CHAPTER 2: DATA INPUT AND MODEL PARAMETERIZATION

2.0 SINGLE-SPECIES ASSESSMENT DATA

This configuration of the MSVPA-X model uses data from each single-species assessment completed in 2002 and 2003, permitting a multispecies analysis through 2002. Below is a summary table of single species stock assessment models used in the MSVPA-X formulation and the current assessment model used for each species.

Species	Assessment model used in MSVPA-X	2002/2003 Assessment model	Current assessment model (2005)
Menhaden	Extended Survivors Analysis (XSA)	Forward Projecting Age Structured model	Forward Projecting Age Structured model
Striped Bass	XSA	ADAPT VPA	ADAPT VPA
Bluefish	Biomass Input	Biomass Dynamic model (ASPIC)	Statistical Catch-at-Age model (ASAP)
Weakfish	XSA	ADAPT VPA	Relative F model

2.1 ATLANTIC MENHADEN

2.1.1 Summary of Fishery and Assessment

The Atlantic menhaden fishery consists largely of purse seine vessels targeting fish for two distinct uses. The reduction fishery typically focuses on relatively young, small fish in the estuaries and coastal waters along the U.S. Atlantic coast, particularly in Chesapeake Bay. Menhaden captured in this fishery are processed for sale as fish meal or fish oil. Purse seine vessels are also the primary component of a fishery that targets larger fish for sale as bait for crab pot and other fishing operations. There are additional small directed and bycatch based gillnet fisheries for menhaden in most states (reviewed in ASMFC, 2004a).

The reduction component of the fishery is intensively monitored, with both catch-at-age and effort data available since 1955. Fishery information on the bait component is less reliable and the catch-at-age matrix from commercial bait landings was used for 1985-2002. Biological sampling for age and size data at the reduction plants has been in place throughout the time series, but sampling of the bait fishery catches is less reliable prior to 1988. Annual size-at-age and length-weight regressions are available from 1955 to the present.

Prior to 2003, the Atlantic menhaden stock assessment used a Murphy Virtual Population Analysis approach. Terminal fishing mortality rates were estimated by a standard catch curve analysis. Population sizes in the last year of the assessment were estimated using a separable

VPA based upon the last 3-7 years of the catch-at-age matrix (Vaughn *et al.*, 2002). However, during the most recent stock assessments, a forward projecting age-structured model was applied to the Atlantic menhaden stock (ASMFC, 2004a). The model incorporated two indices of abundance: an aggregated coast wide age-0 index and a CPUE index for pound net catches. This approach also allows separate treatment of the bait and reduction fisheries, which is particularly appropriate given the different selectivity of the fisheries (reviewed in ASMFC, 2004a).

The newly applied forward-projection model results in similar trends in the Atlantic menhaden population to the previous assessment approach, though there are changes in the absolute estimates of both fishery and natural mortality rates, as well as population sizes. The stock assessment indicates that Atlantic menhaden spawning stock biomass and population fecundity are currently high relative to the population median during the last two decades, though considerably lower than peaks during the late 1950s and early 1960s. The number of recruits (age-0 and age-1) has generally been declining since reaching a peak during the early 1980s. The 2002 estimate of recruits to age-1 falls below the 25th percentile of the time series; however, this recent estimate is highly uncertain. Based primarily upon current estimates of fishing mortality rate and spawning potential, the stock assessment concludes that this population is currently not overfished.

2.1.2 Fishery Catch-at-Age

Time series for predator catch-at-age matrices are restricted to the period from 1982-2002. Thus, the MSVPA-X model uses the Atlantic menhaden catch-at-age data for this period. Unlike the single-species assessment, it is not currently possible to model selectivity for the reduction and bait fisheries separately in the MSPVA-X approach. Thus, a combined catch-at-age matrix is employed including both bait and reduction fishery landings from 1985-2002. Prior to 1985, only reduction landings are included in the catch data. The method for deriving catch data is detailed in ASMFC (2004a), and data are shown in Table D.1.

2.1.3 Fishery-Independent and Dependent Tuning Indices

A fishery-independent coast wide juvenile (age-0) index is available for Atlantic menhaden based upon five seine surveys conducted between North Carolina and Rhode Island. Individual state seine survey indices are derived using a lognormal generalized linear model (GLM). Correlations between surveys are then evaluated to combine individual regional surveys; for example the Virginia and Maryland surveys are highly correlated and reflect trends in Chesapeake Bay. The regional indices are then combined using an average weighting based area of the associated drainage basins. The resultant coast wide index is used as a tuning index for age-0 abundance in the single-species assessment approach used in the MSVPA-X model (Table D.2).

The forward-projection stock assessment model also uses a biomass index based upon CPUE of Potomac River pound net catches. The pound net index reflects total biomass of primarily age 1-3 Atlantic menhaden. The formulation of the MSVPA-X model requires an age-disaggregated index of abundance as opposed to biomass. Based upon the age selection model applied in the forward-projection approach and estimated weights-at-age, the CPUE (biomass) index is

converted to an age-specific index of abundance (numbers) for age classes 1-3 (Table D.3). These age-specific indices are used as tuning indices for adult abundance in the MSVPA-X application.

2.1.4 Age and Growth

Size and weight-at-age derived from von Bertalanffy growth curve parameters and length-weight regression parameters are available annually since 1955 based on commercial fishery sampling (ASMFC, 2004a). However, there is a high degree of interannual variation in predicted sizes and weights-at-age, particularly in the younger age classes. In order to reduce this variability, average size and weight parameters are calculated in five-year intervals from 1982-2002. These average parameters are used to develop size and weight-at-age matrices for use in the MSVPA-X application (Table D.4, Table D.5). In the single-species assessment, the weight-at-age-0 is actually represented by age = 0.75 menhaden because fishery catches do not occur until late in the year (ASMFC, 2004a).

