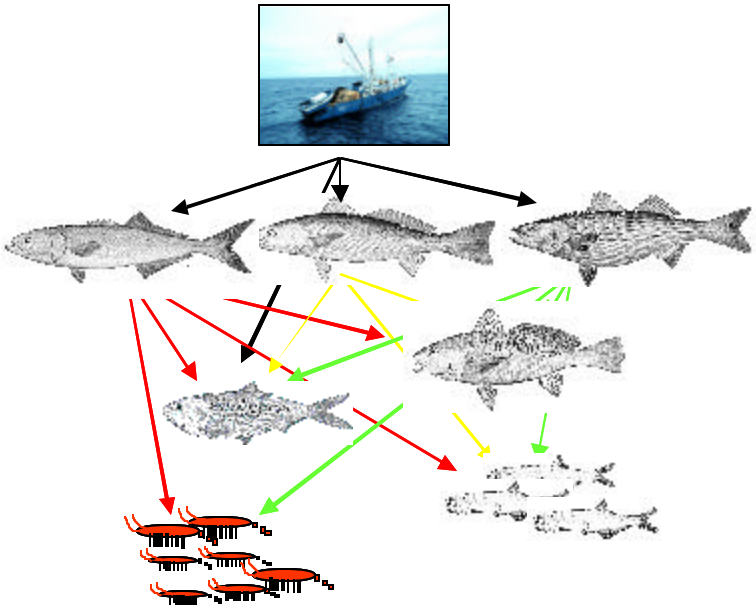
An Expanded Multispecies Virtual Population Analysis Approach (MSVPA-X) to Evaluate Predator-Prey Interactions in Exploited Fish Ecosystems



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Distribution Notes

This distribution updates MSVPA-X version 1.0alpha originally distributed on 2 May 2003. Several significant additions have been made to the program functionality, most notably inclusion of options for estimating predator growth based upon food availability and caloric content of the diet. These additions are discussed in Chapters 3 and 9 of this document. In addition, the extended survivors analysis (XSA) approach for single species assessment was updated to include parameters and options for incorporating "shrinkage to the mean F" (Darby & Flatman, 1994, see Chapter 3). This improves the estimation of terminal fishery mortality rates by the XSA approach. Finally, a number of minor bug repairs and cosmetic changes were made to improve appearance and functionality of the model.

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1- Introduction

Fisheries management has historically taken a single-species approach to evaluating stock status and determining maximum or optimum sustainable removal rates. Fisheries stock assessment models including both aggregate biomass and age-structured models only implicitly include non-fishing mortality as a process limiting population size. In general, this is a simplifying assumption given that natural mortality rates are often difficult to measure in the field. Natural mortality rates are most typically treated as constant values across both age classes and a catch time series.

There are several important implications to this assumption of fixed, age constant natural mortality rates. First, fishery mortality rates (F) are calculated by difference from estimated total mortality (Z) and a (presumed) known natural mortality (M). Where the fixed M is an underestimate of the actual value, F will be overestimated and vice versa. Likewise, if there is a significant interannual trend in M, then estimated Fs will be systematically biased throughout a catch time series. For early age classes that are not fully recruited to the fishery, assessment models provide little or no information on mortality rates. Population sizes cannot be accurately estimated without accounting for natural mortality processes directly and calculating appropriate mortality rates. Thus, ignoring variation and magnitude of natural mortality rates introduces both uncertainty and bias into single species assessments.

However, accounting for natural mortality, in particular trophic relationships, has perhaps more important implications when considering management of fisheries at the system level. In the current assessment environment, each species is managed with little consideration of system level limitations on stock production. The goal of this series of parallel single species management plans is to simultaneously maximize the productivity of all exploited stocks. Given system level constraints on total primary production and thus food availability, this management goal is likely impossible. Multiple, unlinked single species approaches systematically overestimate stock productivity and thus management benchmarks such as maximum sustainable yield when they do not account for species interactions.

The trophic linkages within an ecosystem will be especially important for early age classes of top predators and small forage species that are important prey items for multiple predators and are also heavily exploited by fisheries. The relative size between predator and prey is an important factor limiting capture probabilities and other aspects of the predation process (e.g., Scharf *et al.* 1998; Hartman 2000). As a result, nearly all significant predation by other fish species occurs on early age classes of a particular forage species. Significant changes in predator abundances can therefore have a significant effect on the survivability of new recruits and thus the overall productivity of a forage species stock. Since fisheries generally target the larger members of any given population, fishery removals of top predators may result in important changes in the predation mortality rates of prey species populations. Likewise, fishery removal of prey

species spawning stock may indirectly reduce the availability of young fish and thus the available of preferred prey of top piscivores.

The obvious complexity of trophic interactions places considerable computational and data demands on analytical models designed to quantify species interactions and account for their effects on both predator and prey populations. One approach that has been implemented and used to make management decisions is multispecies virtual population analysis (MSVPA, Gislason & Helgason 1985). This approach is essentially an extension of age-structured approaches that are most typically used in single species assessments. This approach has the advantage of using data inputs (e.g., fishery catch at age) that are similar to those used in standard fishery models. Likewise, model outputs are directly comparable to those of single species approaches, and thus their incorporation into fishery management plans is simplified.

One significant disadvantage of the MSVPA approach is that it still provides an incomplete picture of ecosystem processes and dynamics. MSVPA models typically include only exploited species and all other components of the ecosystem (e.g. zooplankton, benthic secondary production, apex predators) are either left out of the model or are included as fixed inputs of biomass. Thus, important processes such as system level changes in primary production, climate variation that may influence recruitment, and losses to other predators are ignored. Thus, the MSVPA approach should be considered a partial view of ecosystem dynamics that focuses on intermediate trophic levels of greatest direct interest to fishery managers and stock assessment.

This document provides an overview of an expanded version of the MSVPA approach (described as MSVPA-X). The expanded approach addresses several previously recognized weaknesses of the traditional MSVPA as described in following sections. In comparison to the standard MSVPA approach, the MSVPA-X incorporates a more complex expression of predator feeding and consumption rates, a more explicit formulation of prey size and type selection, and includes greater flexibility in the construction of the single species VPA models to calculate population size and fishery mortality rates. The historical MSVPA-X approach is accompanied by a projection model that allows examination of management scenarios and the potential direct and indirect effects of fishery removals on the future trajectories of predator and prey populations.

MSVPA-X is implemented with a graphical interface that allows import and management of data from multiple sources. The program is designed so that each "project file" can contain multiple configurations of both single and multispecies models and outputs from a number of different model historical and projection runs. The package is therefore designed as both an assessment and exploratory tool accessible to technical and non-technical users alike.

2- Review of standard MSVPA model

The MSVPA approach was developed within ICES as a multispecies extension of cohort analysis or virtual population analysis (MSVPA). The basic approach was initially described by Pope(1979) and Helgason & Gislason (1979) and later modified and expressed in Gislason & Helgason (1985). The approach can be viewed essentially as a series of single-species VPA 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 rates (M2s) converge. The basic model is therefore performed in two primary iteration loops. First, all single species VPAs are run to calculate population sizes 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).

Thus, the single species VPAs employ the basic catch equation and VPA approach as described in Gulland (1983). The simple VPA proceeds by solving for each species, *i*, the following equation iteratively given a natural rate, M_{ia}, and either population size or total mortality rate in the oldest age class:

$$(2.1) \qquad N_{ia}(t) = N_{ia}(1)\exp(F_{ia} + M_{ia})(1-t))$$

where for age class, *a*,:

t: is the time within a year (0< t < 1),
$N_{ia}(t)$: is abundance at time t,
$N_{ia}(1)$: is abundance at the *end* of the year and,
F_{ia}: is the fishing mortality rate.

The standard equation for catch at age, C_{ia}, is then given as:

$$(2.2) \qquad C_{ia} = N_{ia}(1)\frac{F_{ia}}{F_{ia} + M_{ia}}[\exp(F_{ia} + M_{ia}) - 1].$$

As noted above, natural mortality rates, M_{ia}, are generally treated as fixed and age-constant in single species VPAs. However, MSVPA further decomposes natural mortality into predation mortality, $M2_{ia}$, and other sources of mortality, $M1_{ia}$. M2 is more appropriately described as predation mortality due to predators included in the MSVPA model. Total mortality rate, Z_{ia}, is thus:

$$(2.3) \qquad Z_{ia} = F_{ia} + M1_{ia} + M2_{ia}.$$

Predation mortalities are calculated based upon a simplified feeding model developed directly from the approach described by Andersen & Ursin (1977) formulated as discrete expressions standardized to a duration of 1 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:

$$(2.4) \qquad R_{ia} = v_{ia} w_{ia}$$

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

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*:

$$(2.5) \qquad S_{jb}^{ia} = O_j^i \cdot A_j^i \cdot B_{jb}^{ia},$$

where O is a spatial overlap index, A is a measure of "general vulnerability", and B reflects size selection (Gislason & 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 therefore interact with one another. The size selectivity index was given by far the greatest analytical weight, and was expressed as a function of the predator/prey weight ratio, w_{ia}/w_{jb}:

$$(2.6) \quad B_{jb}^{ia} = \exp\left[\frac{(\ln\left(\frac{w_{ia}}{w_{jb}} \right) - h_i)^2}{2s_i^2} \right].$$

The equation requires two additional parameters expressing the optimal weight ratio for the predator, h_i, and the "tolerance", s_i^2, expressing the breadth of prey sizes in predator diets.

In addition to standard prey, an additional prey type is included in the MSVPA formulation to account for other, non-fish prey and system biomass that is available to the predator species. As with explicitly included fish prey, selectivity for "other prey" is calculated using equation 2.5. However, the size selection must be calculated based upon an input mean weight, w_x, and its variance, d_x for other food. Assuming a log-normal distribution, the weight distribution for other prey, x, is:

$$(2.7) \quad DB(w)_x = \frac{1}{wb\sqrt{2p}} \exp\left(-0.5\left[\frac{\log w - a}{b} \right]^2 \right),$$

where:

$$b^2 = \log\left[(d_x / w_x^2)^2 + 1 \right], \text{ and}$$

$$a = \log w_x - 0.5b^2 .$$

The suitability index for other prey is therefore

$$(2.8) \quad S_x^{ia} = O_x^i \cdot A_x^i \int B_x^{ia} \cdot BM(l)_x \, dl .$$

Given the size preference function in equation 2.6, selection for other prey is solved as:

$$(2.9) \quad S_x^{ia} = O_x^i \cdot A_x^i \cdot \frac{s_i}{\sqrt{s_i^2 + b_i^2}} \cdot \exp\left[-0.5 \frac{(\log w_{ia} - h_i - a)^2}{s_i^2 + b^2} \right].$$

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

$$(2.10) \quad SB^{ia} = \sum_x S_x^{ia} B_x + \sum_j \sum_b S_{jb}^{ia} \cdot w_{jb} \cdot \overline{N_{jb}} ,$$

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

which is simply 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:

$$(2.11) \quad \overline{N_{jb}} = N(0)_{jb} \cdot \frac{\exp(-aZ) - \exp(-bZ)}{(b - a)Z},$$

where a and ß 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:

$$(2.12) \quad P_{jb}^{ia} = \frac{SB_{jb}^{ia}}{S^{ia}} \cdot C^{ia},$$

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:

$$(2.13) \quad M2_{jb}^{ia} = \frac{P_{jb}^{ia}}{w_{jb}\overline{N_{jb}}}.$$

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

$$(2.14) \quad M2_{jb} = \sum_{i} \sum_{a} M2_{jb}^{ia}.$$

The greatest source of uncertainty in this approach is the actual values of the selectivity indices derived from the simplified feeding model. In the original formulation of the model, these are not well defined, and the choice of selectivity parameters is often arbitrary. The MSVPA approach can therefore be supplemented with diet information and an additional iteration loop to solve for the appropriate values of the selectivity indices. Thus, if diet data is available for all predators and age classes in a particular year of the time series, the proportion of a particular prey in each predator's diet, U, is assumed to be the proportion of the suitable biomass represented by the prey item as in equation 2.12 or:

$$(2.15) \quad U_{jb}^{ia} = \frac{S_{jb}^{ia} w_{jb} \overline{N_{jb}}}{SB^{ia}}.$$

This can be solved for the suitability coefficients if one assumes that they are normalized to sum to 1 across all prey species and age classes for a given predator. This is the case with standardized indices of feeding selectivity for example Chesson's index (Chesson 1983). Thus, if B represents the biomass of a particular prey item, then:

$$(2.16) \quad S_{jb}^{ia} = \frac{U_{pb}^{ia} / B_{pb}}{\sum_{p} \sum_{b} U_{pb}^{ia} / B_{pb}}.$$

To solve for the selectivities in the year where diet data is 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 SVPA and 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 the selectivity values are constant through time and are independent of prey abundance.

The MSVPA approach forms a complex system of non-linear equations. The model is certainly over parameterized, as is the underlying VPA, and there has been no rigorous proof of uniqueness in the numerical solution. However, in a practical sense, lack of unique solutions has not been encountered in the numerous applications of the approach (Magnusson 1995).

The formulation of the MSVPA 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 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 within the MSVPA approach, the solutions of the VPA equations become non-unique under this formulation at even moderate predation mortality rates (Hilden 1988). Thus, active prey switching should not be included in the MSVPA approach.

There has been one major addition to the basic MSVPA formulations. The extended MSVPA to include growth (MSGVPA, Gislason 1999) was implemented to allow a feedback between predator growth rates and food availability. The growth aspect of this model was implemented by assuming a simple linear relationship between growth and food availability. Thus, for a particular predator, i, age class, a, and year, y, the weight at age, w_i, in the following year is expressed as:

$$(2.17)\quad w_i(a+1,y+1) = w_i(a,y) + \frac{Food(a,y)}{\overline{Food(a)}}\left[\overline{w(a+1)} - \overline{w(a)}\right],$$

where *Food(a,y)* represents the available food (suitable biomass in equation 2.10 above) to predator age *a* in year *y*. The remaining terms reflect the average food availability and weight at each age class across the time series of length *ny* or,

$$(2.18)\quad \overline{Food(a)} = \frac{\sum_y Food(a,y)}{ny}, \text{ and}$$

$$(2.19)\quad \overline{w(a)} = \frac{\sum_{y} w(a, y)}{ny}.$$

Therefore, a proportional decline in food availability relative to the average availability results in a proportional decline in the growth increment [*w(a+1,y+1) – w(a,y)*]. Food consumption, or the per capita daily ration R (equivalent to equation 2.4 above), is then directly related to the relative growth rate by:

$$(2.20)\quad R_{ay} = \frac{w(a+1, y+1) - w(a)}{CE_a}$$

where CE is an age specific conversion efficiency of food intake to somatic growth. The MSGVPA approach further allows "other food" biomass to decline as an exponential function of predator consumption as opposed to the strictly donor controlled model implemented in the standard MSVPA where predator consumption does not effect other prey abundance. Results from the MSGVPA applied to the North Sea and implications for multispecies reference points has been explored in Collie & Gislason (2001).

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, results in higher predation rates and lower fishery yields. The analysis from the MSGVPA support these general conclusions such that changes in natural mortality rates due to predation can significantly impact fishery yields, while the effect of changes in growth due to declining food availability is relatively small (Collie & Gislason 2001). The MSVPA approach has also recently been applied to the Georges Bank fish community (Tsou & Collie 2001) with a slightly modified expression for size selectivity and to the groundfish community of the eastern Bering Sea (Livingston & Juardo-Molina 2000).

3- MSVPA-X Approach

The expanded MSVPA (MSVPA-X) approach described here builds upon the framework of the standard MSVPA by modification of the consumption model, formalizing the selectivity parameters within the framework of general feeding selectivity literature, altering the size-selectivity model, and incorporating a broader variety of single species VPA approaches. These additions allow a more clear definition of input parameters that are used to model diets and consumption rates and improve the MSVPA equations to reflect well established processes controlling feeding and predation rates. The MSGVPA equations are not implemented in the base MSVPA-X formulation; however, a modified model can be that includes calculation of predator growth in both historical and forecast models. The approaches including predator growth are discussed in a later chapter.

The implementation of multiple SVPA models also allows greater flexibility in model construction to address the particular data availability and the most appropriate assessment approach for each MSVPA species. In particular, the addition of "tuned" VPA approaches allows improved estimation of mortality rates and stock size in incomplete cohorts at the end of a time series based upon ancillary information such as fishery dependant and independent abundance indices. Tuned VPA approaches are becoming the standard in single species assessments, and the addition of these methods inside the MSVPA approach allows greater compatibility between single and multispecies assessment models.

1) Food consumption and availability

The food consumption equation (equation 2.4) in the base MSVPA assumes that consumption is a constant proportion of body weight across seasons and years. In reality, food consumption rates in fish can vary strongly, particularly between seasons as a function of changing temperatures and metabolic demands. To account for these processes, a somewhat more detailed consumption model was implemented using the Elliot & Persson (1978) evacuation rate approach within the MSVPA equations and including a modified functional relationship between food availability and predator consumption rates.

The daily ration, R, calculated in equation 2.4 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:

$$(3.1)\quad C_{ys}^{ia} = 24E_s^{ia} \cdot \overline{SC_s^{ia}} \cdot D_s \cdot w_{ys}^{ia} \cdot \overline{N_{ys}^{ia}},$$

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:

$$(3.2) \quad E_s^{ia} = a_{ia} \exp(b_{ia} \cdot temp_s),$$

with *temp* equal to seasonal temperature (°C) and α and ß are fitted parameters based upon laboratory feeding experiments, field studies, or other sources (Elliot & Persson 1978, Durbin *et al.* 1983). The evacuation rate (3.2) reflects the temperature dependent metabolic rates of the predator, and requires that the MSVPA 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 standard formulation of the MSVPA assumes that predator feeding rates (i.e., stomach contents) are independent of prey availability. The seasonal stomach contents weight in equation (3.1) reflects only the metabolic demands of the predator and is assumed to be a constant proportion of predator weight across years. The result of this formulation is a Holling Type II predator-prey feeding response (Magnusson, 1995). The Type II feeding response results 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, we implement a weak Type III feeding response in the MSVPA-X model by modifying the consumption equation (eqn 3.1) to incorporate a logarithmic relationship between food availability (measured as total suitable prey biomass) and the amount of prey consumed by a predator.

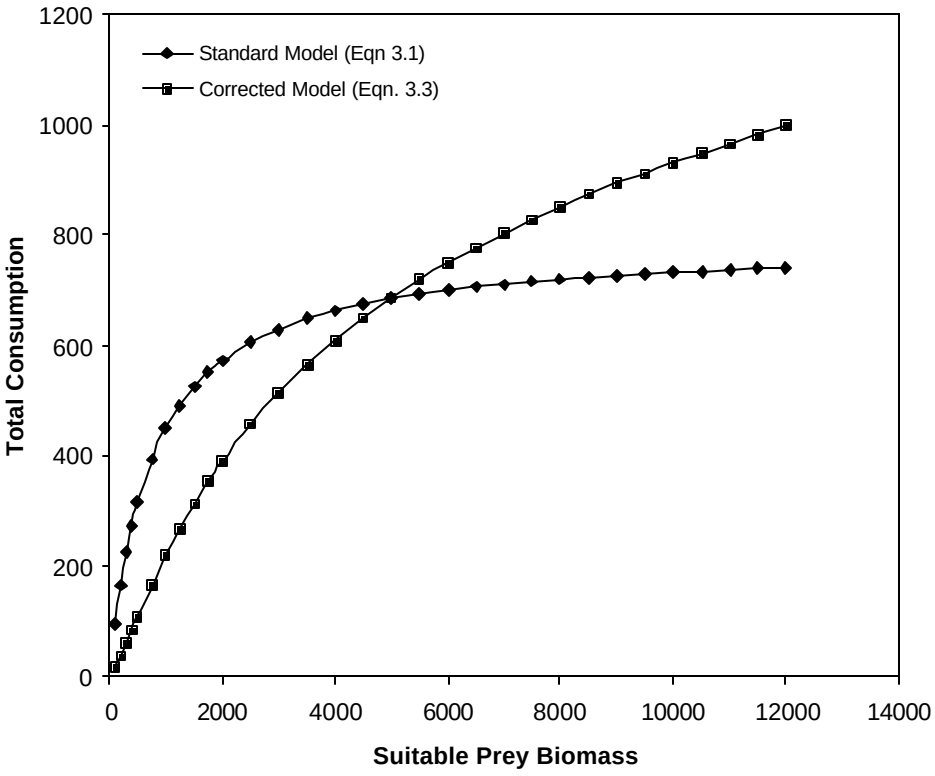
Given an average stomach contents across years for predator *i*, age class *a*, in season *s*, $\overline{SC_s^{ia}}$, as an input to the model, the stomach contents corrected for food availability in a given year, *y*, is calculated as:

$$(3.3) \quad SC_{ys}^{ia} = \overline{SC_s^{ia}} + \log\left(\frac{SB_{ys}^{ia}}{\overline{SB_s^{ia}}}\right) \bullet \overline{SC_s^{ia}}$$

where SB is the total suitable biomass available to the predator. The proportional stomach content weight calculated by equation 3.3 is substituted for the average value in equation 3.1 to calculate total consumption for a predator age, year, and season. The corrected stomach contents is further constrained to be > 10% of the input average value

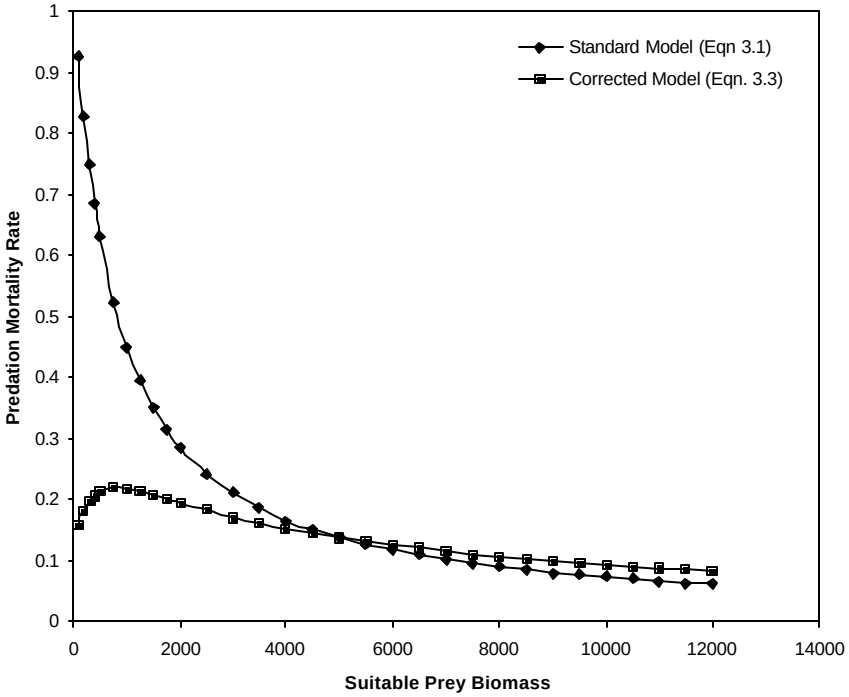
and < 3x the input value. These constraints avoid unrealistically small or large predator feeding rates in very extreme cases. The resulting consumption rate as a function of food availability is shown in Figure 3.1.

Figure 3.1: Predator consumption related to food availability.



In the figure above, 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 3.2.

Figure 3.2: Predator mortality rate related to food availability.



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 an inflection point at which predation mortality declines with further decreases in prey biomass (Figure 3.2). This approach avoids the depensatory dynamics that can result in unrealistic model predictions under the standard model.

2) Feeding selectivity

The predation process has been described mechanistically to include 5 processes that determine the rate at which predators feed on a particular prey item: encounter, detection, attack, capture, and ingestion (Holling 1965). Each of these is associated with a probability value, and the product of these probabilities expresses a predation rate. Relative encounter rates between multiple prey are a function of relative abundance and spatial overlap. The remaining processes are generally a function of relative predator-prey size, prey escape behaviors, prey defenses such as spination, and predator preferences for particular prey species. Ideally, each of these processes would be quantified in feeding experiments for each prey item. However, in practice such detailed

experimental analyses can rarely be accomplished for all species and age classes of predators and prey to be included in an MSVPA model.

The formulation of feeding selectivity (equation 2.5) in the standard MSVPA approach recognizes to some extent the various components of predation. Thus, the spatial overlap index reflects encounter rates and the size selectivity parameter reflects the importance of relative predator to prey size in determining the other processes of predation. However, these terms are not explicitly defined, are often chosen in an *ad hoc* manner, and rely upon the presence of extensive diet information for at least 1 year to "tune" the selectivity parameters.

The MSVPA-X model more explicitly define the parameters entering the basic selectivity equation rather than relying on somewhat the circular argument of back-calculating selectivities in an additional iteration (equations 2.15 and 2.16) based upon diet information which may not be available for all species and age classes. By more carefully defining the indices that go into the selectivity equation, the model can more appropriately model predator diets based upon available data and first principles. Williamson (1993) separated the components of predation into what he termed "density risk" and "prey vulnerability". Density risk reflects the relative encounter rate of the 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 O_{ij}:

$$(3.7) \qquad O_{ij} = \frac{\sum_{z=1}^{m} (N_{jz} N_{iz}) m}{\sum_{z=1}^{m} N_{jz} \cdot \sum_{z=1}^{m} N_{iz}},$$

where $N_{.z}$ is the abundance of each predator or prey in each of m spatial cells (Williamson 1993). In cases where the spatial overlap between predator and prey is less than expected under uniform distributions, the index is less than 1. Where overlap is not different from the uniform expectation, then the index equals 1 and density risk is purely a direct function of predator abundance. Where there is higher than expected spatial overlap, the index is greater than 1 and risk of predation is proportionally higher than the average case. The Williamson spatial overlap index reflecting the increased predation risk at high spatial overlaps between predators and prey is substituted into equation 2.5. The spatial overlap index between predator and prey types can be calculated based upon available survey data across an 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.

As noted above, the probability of prey ingestion is the product of several probabilities reflecting both relative predator and prey size and other factors leading to prey preference. It is unlikely that each of these component probabilities can be estimated for each predator and prey pair, particularly when considering that they must be estimated for each age class of each predator and prey type. In addition, if prey size at

age changes significantly across the time series, then the size-dependant components of feeding success will also change. Thus, 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) selectivity 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:

$$(3.8) \qquad P_i = \frac{a_i n_i}{\sum_{j=1}^{m} n_j},$$

where *n* is the abundance of a given prey type in the environment. The selectivity index, a_i, is the amount of food type in the diet relative to the amount in the environment scaled so that the sum of all a_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:

$$(3.9) \qquad a_i = \frac{r_i / n_i}{\sum_{j=1}^{m} r_j / n_j}.$$

Under a case of random selection (no preference) the $a_i = 1/m$. This is equivalent to the form of the selectivities solved for in the final iteration loop of the standard MSVPA (2.16) which, however, also encompasses 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.

Type selection is entered as a proportionalized 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:

$$(3.10) \quad A_i = \frac{m - r_i + 1}{\sum_{j=1}^{m} r_j},$$

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.

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 for size selectivity (equation 2.6) does not follow this formulation and used the ratio of weights 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 due to gape width limitations, relative swimming speed, and other factors. 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. Howeverthe 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:

$$(3.11) \quad B(a,b) = \int_0^1 t^{a-1}(1-t)^{b-1} dt$$

and this is related to the incomplete beta integral as:

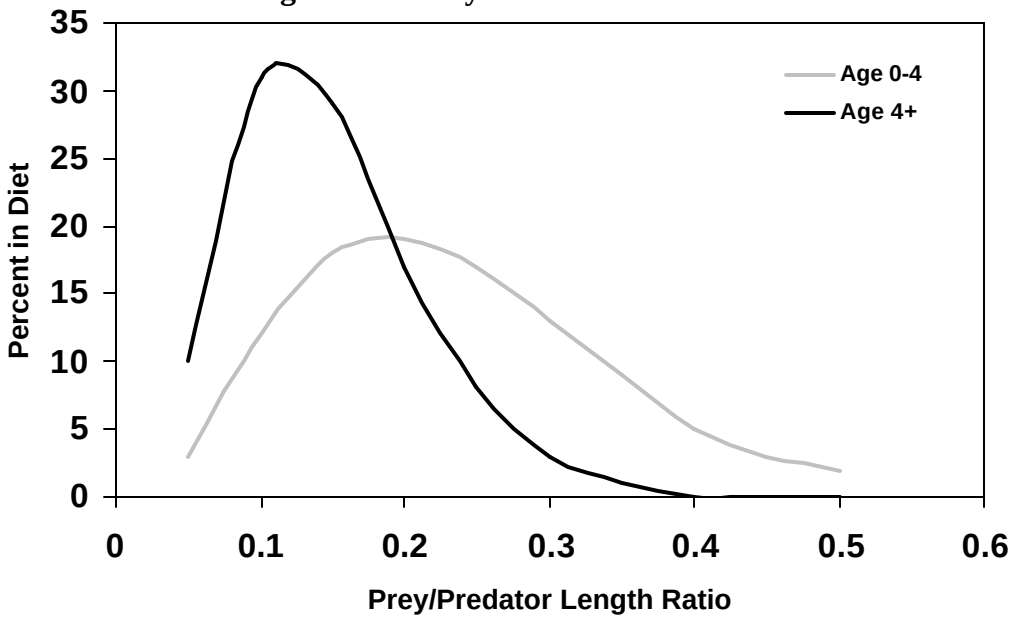
$$(3.12)\ I(z;a,b) = \int_0^z t^{a-1}(1-t)^{b-1} dt \,/\, B(a,b).$$

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

$$(3.13) \quad S(a,b) = I(x_{max};a,b) - I(x_{min};a,b).$$

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 a and ß. This assumes that length distribution of prey in the diet reflects selection rather than availability, which may be a reasonable assumption in datasets of broad spatial and temporal scope. Example size selection curves for different age ranges of a fish predator using the beta function are shown below.

