning of the time step, C is the number consumed during the time step by all predators, and $Z = F + M1 + M2$ where daily values for F and M1 are given. The calculated mortality rates are thus used to project the predator and prey populations forward to the next day.

The model is initialized to a selected year of the reference MSVPA-X historical run. Model outputs include seasonal estimates of predation mortality, predator and prey population sizes in numbers and biomass, fisheries yields (given F), seasonal average predator diets, total seasonal consumption, and seasonal predator size and weight-at-age. The projection model is run for each age class of each predator and prey population on an annual basis, starting from the population abundance at age estimated in the initial year of the projection. It is necessary to include a stock-recruit relationship to calculate the initial abundance of age-0 fish at the beginning of each year. This is accomplished by calculating the spawning stock biomass for each year based upon input maturity information and a stock-recruit relationship that is fit based on data from the MSVPA-X runs and selected by the user. The structure of the forecast model implementation is shown in Figure D.5. Four different stock-recruitment models are provided as options in the forecast model:

1.3.1 Ricker Stock-Recruit Relationship

$$(1.23)\ R = aS\exp(-bS)$$

This is the standard Ricker Stock-Recruit model that includes strong compensatory dynamics resulting in low recruitment success at large stock sizes. The application fits a linear transformation of the model using least-squares regression and displays model fit diagnostics.

1.3.2 Beverton-Holt Relationship

$$(1.24)\ R = \frac{aS}{b+S}$$

A linear transformation of the standard Beverton-Holt model is also fit using least squares regression.

1.3.3 Random from Quartiles

In cases where there is no clear relationship between spawning stock biomass (SSB) and recruitment, it may be appropriate to use a more flexible, stochastic relationship. The “random from quartiles” approach sorts SSB values from the time series into quartiles and determines the minimum and maximum recruitment observed within each SSB quartile. During the projection model, the calculated SSB is compared to the observed quartile ranges, and a value for

recruitment is randomly selected from a uniform distribution ranging between the minimum and maximum recruitment for the appropriate quartile. A weak dependence between SSB and recruitment is maintained with this approach if one exists. Recruitment values are constrained to be between the minimum and maximum values of those observed during the reference MSVPA-X run.

1.3.4 Shepherd Flexible

Shepherd (1982) proposed an alternative stock-recruit relationship that has a more flexible level of compensatory dynamics than the standard Ricker curve. The Shepherd model contains a third term that determines the strength of compensatory declines in recruitment at large stock sizes.

$$(1.25) \quad R = \frac{aS}{1+(S/B)^{\gamma}}$$

The model is non-linear, and therefore it is more difficult to develop a unique and reliable model fit, particularly when there is a large amount of variation in the data.