2.1.5 Single-Species VPA Formulation

In the MSVPA-X application, XSA is used as the single-species assessment model for Atlantic menhaden because it allows including the coast wide juvenile index and the age disaggregated pound net CPUE index as tuning indices and is thus consistent with the approach used in the forward-projection assessment model. A range of XSA options were evaluated to explore the sensitivity of predicted fishing mortality rates to values of shrinkage parameters including the number of years and ages used to calculate terminal fishing mortality rates. Estimated fishing mortality on the last age class was sensitive to the number of age classes used to calculate terminal F (Figure D.6). Four age classes were used to calculate the shrinkage mean to preserve a dome-shaped fishery selection curve to be consistent with the findings of the forward-projection model. The XSA model estimated higher fishing mortality rates on older age classes than the forward-projection approach (Figure D.7). This is likely due to the fact that the reduction and bait fisheries cannot be separately analyzed in the XSA formulation. However, the trends in fishing mortality rates were similar in the two assessment approaches.

The two approaches give similar trends and estimates of total abundance when the same natural mortality vector is applied to each model. For comparison to the assessment results, the natural mortality vector estimated by the forward-projection model was applied to the XSA (age-0 M = 4.31, age-1 M = 0.98, age-2 M = 0.56, age-3+ M = 0.55). The resulting XSA runs gave very similar results to the forward-projection model for ages 0 and 1. However, the abundance of older age classes was underestimated by the XSA in comparison to the forward-projection results, consistent with higher estimates of fishery mortality rates on these age classes. The overall magnitude and trends in abundance were similar between the two approaches (Figure D.8).

In the base MSVPA-X run, the XSA model using four age classes and two years to calculate the "shrinkage" mean was applied. The base natural mortality rate (M1) was set at 0.4 for all age classes.

The Atlantic menhaden stock assessment is scheduled to be updated in 2006 using the forward-projection assessment model.

2.2 STRIPED BASS

2.2.1 Summary of Fishery and Assessment

Striped bass commercial and recreational fisheries occur in nearshore coastal waters, estuaries, and tributaries along the U.S. Atlantic coast, particularly north of North Carolina and in the main-stem and tributaries of the Chesapeake Bay. The stock suffered very high fishing mortality and severe declines in abundance and spawning stock biomass during the late-1970s and early 1980s. Reduced fishery mortality rates during the 1980s and 1990s led to recovery of the stock. Abundance and biomass are currently high. Fishing mortality rates are below target levels for ages 4-11 fish, but exceed management targets for older age classes (ages 8-11; ASMFC, 2003).

The striped bass stock assessment is based upon catch-at-age based VPA using the ADAPT methodology and tag-recovery survival estimation. The VPA analysis is the primary tool used to provide mixed-stock estimates of fishing mortality rate. Catch-at-age matrices for the ADAPT methodology are derived from sampling of the commercial catch. Corrections are made for estimated levels of commercial discard mortality using tag-recovery rates for specific gear types and the spatial distribution of commercial fishing effort (ASMFC, 2003). Recreational harvest and discards derived from MRFSS data following standard methodologies. Length-frequency sampling was converted to catch-at-age by applying state-specific age-length keys (ASMFC, 2003).

Age-length keys for all states are derived from scales. However, there is significant concern over the accuracy of age assignments for fish over age-12 (ASMFC, 2003). To evaluate sensitivity to potential ageing errors, the most recent stock assessment evaluated the effects of designating different “plus-group” configurations including 12+, 13+, 14+, and 15+ categories in the catch-at-age matrix. Based upon this analysis, the 13+ age class was chosen as providing the most appropriate model formulation. In contrast, all previous year assessments applied a 15+ age class. Uncertainty in ageing of older fish remains a considerable challenge in the assessment of the striped bass stock.

For this analysis, we developed XSA runs for direct comparison to the 13+ ADAPT VPA used in the striped bass stock assessment. Numerous age-specific fishery-independent surveys are used as tuning indices for these approaches. The input data and configuration for the XSA and ADAPT approaches are nearly identical, allowing direct comparison of model results.

2.2.2 Fishery Catch-at-age

A catch-at-age matrix is available for 1982-2002. Catch data include commercial and recreational harvest and discard losses; complete details are included in the stock assessment report (ASMFC, 2003; Table D.6).

2.2.3 Fishery-Independent Surveys

Numerous abundance indices are available from fishery-independent and dependent surveys. Age-specific fishery-independent surveys include the Virginia pound net, Maryland gillnet survey, Connecticut trawl survey, New York ocean haul seine survey, New Jersey trawl index, Delaware trawl survey, and the NEFSC spring bottom trawl survey. Fishery-dependent indices include Massachusetts commercial CPUE, Hudson River shad fishery bycatch, and Connecticut volunteer angler CPUE. Juvenile surveys conducted in each state provide YOY indices from Maryland, Virginia, New York, and New Jersey. Yearling indices are available from New York and New Jersey.

The striped bass stock assessment subcommittee eliminates the Maryland spawning stock biomass age-2 index, the NEFSC trawl survey ages 12-15, and the Virginia Pound Net survey based on sampling and ageing concerns. The XSA analysis uses the same suite of indices as the ADAPT analysis, with the exception of age aggregated indices that cannot be used in the current implementation of the XSA.

2.2.4 Age and Growth

Striped bass weight-at-age is derived from several state sampling programs of commercial and recreational catch. Mean weight-at-age in the population is calculated as an average of state values weighted by the commercial catch. The weight-at-age matrix for 1982-1996 was developed for the 1997 stock assessment (NEFSC, 1998), and weights developed for 1997 were applied to 1998 and 1999. Weight-at-age for 2000-2002 were recently updated and applied in the most recent assessment (ASMFC, 2003).

Size-at-age is derived from state specific age-length keys. Seasonal average length-at-age for each state is calculated based upon available data. These state-specific estimates are then used to develop an average length-at-age vector by fitting a von Bertalanffy growth curve.

Due to uncertainties in ageing and questions about the representative nature of the annual weights-at-age derived in the striped bass assessment, the average weight-at-age is used in the base run of the MSVPA-X. Likewise, since there is no information on interannual variation in striped bass length, a single size-at-age vector is applied in the current analysis (Table D.7).