Figure 3.3: Prey Size Selection Curves



3) Single species VPA methods

Previous MSVPA approaches have used solely the cohort analysis method of Gulland to calculate mortality rates and stock sizes. There is no implemented method to calculate the mortality rates in the oldest ages of each cohort or the mortality rates in the terminal year that are necessary to complete the population matrix. In general, these are input into the MSVPA based upon results from single species assessments. However, single species assessments and the methods used to calculate terminal mortality rates are contingent upon assumptions about natural mortality rates that are calculated within the MSVPA approach. The input mortality rates are thus not consistent with the rest of the model, and it is therefore desirable to calculate these within the MSVPA iterations. Second, the standard cohort analysis approach may not be the best option for assessment of any given fish stock, in particular for estimating mortalities for recent, incomplete cohorts. Separable VPA (Pope & Shepherd 1982), for example, may be a more appropriate tool for a given species. Likewise, most VPA assessments currently employ "tuning" indices such as fishery CPUE and/or fishery independent indices to calculate

population sizes in terminal years. For example, the extended survivors analysis (XSA, Shepherd 1999) or the ADAPT VPA methods (Gavaris 1988) have become standard tools for single species VPAs.

It is desirable that the results from multispecies assessments be directly comparable to those for single species assessments. However, differences in the single species models used would preclude these direct comparisons. Therefore, a suite of single species VPA approaches are implemented within the MSVPA-X. These include separable VPA, cohort analysis using a catch curve to calculate terminal mortality rates, *ad hoc* effort tuned VPAs (Pope & Shepherd 1985, Darby & Flatman 1994), and extended survivors analysis (Shepherd 1999). The last two methods employ either fishery effort information and/or external abundance indices to tune single species VPA assessments. The suite of single species VPA tools is equivalent to that distributed in the Lowestoft VPA assessment package (Darby & Flatman, 1994). Greater detail on the VPA methods and data requirements is given in the implementation description below.

While the ADAPT VPA method is becoming the standard assessment tool in North America, it is not possible to implement this method within the MSVPA. Primarily this is due to the extreme computational complexity of using multiple nested non-linear optimization routines. Further, the ADAPT approach often requires complex model building and decision making regarding the most appropriate tuning indices to use. This type of complex model building cannot be reliably implemented within the iterative framework of the MSVPA. However, the extended survivors analysis approach provides an intermediate level of complexity that allows tuning with fishery independent indices without the additional complexity of the full statistical approach implemented in ADAPT (Shepherd 1999)

The implementation of multiple SVPA approaches is consistent with the general structure of the MSVPA model. In each case, the SVPA method uses natural mortality rates, which are easily implemented as being time and age variant, as inputs to the models. The MSVPA iteration loop calculates these mortality rates, which can then be fed downward into the SVPA models. Thus, MSVPA is appropriately viewed as a series of parallel SVPA models, linked by the calculated predation mortality rates.

4) Biomass Predators

One potential limitation of the previous MSVPA application is that all predator species must be explicitly modeled within the MSVPA, and therefore must have age structured catch data and meet other assumptions of the model. While there is a capability to include "other prey" in the model that do not correspond to these assumptions, there was no mechanism to incorporate removals by other predators for which only biomass or abundance information is available. This would include fish species where age structured models are inappropriate, birds, or marine mammals that may have a significant predatory impact on a species of interest.

To account for these types of predators, an approach to incorporate "biomass predators" has been implemented in the model. 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 3.13 a and ß) 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:

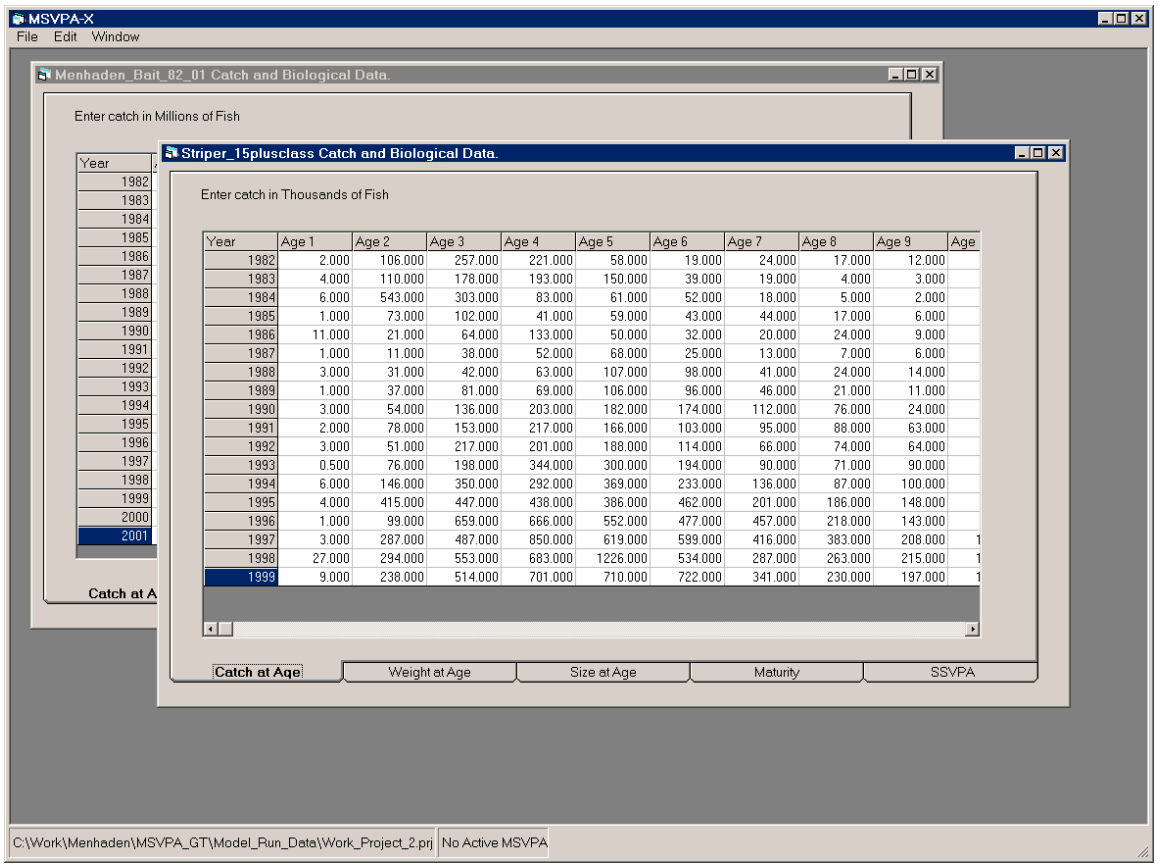
$$(3.14)\quad S = \int_{l\min}^{l\max} S(x/l; a, b)\,dl\,.$$

Where l is the predator length, x is the prey length, and the function in the integral is the size selectivity function (equation 3.13). 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.

Program Implementation

The MSVPA-X is implemented as a MS Windows application written in Visual Basic 6.0. The program includes interface screens for the entry and management of species data, model inputs, and both graphical and data outputs. All data and outputs are stored and managed within a relational database created by the program termed a "project file". The project file stored entered catch and other biological data for individual species that can be included within MSVPA executions. This list of species is termed the "species collection" and all data entry is handled through the species form described below. Multiple species forms can be opened and manipulated at the same time. The project file also allows development and storage of multiple MSVPA-X runs. A multispecies forward projection model is also implemented within the program along with procedures for viewing and management of model outputs. The main program form, viewed on startup, contains menu options to allows the user to select a save project file, then proceed to create or manage species data or MSVPA applications.

Figure 3.4: MSVPA-X Multiple Document Interface



4- The Species Collection

Using the file menu on the main program form, the user first loads a project file then can choose to either create a new species or view data from a previously saved species. Two species "types" can be entered into the species collection. The first is described as an "MSVPA species" and includes both predator and prey species that are explicitly included in the MSVPA-X model. The population sizes and mortality rates for these species are estimated from catch data and information on predator-prey interactions and are the primary focus of the analysis. The second species type is the "biomass predator" so called because the biomass and feeding information for these species are inputs in the model. This information is used to calculate the prey consumption rates, diets, and predation mortality rates on prey species due to the biomass predators; however, the populations of biomass predators are not directly modeled. Both MSVPA and biomass species information are stored in the project database for inclusion in MSVPA-X configurations.

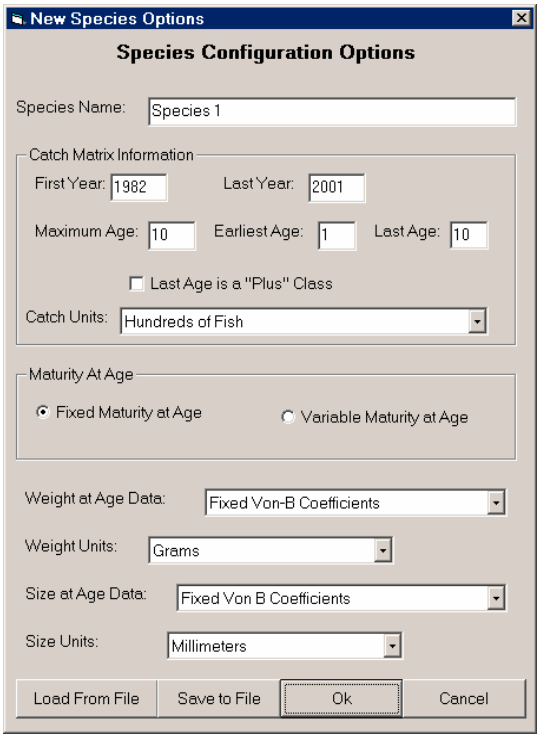
Clicking the "New Species" item on the main program menu bar prompts the user to enter information for either a MSVPA species or a biomass predator. Clicking "Open Species" presents the user with a list of previously saved species. Selecting the species from the list opens the appropriate dialogs and data depending on the species type.

MSVPA Species

The species form allows entry and storage of all relevant catch and biological information for each species in the species collection. In addition, the species form allows the configuration of single species VPA approaches for the species. A large number of species configurations can be stored within the database, and any combination of these can be included in a particular MSVPA-X application.

The new species form contains the basic configuration information for a given species.

Figure 4.1 New Species Configuration Form



This information includes the configuration of the catch matrix. The "Maximum Age" is the maximum attainable age of the species whereas the "earliest age" and "last age" represent those age classes that are represented in the catch matrix. The program allows inclusion of a "plus class" for the last age class.

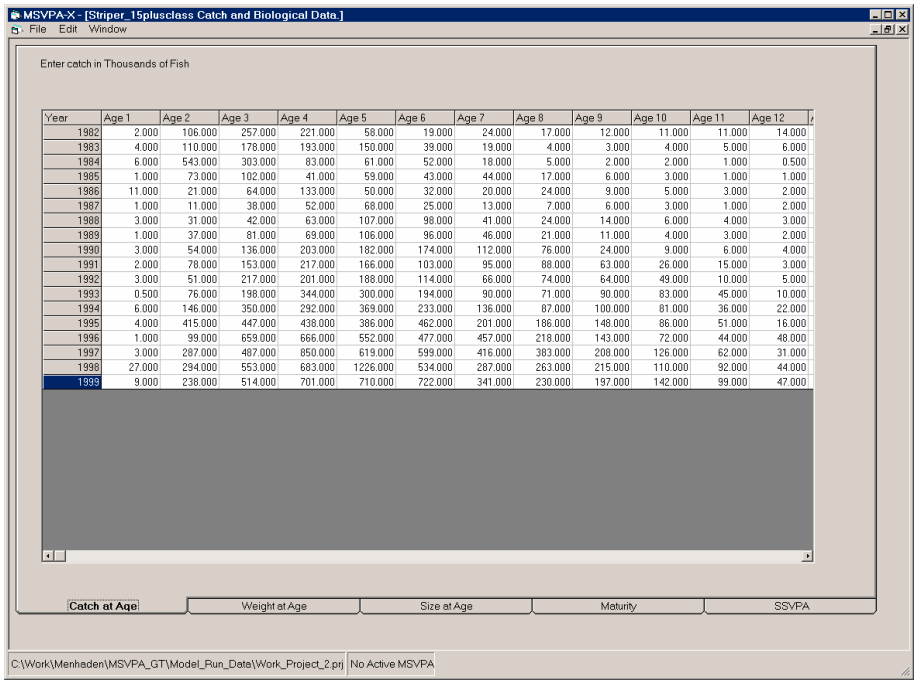
The maturity at age schedule can be fixed throughout the time series or vary from year to year. Likewise, weight and size at age can be fixed or vary interannually and can be entered through a variety of data types including Von Bertalanffey growth equation parameters or directly entered weight or size at age values. These options are selected through the drop down list boxes on the form. In addition, appropriate units for all parameters can be selected. After entering all selections and clicking "OK" the user is shown a species form with data entry formats reflecting the configuration of the new species.

The species form allows entry of catch, weight at age, size at age, maturity, and single species VPA (SSVPA) data by selecting the appropriate tabs at the bottom of the form.

The first four tabs contain spreadsheet data entry forms to allow manual entry of data. In addition, data may be loaded from comma delimited and Excel data files using options on

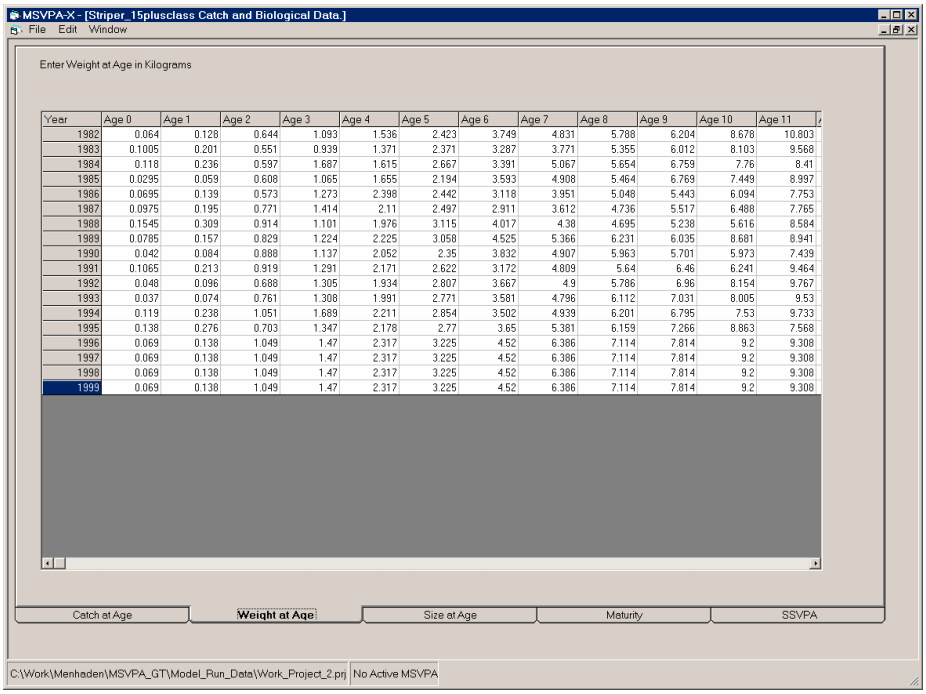
the file menu. The spreadsheet data entry interface contains options for editing (i.e. copy, cut, paste) that can be accessed through the Edit menu or using control keys (e.g. Ctrl-X for cut). The user is required to enter catch, weight at age, size at age, and maturity at age by selecting each of the appropriate tabs.

Figure 4.2 Species Form – Catch at Age



Year	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11	Age 12
1982	2.000	106.000	257.000	221.000	58.000	19.000	24.000	17.000	12.000	11.000	11.000	14.000
1983	4.000	110.000	178.000	193.000	150.000	39.000	19.000	4.000	3.000	4.000	5.000	6.000
1984	6.000	543.000	303.000	83.000	61.000	52.000	18.000	5.000	2.000	2.000	1.000	0.500
1985	1.000	73.000	102.000	41.000	59.000	43.000	44.000	17.000	6.000	3.000	1.000	1.000
1986	11.000	21.000	64.000	133.000	50.000	32.000	20.000	24.000	9.000	5.000	3.000	2.000
1987	1.000	11.000	38.000	52.000	68.000	25.000	13.000	7.000	6.000	3.000	1.000	2.000
1988	3.000	31.000	42.000	63.000	107.000	98.000	41.000	24.000	14.000	6.000	4.000	3.000
1989	1.000	37.000	81.000	69.000	106.000	96.000	46.000	21.000	11.000	4.000	3.000	2.000
1990	3.000	54.000	136.000	203.000	182.000	174.000	112.000	76.000	24.000	9.000	6.000	4.000
1991	2.000	78.000	153.000	217.000	166.000	103.000	95.000	88.000	63.000	26.000	15.000	3.000
1992	3.000	51.000	217.000	201.000	188.000	114.000	66.000	74.000	64.000	49.000	10.000	5.000
1993	0.500	76.000	198.000	344.000	300.000	194.000	90.000	71.000	90.000	83.000	45.000	10.000
1994	6.000	146.000	350.000	292.000	369.000	233.000	136.000	87.000	100.000	81.000	36.000	22.000
1995	4.000	415.000	447.000	438.000	386.000	462.000	201.000	186.000	148.000	86.000	51.000	16.000
1996	1.000	99.000	659.000	666.000	552.000	477.000	457.000	218.000	143.000	72.000	44.000	48.000
1997	3.000	287.000	487.000	850.000	619.000	599.000	416.000	383.000	208.000	126.000	62.000	31.000
1998	27.000	294.000	553.000	683.000	1226.000	534.000	287.000	263.000	215.000	110.000	92.000	44.000
1999	9.000	238.000	514.000	701.000	710.000	722.000	341.000	230.000	197.000	142.000	99.000	47.000

Figure 4.3 Species Form – Weight at Age Tab



Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10	Age 11
1982	0.064	0.128	0.644	1.093	1.536	2.423	3.749	4.831	5.788	6.204	8.678	10.803
1983	0.1005	0.201	0.551	0.939	1.371	2.371	3.287	3.771	5.355	6.012	8.103	9.568
1984	0.118	0.236	0.597	1.687	1.615	2.667	3.391	5.067	5.654	6.759	7.76	8.41
1985	0.0295	0.059	0.608	1.065	1.655	2.194	3.593	4.908	5.464	6.769	7.449	8.997
1986	0.0695	0.139	0.573	1.273	2.398	2.442	3.118	3.951	5.048	5.443	6.094	7.753
1987	0.0975	0.195	0.771	1.414	2.11	2.497	2.911	3.612	4.736	5.517	6.488	7.765
1988	0.1545	0.309	0.914	1.101	1.976	3.115	4.017	4.38	4.695	5.238	5.616	8.584
1989	0.0785	0.157	0.829	1.224	2.225	3.058	4.525	5.366	6.231	6.035	8.681	8.941
1990	0.042	0.084	0.888	1.137	2.052	2.35	3.832	4.907	5.963	5.701	5.973	7.439
1991	0.1065	0.213	0.919	1.291	2.171	2.622	3.172	4.809	5.64	6.46	6.241	9.464
1992	0.048	0.096	0.688	1.305	1.934	2.807	3.667	4.9	5.786	6.96	8.154	9.767
1993	0.037	0.074	0.761	1.308	1.991	2.771	3.581	4.796	6.112	7.031	8.005	9.53
1994	0.119	0.238	1.051	1.689	2.211	2.854	3.502	4.939	6.201	6.795	7.53	9.733
1995	0.138	0.276	0.703	1.347	2.178	2.77	3.65	5.381	6.159	7.266	8.863	7.568
1996	0.069	0.138	1.049	1.47	2.317	3.225	4.52	6.386	7.114	7.814	9.2	9.308
1997	0.069	0.138	1.049	1.47	2.317	3.225	4.52	6.386	7.114	7.814	9.2	9.308
1998	0.069	0.138	1.049	1.47	2.317	3.225	4.52	6.386	7.114	7.814	9.2	9.308
1999	0.069	0.138	1.049	1.47	2.317	3.225	4.52	6.386	7.114	7.814	9.2	9.308

Figure 4.4 Species Form – Size at Age Tab

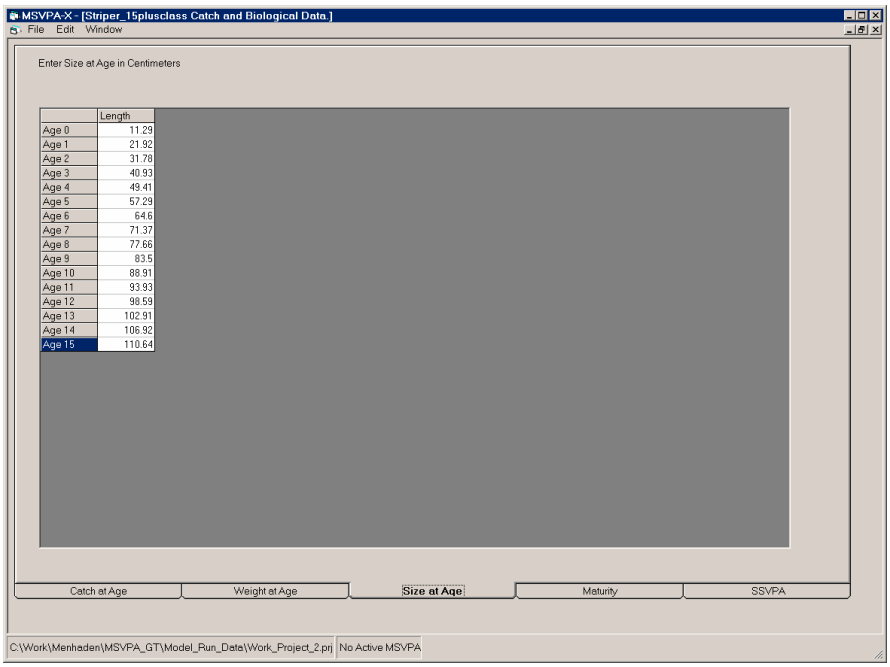
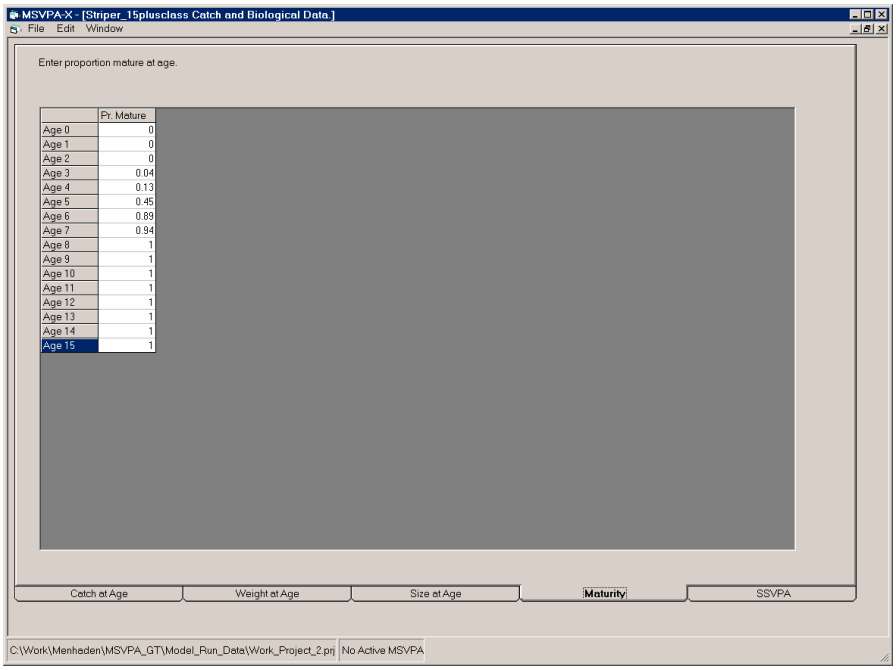


Figure 4.5 Species Form – Maturity Tab



Following entry of these required data, the user must save the species to the project file database by selecting "Save Species to Database" from the file menu. After saving the species, the user is able to configure the SSVPA models for the species by selecting the "SSVPA" tab.

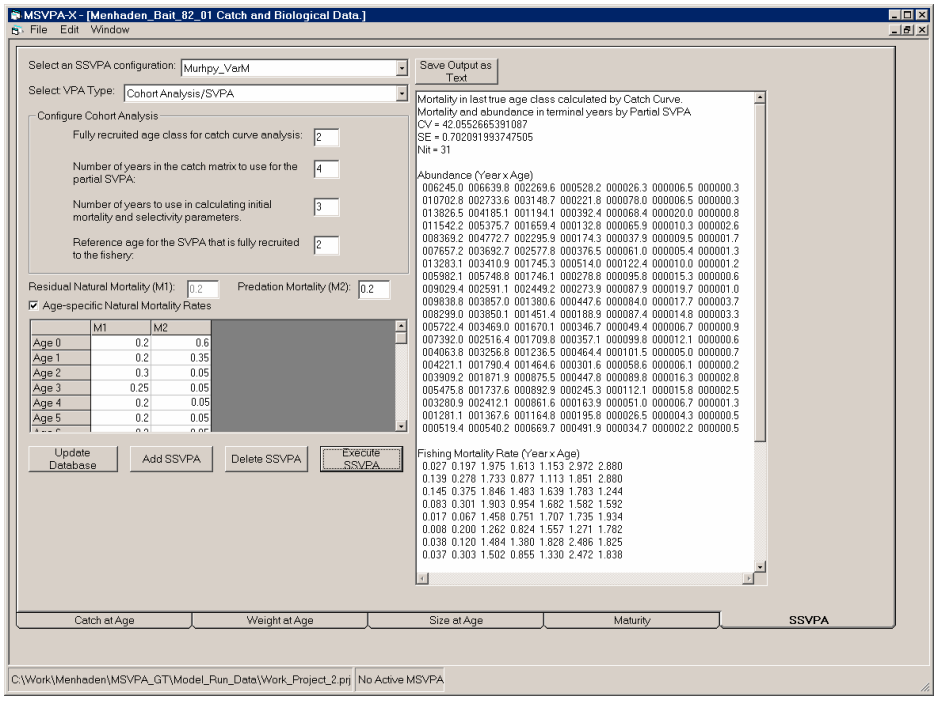
The SSVPA tab contains options for entering several types of single species VPA configurations, each described below. In each case, natural morality rates (M1 and M2)

can be entered as fixed or age-specific using the appropriate text boxes or the spreadsheet on the form. The entered M2 values will be used as initial values in MSVPA-X model runsreferencing the SSVPA configuration. To add a new SSVPA, the user clicks on the "Add SSVPA" command button and will be prompted to enter a name for the configuration. The new configuration name will be stored in the drop-down list at the top of the form. The user then selects the SSVPA type for the new configuration and enters the appropriate parameters (described below). After configuring the SSVPA, the user clicks the "Update Database" button to store the information in the project file. After saving the SSVPA, clicking the "Execute SSVPA" command button will run the SSVPA and results will be displayed in the text box on the form. This output can be saved to a text file by clicking on the "Save Output As Text" command button.

This implementation therefore allows the user to evaluate the performance of multiple SSVPA configurations relative to more developed single species assessments that may be available for the species. Ideally, the results of these preliminary SSVPAs with similar parameter entries should closely match the outputs of other age-structured assessments for the species. However, it may not be possible to match outputs particularly recent years due to differences in methodology or data inputs. For each species, the user should undergo an exploratory analysis of the multiple SSVPA types to find the configuration that best matches the data availability, assumptions, and assessment results for a given species.