2.2.5 Single-Species VPA

Extended survivors analysis (XSA) is used as the single-species VPA model for striped bass in this application. The XSA approach is similar to the ADAPT methodology in that it utilizes tuning indices in the estimation procedures for fishery mortality rates. The tuning index data used in the 2003 striped bass stock assessment are used in the XSA, with the exception of age-aggregated and biomass indices. As in the ADAPT assessment, a 13+ age class is used and natural mortality set at 0.15 (ASMFC, 2003).

A series of XSA evaluation runs were conducted to evaluate sensitivity to XSA parameters and to compare results to the ADAPT assessment. Estimation of fishery mortality rates on older age

classes was sensitive to the selection of the number of age classes used to calculate the shrinkage mean F (Figure D.9). Calculating the shrinkage mean using 4 age classes most closely approximated the ADAPT results and will be used in the MSVPA-X application. The estimates of F were insensitive to other XSA parameters including the number of years used to calculate the shrinkage mean F in the last year. Trends in F were qualitatively similar for age classes 3-8 and 8-11 for the two approaches (Figure D.10). There was a tendency for the XSA to estimate slightly higher values of F relative to the ADAPT approach for older age classes during the last years of the assessment (Figure D.11). However, the selection curve and average F at-age were comparable between the two models.

The time series of estimated recruit abundance differed significantly in the last two years of the time series with ADAPT estimating much higher age-1 abundance during 2001 and 2002 compared to XSA (Figure D.11). For both assessment approaches, estimates of F and abundance for pre-recruit age classes is highly uncertain, so it is difficult to evaluate which model provides the "better" assessment. The trends and estimates of abundance for the remaining age classes are similar between the two approaches, though there is a tendency for the XSA to underestimate abundance relative to the ADAPT model (Figure D.11).

The striped bass stock assessment is updated annually and the next benchmark stock assessment is scheduled for 2007.

2.3 WEAKFISH

2.3.1 Summary of Fishery and Assessment

Weakfish are harvested commercially and recreationally along the U.S. Atlantic coast and in estuaries from Florida to the southern Gulf of Maine. Adult fish are harvested in offshore waters off of Virginia and North Carolina by gillnet and trawls. During spring and summer, gillnets and trawls are used to harvest fish in more northern coastal waters, and primarily gillnets are used in estuarine waters along the U.S. Atlantic coast. Recreational catch is concentrated in estuarine waters in the mid-Atlantic; however, there are significant recent recreational catches in southern New England states (Kahn, 2002a).

The weakfish stock biomass was generally low throughout the 1980s into the early 1990s. Fisheries regulations were put into place to restore the stock in the mid-1990s (Amendment 3 to the Interstate Fishery Management Plan for Weakfish), and estimated stock abundance and biomass has been generally increasing since at least 1990. The estimate of fishing mortality rate in the terminal year (2000) was below both the target and threshold values of F under the current FMP (Kahn, 2002a).

Kahn (2002a) applied the ADAPT VPA approach to a catch-at-age matrix derived from commercial and recreational catches through 2000. There is significant concern with the very low estimates of terminal fishing mortality and associated large population size estimates. Retrospective analyses of the ADAPT assessment indicate that the terminal F estimate may be underestimated by 100% (Kahn, 2002a). Additional concerns include the relatively limited geographic scope of biological sampling of the commercial catch, lack of data on commercial

discard mortality, and lack of information on recreational discards. The weakfish stock was assessed in 2004, but confounding signals from fishery-independent and fishery-dependent data prevented the ASMFC Weakfish Technical Committee from completing an ADAPT VPA.

An XSA analysis is applied to the weakfish stock for direct comparison to the ADAPT results. Four age disaggregated fishery-independent indices are used in both the ADAPT and XSA analyses. In addition, several indices of juvenile abundance are employed in the XSA analysis (data provided by ASMFC Weakfish Stock Assessment Subcommittee). Indices are developed for the period from 1982-2001, while the fishery catch-at-age matrix and associated data are currently available only from 1982-2000. In addition, XSA evaluation runs were compared to an integrated catch-at-age analysis (ICA) of the weakfish stock that was explored during the 2001 assessment (Kahn, 2002a).

2.3.2 Fishery Catch-at-age

The fishery catch-at-age matrix reflects both commercial and recreational landings, but includes discards from only the recreational fishery. Catch-at-age data are supplied either individually by state, or by estimating catch-at-age from length-frequency data and applying regional length-weight and age-length relationships as appropriate (Kahn, 2002a). The resulting catch-at-age matrix includes the period from 1982-2000 and includes age classes 1-6+ (Table D.8). For MSVPA-X evaluation runs, the catch matrix is projected forward to include 2001 and 2002 based upon fishing mortality rates and population sizes calculated through 2000.

2.3.3 Fishery-Independent Surveys

Four fishery-independent surveys provide age-specific indices of weakfish abundance for use in tuning the ADAPT and XSA approaches. Only surveys encompassing the region between North Carolina and Delaware are used: the New Jersey coastal trawl survey, a Delaware Bay survey, the SEAMAP fall coastal survey in North Carolina waters, and the NMFS fall inshore survey (Kahn, 2002a). In addition, several juvenile indices based upon haul seine surveys in estuarine waters are included: the VIMS haul seine (age-1), the North Carolina DMF survey (ages-1 and -2), two surveys by Maryland DNR (both age-1), and a Delaware Bay survey age-1).

2.3.4 Age and Growth

Size and weight-at-age are estimated from year specific von Bertalanffy parameters developed by Vaughan (unpublished data) for the period from 1990-1999 based upon otolith data (Kahn 2002b, pers. comm., D. Vaughn, SEFSC). Due to uncertainties in the methods used for length and weight analyses, the average derived weights and lengths from the 1990-1999 period are used in the MSVPA-X base run (Table D.9).

2.2.5 Single-Species VPA

The XSA model is used as the single-species VPA approach for weakfish. A series of XSA evaluation runs were developed for the period from 1982-2000 for comparison to the ADAPT VPA and integrated catch-at-age (ICA) analysis used in the 2002 assessment document. The

catch matrix included ages 1-6+ and the same indices were used in the XSA as in the standard assessment models. A constant natural mortality rate of 0.25 was assumed for weakfish.

The XSA for weakfish was largely insensitive to shrinkage parameters, and varying the number of years or age classes used to estimate terminal F values had little effect. The qualitative trends are similar for the ICA, XSA, and ADAPT models with the exception of the last two years of the assessment (Figure D.12). The XSA tends to underestimate fishery mortality rates on older age classes through most of the time series compared to the other two models. However, in the last two years of the assessment, the ADAPT approach estimated very low fishery mortality rates for ages 3-5 compared to the other two approaches (Figure D.13). Concern was expressed in the 2002 assessment about severe retrospective bias in the ADAPT approach and significant underestimation of F in the terminal year (Kahn 2002a). The fishing mortality rate estimates in the last two years for the XSA are more similar to those estimated by the ICA model (Figure D.13).

Abundance estimates from the three approaches diverge from one another beginning in the mid-1990s. From 1997-2000, the ICA and XSA models estimate declining abundance of older age classes, while the ADAPT estimates significant increases in the abundance of older fish during this time period (Figure D.14). For younger age classes, the ICA and XSA both predict declines during 1994-1997, while the ADAPT predicts continued increases. The ICA model indicates increases in the abundance of young weakfish during 1998-2000, while the XSA model indicates continued decline (Figure D.14).

The divergent results of the three age-structured assessment models used here likely reflect problems with the catch-at-age matrix described in the 2002 assessment. Another problem is that only two fully recruited true age classes are in the current assessment.

2.4 BLUEFISH

2.4.1 Summary of Fishery and Assessment

Bluefish landings are primarily from recreational fisheries along the U.S. Atlantic coast and in estuaries between Maine and Florida. Commercial fishery operations in coastal waters also land bluefish in several gillnet and trawl fisheries; however, the commercial landings are consistently below those of the recreational fishery (Lee, 2003). The biomass of the bluefish stock declined during the period from 1982-1992 and continued at low levels through 1998. Amendment 1 to the FMP was adopted in 1998 in an effort to rebuild the stock by 2007 through gradual reductions in fishery mortality rate. The stock assessment model results used in the MSVPA-X indicate that fishing mortality rates in the terminal year (2002) are below target levels and there have been recent increases in stock abundance.

The biomass dynamics model (ASPIC) previously used to assess the bluefish stock utilized commercial and recreational landings data. The recreational CPUE and NEFSC inshore fall survey are used as tuning indices in this approach. The stock had not been assessed using an age-structured approach, primarily due to concerns at the time, about the validity of reliable ageing. Prior to the 2005 stock assessment, the most recent age-structured assessment included catch-at-

age through 1997 (NEFSC, 1997), and at that time age-length keys were available only from North Carolina. In 2005, a forwarding projecting model (ASAP) was used to assess the bluefish stock and also determined fishing mortality to be below target levels and population abundance has been increasing since 2000. Though the peer reviewers had concerns regarding the 2005 assessment, it was accepted for management purposes (NEFSC, 2005).

Due to the unavailability of catch-at-age information from a peer reviewed stock assessment during the model reference period (1982 – 2002), bluefish is included in the MSPVA-X application as a "biomass predator". In this formulation, the predator population dynamics are not modeled. Model input requirements include a time series of total predator biomass, limited information on predator size structure, and feeding selectivity parameters.

2.4.2 Biomass Input

The time series of bluefish stock biomass from 1982-2002 is derived from the ASPIC Biomass Dynamic model used in the ASMFC stock assessment (Lee, 2003). The model uses recreational CPUE and the NEFSC inshore fall bottom trawl survey as tuning indices. Lee (2003) points out several areas of concern with this assessment model including: uncertainty as to the appropriateness of the NEFSC survey as an index of total biomass, assumptions of constant catchability in the fishery, and general concerns with the base assumptions of the simplified biomass dynamic model. The time series of total bluefish biomass is shown in Figure D.15.

2.4.3 Size Structure

An analysis of bluefish diet information based upon the Northeast Fisheries Science Center Food Habits database indicated significant breaks in bluefish diets in three size classes: 10-35 cm (ages 0-1), 35-55 cm (ages 2-3), and > 55 cm (ages 4+). These three size classes were used in the MSPVA-X model to account for ontogenetic changes in feeding selectivity and consumption parameters. The proportion of the total biomass in each age class was estimated based upon the average size distribution from the previous age-structured assessment (NEFSC, 1997). The proportion of biomass calculated for each size class was: Size 1 – 0.07; Size 2 – 0.21; Size 3 – 0.71.

2.5 'OTHER PREY' COAST WIDE BIOMASS ESTIMATES

2.5.1 Benthic Invertebrates

The three primary benthic invertebrate taxa important in the diets of weakfish, bluefish, and striped bass include gammarid amphipods, isopods, and polychaetes. The benthic invertebrates, particularly gammarids, are most important in the diets of young striped bass in the Chesapeake Bay, with gammarids accounting for up to 80% of the diet during some seasons (Hartman and Brandt, 1995). Over the continental shelf, gammarids are also the primary benthic invertebrate consumed by weakfish and striped bass, typically accounting for 5-15% of the observed diet Northeast Fisheries Science Center Food Habits database. Bluefish tend to have low amounts of benthic invertebrates in their diets.

Regional density estimates for these benthic invertebrate taxa were developed from a systematic benthic sampling program of the U.S. Atlantic continental shelf described in Wigley and Theroux (1981) and Theroux and Wigley (1998). This study was a comprehensive quantitative sampling of the benthic invertebrate community conducted during the 1950s and 1960s. Sampling was conducted using quantitative grab samplers. Results in the referenced reports provide maps and taxa specific density estimates in areas consistent with the regional definitions used in the current analysis. Densities are provided as g m^{-2}, and these were converted into biomass by multiplying regional density values by area, calculated using GIS tools (Table D.10). These data are not seasonally or annually resolved; therefore, constant biomass values were used across seasons and years in the current MSVPA-X application. While these estimates of benthic invertebrate biomass are based upon data several decades old, there is no more recent broadscale estimate of benthic biomass available over the U.S. Atlantic continental shelf. The resulting total estimated biomass of benthic invertebrates is 3,357,000 mt.