SSVPA Type 1: Cohort Analysis / Separable VPA

Figure 4.6 SSVPA Tab – Cohort Analysis/SVPA

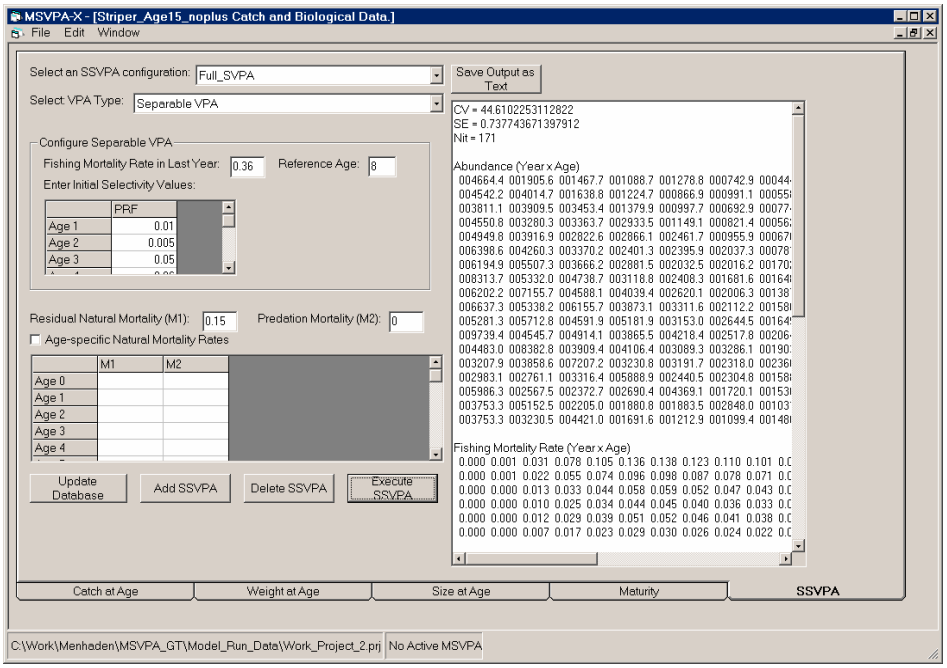


The first SSVPA type implements the Murphy VPA (Murphy 1965, Tomlinson 1970) to solve for fishery mortality rates and abundances. This is equivalent to Gulland's (1983) solution for the catch curve implemented in the standard MSVPA approach. Mortality rates on the oldest true age class are solved using catch curve analysis (Chapman & Robson, 1961; Cadrin & Vaughn 1997). However, since the catch curve analysis requires at least two age classes above the fully recruited age class, the mortality on the oldest age for the last several cohorts cannot be calculated. To complete the output matrices, a separable VPA (SVPA, Pope & Shepherd 1982) is performed for a user defined period at the end of the catch time series. Initial fishery selectivities and mortality rates are calculated based upon a user selected number of years at the end of the completed matrix from the cohort analysis. Each of these parameters is entered in the text boxes displayed when this VPA type is selected. The user is also required to enter a "reference age" for the SVPA, or an age with a selectivity of 1, which should generally match the fully recruited age for the catch curve. The results windows includes the standard error (SE) and coefficient of variation (CV) that measure the reliability of the SVPA solution. The user should explore variation in these results using various numbers of years in the catch series to minimize the CV of the solution.

This SSVPA configuration closely mirrors that implemented for the standard Atlantic Menhaden stock assessment (Vaughn *et al.*, 2002) and gives equivalent results with the same input parameters. It is most appropriate for species with constant selection above a given age in the fishery ("flat-topped selectivity") given the assumptions of the catch curve analysis and where separability may be assumed in the last several years of the catch matrix. This approach does not incorporate tuning by external abundance or CPUE indices.

SSVPA Type 2: Separable VPA

Figure 4.7 SSVPA Tab – Separable VPA

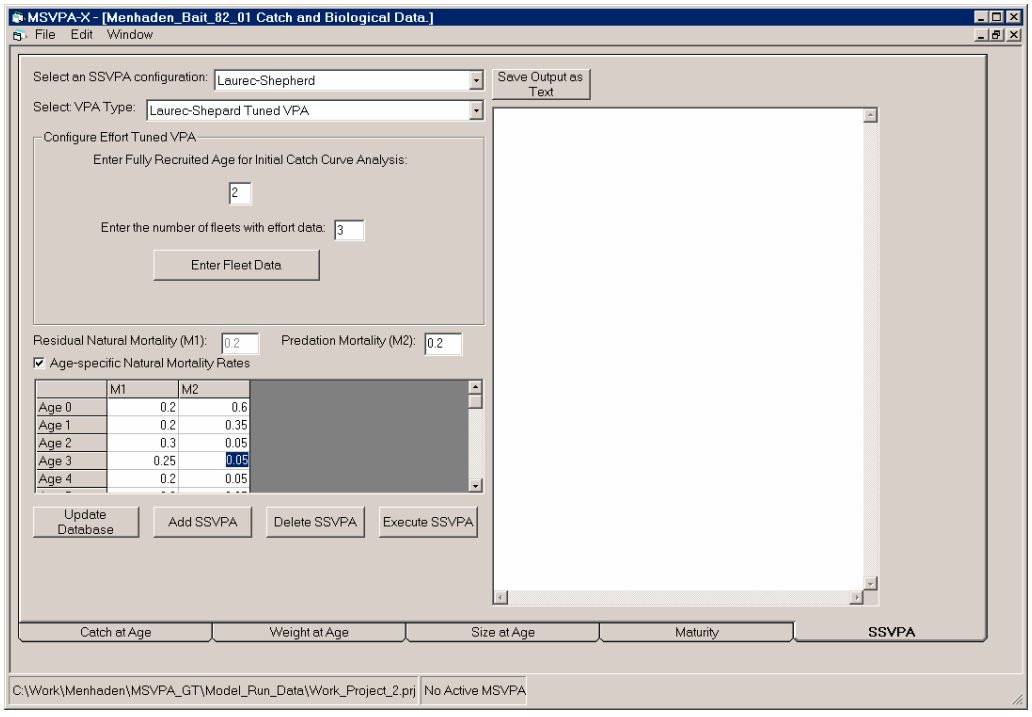


This VPA type implements a full separable VPA (SVPA, Pope & Shepherd 1982) for the entire catch series. This approach is based upon a statistical evaluation akin to a two-way analysis of variance of the catch matrix. The model explicitly assumes a constant selectivity pattern across the time series. It thus calculates the overall fishing mortality rate in each year, then multiplies by a constant selection rate at age vector to calculate F at age throughout the complete catch matrix. The SVPA analysis is performed on all true age classes, and the fishery mortality on the oldest true age is applied to any plus class by convention.

The SVPA requires entry of a reference age that is fully recruited to the fishery, an initial selectivity vector (Partial Recruitment Factors), and a fishing mortality rate in the terminal year. Outputs include an evaluation of model fit using the CV and SE of estimates from the SVPA equations.

SSVPA Type 3: Laurec-Shepherd Tuned VPA

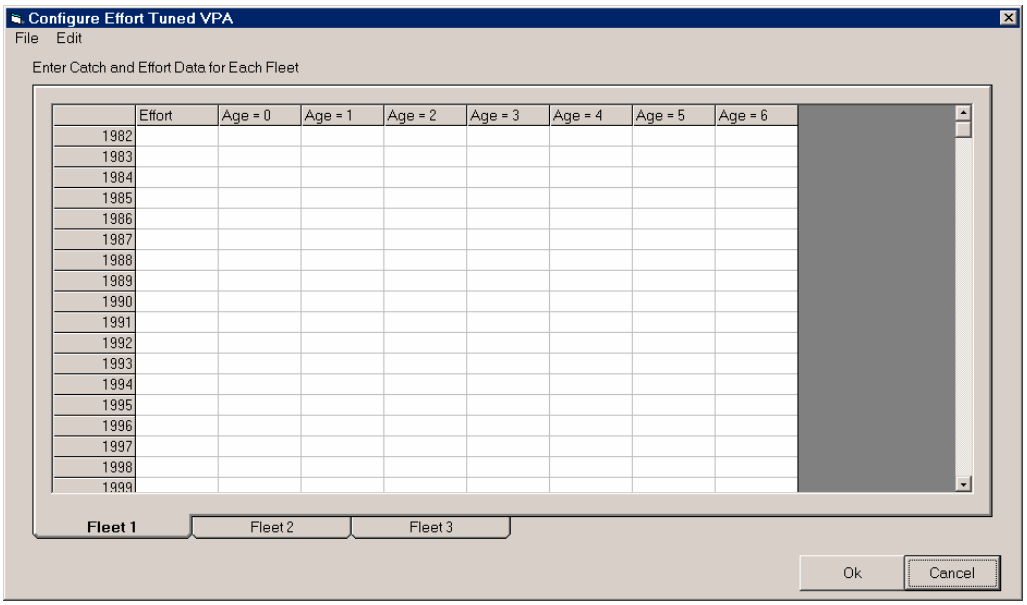
Figure 4.8 SSVPA Tab – Laurec-Shepherd VPA



This SSVPA type implements what has been described as an *ad hoc* tuning method using supplemental information on catch and effort in a number of different fisheries or "fleets" to solve for fishing mortality rates in the terminal year. The method and other *ad hoc* tuning methods are described in detail in Pope & Shepherd (1985). The

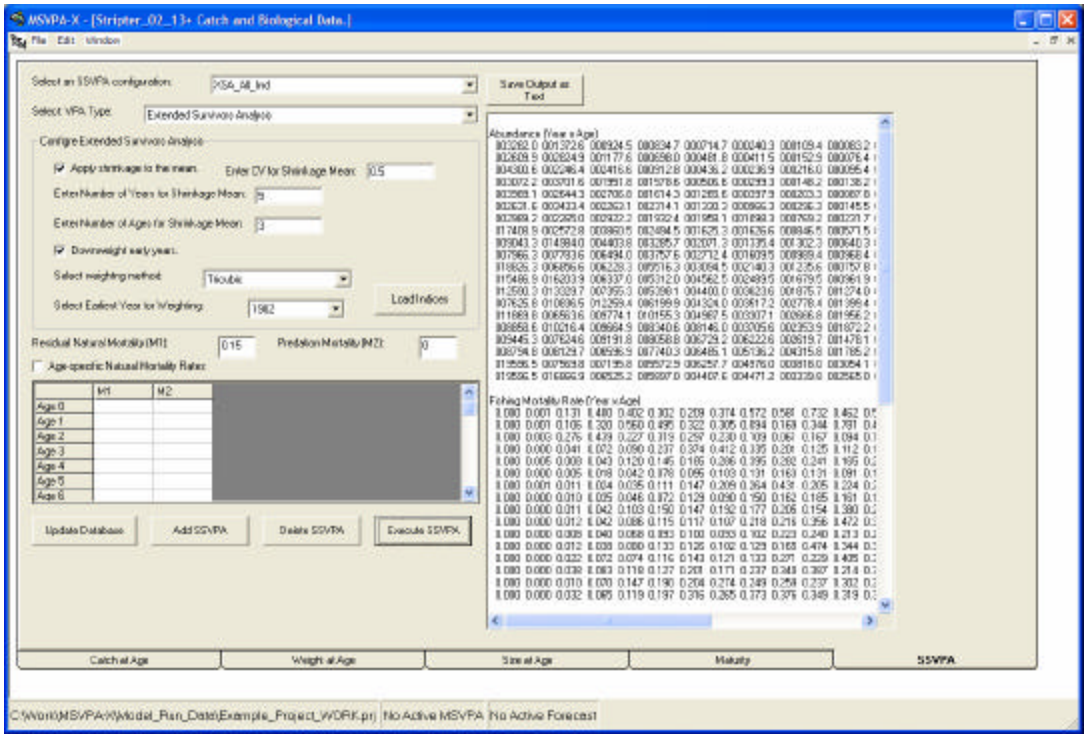
Laurec-Shepherd (LS) tuning method assumes that age-specific catchability coefficients (q) are independent of abundance, consistent with many of the basic assumptions of the VPA and the catch equation. Based upon an initial cohort-analysis, catchabilities for each fleet and Fs are calculated given an input on annual effort in the fleet. These are then used to calculate mortality rates in the final year of the catch matrix and thus to calculate mortalities for incomplete cohorts. The effort tuned VPA is iterated, recalculating mortality on the oldest true age class for each year, until the mortalities in the terminal years converge (Pope & Shepherd 1985; Darby & Flatman 1994).

The SSVPA is initialized using a catch curve analysis to calculate mortality on the oldest true age, and thus the user is asked to enter the fully recruited age class. The user is also asked to enter the number of "fleets" for entry of effort data, and clicking on the "Enter Fleet Data" command button displays a spreadsheet for entry or loading of fleet specific catch and effort data. The total catch at age across all fleets must equal the total catch at age in the basic catch matrix. Catch and effort data can be entered for up to 5 fleets.



SSVPA Type 4: Extended Survivors Analysis

Figure 4.10 SSVPA Tab – Extended Survivors Analysis



The extended survivors analysis (XSA, Shepherd 1999) is an additional tuned VPA method that allows solution of mortality rates in incomplete cohorts based upon multiple fishery dependent and/or independent abundance indices. The approach is related to the ADAPT VPA methodology currently implemented in many single species stock assessments. However, the ADAPT method requires extensive model building and minimization routines involving perhaps hundreds of parameters. This full statistical treatment generally requires considerable analytical expertise and judgment as to the most appropriate model based upon input parameters. Within the MSVPA-X approach, a required input parameter, natural mortality rates, are iteratively recalculated. Thus, at each iteration step the most appropriate statistical model for the ADAPT method must be reevaluated, something which cannot be reliably performed in an automatic procedure. Further, the computational demands of a single ADAPT implementation are extreme, and an iteration of multiple linked ADAPT runs would results in excessive computational overhead. The XSA analysis does not reflect the full statistical approach of the ADAPT methodology, but does have a similar basis, provides similar results, and does not have the same level of computational or model-building demands. The XSA approach is therefore useful within the MSVPA-X framework because it does provide a SSVPA assessment tuned to external abundance indices.

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. The approach is identical to that described in Darby and Flatman (1994), and the parameter entry boxes on the XSA form conform to the parameters required to implement the "shrinkage" approach. In general, applications not applying 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 senstitive 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 described 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 contrained by the average F over the previous N age classes as determined by this parameter value.

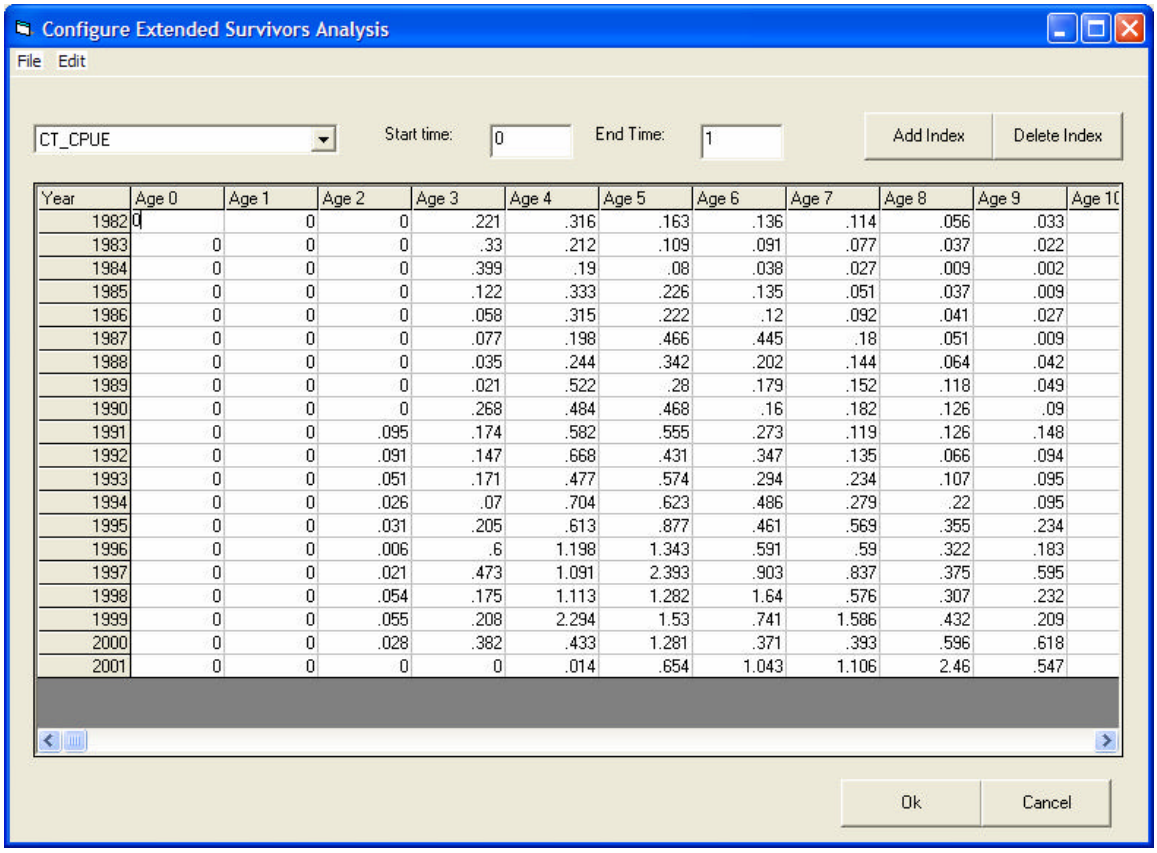
Downweight Early Years: In the calculation of shrinkage means and terminal Fs, early years of the catch matrix are "downweighted" on the assumption that catchabilities and average Fs in recent years are more similar to those of the terminal years. It is highly reccommended that downwieghting be applied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

Select Earliest Year for Weighting: This selects the range for the downweighting, all years prior to the selected year have a weight of zero in the XSA equations.

The XSA requires entry of tuning index data in addition to natural and predation mortality rates that can be age specific. Clicking on the "Load Indices" command button displays the index data entry form.

Figure 4.11 XSA Index Entry Form



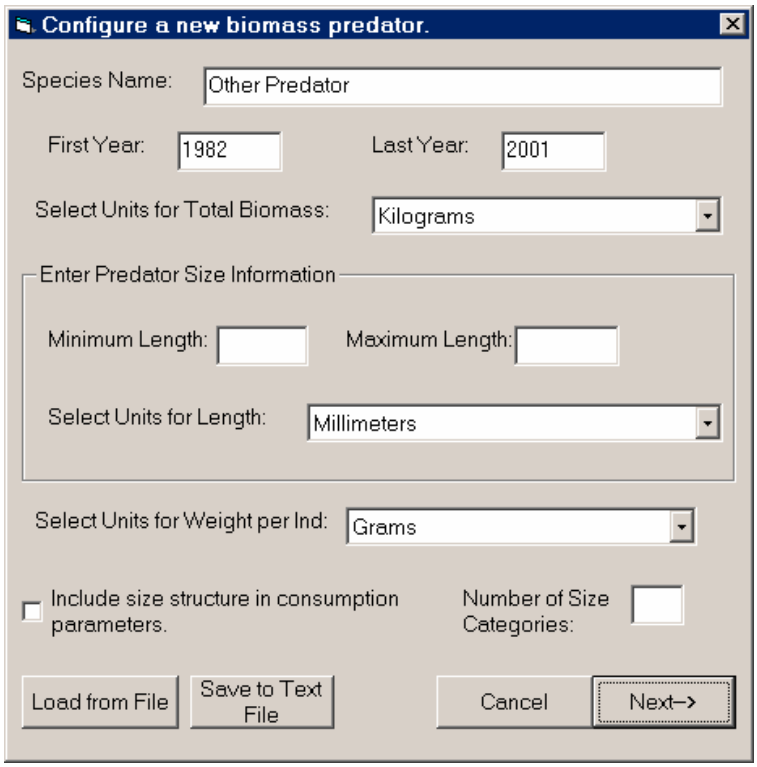
Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	Age 10
1982	0	0	0	.221	.316	.163	.136	.114	.056	.033	
1983	0	0	0	.33	.212	.109	.091	.077	.037	.022	
1984	0	0	0	.399	.19	.08	.038	.027	.009	.002	
1985	0	0	0	.122	.333	.226	.135	.051	.037	.009	
1986	0	0	0	.058	.315	.222	.12	.092	.041	.027	
1987	0	0	0	.077	.198	.466	.445	.18	.051	.009	
1988	0	0	0	.035	.244	.342	.202	.144	.064	.042	
1989	0	0	0	.021	.522	.28	.179	.152	.118	.049	
1990	0	0	0	.268	.484	.468	.16	.182	.126	.09	
1991	0	0	.095	.174	.582	.555	.273	.119	.126	.148	
1992	0	0	.091	.147	.668	.431	.347	.135	.066	.094	
1993	0	0	.051	.171	.477	.574	.294	.234	.107	.095	
1994	0	0	.026	.07	.704	.623	.486	.279	.22	.095	
1995	0	0	.031	.205	.613	.877	.461	.569	.355	.234	
1996	0	0	.006	.6	1.198	1.343	.591	.59	.322	.183	
1997	0	0	.021	.473	1.091	2.393	.903	.837	.375	.595	
1998	0	0	.054	.175	1.113	1.282	1.64	.576	.307	.232	
1999	0	0	.055	.208	2.294	1.53	.741	1.586	.432	.209	
2000	0	0	.028	.382	.433	1.281	.371	.393	.596	.618	
2001	0	0	0	0	.014	.654	1.043	1.106	2.46	.547	

A new index is added or deleted by clicking the appropriate command button and entering the index name. Start and end time is entered as a proportion of a year (0-1) and reflects the time frame for which the index is considered representative. For example, an autumn index collected between September – December would have a start time of 0.75 and an end time of 1. Index values for each age class are entered. Both true zero values and missing data are ignored in the XSA calculations, and hence are represented by 0 in these matrices. Clicking "Ok" saves the data to the database and returns the user to the species form.

Biomass Predators

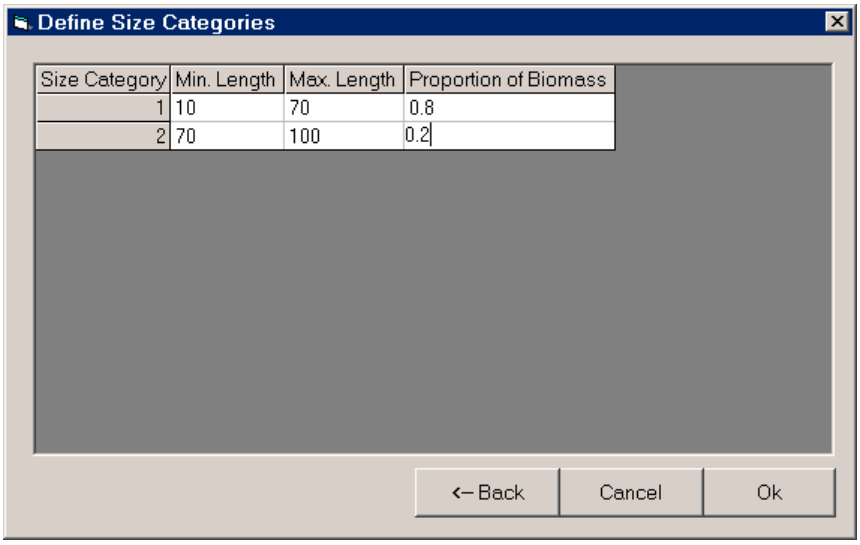
As with MSVPA species, biomass predator information is developed through a series of configuration forms and is stored in the project database for application during MSVPA-X runs. Choosing the "Biomass Predator" option from the form displayed after clicking "New Species" on the main file menu will display the biomass predator configuration form.

Figure 4.12 Biomass Predator Configuration



Here the user selects the appropriate time frame, biomass units, weight units, and size units. Minimum and maximum sizes for the predator are chosen. Because diets and feeding rates vary with predator age/size, it is often desirable to include some degree of size structure in calculated predation rates. To include size structure, the user clicks the appropriate check box on the form and enters a number of size categories. If this box is checked, clicking "Next" displays the size category form:

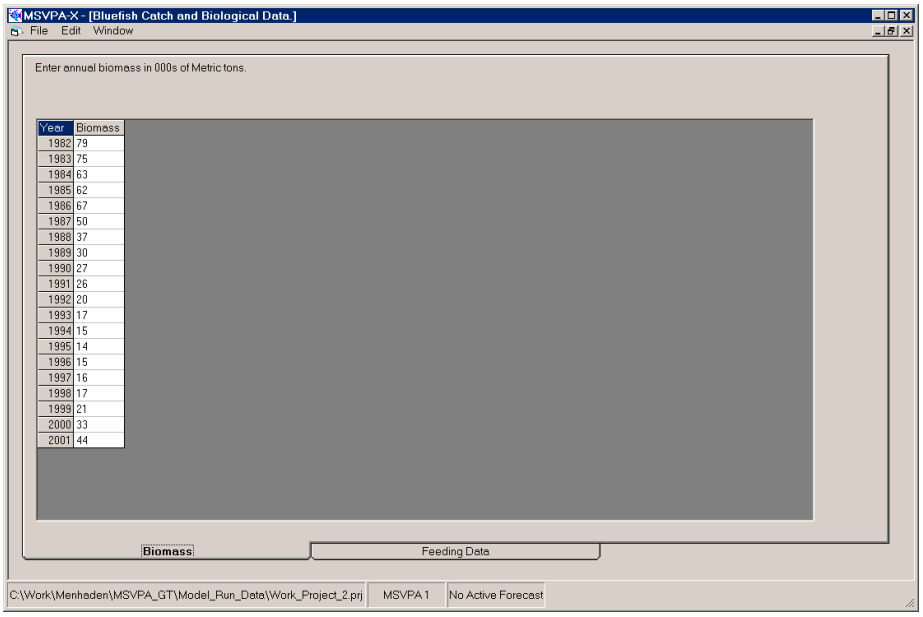
Figure 4.13 Biomass Predator Size Categories



The user is prompted with the minimum and maximum sizes of the predator on the spreadsheet. The cutpoints for the size interval are entered along with the proportion of total biomass for the species in each size class. Clicking Ok saves the predator configuration to the database and displays the biomass predator species form.

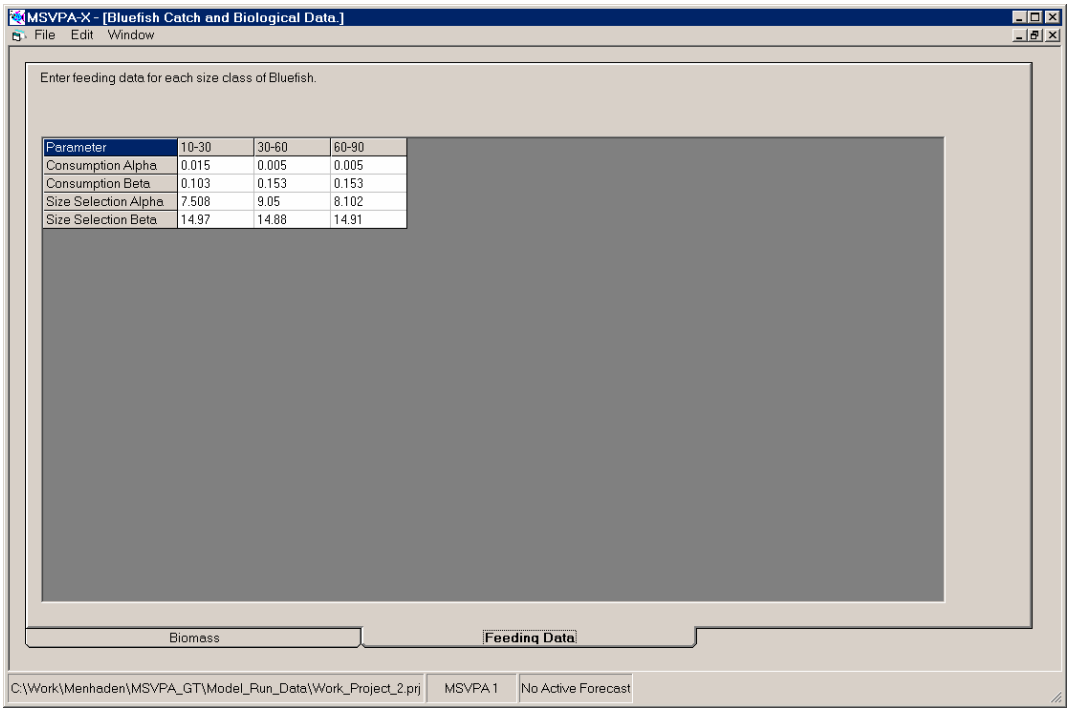
The biomass predator from contains two data entry spreadsheets and will display any stored data for the predator in the database. The first tab allows entry of total biomass by year while the second enters feeding data for each size category.

Figure 4.14 Biomass Predator Data – Total Biomass



The required feeding data includes alpha and beta parameters for the consumption equations (equation 3.2) and parameters for the prey size selectivity beta function (equation 3.11). Following entry of data, the species can be saved to the project database using the File menu.