The size structure of the benthic invertebrate taxa was inferred from general descriptions of the observed size ranges in these habitats. This prey type was assumed to range between 1-7 cm in body length with peak biomass occurring at 3 cm. The resulting biomass distribution input into the MSVPA-X application is shown in Figure D.16.

2.5.2 Macrozooplankton

Crangonid shrimps, mysids, and other large zooplankton are primary prey items for young age classes of each predator species. However, there is no systematic information available on densities or biomass of these along the mid-Atlantic coast. Monaco and Ulanowicz (1995) report total density of "mesozooplankton" in the Chesapeake, Delaware, and Narragansett Bays as part of a trophic food web model examining energy flow in these systems. The total carbon density (mg C m^{-2}) was converted to total biomass assuming that carbon accounts for 90% of dry weight and that dry weight is 10% of live weight. These estuarine densities were averaged to generate an estimated coast wide biomass density estimate of 13.3 mt per km^2. Multiplying this value by the regional areas generated a total biomass estimate of 1,994,000 mt. An approximate length-frequency for macrozooplankton biomass based upon literature descriptions of these taxa is shown in Figure D.17.

2.5.3 Benthic Crustaceans

Benthic crustaceans including crabs and lobsters make up a small, but consistent, proportion of the diet of striped bass, bluefish, and weakfish. For striped bass, blue crabs have been observed to make up a significant proportion of the diet (typically 10-20%) in some seasons in estuarine habitats (Hartman and Brandt, 1995). Over the continental shelf, the Cancer crabs (rock and Jonah crabs) are observed at low levels (1-3%) in striped bass diets, and in the inshore Gulf of Maine, lobsters accounted for 20-40% of adult diets in localized studies (Nelson *et al.*, 2003). The proportion of benthic crustaceans is lower in weakfish and bluefish diets, typically ranging between 1-3%.

As important commercially exploited species, both blue crabs and lobsters are the subject of detailed assessment work along the U.S. Atlantic coast. For blue crabs, assessment documents

provide biomass estimates in 10mm size intervals for Chesapeake Bay, Delaware Bay, and North Carolina (Eggleston *et al.*, 2004; Kahn and Helser, 2005; Sharov *et al.*, 2002). The total annual biomass estimates derived from assessment data are shown in Table D.11. The average biomass of blue crabs across the time series is 85,961 mt.

Data on lobster abundance along the Atlantic coast of U.S. were obtained from the ASMFC American Lobster Stock Assessment Report (ASMFC, 2000). Absolute abundance was reported for recruits, post-recruits and total for the Gulf of Maine, Cape Cod and Long Island areas for the period of 1982-1997 (Tables D.12 and D.13). Size distribution of lobster recruits from the intertidal study in the Gulf of Maine (Cowan, 1999) was similar to the size frequency of lobsters in striped bass stomach reported by Nelson *et al.* (2003). An estimated mean weight of recruits was applied to the absolute abundance estimates to produce total biomass of recruits for each year (Table D.14).

For rock and Jonah crabs, there is no detailed assessment data from which to derive information on total biomass. However, the NEFSC bottom trawl survey samples and quantifies both species. Trawl survey estimates of seasonal (Fall and Spring) and regional catch rates (number per tow) were summarized in Stehlik *et al.* (1991). These catch rates were converted into biomass per km2 (Table D.15) assuming a trawl swept-area of 0.0315 km^2 and a mean weight of 63g per individual as reported in Stehlik *et al.* (1991). Rock crab densities in the Chesapeake Bay were assumed to be equal to those in the mid-Atlantic coastal waters based upon the spatial distribution described in Stehlik *et al.* (1991). Regional biomass estimates based upon swept area were 2,220 mt during fall and 253 mt during spring. These are recognized to be underestimates of total biomass since the trawl does not catch crabs with 100% efficiency.

Estimates suggest that the biomass of available benthic crustaceans is dominated by blue crabs. Averaged across the time series, the total estimated biomass for these three taxa is 91,471 mt. Due to the dominance of the blue crab component, the size distribution is based upon those developed for blue crabs from assessment data. The peak biomass is in the adult size classes between 13-16 cm carapace width (Figure D.18). This size range is larger than the range of prey consumed by striped bass and other species. Therefore, the available biomass of benthic crustaceans will be in the lower portion of this size range, consistent with the findings of diet studies showing that these predators feed primarily upon juvenile crabs.

2.5.4 Squid and Butterfish

Butterfish were last assessed using a forward-projection model (NEFSC, 2004). Length-frequency data for the commercial fleet are provided therein. Fishery-independent length-frequencies are available from the NEFSC fall bottom trawl survey (pers. comm., William Overholtz, NEFSC).

Northern Short-finned squid (*Illex*) were assessed in 2003 (NEFSC, 2003). This assessment uses various methods, including a fishery-independent index based on the NEFSC fall bottom trawl series, a maturation-natural mortality model, and both yield-per-recruit and egg-per-recruit models. Data on length-frequency were provided using the NEFSC fall bottom trawl survey (pers. comm., Larry Jacobson, NEFSC).

Long fin squid (*Loligo*) data are available through a peer reviewed assessment (NEFSC, 2002). *Loligo* were assessed using both a length-lased VPA and an index based assessment. Fishery-independent and dependent length-frequencies are available.

2.5.5 Clupeids

Clupeids (other than Atlantic menhaden) are abundant in estuaries and coastal waters along the U.S. Atlantic coast, and may constitute an important prey for each of the predators included in the MSVPA-X model. Landings were accumulated as available for four species, including Atlantic herring, Atlantic thread herring, Spanish sardine, and scads. Additionally, the MSVPA-X Assessment Subcommittee recognized the shads (American shad, hickory shad and the river herrings) as a regionally important prey item, but was unable to develop a coast wide estimate of abundance for these species due to data limitations. A coast wide assessment for American shad is scheduled for completion in 2006.

2.5.5.1 Atlantic Herring

Monthly landings of Atlantic herring (mt) were obtained for 1982-2004 from the northeast commercial fishery database (CFDB) as used in a recent stock assessment for Atlantic herring (Overholtz *et al.*, 2003). Annual landings are summarized in Table D16. Seasonal landings across years are summarized in Table D.17.