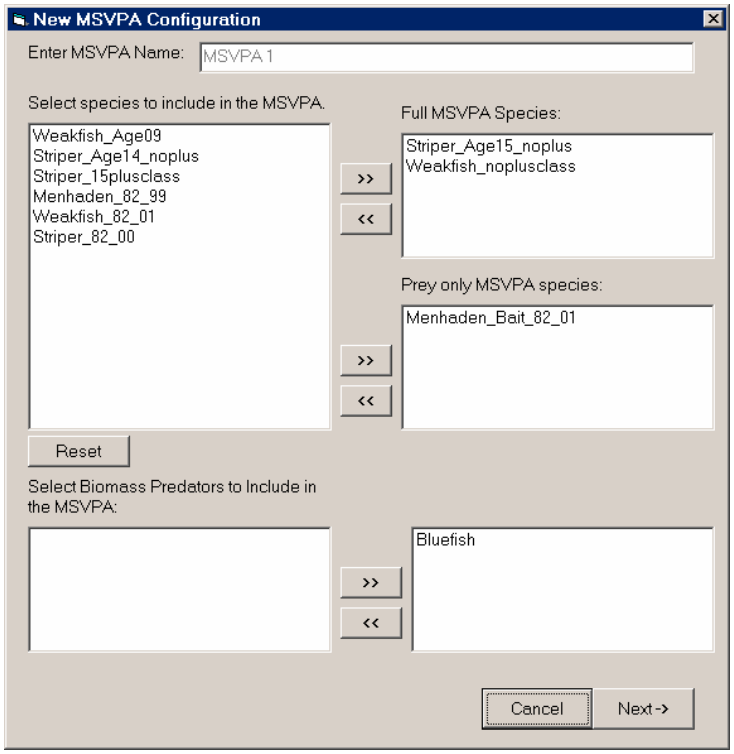
Figure 4.15 Biomass Predator Data – Feeding Data



5- Implementing a MSVPA-X

Multiple MSPVA-X configurations, and their associated output, can be stored within the project and each uses a group of species selected from the species collection. To configure a new MSVPA-X, or load a saved MSVPA-X, the user selects the appropriate item from the main form File menu which is available after closing all species forms. The MSVPA-X configuration begins with a screen to select species from the species collection including MSVPA species and "biomass predators".

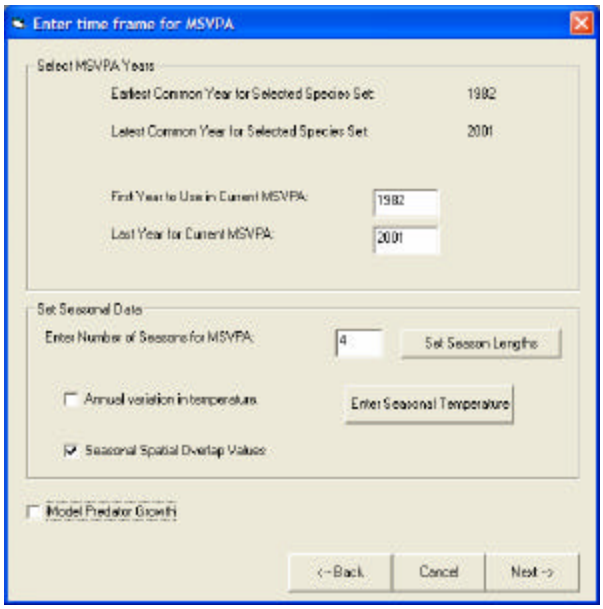
Figure 5.1 MSVPA Species Selection



Species are selected by selecting them on the list to the right of the screen, then clicking on the appropriate arrow to add them to either the "Full MSVPA Species" list or "Prey Only MSPVA species". Full MSVPA species are those that can be both predators and prey in the model. This distinction is only made to avoid having to enter predation parameters for forage species. Biomass predator species are likewise selected and added to the MSVPA-X species collection.

Clicking on the "Next" command button shows a screen to configure the time frame, seasons, and seasonal temperatures for the MSVPA-X run.

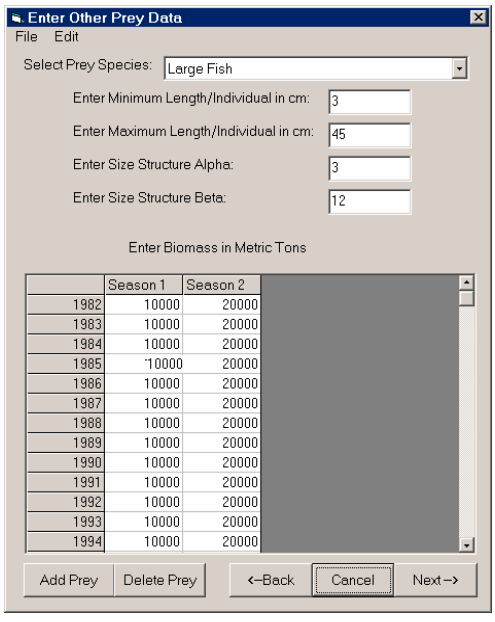
Figure 5.2: MSVPA-X Configuration



The MSVPA-X is limited to the smallest common set of years for the catch matrices of all species since all species abundances must be available for all years. Up to 6 seasons can be included, and these can be of variable length (in days) as set by clicking the appropriate command button. Seasonal temperatures for use in the evacuation rate equation (3.2) are entered by clicking the command button and can vary between years, if desired. Finally, spatial overlap values may be seasonally variable to reflect seasonal movements of predators and prey. Predator growth may be modeled by clicking the labeled check box (see Chapter 9).

Clicking the "Next" command button displays the data entry form for "other prey" types.

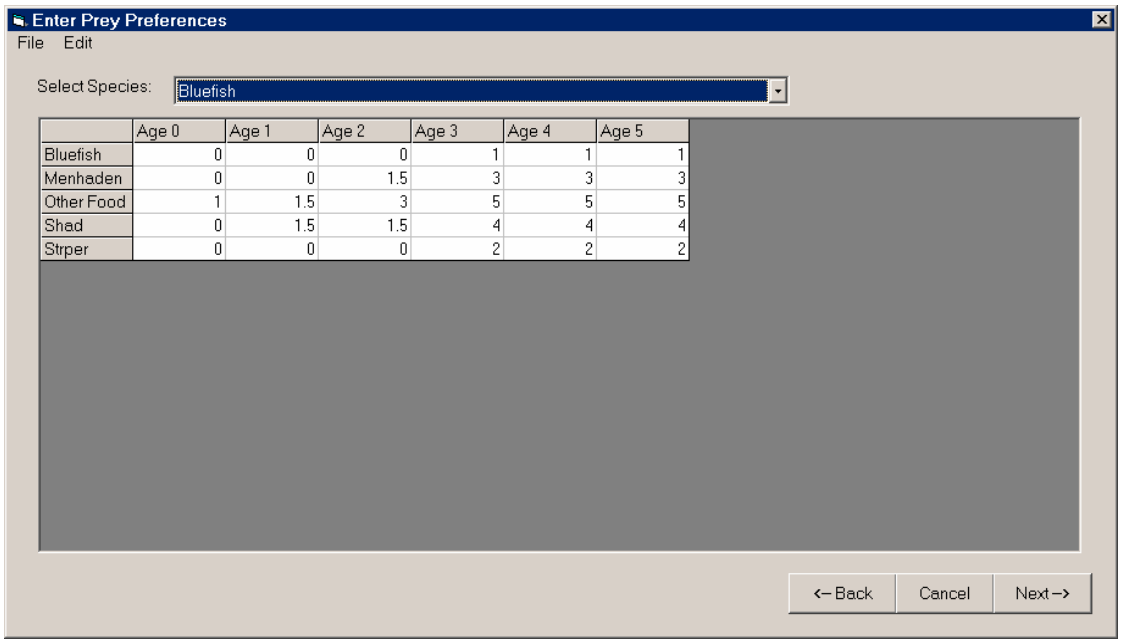
Figure 5.3 MSVPA-X Other Prey



Clicking the add prey button at the bottom of the form prompts the user to enter a unique name for a new prey type. The form includes a data entry spreadsheet to enter seasonal biomass of the prey. Minimum and maximum prey size (in cm) are entered with text boxes along with alpha and beta parameters describing the size structure of the prey population using the beta curve similar to the selectivity parameters as described above.

Clicking the "Next" command button presents a spreadsheet screen to enter ranked prey type preferences for each MSVPA predator (see equation 3.10 and type selectivity section above).

Figure 5.4 MSVPA-X Type Selectivity

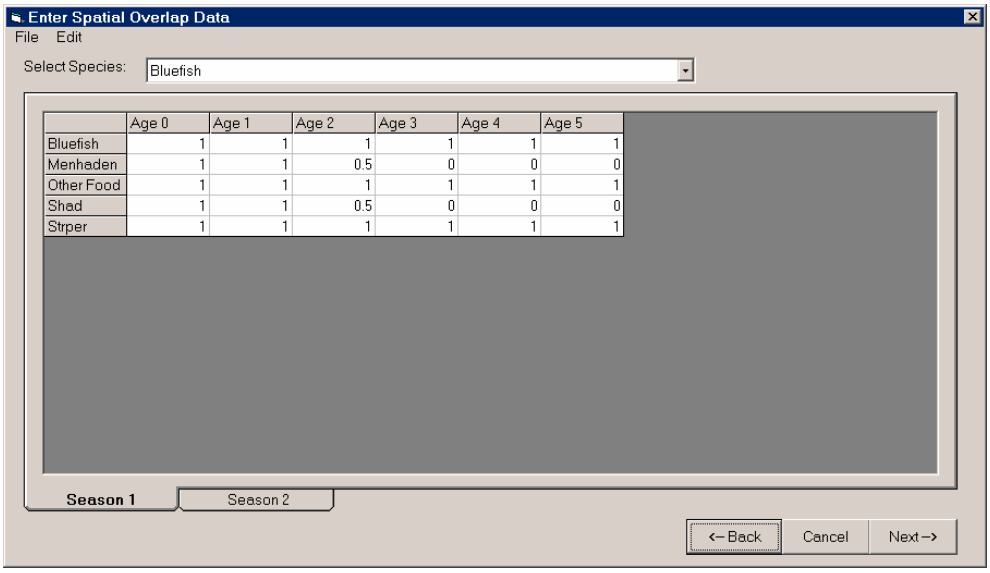


	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5
Bluefish	0	0	0	1	1	1
Menhaden	0	0	1.5	3	3	3
Other Food	1	1.5	3	5	5	5
Shad	0	1.5	1.5	4	4	4
Strper	0	0	0	2	2	2

The predator species is selected from the drop down list, and age-specific prey type ranks are entered. If a prey type is not included in the predators diet, it is given a rank of zero. The most preferred prey type is given a rank of 1 and the least a rank equal to the total number of ranked prey. Tied prey species are represented by half-ranks.

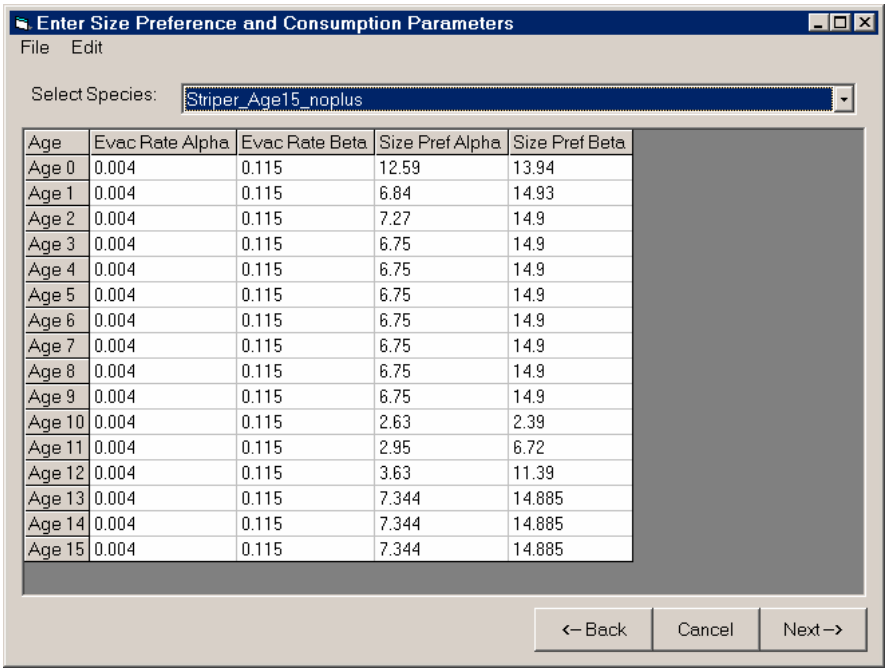
The next screen has a similar format and allows entry of spatial overlap values (equation 3.7) for each predator age class and prey type. Seasonal spatial overlap values can be entered if necessary.

Figure 5.5 MSVPA-X Spatial



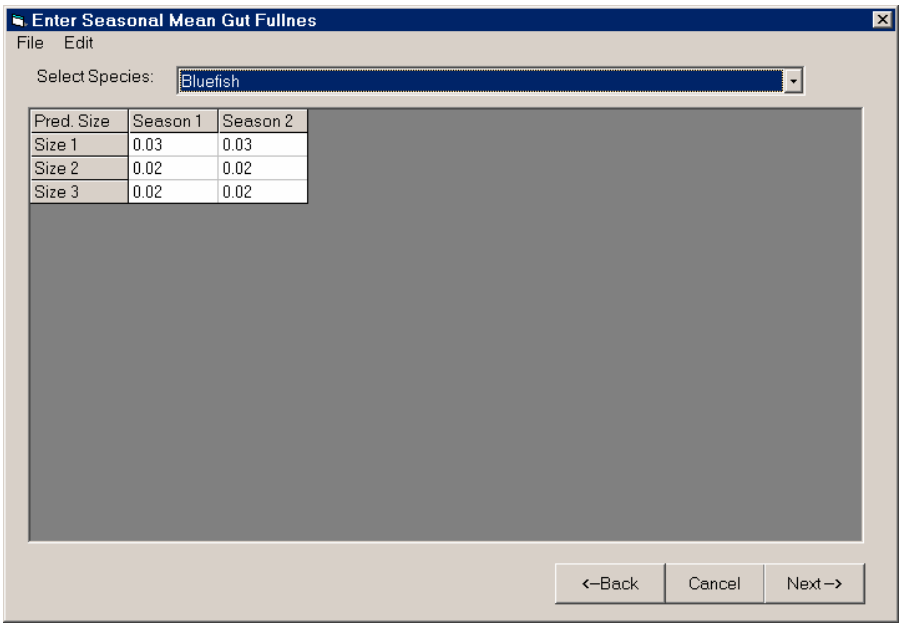
The next screen requires entry of age-specific evacuation rate parameters (equation 3.2) and parameters for the size selectivity function (equation 3.11). The size-selectivity parameters can be derived from a utility to fit the beta function to prey size data with a utility that will be provided with the distributed version of the program.

Figure 5.6 Consumption and Size Selection Parameters.



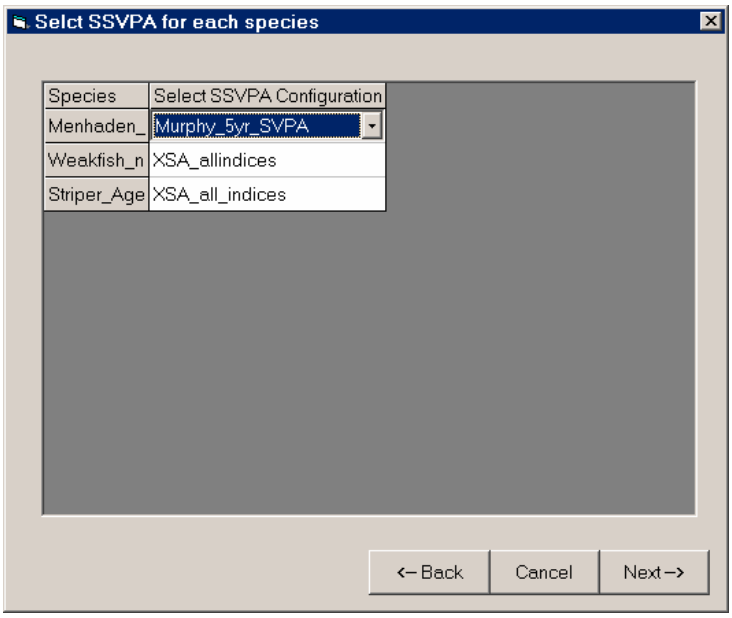
Clicking the "Next" button shows a form to enter mean seasonal gut fullness entered as a proportion of body weight. This value is used to calculate mean stomach content weights for use in the consumption equations (equations 3.1-3.4). Again, the value is age specific for each predator selected from the drop down list.

Figure 5.7 MSVPA-X Predator Seasonal Gut Fullness



The final screen for configuring the MSVPA species allows the user to select the SSVPA configuration for each species that will be used in the MSVPA-X loops. The predation mortality rates (M2) entered in the SSVPA configurations will serve as the initial values in the MSVPA-X.

Figure 5.8 SSVPA Configuration for Each Species

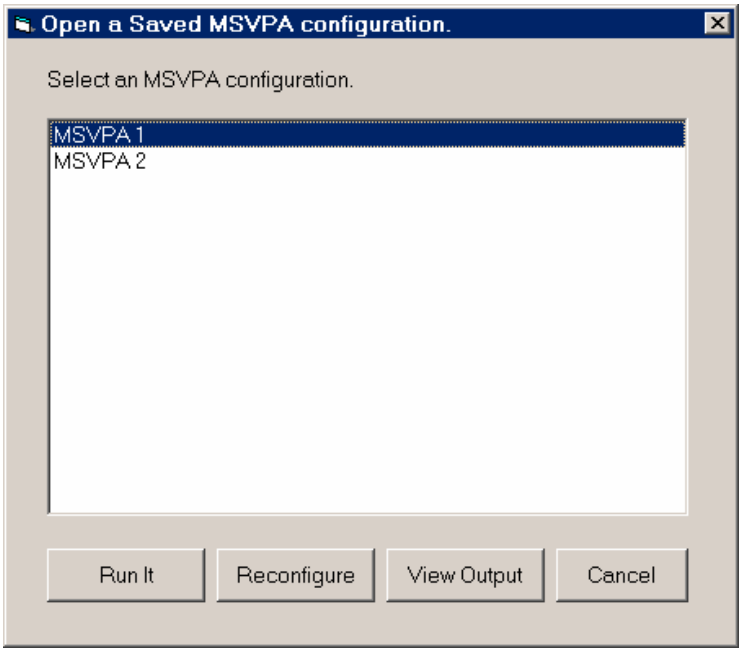


After all data entry is complete, the configuration screen summarizes the MSVPA-X configuration. Clicking the "Go" button executes the model. Following execution, the program informs the user that the analysis is complete and presents options for display of outputs.

Figure 5.9 Review of MSVPA-X configuration.

The configuration and output from the MSPVA is saved within the project database file. To open and reconfigure a previously stored MSVPA-X or view outputs, click "Open MSVPA" on the main application File menu. The following form is displayed and the user selects the MSVPA-X from the list and clicks the appropriate command button.

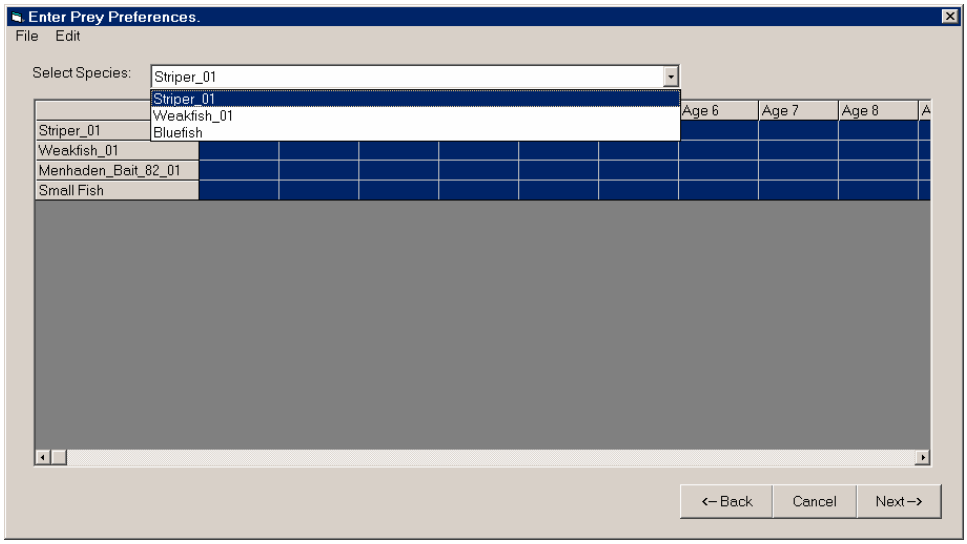
Figure 5.10 Saved MSVPA-X Configurations



Spreadsheet Controls

Data entry throughout the program is accomplished with spreadsheet forms that have common functionality. The spreadsheets do not provide advanced options, but do contain basic tools for navigating, entering, importing, and exporting model input and outputs. Below is a review of the basic functionality of the spreadsheet forms used in the program.

Figure 5.11 Common Spreadsheet Form



On many spreadsheet forms, the user is asked to enter data for a number of different species. For example, preferences for each prey type by predator age class. In these cases, a list box is used to provide a list of the species for data entry. Selecting a species from the list modifies the spreadsheet as appropriate and displays any previously entered data. The entered data is checked and saved to the project database on clicking the "Next" command and proceeding to the next form.

Functional navigation keys:
Up Arrow – Move focus up one cell
Down Arrow – Move focus down one cell
Left Arrow – Move focus left one cell
Right Arrow – Move focus right one cell
Page Up – Move focus to top of spreadsheet
Page Down – Move focus to bottom of spreadsheet

Editing Functions for data entry forms:
Copy - Menu > Edit > Copy or ctrl+C: Copies selected cells to clipboard
Paste - Menu > Edit > Paste or ctrl+V: Pastes clipboard contents to highlighted cells
Clear – Menu > Edit > Clear: Deletes selected cell contents without storing to clipboard
Cut – Menu > Edit > Cut or ctrl+X: Copies selected cells to clipboard, then clears cells

Select All – Menu > Edit > Select All or ctrl+A: Selects all spreadsheet cells.

File Save and Import Options (File menu):

Files can be saved or imported as comma delimited files or as Microsoft Excel files. When loading Excel files, a small form provides the ability to select from among spreadsheets saved in an Excel workbook

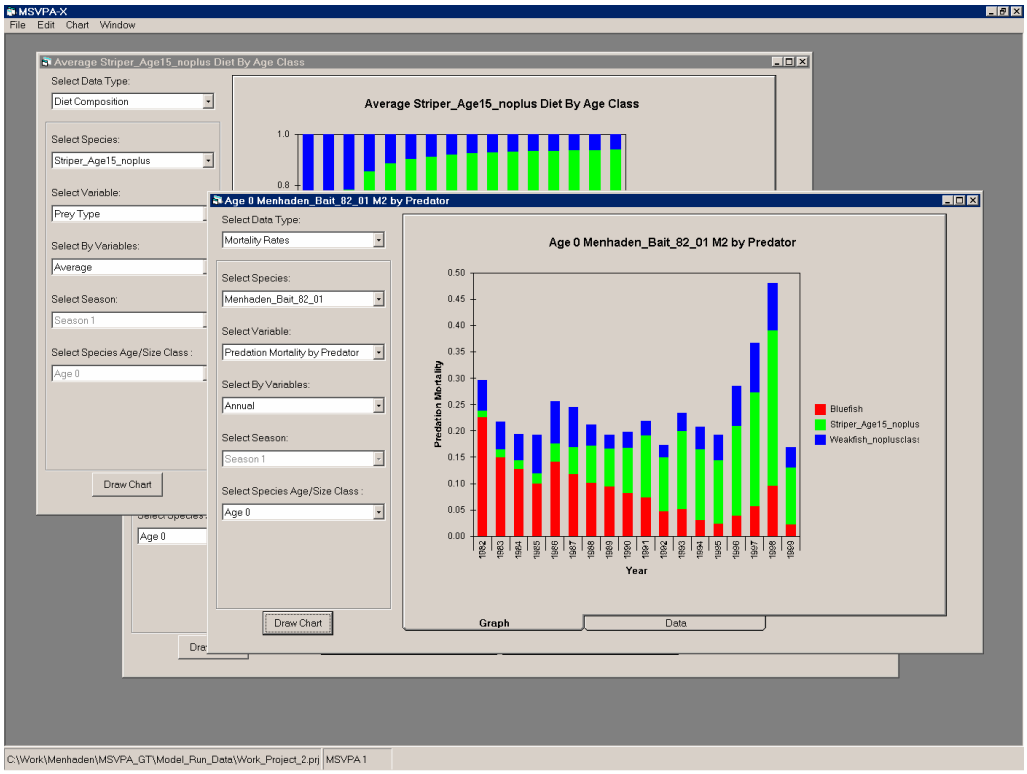
NOTE: The control used to access Excel may cause a software conflict. In general, importing or saving Excel files does not cause a conflict if there is already a instance of Excel open on the system. However, attempting to open Excel after using the control often causes a conflict while the MSVPA-X is running. Closing the MSVPA-X program will relieve this problem.

6- Exploring MSVPA-X Results

MSVPA-X outputs include population sizes, mortality rates, prey consumption, and predator diets. Each of these variables is age specific and includes both seasonal and interannual variation. The multitude of outputs from an MSVPA-X run are stored in the project database file. Model outputs are explored through graphical data forms implemented within the MDI of the MSVPA-X implementation.

To view model outputs, select "Open MSVPA" from the File menu of the main application. A list of saved MSVPA-X runs is displayed and viewing model output is accomplished by selecting the appropriate command button.

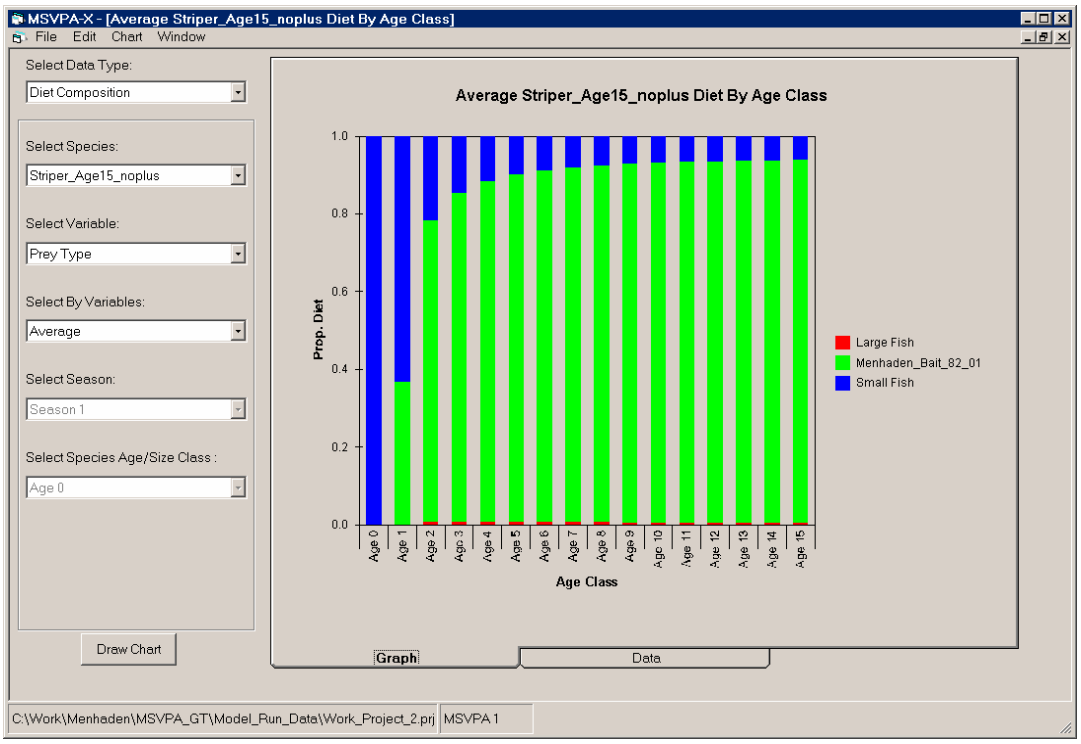
Figure 6.1 Data forms in the MSVPA-X multiple document interface



The data form contains a series of list boxes that allow the user to select the parameters to be used in a query of the project database and the display of data on the form. The form contains a chart showing a graphical output and a "data" tab that displays the numerical results. The first list titled "Select Data Type" allows the user to select among 7 major output types from the model. The subsequent list boxes are configured depending upon the data type. In each case, the user selects parameters for the data query and clicks the "Draw Chart" command button to display the results.

I. Diet Composition

Figure 6.2 Data Form – Diet Composition



Diet compositions for both MSVPA species and biomass predators are derived from the MSVPA-X equations. Diet composition is expressed as a proportion by biomass. The box labeled "Select By Variables" allows output to be displayed in four formats:

Average – Diets by predator age class averaged across seasons and years.

Average by Year – Annual average diets for a specific age/size class of the predator as selected in the box labeled "Select Species Age/Size Class"

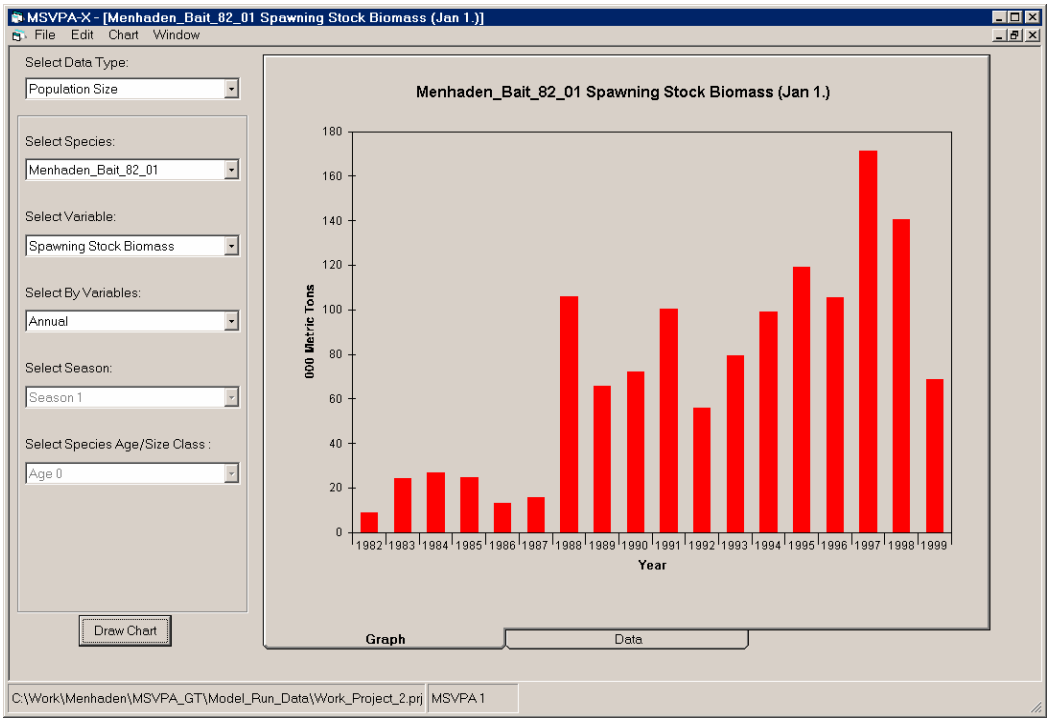
Average by Season – Seasonal average diets for a particular predator age/size class.

By Year and Season – Diet composition for each year in a particular season and predator size class as selected by appropriate list boxes.

The numerical data displayed in the chart is shown in a matrix on the "Data" tab. The charts can be displayed as either stacked bars (shown) or by series by selecting the appropriate option under the "Chart" menu item.

II. Population Size

Figure 6.3 Data Form – Population Size



Population size outputs are available for the MSVPA species whose abundances, biomasses, and mortality rates are calculated within the model. For each population size metric, data can be presented as annual or seasonal information, and this option is chosen in the list box labeled "Select By Variables". Annual data reflects the population size at the beginning of each year, while seasonal data reflects population size at the mid-point of each season. There are seven variable types within the population size data type. Biomass is presented in 000 metric tons for all species, and abundance is in the same units as the input catch data.

Total Biomass – Total biomass for the species by year.

Biomass by Age – Biomass of each age class. The chart displays the age class selected in the appropriate list box, however the data matrix displays biomass for all age classes.

Spawning Stock Biomass – Spawning stock biomass as calculated from input maturity data and assuming a 50% female population.

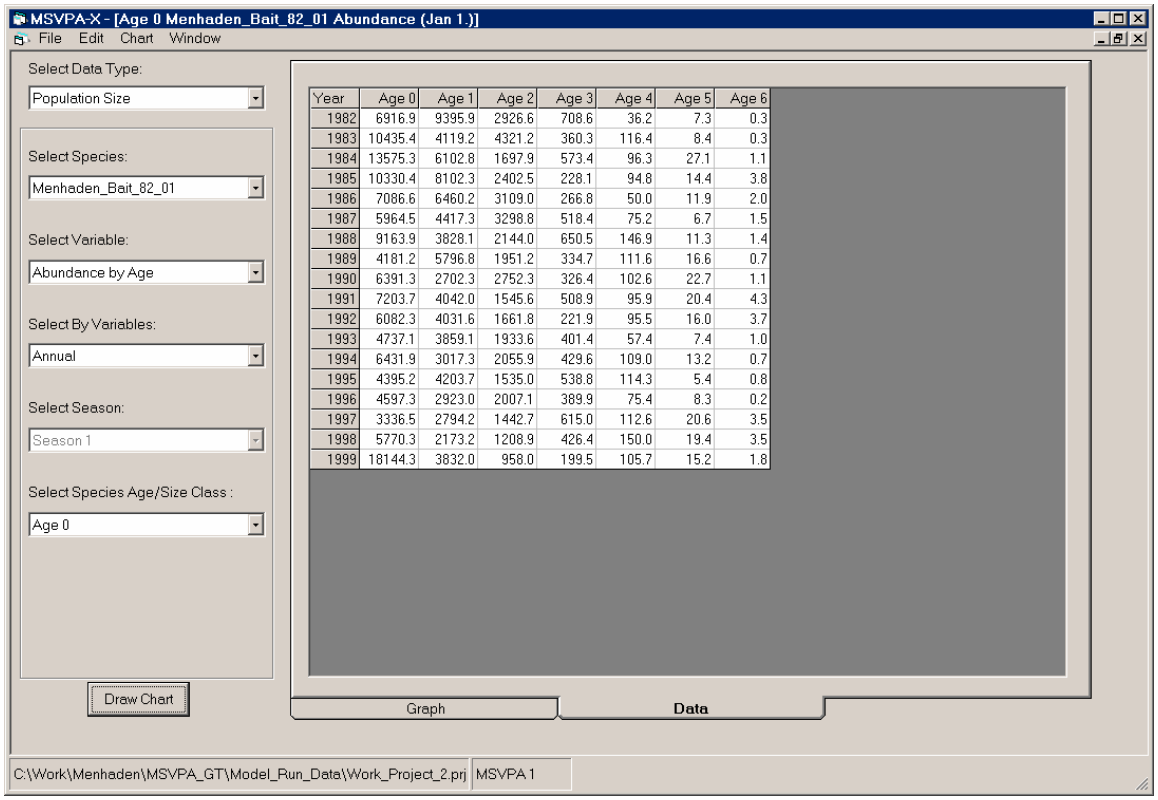
Total Abundance – Total abundance in numbers of fish by year

Abundance by Age – Abundance of each age class. The chart displays results for a specific age class, but the data matrix presents abundance for all ages.

Recruit Abundance - Calculates the total abundance for all age classes above the age class selected by the user. For example, selecting age 2 under this option will calculate the total abundance of fish in age classes >= 2.

Recruit Biomass - As with Recruit Abundance, but using biomass units.

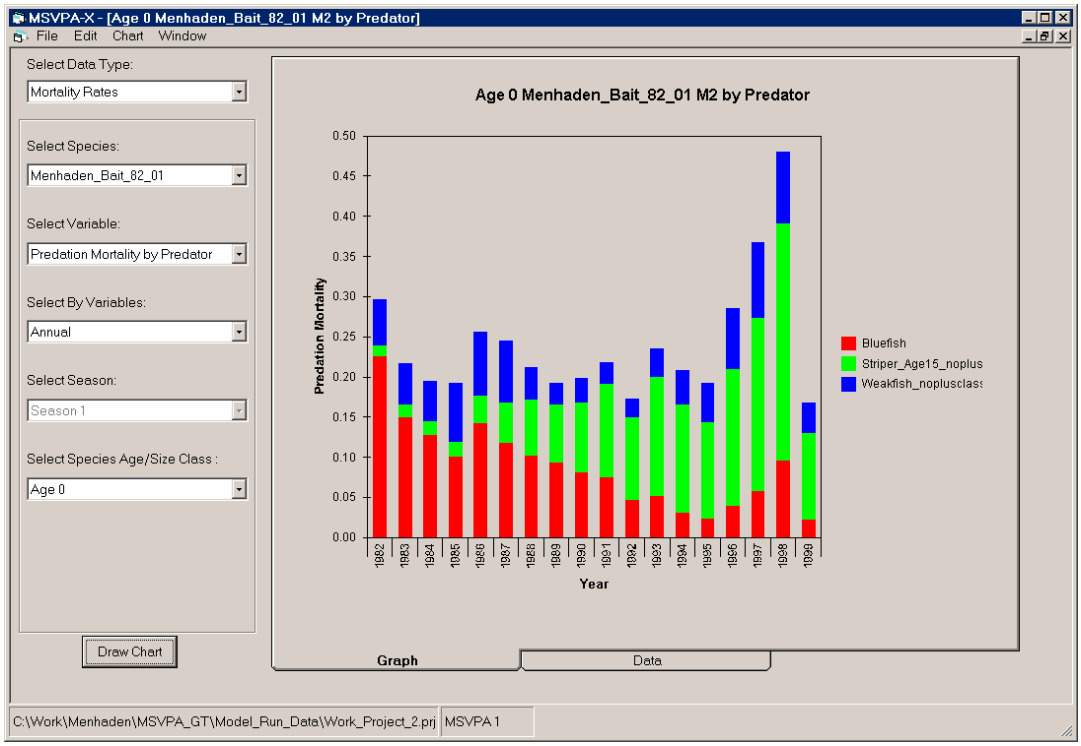
Figure 6.4 Data Form – Population Size Data



Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
1982	6916.9	9395.9	2926.6	708.6	36.2	7.3	0.3
1983	10435.4	4119.2	4321.2	360.3	116.4	8.4	0.3
1984	13575.3	6102.8	1697.9	573.4	96.3	27.1	1.1
1985	10330.4	8102.3	2402.5	228.1	94.8	14.4	3.8
1986	7086.6	6460.2	3109.0	266.8	50.0	11.9	2.0
1987	5964.5	4417.3	3298.8	518.4	75.2	6.7	1.5
1988	9163.9	3828.1	2144.0	650.5	146.9	11.3	1.4
1989	4181.2	5796.8	1951.2	334.7	111.6	16.6	0.7
1990	6391.3	2702.3	2752.3	326.4	102.6	22.7	1.1
1991	7203.7	4042.0	1545.6	508.9	95.9	20.4	4.3
1992	6082.3	4031.6	1661.8	221.9	95.5	16.0	3.7
1993	4737.1	3859.1	1933.6	401.4	57.4	7.4	1.0
1994	6431.9	3017.3	2055.9	429.6	109.0	13.2	0.7
1995	4395.2	4203.7	1535.0	538.8	114.3	5.4	0.8
1996	4597.3	2923.0	2007.1	389.9	75.4	8.3	0.2
1997	3336.5	2794.2	1442.7	615.0	112.6	20.6	3.5
1998	5770.3	2173.2	1208.9	426.4	150.0	19.4	3.5
1999	18144.3	3832.0	958.0	199.5	105.7	15.2	1.8

III. Mortality Rates

Figure 6.5 Data Form – Mortality Rates



Mortality rate outputs are also available for all MSVPA species and are calculated within the model. Mortality rates can be presented on an annual or seasonal basis by selecting the appropriate by variable. In the case of fishing mortality, seasonal rates are simply the annual rates prorated by the length of the selected season. Four variable types are available.

Fishing Mortality - Age specific fishing mortality rates as calculated by the MSVPA-X. F for a single selected age class is displayed in the chart, but the data matrix displays the entire F-at-Age matrix.

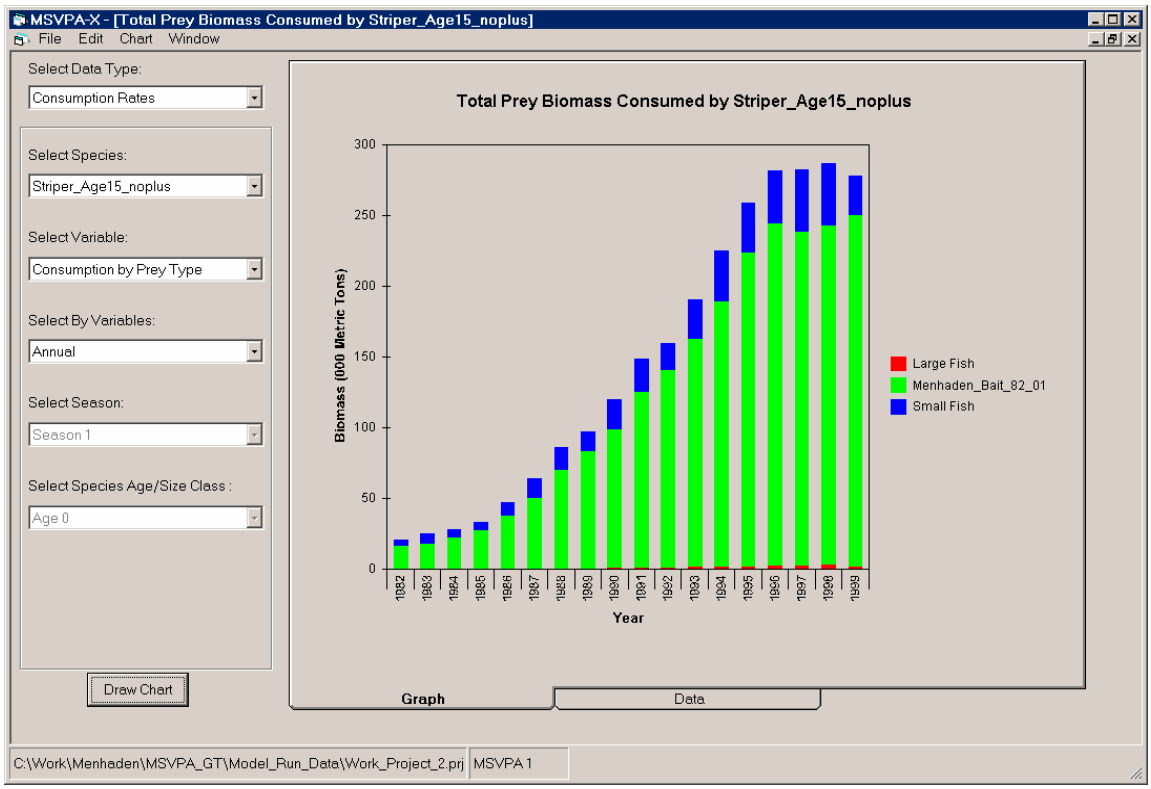
Average Recruited F - The average fishing mortality weighted by catch at age above a selected age of recruitment. For example, selecting age 3 would calculated the catch weighted average F for ages 3+.

Predation Mortality - Predation mortality rates by age class. A single selected age is presented in the chart, but M2 by age class is shown in the data matrix.

Predation Mortality by Predator – Age specific predation mortality partitioned among the predator types including both MSVPA and biomass predator species.

IV. Consumption Rates

Figure 6.6 Data Form – Consumption Rates



Total consumption rates in prey biomass are calculated for both MSVPA species and biomass predators. Five variable types are available under this data type and can be resolved seasonally or annually. Annual data reflects the sum of season specific totals. Prey biomass consumed by each predator is expressed in thousands of metric tons.

Total Biomass Consumed – Total biomass of prey consumed by the predator summed across predator age classes.

Consumption by Predator Age – Prey biomass consumed by a particular age or size class for the selected predator.

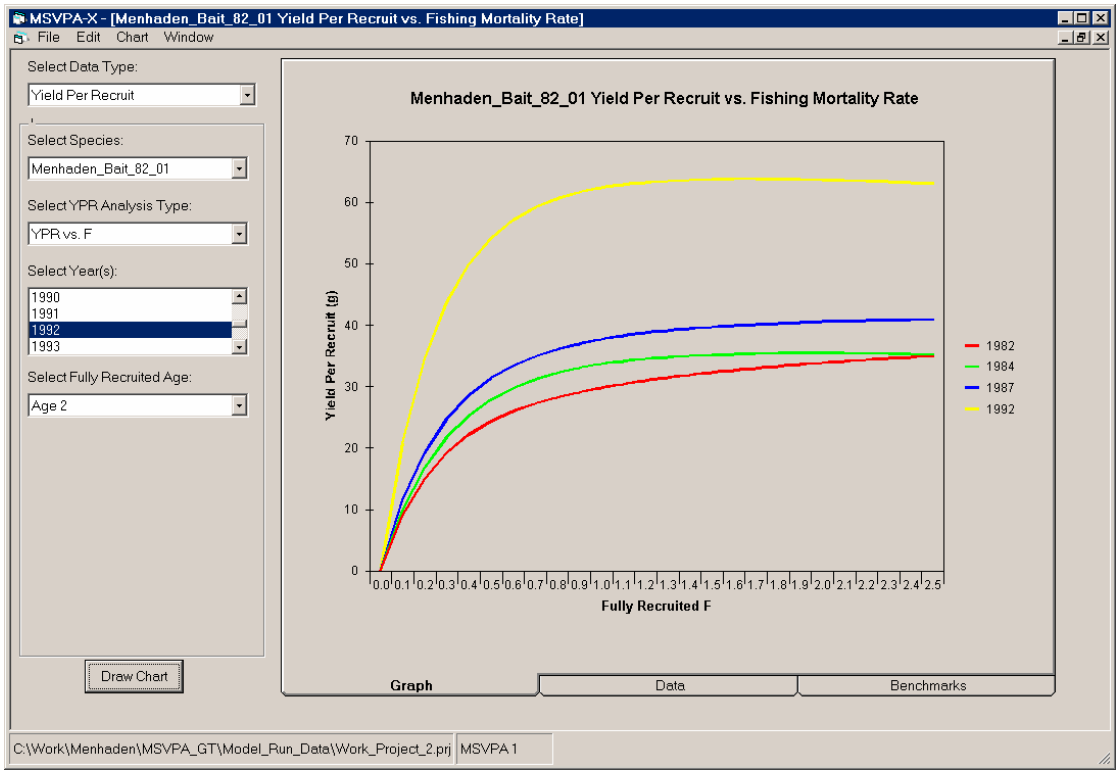
Consumption by Prey Type – Total consumption across predator ages partitioned by prey types. Includes both MSVPA-X prey and other prey types.

Cons. By Pred Age and Prey Type – Predator age specific consumption partitioned by prey type.

Consumption by Prey Age – Predator age specific consumption of a particular prey species partitioned by age class of the prey. The prey species is selected in the "Select Prey Species" list box that is available when this variable type is selected.

V. Yield Per Recruit

Figure 6.7 Data Form – Yield Per Recruit



Yield per recruit (YPR) and spawning stock biomass per recruit (SSB/R) analyses are not a direct output from the MSVPA-X approach, but they are calculated from mortality rates for the MSVPA species. The metrics provided here are useful for evaluating changes in the productivity of these stocks over time as a function of both varying predation mortality rates and growth rates.

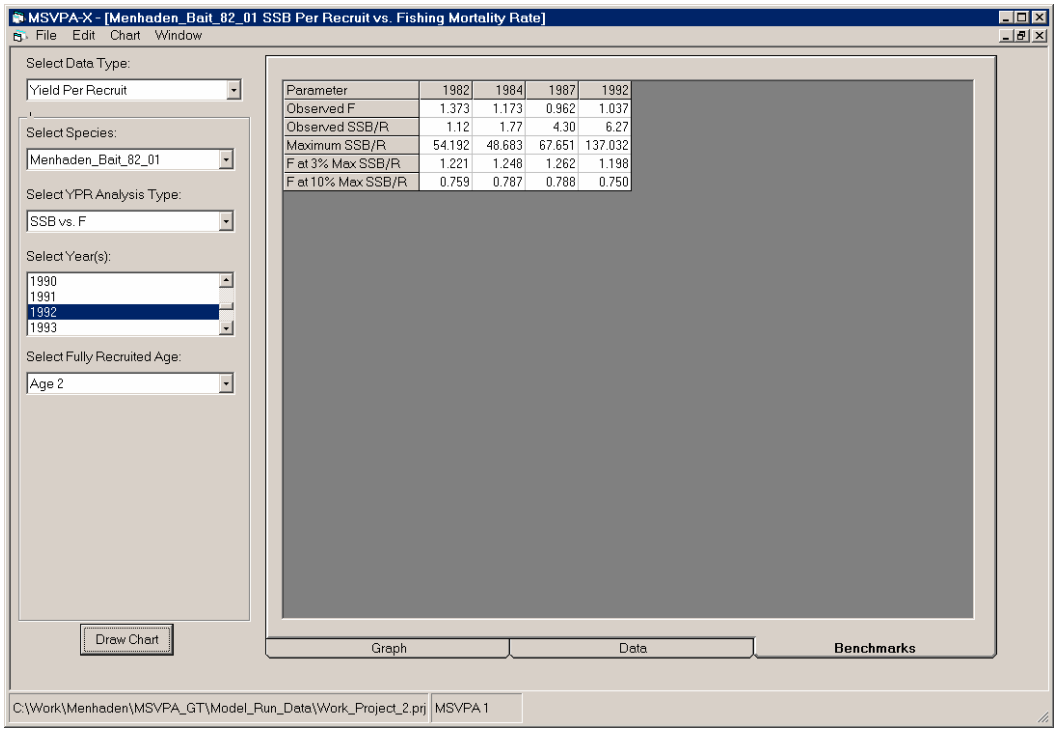
On selecting the "Yield Per Recruit" data type, a different set of list boxes for selecting query options becomes available. The first is the species list including all MSVPA species, the second selects the analysis type, the third allows selection of years for a particular analysis, and the last selects the fully recruited age class for the species. In all cases, "flat-topped" recruitment is assumed when calculating average fully recruited fishing mortality rates and partial recruitment factors. The age specific fishery, predation and natural mortality rates from the MSVPA-X model are used in calculating YPR indices. SSB/R values also include input data on maturity at age and assume a 50% female sex ratio. Biomasses are calculated based on the weight at age data or equations input for the species and reflect weights at the beginning of each year. Five YPR analysis types are available.

For each analysis type, an appropriate set of benchmarks is displayed in a data matrix on the "Benchmarks" tab.

YPR vs. F –YPR as a function of fully recruited fishing mortality rates for a selected year or years. Multiple years can be selected for display by holding the "Ctrl" button and clicking on the "Select Year(s)" list. Observed fishing mortality, observed YPR, the Fishing mortality rate providing maximum YPR (Fmax), and the Fishing mortality rate where the slope is $1/10^{th}$ that at the origin ($F_{0.1}$) are displayed on the benchmarks page.

SSB vs. F – SSB/R as a function of fully recruited fishing mortality rates for a selected year or years. Observed F, observed SSB/R, maximum SSB/R (no fishing), F resulting in 3% maximum SSB/R and F resulting in 10% maximum SSB/R are shown on the benchmarks page.

Figure 6.8 Data Form – SSB/R Benchmarks

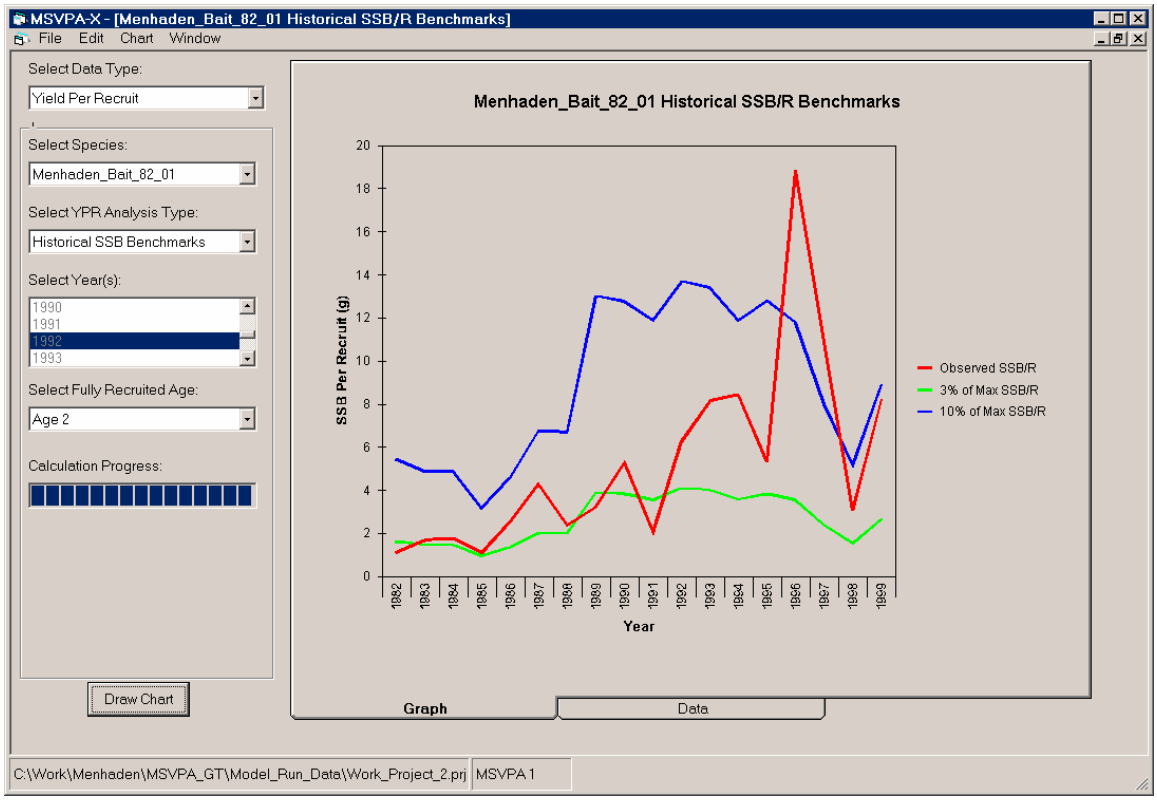


Historical YPR – Shows trends in calculated observed and maximum YPR values across the MSVPA-X time series.

Historical F Benchmarks – Trends in observed fully recruited fishing mortality rate and F benchmarks across the time series. F benchmarks include Fmax, $F_{0.1}$, F at 3% maximum SSB/R, and F at 10% maximum SSB/R.

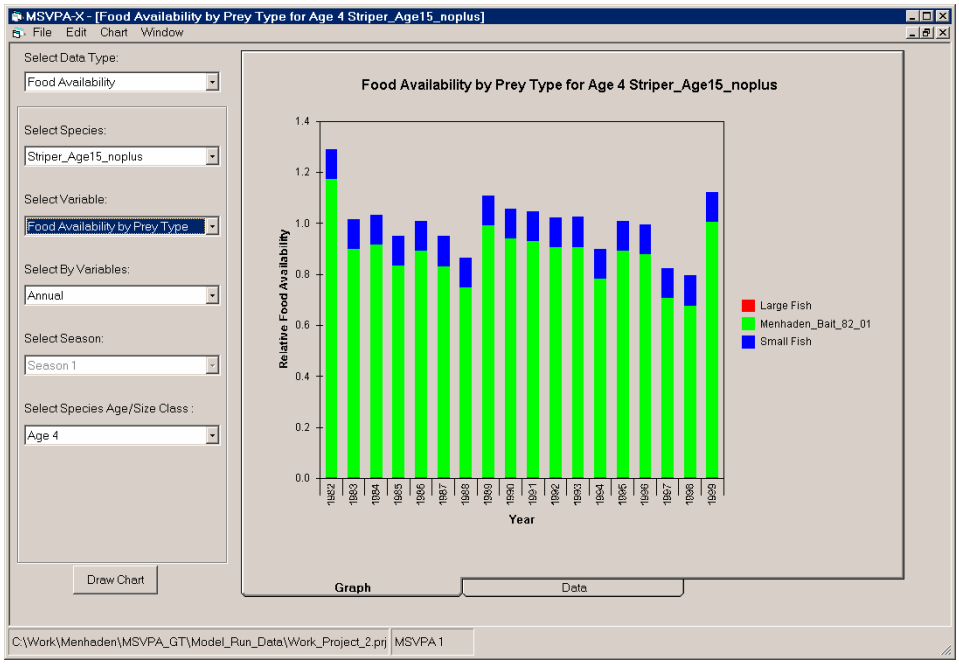
Historical SSB Benchmarks – Trends in observed SSB/R, 10% of Max SSB/R, and 3% of Max SSB/R. Maximum SSB/R for each years is also shown in the data matrix.

Figure 6.9 Data Form – Historical SSB Benchmarks



VI. Food Availability

Figure 6.10 Data Form – Food Availability



Food availability may adversely affect predator growth rates in cases where there are dramatic changes in forage species availability over time, and the suitable prey biomass calculated in the model is an index of the food available that a predator may consume. Food availability outputs are presented as relative values against average suitable prey biomass across the time series. A value of 1 for a given time period indicates that food availability was equal to the time series average, a value > 1 indicates higher than average suitable prey biomass, and a value < 1 indicates lower than average suitable prey biomass. Four variable types are available and can be displayed seasonally or annually.