Length composition data representing Atlantic herring for 1982-2004 (n = 253,274) were also available from the recent stock assessment (pers. comm., Matthew Cieri, Maine DMR). These data are summarized in Table D.18.

2.5.5.2 Atlantic Thread Herring

The biology of and fishery for Atlantic thread herring along the North Carolina coast is reported in Smith (1994). Monthly landings of Atlantic thread herring in North Carolina were obtained from NMFS's menhaden sampling program (pers. comm., Joseph W. Smith, SEFSC). Additional monthly landings of Atlantic thread herring from the east coast of Florida were obtained from the NMFS website for commercial landings statistics (http://www.st.nmfs.gov/st1/commercial/index.html). Annual landings are summarized in Table D.16. Seasonal landings across years are summarized in Table D.17.

Length (n = 990) and age (n = 628) compositions were also available from the NMFS menhaden sampling program (pers. comm., Joseph W. Smith, SEFSC). These data, from fish collected between 1982 and 2002, are summarized in Table D.19.

2.5.5.3 Spanish Sardines and Scads

Monthly landings of Spanish sardines and scads were also obtained from the NMFS website for commercial landings statistics cited above. Annual landings are summarized in Table D.16. Seasonal landings across years are summarized in Table D.17.

2.5.5.4 Stock Abundance

The recent assessment of the Atlantic herring stock suggested an approximate F = 0.05 (age-1+ in 2002). Based on this result, and noting that the landings of Atlantic herring are several orders of magnitude larger than the aggregate of other species presented here, combined landings were divided by F to obtain an estimate of population biomass for these species in aggregate. These values are presented annually from 1982-2004 (Table D.16).

2.5.6 Anchovy

Bay anchovy, *Anchoa mitchilli*, is one of the most abundant fish species in mid-Atlantic estuaries and coastal waters and is a primary prey item during some seasons and age classes for each of the predators included in the MSVPA-X model. Relatively little information is available regarding biomass and population dynamics outside of estuarine waters. However, there has been intensive study of larval dynamics, life history, and seasonal patterns in biomass inside of Chesapeake Bay (Lou and Brant, 1993; Newberger and Houde, 1995; Rilling and Houde, 1999).

2.5.6.1 Estuary Biomass Estimates

Bay anchovy are a short-lived species in Chesapeake Bay, rarely are there more than three age classes in the population. During most of the year, bay anchovy biomass in the bay is relatively constant; however, during the late summer and fall following recruitment, anchovy biomass increases dramatically as age-0 fish undergo rapid growth (Newberger and Houde, 1995). Rilling and Houde (1999) estimated baywide biomass during June and July at approximately 23,000 mt. During peak densities during fall, they cite studies indicating biomass levels peaking at over 100,000 mt. Biomass levels of 23,000 mt are assumed typical of winter and spring. Biomass is assumed to increase to 100,000 mt summer (July – September) and then decline to 60,000 mt during the fall.

2.5.6.2 Coastal Biomass Estimates

The New Jersey Ocean Trawl Survey (NJ OTS) database was used to develop bay anchovy biomass estimates for nearshore coastal waters. The survey started in 1989 and samples nearshore waters (3 fathom – 15 fathom isobaths) from the entrance of New York Harbor south to Delaware Bay five times a year (January, April, June, August and October). There are 15 strata – 5 strata assigned to 3 different depth regimes (inshore – 3 to 5 fathoms, mid-shore – 5 to 10 fathoms, and offshore – 10 to 15 fathoms). Station allocation and location is random and stratified by strata size. The total weight (kg) of each species is measured and the length of all individuals, or a representative sample by weight for large catches, is measured to the nearest cm.

The average area swept per tow (km^2) was derived from the trawl mouth opening (wing spread x vertical opening) and the average distance covered per trawl. We then determined the average total area swept by season (**season 1** – 1 survey cruise and 30 stations, **season 2** – 2 survey cruises and 80 stations, **season 3** – 1 survey cruise and 40 stations, **season 4** – 1 survey cruise

and 40 stations) and determined the multiplying factor (area swept per season / total survey area) to develop estimates of absolute abundance and biomass. We developed a yearly, weighted (by stratum size) CPUE index (by number and biomass per tow) by season, and then multiplied that value by the number of tows within the season to determine the average total abundance or biomass caught for the season. By multiplying that value by the multiplying factor, we developed estimates of absolute abundance or biomass (mt) for that year and season. Using the mean biomass estimate for the time series (1989-2004), the total seasonal biomass estimate along the New Jersey coast was derived.

The seasonal biomass estimates and seasonal trends for bay anchovy off the New Jersey coast are different than those for Chesapeake Bay (Figure D.19). Anchovy biomass along the coast increases throughout the year and reaches its peak biomass in the fall as anchovies begin to move out of the estuaries and into the coastal waters.

2.5.6.4 Estuary Time Series Index

Data from the New Jersey Department of Environmental Protection (NJ DEP) Delaware River seine survey, Virginia Institute of Marine Science (VIMS) trawl survey, VIMS seine survey, Maryland Department of Natural Resources seine survey, Maryland DNR coastal bay seine survey and Delaware Department of Natural Resources and Environmental Control Delaware Bay juvenile trawl survey were used to develop a yearly *estuary* bay anchovy index. We first developed separate Chesapeake Bay and Delaware Bay indices using the appropriate surveys. We z-transformed (+ 2) the annual CPUE indices in order to normalize and standardize the data. The Chesapeake Bay indices are highly correlated and all surveys show a clear decline in anchovy abundance (Figure D.20); the Delaware Bay indices are not correlated and are much more variable and neither survey shows a clear trend in abundance (Figure D.21). To create one index for the Chesapeake Bay, we weighted the surveys according to length of time series, number of samples, and the spatial and temporal range of the survey – the surveys had the following weighting factors: VIMS seine – 0.3, VIMS trawl – 0.3, MD DNR seine – 0.3 and MD DNR coastal bay – 0.1. The same procedure was followed to develop the Delaware Bay index, with both surveys assigned a weighting factor of 0.5. In order to combine the two surveys into one grand estuary index that would be applied to other estuary waters along the Atlantic coast, we re-weighted the two surveys in reference to each other by their total area (km^2) – Chesapeake index weighting, 0.788 and Delaware index, 0.212. Figure D.22 shows the combined Chesapeake Bay index, the combined Delaware Bay index and the combined *estuary* index.