Food Availability: Relative suitable prey biomass

Per Capita Food Availability: Suitable prey biomass divided by the total biomass of the predator/age class. This reflects changes in the food availability to each individual as a function of changes in both prey and predator populations.

Food Availability by Prey Type: Relative food availability partitioned by the proportion of each prey type.

Food Availability by Prey Age: Relative food availability by age class for a prey species.

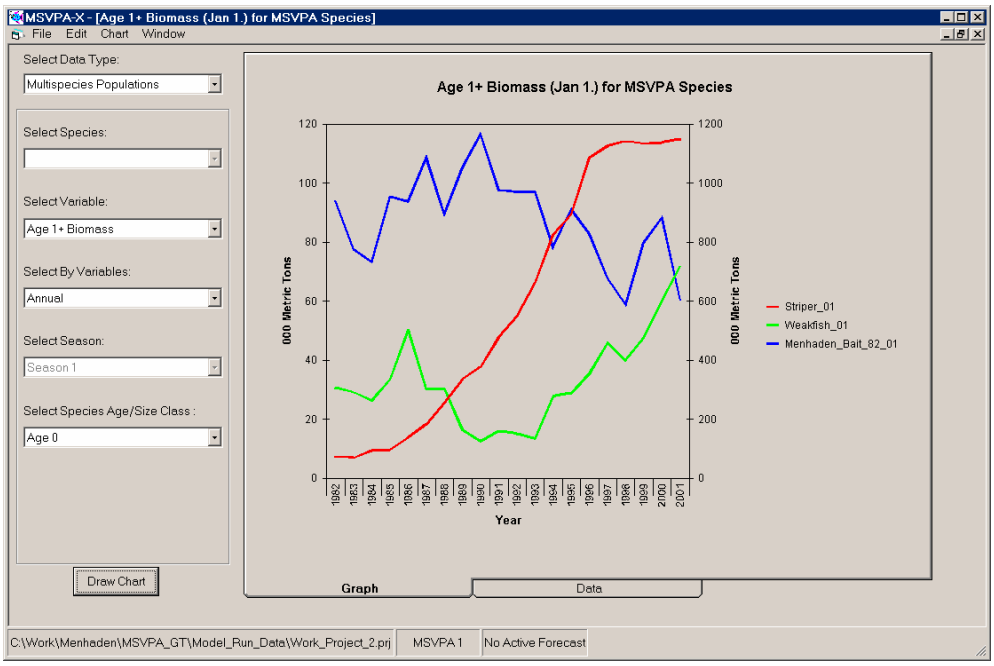
Stomach Content Weight: This displays the proportional stomach contents weight as predicted from food availability.

Caloric Content of Diet: This option is active only if predator growth is modeled (see Chapter 9). This displays the total energy content of the diet based upon diet composition and prey energy density.

Caloric Content by Prey Type: This displays the proportion of the diet caloric content as contributed by different prey types. This option is active only when growth is modeled (see Chapter 9).

VII. Multispecies Population Trends

Figure 6.11 Data Form – Multispecies Populations



The final output type displays population information for multiple species simultaneously. The output values for each species are identical to those calculated in the "Population Size" variable type. This output allows exploration of trends in population size for MSVPA predator and prey species. Five variable types are available and can be presented annually or seasonally as with single species population size outputs.

Total Biomass: Total biomass of each species.

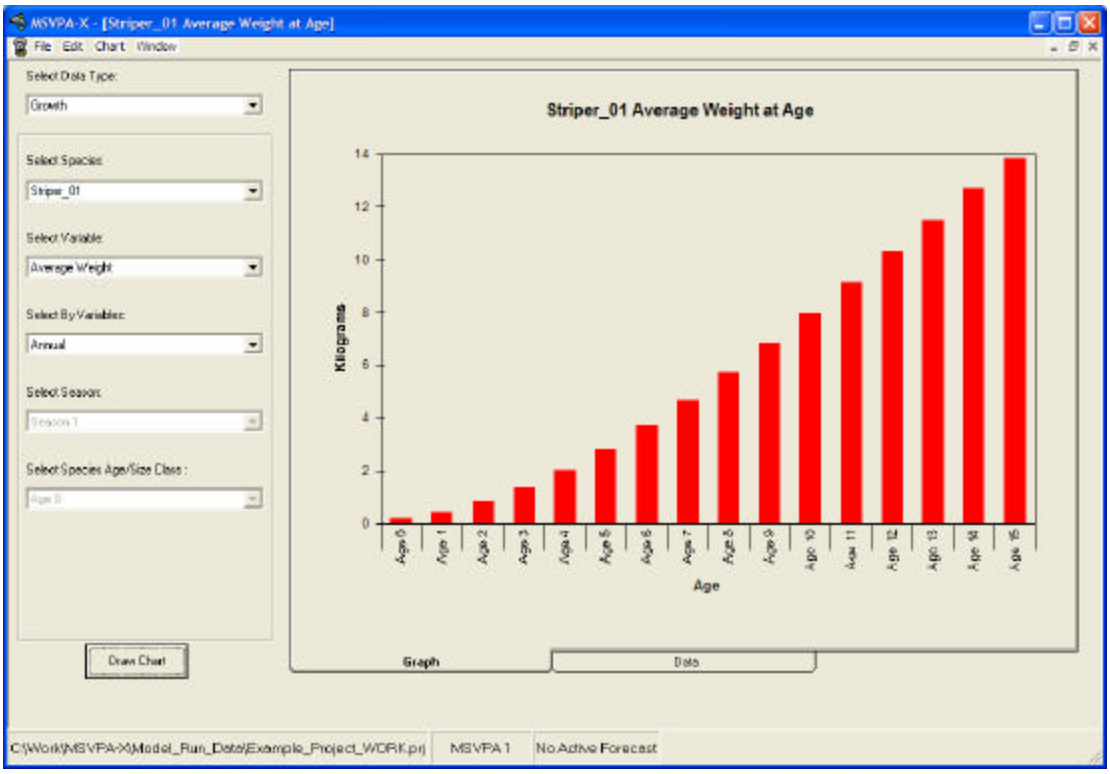
Total Abundance: Total abundance of each species.

1+ Biomass: Total biomass of age classes >= 1 for each species.

1+ Abundance: Total abundance of age classes >= 1 for each species.

Spawning Stock Biomass: Spawning stock biomass as calculated from input maturity data and assuming a 50% female population.

VIII. Growth



Predator growth in size and weight at age can be examined in this data type. When predator growth is modeled, these results will reflect predicted growth based upon food availability and caloric content of the diet. Four variable types can be displayed for the MSVPA predators included in the model and may be displayed seasonally or annually.

Average Weight: Seasonal weight for each age class averaged across years. The "annual" weight reflects the mid point of season 1.

Average Size: Seasonal size for each age class averaged across years. The "annual" size reflects the mid point of season 1.

Weight At Age: Time series of seasonal weight for the selected age class and season.

Size at Age: Time series of seasonal size for the selected age class and season.

Additional Menus on Data Forms

The data forms include options under the chart menu to control some aspects of the appearance of the graphs. Future versions of the program may expand these options to allow modification of series colors, chart labels, and other cosmetic aspects of the charts. The options included in this version are designed to assist in display and interpretation of model data. In each case, selecting the option automatically redraws the chart. Default chart characteristics are set for each variable type. Selections under the chart menu include:

Chart > Chart Type >

Line Chart: Displays the data series as lines.

Bar Chart: Displays the data series as vertical bars.

Stack Chart Series: "Stacks" series to present cumulative totals. Useful for presenting proportional diets that sum to 1.

Unstack Chart Series: Deactivates stacking.

Chart > Series >

The user must first select a series by a single click on the plot to activate these controls.

Plot Series on Primary Y-Axis: Plots a selected series on the main (left) Y-axis

Plot Series on Secondary Y-Axis: Activates and plots a selected series on a secondary (right) Y-axis. Useful in cases where one is interested in comparing trends of measures that have very different magnitudes. For example, multispecies population sizes.

Edit > Copy Graph

This menu selection copies an image of the graph to the clipboard for pasting into other programs. The bitmap image of the graph can be pasted into other applications, for example MS Word or Excel, by selecting Paste Special on the menu item. The associated data plotted in the chart may be pasted into other programs by selecting "Text" in the Paste Special Menus.

Remaining Edit commands apply to the data spreadsheet (see pg. 38: Spreadsheet Controls).

7- Multispecies Forecast Model

The MSVPA-X provides a historical perspective on the interactions between species and a basis of comparison to historical population trends, benchmarks, and predator diets across a time series. In addition to this perspective on multispecies interactions, it is a primary goal of multispecies and ecosystem fisheries models to evaluate potential short and medium term effects of management actions or ecological events. In single species assessments, this is generally accomplished by fairly simple age structured population models with inputs regarding target catches, fishery mortality rates, and stock recruit relationships. For multispecies models, one must consider these for each species and the potential linkages between species through predator-prey interactions. Thus, management scenarios for one species may have direct effects on the mortality rates, population sizes, and fishery yields for another species. The MSVPA-X application includes a forecast model that allows exploration of the 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 implented in the project file. Prey selection, predator consumption rates, and diet composition are calculated in an equivalent manner to the equations described in chapters 2 and 3. Predator growth may be modeled in the forecast approach, and this formulation is discussed in Chapter 9.

The forecast model is built upon the basic age structured population model:

$$(7.1)\quad N_{t+1} = N_t \exp[-(F + M1 + M2)],$$

Where the mortality terms are used as previously (equation 2.2) and N_t indicates the population size in numbers of a particular cohort at time t. Population biomass is then simply:

$$(7.2)\quad B_t = N_t w_t$$

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 the 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 (see Chapters 2 and 3), 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 wieght 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 are calculated based upon biomasses at the beginning of the day. Predator consumption is modeled as in the historical MSVPA-X approach (see Chapter 3). The correction for food availability is relative to the historical time series average 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:

$$(7.3)\quad \frac{C}{N} = \frac{M2}{Z}(1 - \exp(-Z)),$$

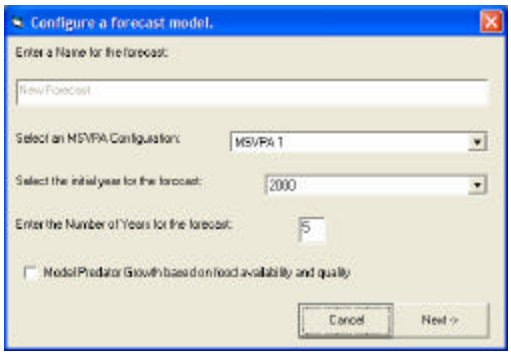
where *N* is prey abundance at the beginning of the time step, *C* is the number consumed during the time step by all predators, and $Z = F + M1 + M2$ where daily values for F and M1 are given. The calculated mortality rates are thus used to project the predator and prey populations forward to the next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

The model is intialized to a selected year from 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 in MSVPA predator and prey populations on an annual basis given the initial population size for each age class. 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. Several functional forms of the stock recruit relationship are included in the model implementation and are described more fully below.

8- Implementing a Forecast Model

Forecast configurations are saved in the project file and refer to a previously executed MSVPA-X run. Assuming at least one MSVPA-X model has been executed, a new forecast configuration can be developed by selecting the appropriate menu item from the main file menu.

Figure 8.1 New Forecast



The "new forecast" form is displayed and includes a list of available reference MSVPA-X runs. A list of years associated with the selected MSVPA-X is also shown, and the user is prompted to select a year containing initial population sizes, mortality rates, weights, etc. The number of years for the forecast is entered in a text box and cannot exceed 20 years. The same number of seasons, season lengths, and temperatures as those in the reference MSVPA-X will be used in the forecast. The predator growth model can be implemented by checking the appropriate box, and this approach is discussed further in Chapter 9.

Clicking "next" displays a data entry form to enter Von Bertalanffey growth and length-weight parameters for MSVPA-X species. All length data is in centimeters and weights are in kilograms for these parameters. The form behaves identically to spreadsheet forms used in the configuration of an MSVPA-X run.

Figure 8.2 Growth Parameters

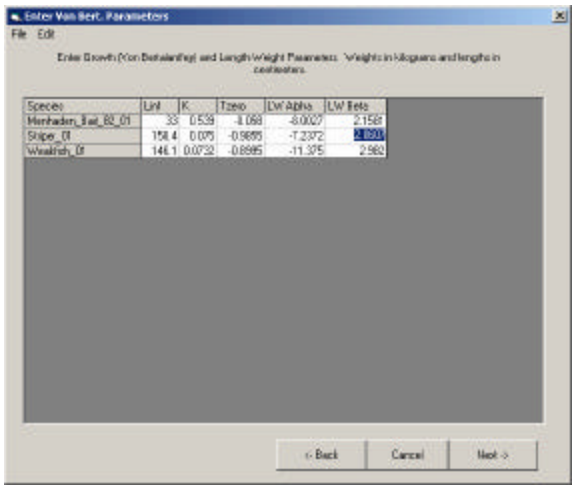
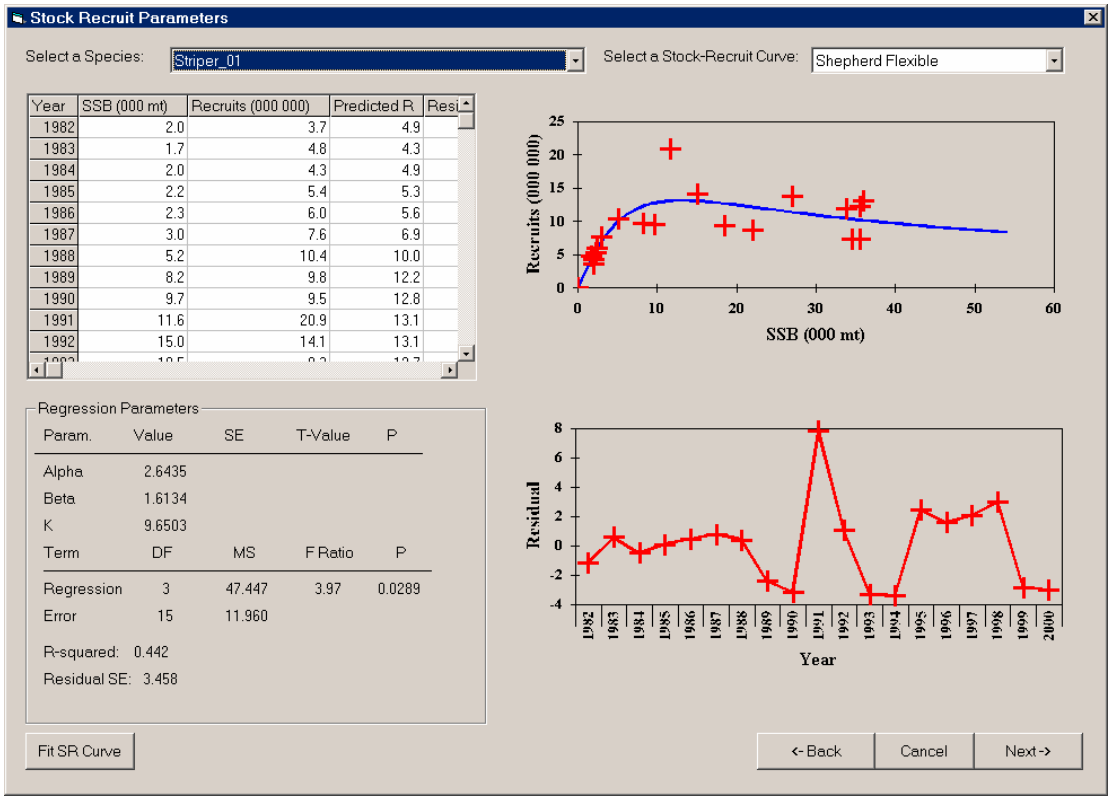


Figure 8.3 Stock-Recruit Relationships



Following the growth parameter form, the stock-recruit form allows the user to select and fit one of four different stock-recruit relationships for each of the MSVPA predators and prey. The model types are selected from the appropriate list box, and the "Fit SR Curve" button is clicked to fit the curve and display results. Linear and non-linear regression diagnostics are displayed along with plots of the model fit (upper panel) and residuals (lower panel). In each case, the stock-recruit models fit the number of (age 0) recruits (R) at the beginning of season 1 as a function of spawning stock biomass (S). The model types are described below.

1) Ricker Stock Recruit Relationship

$$(8.1)\quad R = aS\exp(-bS)$$

This is the standard Ricker SR 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 in the frame labeled "Regression Parameters".

2) Beverton-Holt Relationship

$$(8.2) \quad R = \frac{aS}{b+S}$$

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

3) Random from Quartiles

In cases where there is no clear relationship between 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 R for the appropriate quartile. A weak dependence between SSB and R 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.

4) Shepherd Flexible

Shepherd (1982) proposed an alternative SR 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.

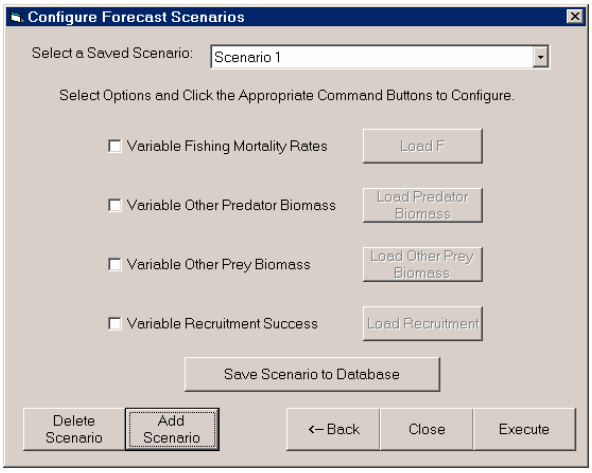
$$(8.3) \quad R = \frac{aS}{1+(S/B)^g}$$

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. Warning messages will be shown in the regression parameters frame when the fitting procedure fails to converge on an appropriate model.

Forecast Scenarios

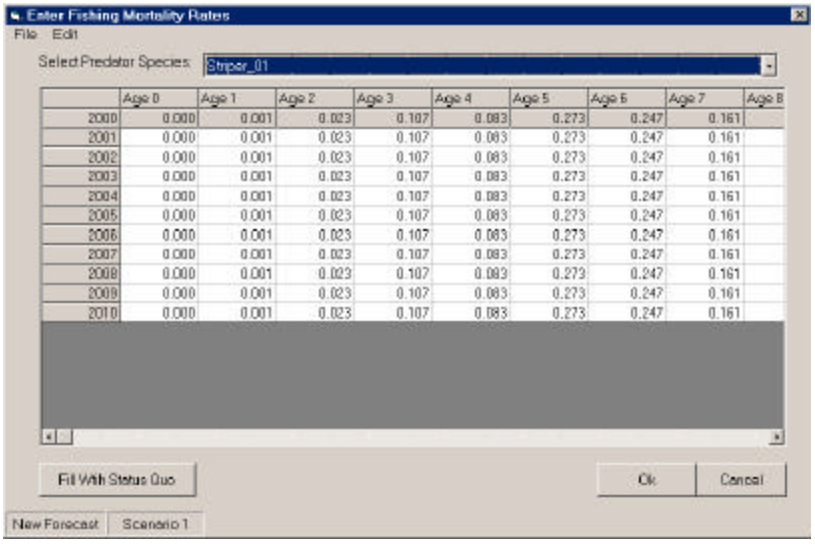
Each forecast configuration can be associated with a number of "scenarios" to facilitate exploratory analyses changes in fisheries management strategies and environmental effects for the assemblage being considered.

Figure 8.4 Scenario Configuration



The user can choose to add a new scenario or delete a saved one by clicking the appropriate command button. It is possible to configure each of 4 parameters that can vary through the course of the forecast: fishing mortality rates, other predator biomass, other prey biomass, and recruitment success. Clicking the appropriate check box activates the associated command button, and clicking on that button displays a data entry form:

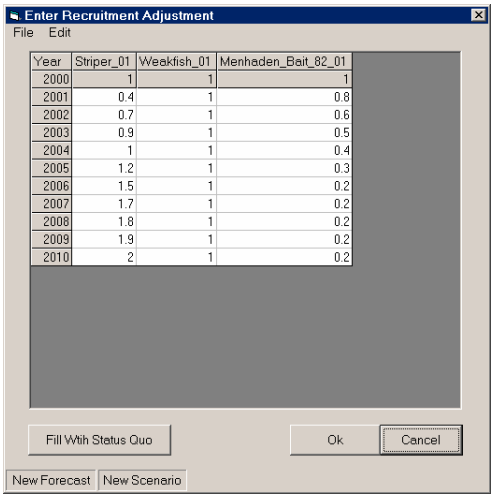
Figure 8.5 Scenario Fishing Mortality



In each case, the form contains a command button allowing the user to fill the matrices with status quo values (last year of results from historical MSVPA-X run) for a particular species.

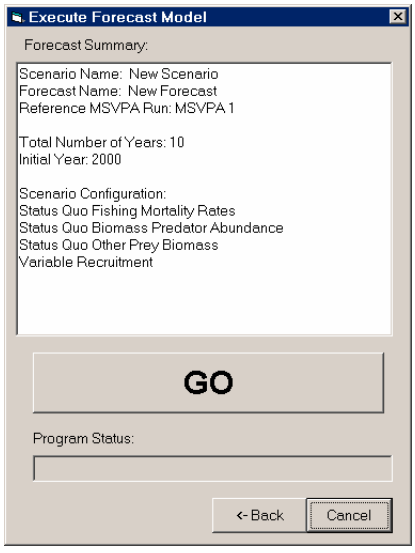
Recruitment success can be variable for each species. In this case, the scenario specifies that recruitment is above or below the predicted recruitment for the calculated SSB. This formulation is meant to simulate the effects of "good" or "poor" recruitment success during the simulation as a result of changing environmental conditions. A value of 1 indicates predicted recruitment levels, a value > 1 indicates above average recruitment success, and a value below 1 (greater than 0) indicates below average recruitment.

Figure 8.6 Scenario Recruitment Variation



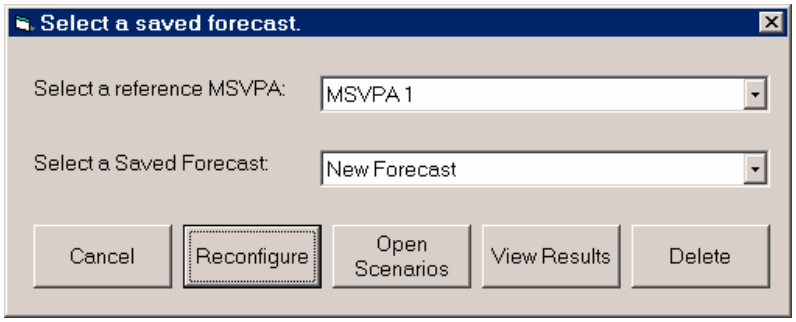
After entering all scenario data and clicking "execute" on the scenario configuration form, a summary form is displayed to execute the model and indicate program status.

Figure 8.7 Execute Forecast Model



After execution, the forecast run and outputs are saved to the project file and can be selected by choosing “Open Forecast” from the main file menu. Saved forecasts can be selected and reconfigured, or output forms can be display by clicking “View Results”.

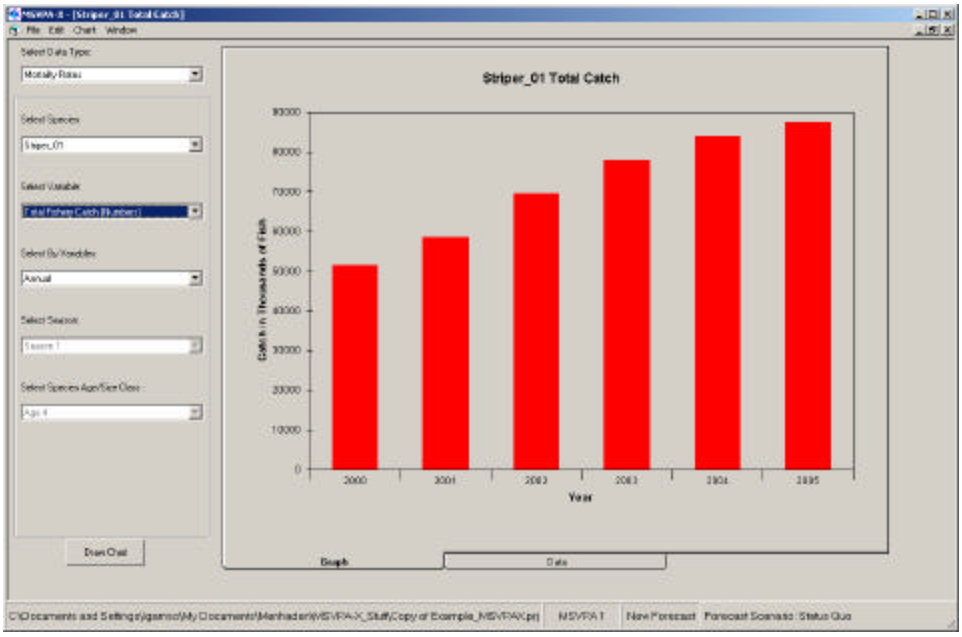
Figure 8.8 Execute Forecast Model



Forecast Results

Forecast scenario results are displayed on data forms that are nearly identical to those used to display MSVPA-X outputs. Multiple forecast data display forms can be opened simultaneously to explore results within a scenario. The only significant change for the forecast data form is that fishery catch (numbers) and yields (biomass) are displayed in the mortality data type as opposed to fishery mortality rates for the forecast model. These are predicted from input target F at age values and calculations of population size during the model. The forecast ouputs for fishery removals include total and age specific catch in thousands of fish and yields in thousands of metric tons.

Figure 8.9 Forecast Output form and Fishery Yields



9- Modeling Predator Growth

The potential feedbacks between predator growth and prey availability are potentially important when considering the dynamics of interacting exploited species. The MSGVPA application (Gislason, 1999) was developed explicitly to explore these processes, and the implications for multispecies reference points has been discussed in Collie & Gislason (2001). The development and application of bioenergetics models in the Chesapeake Bay also highlighted the potential for limitation of predator growth by reductions in prey species abundance with particular reference to the interactions between striped bass and Atlantic menhaden (Hartman & Brandt, 1995a; 1995b). The MSVPA-X application includes alternative model formulations for both the historical and forecast components of the model that include changes in predator growth in response to changes in prey availability and diet composition.

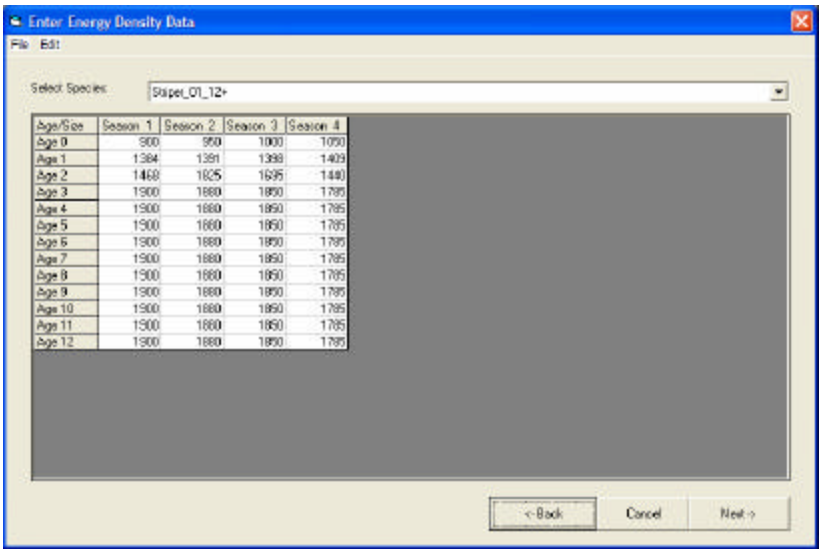
The formulation applied here is similar to the approach developed in the MSGVPA in that predator growth is modified as a function of deviations in food availability from an average level. Predator growth is thus constrained to vary around a mean growth rate that is input by the user. This contrasts with a fully developed bioenergetic approach that explicitly models predator metabolism (e.g., Hartman & Brant, 1995b). However, the fully developed bioenergetic approach requires a large number of additional parameters determined from laboratory experiments, the bioenergetic approach is sensitive to relatively small changes in prey diets, and the prediction of growth from this model is very sensitive to uncertainty in parameter values. We have taken a more simplistic approach to expand upon the MSGVPA equations by including considerations of food quality (i.e., caloric content) into the growth model implemented in the MSVPA-X.

Additional Data Input Requirements

In both the historical and forecast components of the model, the user may select to include predator growth formulations by clicking the appropriate check boxes on configuration forms (see Figures 5.2 and 8.1, respectively). Checking these boxes will change the sequence of data entry forms to allow the user to enter additional data required by the growth model. These data forms are similar for both the historical and forecast components of the application.

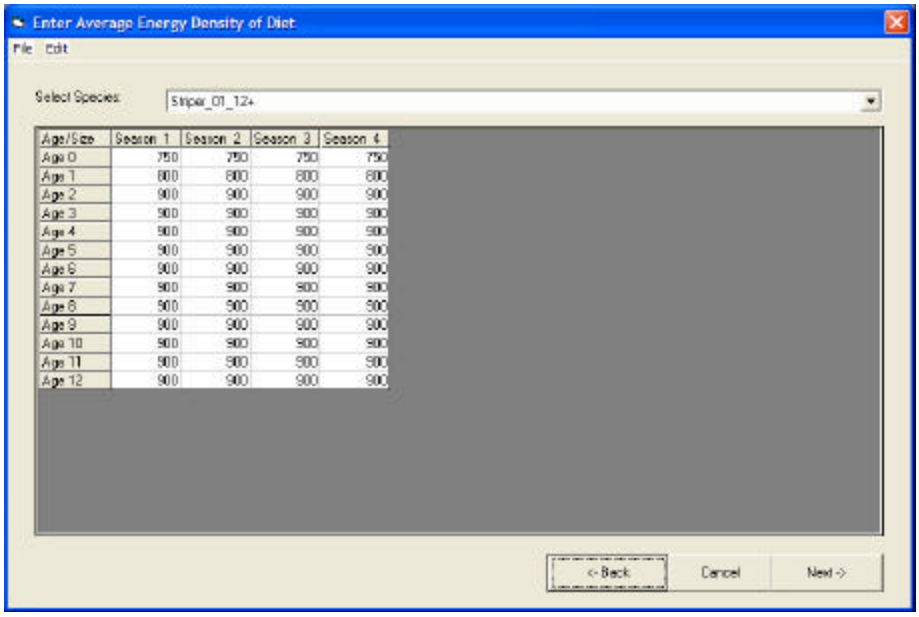
The growth model requires inputs of the energy density (Energy kg^{-1}) for all MSVPA predators and all prey species. Energy densities are known to vary seasonally and by size, and hence seasonal and size based energy density values are required data inputs. Energy densities for fish and invertebrate species are available from the literature (see Hartman & Brandt, 1995a and references therein).

Figure 9.1 Energy Density Data Entry



In addition to the seasonal average energy density, the model requires and estimate of average seasonal caloric value of the diet. Because the model is constrained to the average growth of the predators based upon input weight at age or growth parameters, it is necessary to know the average predator energy intake used to support that growth. In parameterizing the model, average predator diet composition should be calculated based upon either MSVPA-X runs not including predator growth or from literature sources. The average caloric content for input into the growth model is calculated from energy densities and the expected diets under average conditions.

Figure 9.2 Average Seasonal Caloric Content of Diet



Growth Model Formulation

Based upon either input size and weight at age or growth parameters, the average seasonal growth increment (i.e., change in weight) for each predator age class is calculated across years. In the case of the forecast model, the daily average growth increment is calculated, while the seasonal increment is calculated in the historical model. The average growth increment is converted from weight to energy by multiplying by the seasonal energy density for the predator. Growth (G) is the balance between consumption and respiration plus metabolic costs (e.g., assimilation loss, excretion). Thus, the average seasonal energy loss is calculated as the difference between average growth and average energy consumed. Thus, the average seasonal energy loss is:

$$(9.1) \quad \overline{R} = \overline{G} \cdot E_p - \overline{C} \cdot \overline{E^{diet}} \ ,$$

where E_p is the energy density of the predator, E^{diet} is the average caloric content of the diet as a data input, and C is the average wieght specific consumption (biomass) as calculated from input proportional stomach contents weight (see equation 3.1).

For a given year, *y*, the caloric content of the diet is calcluated as:

$$(9.2) \quad E_y^{diet} = \sum_i P_i \cdot E_i \ ,$$

where P_i is the proportion of each prey type, *i*, in the diet based upon the feeding selectivity model and E_i is the input seasonal prey energy density. The weight specific consumption, C_y, is calculated based upon total available prey biomass using equation 3.3. The "observed" consumption in energy for a given season is thus the product of C_y and E_y.

Growth is estimated as the difference between the energy consumed during the season and the average losses as calculated from eqn. 9.1. However, an additional constraint on predator growth is imposed by including a relationship between consumption and respiration. In most bioenergetic models, there is a negative relationship between predator consumption and respiration rate. Thus, at low food availabilities and low consumption, respiration declines preventing severe reductions in weight. Likewise, growth rates are constrained at high food availability and consumption rates by proportional increases in respiration. In the absence of these constraints, unrealistic predictions of predator growth occur. The constraint also imparts some degree of biological reality, as respiration rates may be reduced during periods of low food availability by, for example, reducing activity levels. In this application, the constraint on growth is implemented as a linear change in respiration proportional to the deviation of consumption (in energy units) from the average value:

$$(9.3) \quad R_c = 1 - \frac{C_y \cdot \overline{C}}{\overline{C}}.$$

Predator growth (in mass units) during the time interval is calculated as:

$$(9.4) \quad G_y = \frac{(C_y \cdot E_y^{diet}) - (\overline{R} \cdot R_c)}{E_p}.$$

Growth in length is calculated for the time interval from the appropriate length-weight relationship. This model results in a linear relationship between caloric intake in the diet and growth rates.

Additional outputs are included in both the forecast and MSVPA data screens to examine the results of the growth model. Under the "Food Availability" data type, the caloric content of the diet and proportional stomach contents can be plotted. In addition, the "Growth" data type allows examination of wieght and size as predicted by the model.

10- An Example MSVPA-X Analysis

The MSVPA-X model development was primarily focused on evaluating the interactions between Atlantic menhaden and its major predators along the U.S. Atlantic coast. Atlantic menhaden is a commercially and economically important species and serves as the primary forage base for commercially important fish including striped bass, weakfish, and bluefish. Atlantic menhaden can account for the majority of the diets of each of these species at some point during their life history.

Recent trends in the populations of these species have highlighted the potential importance of species interactions. The striped bass population declined to very low levels during the early 1990s and has recently undergone a strong recovery. The stock is currently at or near historically high levels (ASMFC, 2000). Likewise, weakfish populations have recently increased to high levels (Kahn 2002), and the bluefish stock is currently in a rebuilding phase (Gibson and Lazar, 1999). At the same time, Atlantic menhaden has shown poor recruitment in recent years. While the spawning stock biomass is at high levels, the recruitment of age 1 menhaden has been declining in recent years (Vaguhn *et al.* 2002).

These patterns raise two important issues from a multispecies management perspective. First, it is important to evaluate the potential effect of increasing predator populations on the dynamics of the menhaden stock. Increasing predator abundances may be associated with greater predation mortality rates and hence anticipated declines in menhaden productivity. Second, there is a concern that increasing predator stocks in combination with declining abundance of small menhaden may result in food limitation for the predator stocks. Suggestions of increased disease prevalence and "skinny" striped bass in the Chesapeake Bay are consistent with this hypothesis (Uphoff, in press).

Multispecies models in general and the MSVPA-X in particular are a useful framework in which to explore these potential interactions. The model can be used to evaluate historical patterns in interactions between the species, calculate predation mortality rates on menhaden, examine patterns in food availability to the predators, and model expected changes in predator diets associated with changes in the forage base.

An example MSVPA-X run is described here as an example of the data types, procedures, and outputs associated with a multispecies assessment. The data sources, configuration, and model results should be considered preliminary pending further refinement of model inputs.

Time Frame and Seasonal Temperatures

This example run encompassed the time period between 1982-2000 and included four seasons of even length. The seasons and associated temperatures (°C) were:

Winter	Jan – March	10
Spring	April – June	12
Summer	July – September	22
Fall	October-December	18

These temperatures were taken to be large scale seasonal averages reflecting both estuarine and Atlantic waters. They were treated as constant across the time series, but can be refined in full assessments.

MSVPA Predators

Striped bass and weakfish are the two predators that will be explicitly incorporated in this example MSVPA-X run. Data on catch at age, weight at age, size at age, and maturity for these species were taken from recent assessment documents (Kahn, 2002; ASMFC, 2000) and include fishery catches from 1982-2000. The assessments for these species currently use the ADAPT methodology and include multiple tuning indices. Therefore, the extended survivors analysis (XSA) single-species VPA was applied to these species for the current MSVPA-X run.

Figure 10.1 XSA and Adapt estimates of Age 4-14 abundance of Striped Bass. The Adapt model is based on catches from 1982-1999.

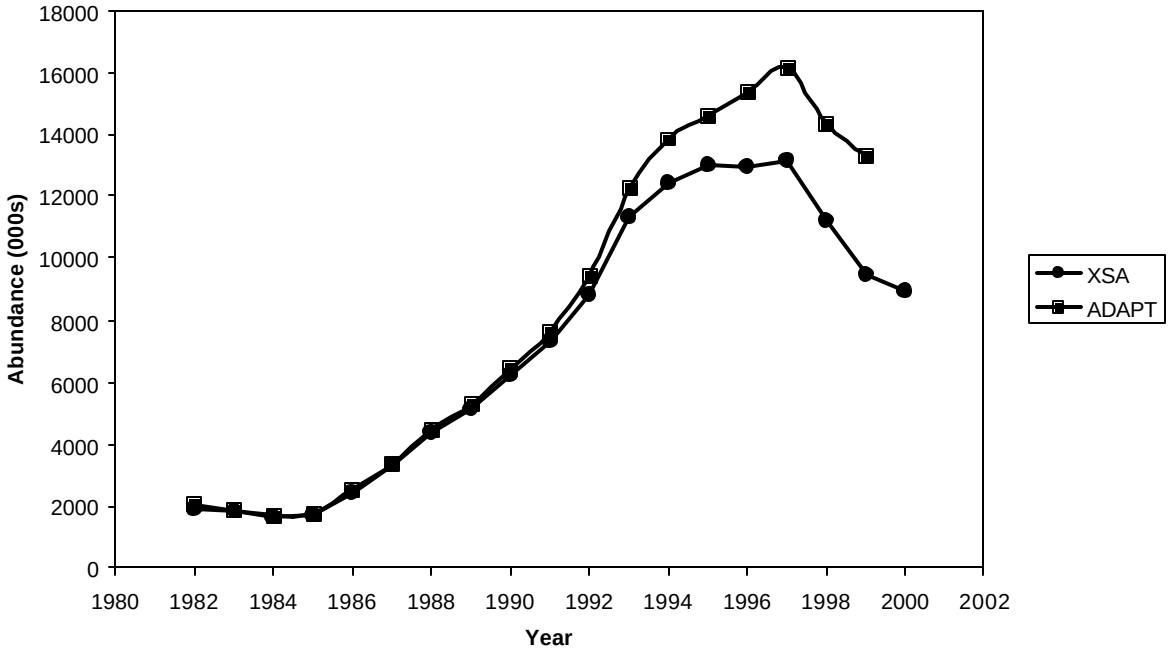
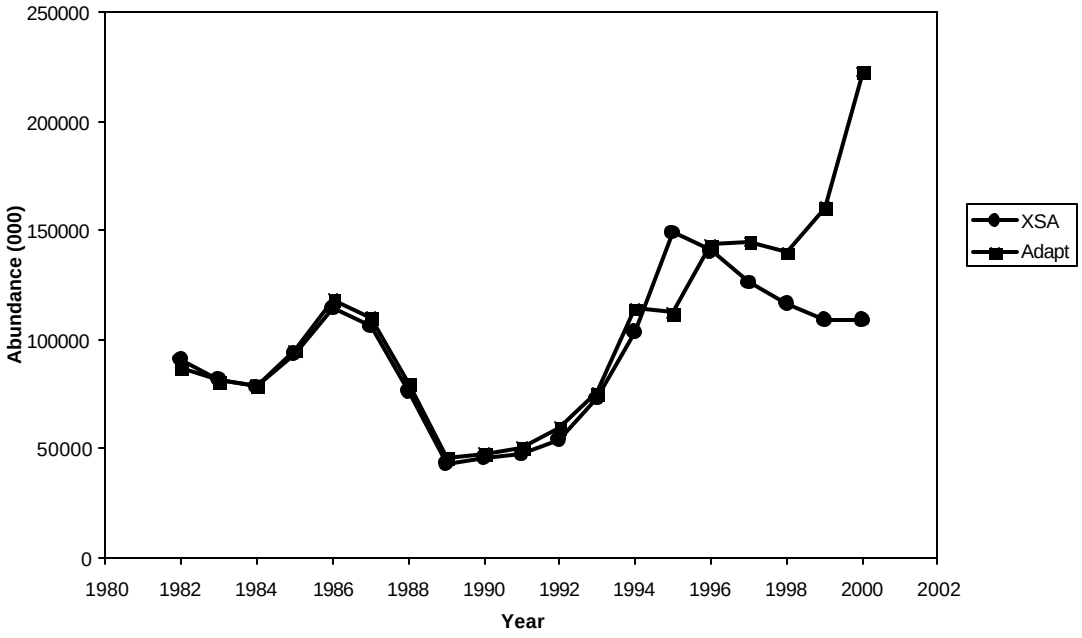


Figure 10.2 XSA and Adapt Estimates of Age 1+ Abundance of Weakfish.

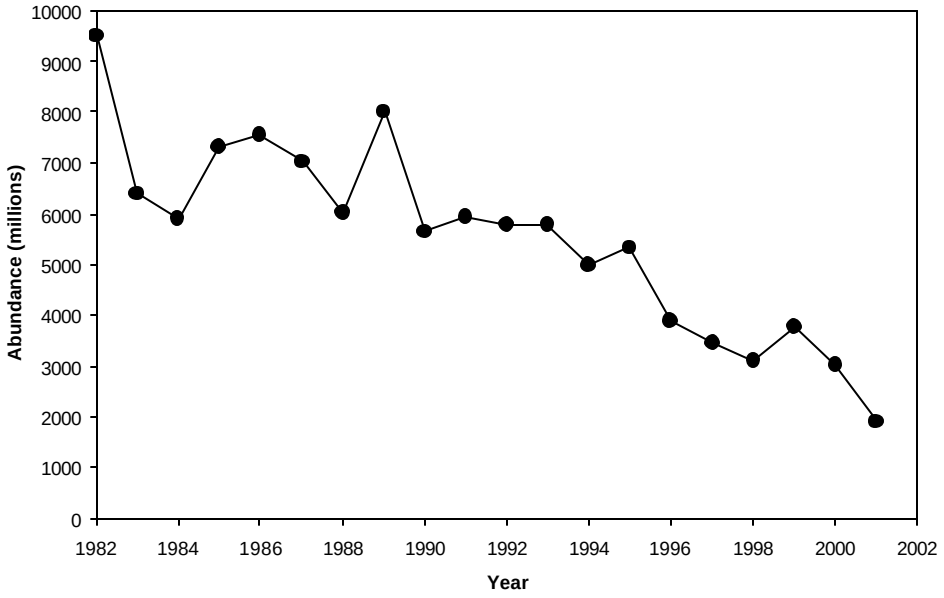


Note that the XSA generally results in a lower abundance estimate in recent years compared to the adapt methodology. The ADAPT assessment for weakfish demonstrated a strong positive bias in abundance estimates for recent years (Kahn, 2002). It is possible that the XSA approach is not as sensitive to this source of bias.

MSPVA Prey

Atlantic menhaden was the only MSPVA prey species included in the example model run. Catch at age, weight, size, and maturity data are taken from recent assessment documents for menhaden (Vaughn *et al.* 2002). The cohort analysis/separable approach implemented in the MSVPA-X and single-species results are identical to that used for the single species assessment and was applied to the catch at age matrix. Results shown in figure 10.3 are for the standard assessment assuming M= 0.45 for all age classes. The MSPVA-X recalculates the predation mortality rates based on predator consumption.

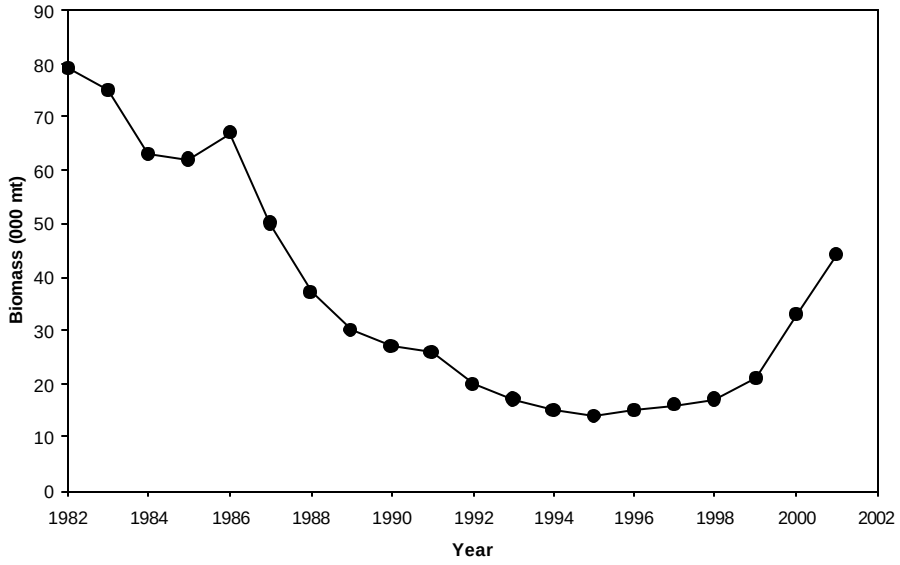
Figure 10.3 Abundance of age 1+ Atlantic menhaden based on single species assessment.



Biomass Predator

The bluefish stock is currently assessed using the ASPIC production model as opposed to age-structured MSVPA assessments. Therefore, bluefish is incorporated into the current example run as a biomass predator using the total biomass estimated from the ASPIC assessment (Lazar, 2000).

Figure 10.4 Biomass of bluefish from ASPIC model.



Three size classes were defined for bluefish to account for differences in prey preference. The proportion of total biomass for each size class was based upon results from previous age structured assessments for the species, and it is assumed that size structure is constant through the time series.

Table 10.1 Bluefish size structure

Size Class	Length Range (cm)	Age Range	Proportion of Biomass
1	10 - 30	0-1	0.025
2	30 - 60	1-4	0.267
3	> 60	5+	0.711

Other Prey

Inclusion of an appropriate set of "other prey" types and quantification of appropriate biomass levels is often the most subjective aspect of developing an MSVPA-X run. The prey field selected must accurately account for the major prey types available to and consumed by the predator species to develop appropriate modeled diet compositions. Based upon a review of available diet literature for the three predators being considered here, the example MSVPA-X run used three "other prey" types that are commonly consumed by the three predators.

1) Macrozooplankton: In younger age classes (primarily age 0) all three species had a significant amount of shrimps, mysids, and other small crustaceans in their diets. In addition, gammarid amphipods are often important components of juvenile diets for striped bass. The macrozooplankton prey type is meant to reflect these small crustacean prey. For the example run, a biomass of 600k metric tons was used for this prey type with a size range from 0.5-3 cm. The biomass was constant both seasonally and annually. Beta function parameters were selected so that the biomass distribution was approximately normally distributed across the size range.

2) Spot/Croaker: Small sciaenid fish are frequently significant dietary components for all three predators accounting for 10-40% of the diets. This prey category is meant to more generally represent other small to medium sized fish prey aside from menhaden that are consumed by large size classes of each predator. For the example run a constant biomass of 120k mt was selected based on fishery catches, and a size range of 4-15 cm was used. The size distribution was selected to also be approximately normally distributed.

3) Anchovy/Sm. Fish - A number of small fish species are important seasonal diet components for juveniles and young adult fish (ages 0-2). Bay anchovy is the most important of these and can account for >50 % of the diets of these predators

in some seasons. The availability of anchovy varies seasonally and can peak above 200k mt in Chesapeake Bay alone during summer and fall. For the example run, seasonal biomass values were set at: Winter (Season 1): 125k mt, Spring (Season 2) 125k mt, Summer (Season 3) 300k mt, and Fall (Season 4) 250k mt. The size range was 3-7 cm and biomass was approximately normally distributed across this range.

These values are intended only as approximations for the example run and should be further refined in more detailed assessments.

Type Selection and Spatial Overlap For Predator Species

Type selectivity and spatial overlap parameters were selected to reflect the major seasonal features of predator diets and the relative spatial distribution of the predators and Atlantic menhaden. Size selection parameters were fit based upon available data on the size distribution of fish prey in the diets. Summary diet information for each species and selected parameter values used in this run are included with the Version 1.0alpha distribution package. Major characteristics of the predator diets from literature sources (see documentation) are summarized here briefly.

Weakfish: Age 0 weakfish had high proportions of Bay Anchovies in their diets in summer and fall months along with shrimps and other macrozooplankton. Age 1-3 fish consumed larger fish, but generally did not consume menhaden during cold (winter and spring) months. Bay anchovy is important for age 1 fish, and spot and croaker are important dietary components during these months for larger fish. During summer and fall, menhaden becomes a large proportion of Age 1-2 weakfish diets. For larger sized weakfish living primarily in coastal waters, the proportion of menhaden in the diets is very low for all seasons.

Striped Bass: Age 0 striped bass consumed exclusively small fish and macrozooplankton. Age 1 fish consumed primarily shrimps and small fish during winter and spring, but over 50% of their diets were menhaden during summer and fall. Age 2+ fish consume high proportions of menhaden year round along with larger fish including spot and croaker.

Bluefish: Bluefish are piscivorous at a very early age and had high proportions of menhaden in their diets in summer months at Age 0. The remainder of age 0 diets is generally macrozooplankton and small fish. Menhaden is an important component of bluefish diets inside estuaries at all age classes and seasons. Larger (age 3+) bluefish in oceanic waters consume primarily larger fish including spot and croaker along with relatively low proportions of menhaden in their diets.

Evacuation rate parameters and the mean weight of stomach contents by season were summarized from previous analyses, published sources, and unpublished data.

The MSVPA-X run converged after 16 iterations, and was completed in approximately 45 minutes on a laptop computer with an 800 mHz Pentium 3 processor.

Example Outputs-Predator Diets and Consumption

Calculated average predator diets from the MSVPA-X run reflected the expected diet composition for each species. Model outputs of average predicted diet composition are shown below.

Figure 10.5 Average Diet Composition for Striped Bass Predicted from MSVPA-X

Figure 10.6 Average Diet Composition for Weakfish Predicted from MSVPA-X

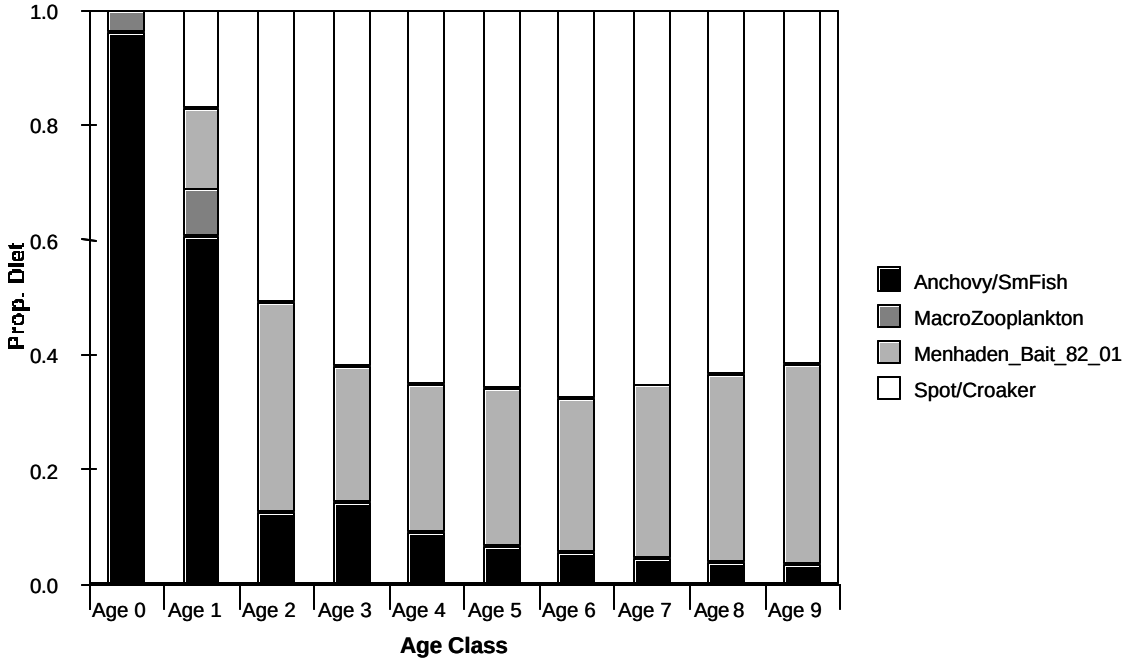
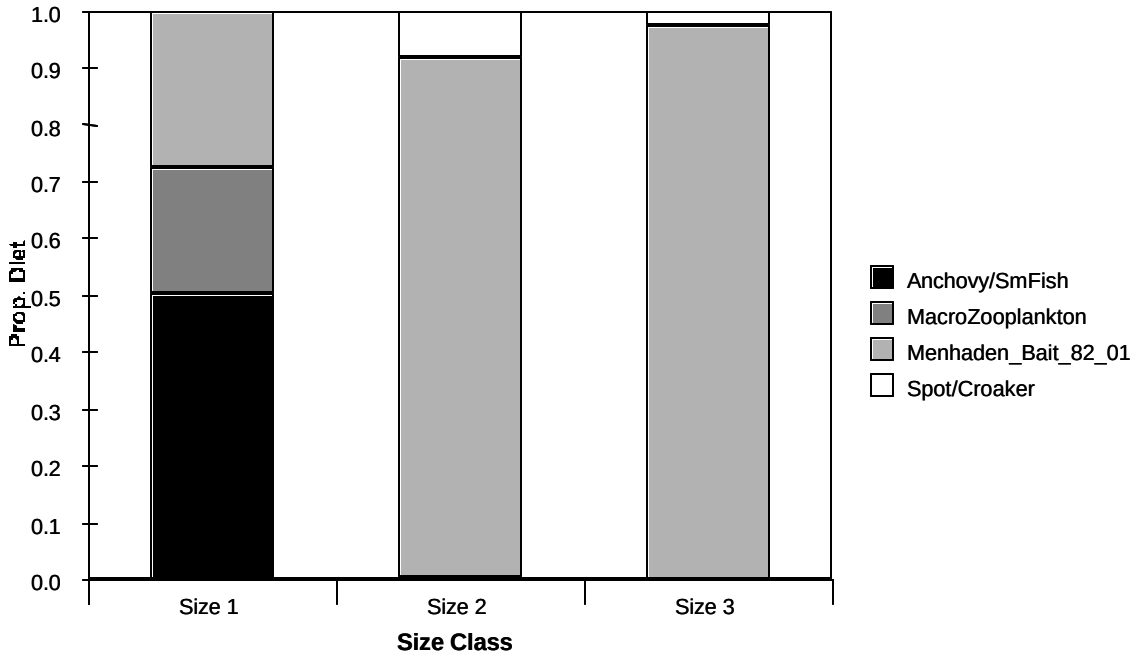
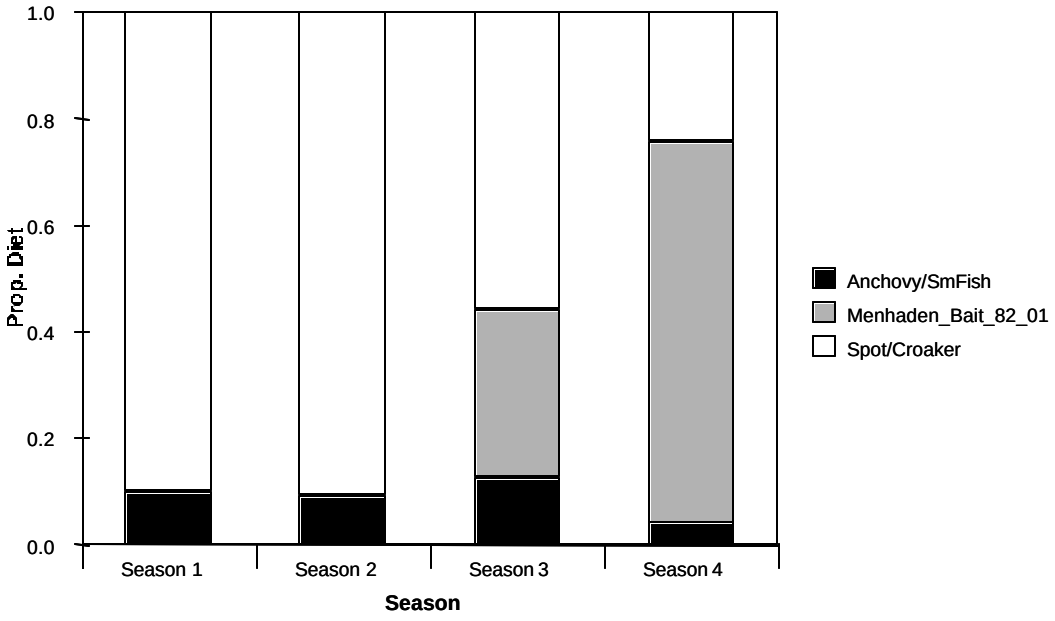


Figure 10.7 Average Diet Composition for Bluefish Predicted from MSVPA-X



The modeled diet composition for striped bass closely reflects the expected diets by age class based upon available data. The diet composition for weakfish reflected the expected seasonal patterns in that all menhaden consumption occurred during summer and fall. However, the proportion of menhaden in large weakfish diets during fall is higher than would be expected from observed diet data.