2.5.6.5 Coastal Time Series Index

Data from the NJ OTS and the Southeast Area Monitoring and Assessment Program (SEAMAP) survey were used to develop the yearly *coastal* bay anchovy index. As with the estuary indices to normalize and standardize the surveys, we z-transformed (+3) the annual CPUE values. The surveys were not significantly correlated but both show a decrease in anchovy abundance over the course of the time series – NJ OTS 1989 – 2004, SEAMAP 1990 – 2004 (Figure D.23). In order to combine the two indices and develop one coast wide annual index, we weighted each z-transformed index. Weighting factors were estimated by comparing the survey area sampled, time series length, number of samples collected and the temporal range of the surveys. For this

case both the NJ OTS and the SEAMAP survey were assigned a weighting factor of 0.5. Those values were then added to derive the single annual *coastal* index value (Figure D.23).

2.5.6.6 Time series of Seasonal Density and Biomass Estimates

Estuaries: The seasonal estuary biomass estimates developed by Rilling and Houde (1999) were determined from data collected in 1993. Since we developed a single seasonal biomass estimate, we used 1993 as the 'reference year' and scaled the annual (1982 – 2002) estuary indices to the 1993 index to determine the annual seasonal biomass estimates. We first determined the annual seasonal densities (biomass km^{-2}) for each of the estuaries along the coast – Buzzards Bay, Long Island Sound, Hudson River Estuary, Delaware Bay, Chesapeake Bay, Neuse River and Pamlico Sound (GIS tools were used to determine estuary and coastal water area – km^2). We assumed the density inside Chesapeake Bay is similar to that in other estuaries, but applied the appropriate scaled index value to the appropriate estuary to develop the season densities (ex. formula: {season biomass * scaled index value} / area). The calculated seasonal densities were then multiplied by the respective estuaries total area (km^2) to determine the annual seasonal biomass estimates for each estuary. We then summed all of the individual estuary estimates to determine the total estuary bay anchovy biomass.

Coast: A similar procedure was followed with the coastal estimates. For consistency with the estuary estimates, we scaled the annual coastal estimates to the 1993 reference year to determine the annual seasonal biomass estimates (Note: from 1982 through 1988, coastal biomass estimates are constant and are equivalent to the 1993 reference year because the coastal surveys used in this analysis began in 1989). We determined the annual seasonal densities (biomass km^{-2}) for the New Jersey coast and the remaining coastal waters (out to 10 nautical miles from shore) and assumed the density along the Jersey coast was similar to that along other parts of the coast and applied the appropriate scaled index value to develop the seasonal densities. As with the estuarine estimates, the calculated densities were multiplied by the corresponding coastal total area and then all of the coastal areas were summed to get the total coastal bay anchovy biomass.

The total estuary and coastal estimates were then summed to develop the overall annual seasonal bay anchovy biomass (Table D.20).

The length-frequency of bay anchovy is summarized in Newberger and Houde (1995) and length-frequency data from the New Jersey Ocean Trawl Survey show a similar size range.

2.6 DIET SELECTIVITY INDICES

The selectivity model used in the MSVPA-X relies upon a rank index for prey type preference. These indices are derived from summaries of available diet composition data when they are available. For the predators considered here, there are multiple diet studies published in the literature; however, these are generally smaller scale studies focusing on particular places, seasons, and time periods. The most spatially and temporally comprehensive data set for all three species is the Northeast Fisheries Science Center Food Habits database. However, this survey is limited to the coastal (i.e., non-estuarine) waters, is only available during spring and fall, and generally does not have large sample sizes for older fish. For each species, there are additional

regional studies that provide diet information for estuarine waters and/or other times of the year. A compilation of regional studies and NEFSC Food Habits database was used to develop overall rank indices of type preference for each predator species and age class.

The strategy used to develop type indices for each predator is outlined as follows:

1) For each region, summarize available data to develop an average diet for each season and age class.

2) Calculate the seasonal biomass of each prey type in the region based upon the estimated biomass and spatial distribution of each prey type (used in the spatial overlap analyses).

3) Calculate a quantitative electivity index as the ratio between the proportion of the prey in the diet versus the proportion of the prey biomass, and normalize so that these electivity values sum to one. This is equivalent to calculating Chesson's electivity index.

4) For each predator age and prey type, calculate the average of this quantitative index weighting by the proportion of the predator biomass in each region. Thus, the average selectivity will therefore reflect data from the region(s) containing the majority of each predator's biomass.

5) Rank the resulting overall values, and use these as the rank type-preference index in the model. The rank indices reduce the effects of poor estimation of biomasses in each region that may result in biases in the quantitative indices.

As an example of the data used to derive these indices, we present the diet information for striped bass from Chesapeake Bay. There are a number of primary sources of diet information in the published literature for striped bass (Table D.21) encompassing all of the regions, age classes, and seasons used in the current application. For early age classes of striped bass, the most comprehensive available data set is from Hartman and Brandt (1995). This study includes fish sampled across most of the Chesapeake Bay including the main-stem and tributaries. Samples were collected during the early 1990s and across most months. The seasonal diet compositions used for age classes 0, 1-2, and 3-5 based upon this study are shown in Figure D.24. Generally, age-0 fish fed primarily upon benthic invertebrates during the early part of the year and anchovies and macrozooplankton during the later part of the year. Age 1-2 and 3-5 fish were more piscivorous, and their diets were dominated by menhaden except for season 2 when sciaenids were more important (Figure D.24a).

The samples collected in Hartman and Brandt (1995) did not include older age classes. Therefore, diet information for older fish was taken from Walter and Austin (2003) using samples collected during 2000-2001 across most of the Chesapeake Bay and most seasons. The seasonal patterns for both age groups are similar with medium forage fish (made up primarily of *Alosa* spp.) comprising the majority of the large fish diets during the early part of the year and menhaden and sciaenids during the later part of the year (Figure D.25). Benthic crustaceans (primarily blue crabs) were also an important component of the diet for age 6-7 fish during the spring (Figure D.25a).