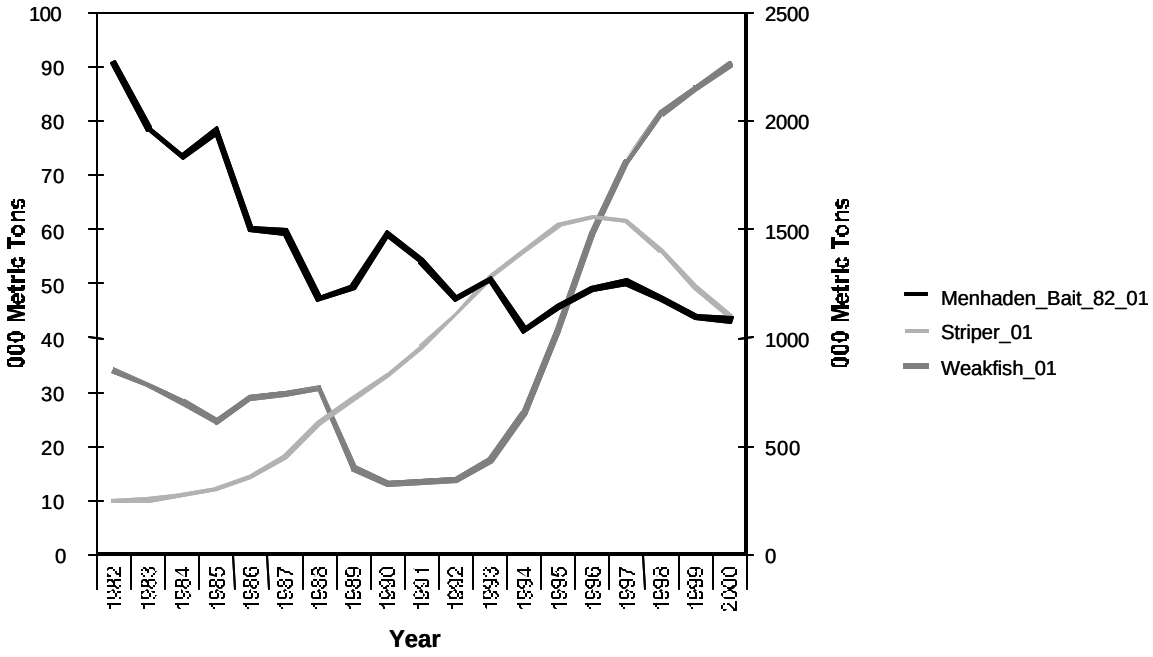
Figure 10.8 Average seasonal diet composition for age 4 Weakfish



The proportion of menhaden in large bluefish (Size 3, ages 5+) is also higher than would be expected from available diet data. Additional refinement of input parameters can improve the agreement between model outputs and expected diets for large bluefish and weakfish.

Total biomass trends for the three modeled species reflect the patterns observed in the single species VPAs for striped bass and weakfish as no additional predation mortality was included from the multispecies model. The downward trend in overall abundance and biomass of menhaden observed in the single species VPA was also seen in the MSVPA-X results.

Figure 10.9 Total biomass trends from the MSVPA-X example run. Menhaden biomass is shown on the right axis.



However, due to differences in calculated mortality rates, the abundance and biomass of menhaden differs between the multispecies and single species models. This is particularly the case in early years of the time series where the abundance estimates from the multispecies model is consistently higher than that for the single species assessment. The abundance estimates for age 0 menhaden are also consistently higher from the multispecies assessment compared to the single species assessment.

Figure 10.10 Age 1+ Menhaden abundance from single species and MSVPA-X models.

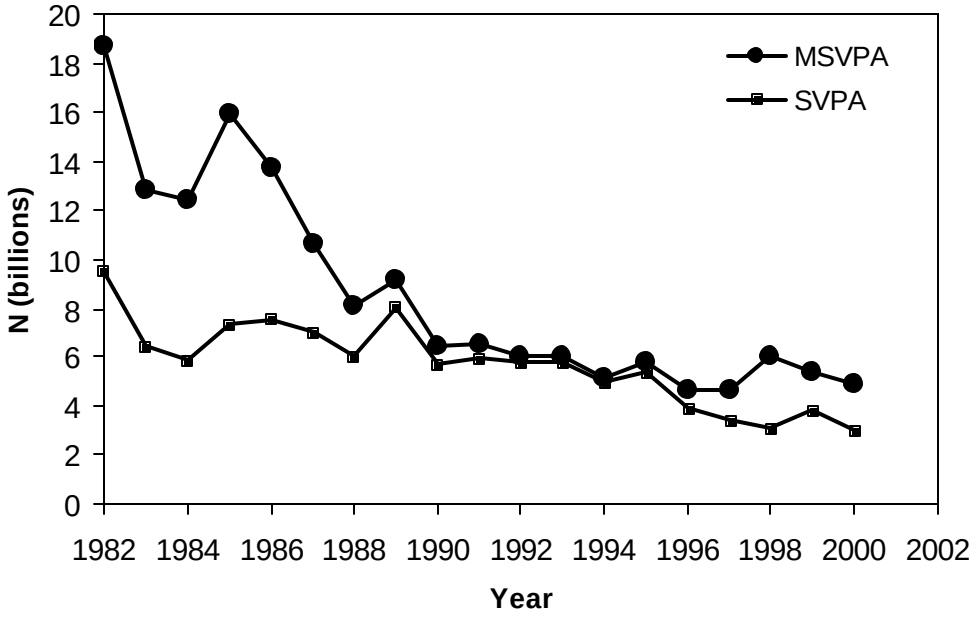
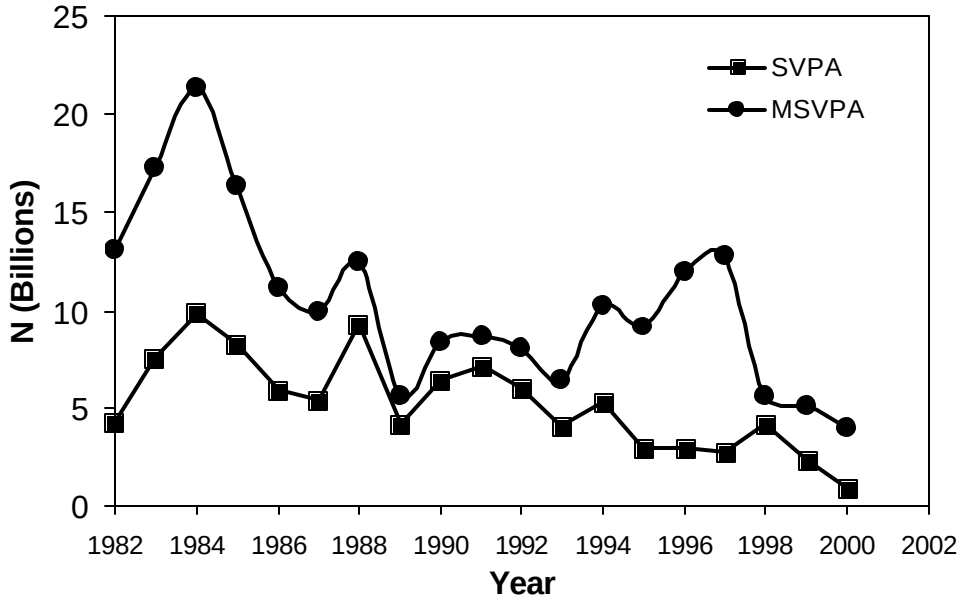
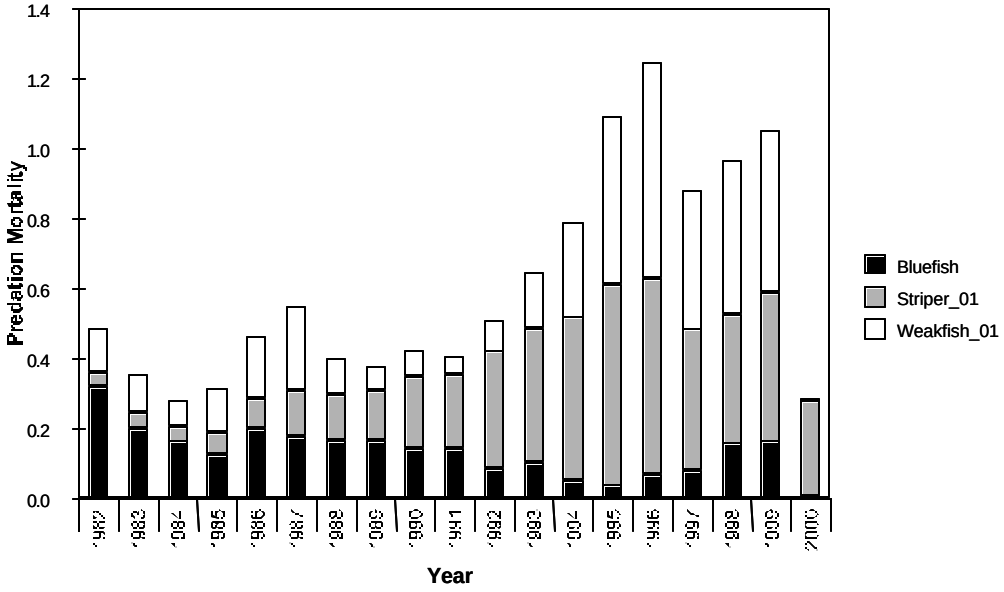


Figure 10.11 Age 0 Menhaden abundance from single species and MSVPA-X models.



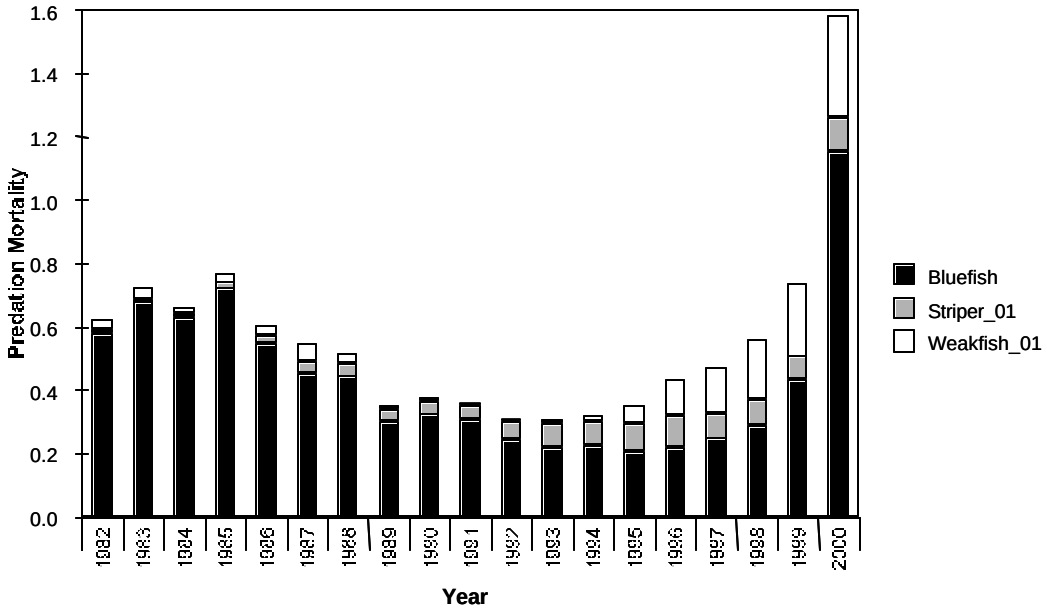
The higher abundance estimates from the MSVPA-X reflect the overall higher calculated mortality rates on earlier age classes due to the inclusion of predation in the multispecies model.

Figure 10.12 Age 0 menhaden annual predation mortality rate by predator species.



The predation mortality rates on age-0 menhaden increased over the course of the time series in this model configuration. The recent increases are associated primarily with the increased biomass of striped bass and weakfish during recent years.

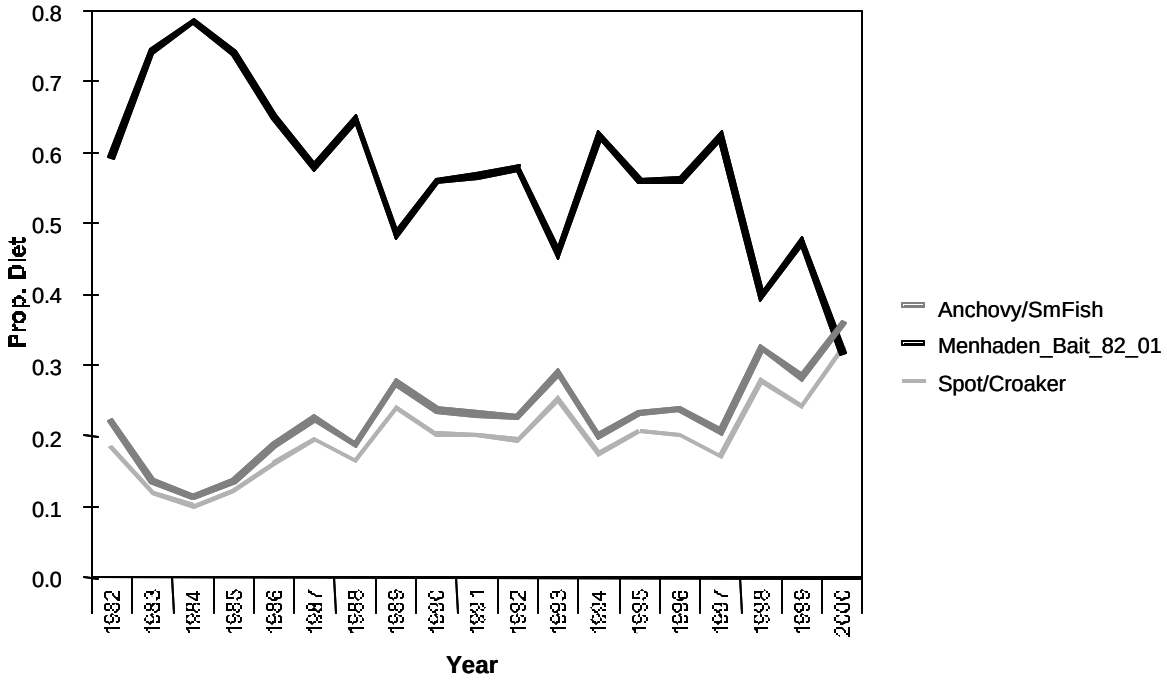
Figure 10.13 Age 1 menhaden annual predation mortality rate by predator species.



The model also predicts that predation mortality rates on age 1 and older menhaden have increased to very high levels in recent years associated primarily with an increase in bluefish abundance. This results from the prediction of high proportion of menhaden in large bluefish diets, which may not be supported by the available data.

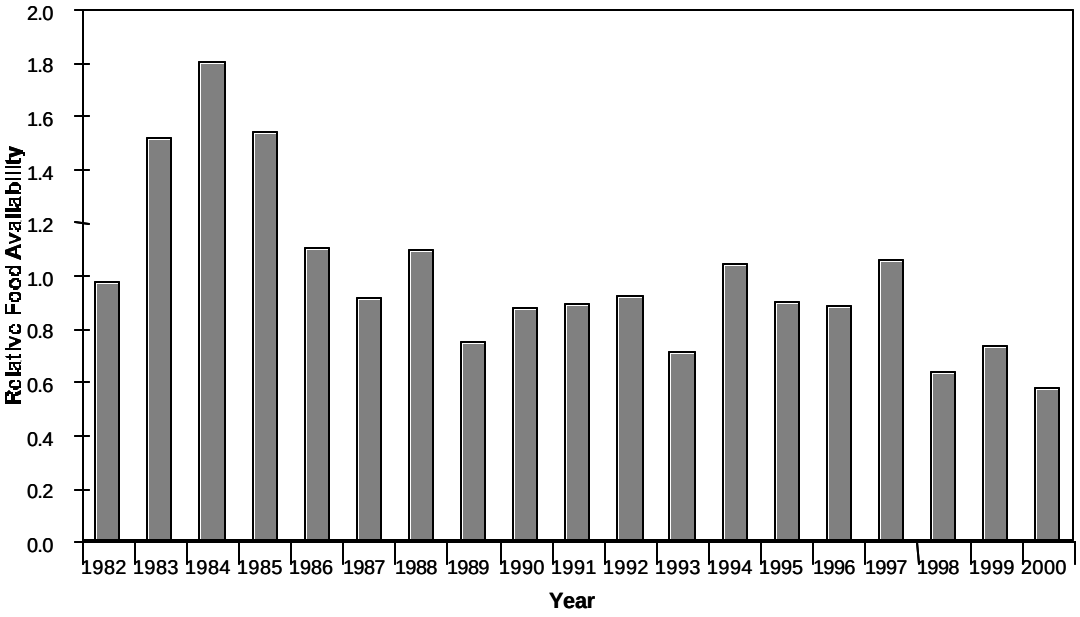
The feeding selectivity component of the model allows predator diet compositions to change as a result of changes in prey population sizes. Thus, as small menhaden abundance has declined over time, the proportion of menhaden in predator diets has changed. For example, the proportion of menhaden in Age 5 striped bass diets is predicted to have declined from between 60-80% during the early portion of the time series to approximately 30% in recent years.

Figure 10.14 Annual average proportion of menhaden in Age 5 striped bass diets.



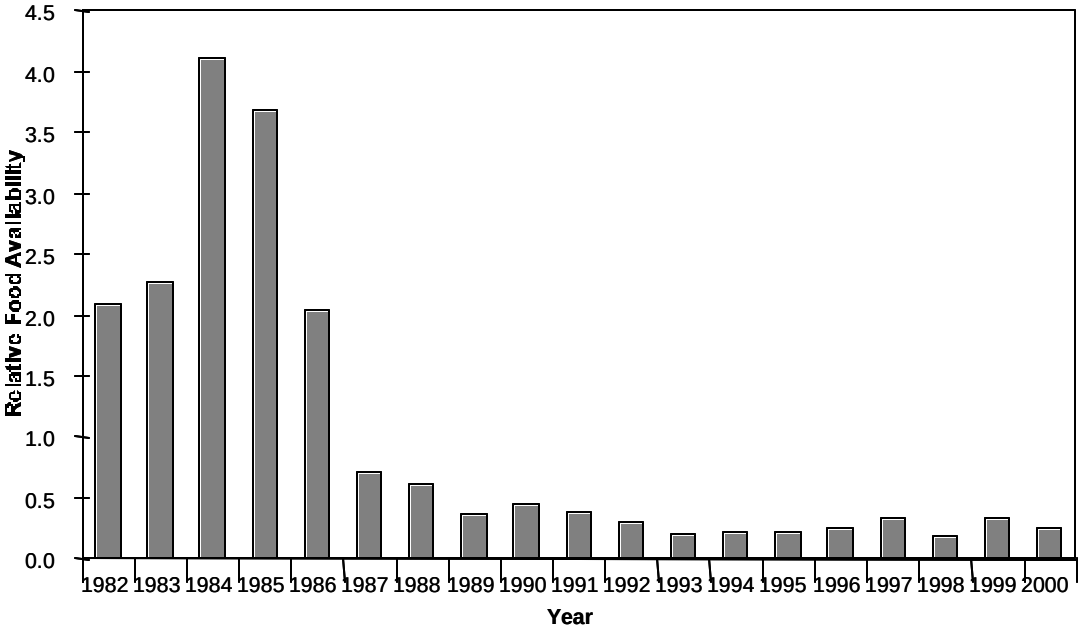
This declining availability of Age 0 menhaden also is predicted to result in declining food availability over time for larger age classes of striped bass. In recent years, the suitable prey biomass for age 5 striped bass declined to approximately 60% of the time series average.

Figure 10.15 Annual relative food availability of age 5 striped bass.



When expressed on a per capita basis, the recent increases in striped bass abundance coupled with declining young menhaden populations predict very low relative food availability in recent years compared to the 1980s when striped bass populations were low.

Figure 10.16 Annual per capita relative food availability of age 5 striped bass.

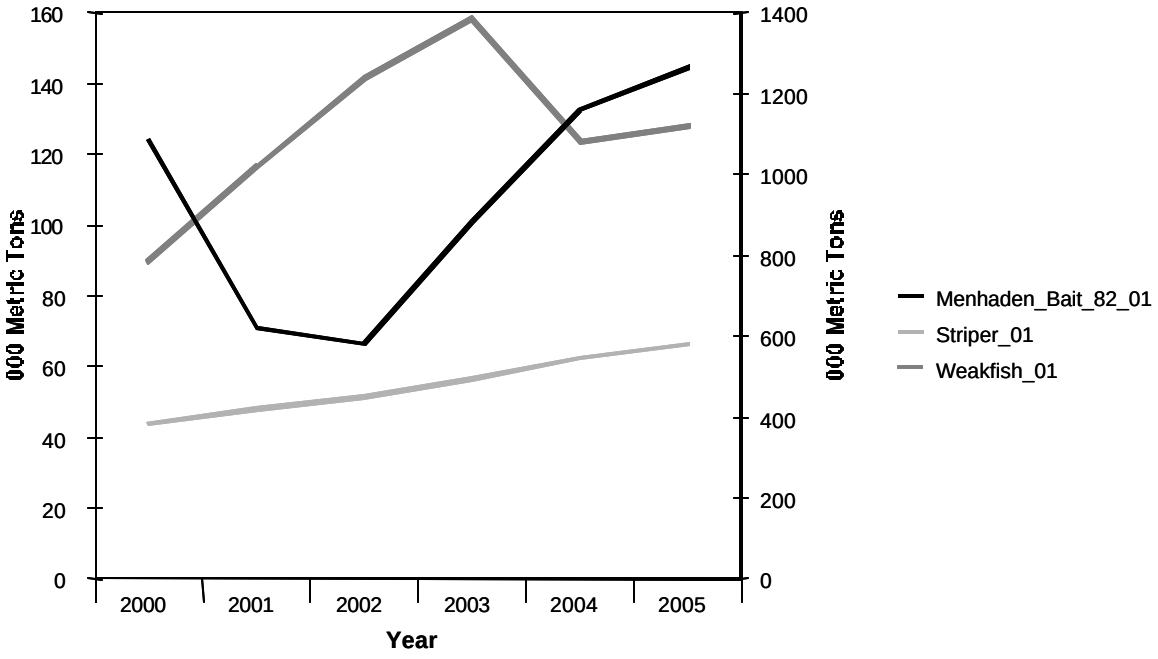


Short Term Projection of the Status Quo

Based on the example MSVPA-X runs and current levels of fishing mortality rates, other prey biomass, other predator biomass, and recruitment levels a short term projection of the multispecies population trends was developed and outputs are stored in the example project provided with the distribution package.

The short term forecast predicts that populations of striped bass and weakfish will continue to increase over the next several years under the current fishery mortality rates. Menhaden biomass is predicted to decline between 2000-2002 then begin to recover.

Figure 10.17 Short term forecast of total biomass based on example MSVPA-X run



The predicted patterns in these populations are likely to be strongly influenced by the selected stock recruitment curves. The predicted increase in menhaden population sizes is driven by both high predicted recruitment and declining predation mortality rates as the proportion of menhaden in predator diets declined.

Figure 10.18 Predicted abundance of Age 0 menhaden.

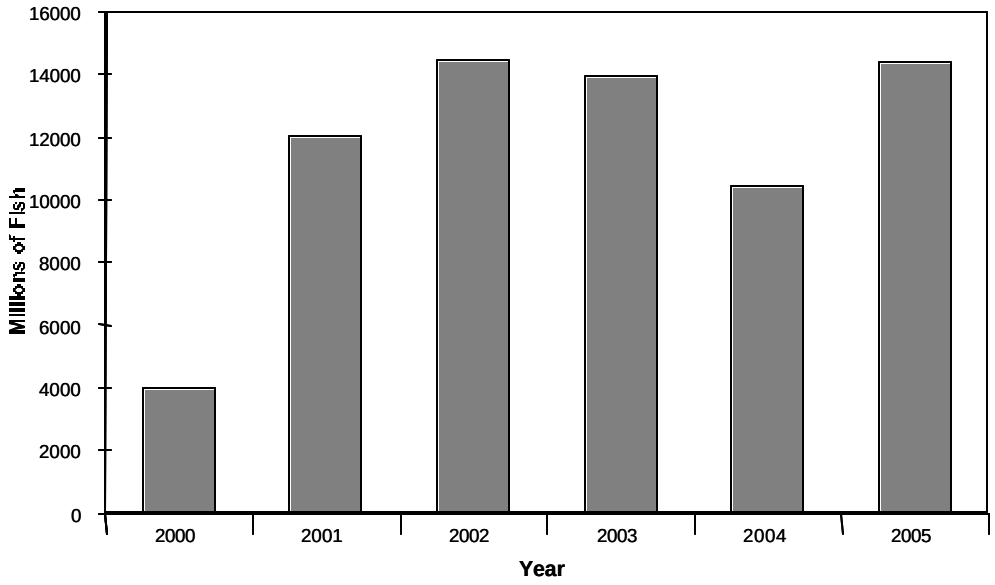
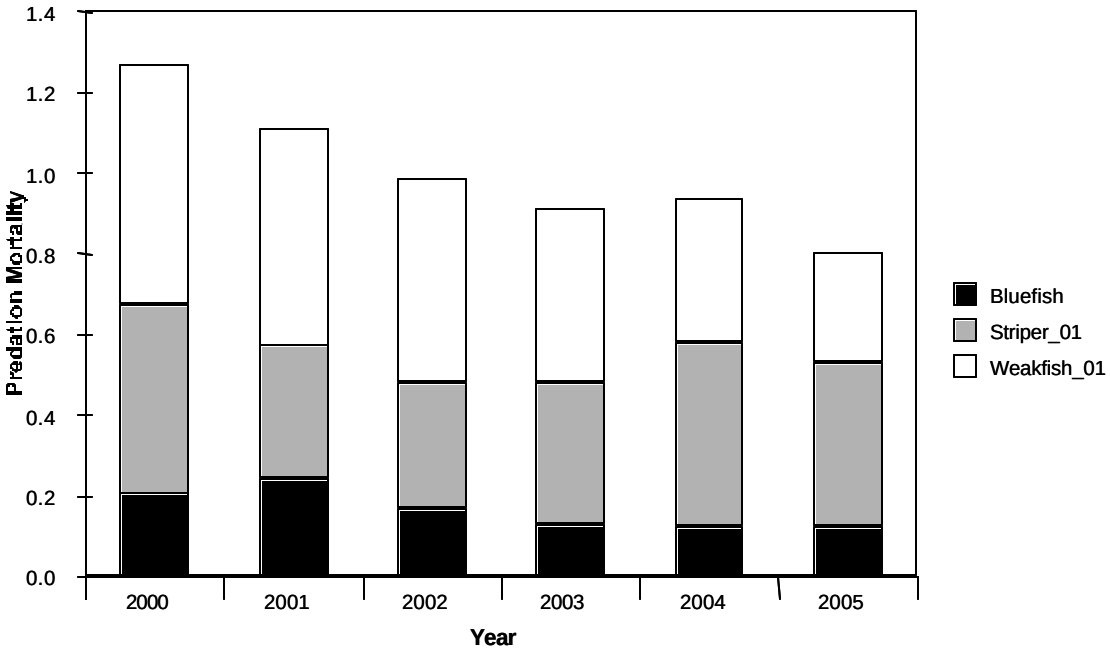


Figure 10.19 Predicted predation mortality rate on Age 0 menhaden.



Conclusions and Continuing Work

There are numerous additional model outputs that can be explored to evaluate historical and projected patterns of interactions between predators and prey. The example MSVPA-X run described here is intended only for illustrative purposes to describe the types of outputs that can be explored within the model. The example model inputs are very preliminary summaries of available data and must be more fully defined before drawing any firm conclusions about species interactions. However, these inputs demonstrate the flexibility of the model and its ability to capture important dynamics of predator-prey systems. The range of single-species VPA models provides the ability to match the model structures of the MSVPA-X with those of single species assessments to insure consistency across different approaches. The model provides concrete predictions that can be compared to available data to further refine input parameters. Finally, the projection model provides a framework to evaluate the potential effects of management actions in the short and medium term (5-10 years) under different assumptions about recruitment and prey availability. The continuing focus of the MSVPA-X model development will be on refining input parameters and developing multiple runs of the historical and forecast models to evaluate model sensitivity.

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