The proportion of total biomass in the Chesapeake Bay by prey type is shown in Figure D.26. These seasonal values are derived from information on the seasonal spatial distribution of each taxon and the estimated total biomass of each. It is important to note that the "medium forage fish" category does not well represent the biomass of that prey type in the Chesapeake Bay since biomass estimates for *Alosa* spp. and other small fish were not available. Based upon the available data, anchovies represent the majority of the prey biomass in the Chesapeake Bay in all seasons.

Quantitative values for Chesson's electivity index were calculated as the ratio between the proportion of each prey in the diet and the proportion of total prey biomass in the region. The seasonal values for each striped bass age class and prey type are shown in Table D.22. A similar analysis was conducted for all other regions using the data sources listed in Table D.21. These quantitative scores were then averaged across regions and seasons weighed by the biomass of each age class of striped bass. These averages were ranked to provide the indices input into the MSVPA-X application shown in Table D.23.

In contrast to striped bass, there are very few references for regional and seasonal diet composition for weakfish. Hartman and Brandt (1995) is the primary data source for the Chesapeake Bay, while diet information for the remainder of the study is limited to the Northeast Fisheries Science Center Food Habits database (Table D.24). Based upon this somewhat incomplete picture of weakfish diets, the resulting type preference ranks are shown in Table D.25.

The primary data source for bluefish diets is also Hartman and Brandt (1995) for the Chesapeake Bay and the NEFSC food habits database for larger fish in the remaining regions (Table D.26). The NEFSC food habits data are also described in Buckel *et al.* (1999). There are a number of additional studies (Buckel *et al.,* 1999, Juanes *et al.*, 2001, Buckel and Conover, 1992), primarily in the New England region, examining the diets of age-0 bluefish and these were also incorporated into the current analysis. The resulting type preference ranks are shown in Table D.27.

2.7 SPATIAL OVERLAP INDICES

2.7.1 Model Spatial Domain

While the MSVPA-X model is not fully spatially explicit, it is necessary to define a spatial domain and strata at regional scales to evaluate seasonal spatial overlap between predators and prey. The spatial resolution of these strata is primarily limited by available data on the spatial distribution of the species included in the model. Ideally, a broad scale scientific survey would capture all predator and prey species at a relatively high spatial resolution. However, this is rarely the case, and in particular spatial data on invertebrate and small fish prey are typically limited.

The spatial domain for the current model application was developed based upon the known spatial distribution of the four primary species. Five regional strata were defined (Figure D.27,

Table D.28) ranging from North Carolina to the Gulf of Maine. The offshore extent of the model was defined as 20 nautical miles from shore for coastal strata. Georges Bank (defined by the 200m isobath) was included in the Gulf of Maine (GM) stratum. These strata areas are used to expand the densities of invertebrate and other prey to total biomass. In the case of data from the NMFS bottom trawl survey, stations were assigned to strata based upon their reported latitude and longitude locations.

Commercial and recreational landings data were used to evaluate the spatial distribution of several species. While landings data are subject to several biases, there is no comprehensive regional survey providing spatial distribution data for the larger predators. The NMFS bottom trawl survey provides some data; however, it is inefficient at catching these larger more pelagic predators, does not sample nearshore waters, and does not include sampling in Chesapeake Bay. The bottom trawl survey is also limited to primarily the fall and spring seasons. Landings data therefore provide the best available measure of the relative spatial distribution of the predators included in this model.

Landings data were matched to the regional strata based upon the reported state (Table D.28). Landings data were downloaded for the period from 1982-2002 (where available) from the NMFS website (http://www.st.nmfs.gov/st1/commercial/index.html) by state, month, and area (inland versus offshore). For the recreational (MRFSS) data, the two-month "waves" were divided evenly into monthly landings so as to define the seasonal totals. For Virginia and Maryland, nearly all commercial and recreational landings are from the Chesapeake Bay region. The total landings were thus calculated for each season and region

The spatial distribution of each taxon was evaluated on a seasonal basis using landings, survey, or regional density data as appropriate. These relative spatial distributions were then used to calculate the seasonal spatial overlap (using Schoener's index) between each predator age class and each prey species.

2.7.2 Striped Bass

The seasonal spatial distribution of striped bass based on landings data is shown in Figure D.28. During the winter months (season 1), striped bass is concentrated in the southern portion of the range, particularly in North Carolina and Chesapeake Bay. During spring, the landings increased in the northern portion of the area, and this trend continued through season 3 where the majority of landings are concentrated in the New England and Gulf of Maine strata. During the fall months, the landings were highest in the mid-Atlantic and Chesapeake Bay regions as the stock moves south (Figure D.28). These spatial patterns in the total biomass were converted into age-specific spatial distribution based upon the observed age-structure of the catch within each region (Figure D.29).

2.7.3 Weakfish

Weakfish seasonal distribution patterns were similar to those observed for striped bass; however, weakfish did not occur as far north during the spring and summer (Figure D.30). In the winter, weakfish landings primarily occurred in the North Carolina region. The weakfish stock

progressed north during the spring and summer with landings concentrated in the mid-Atlantic region, and occurring in the Gulf of Maine area only during the summer months. During fall, the stock again moved south and was concentrated in the mid-Atlantic and Chesapeake Bay areas. The regional age structure of the catch is shown in Figure D.31 and was used to calculate age-specific seasonal spatial distribution of the stock.

2.7.4 Bluefish

The spatial distribution of the bluefish stock showed a similar seasonal progression to that of the other predator species (Figure D.32). During the winter, the landings were concentrated in the North Carolina and mid-Atlantic regions. Landings increased in the northern regions during spring. In summer and fall, the landings were highest in the southern New England stratum. Unlike weakfish and striped bass, there are no available data on the regional age structure from commercial landings; therefore, the spatial distribution of different size classes used were derived from the NMFS bottom trawl survey. The spring bottom trawl survey was used as the proxy for the winter and spring seasons while the fall survey was used for the summer and fall. The relative mean catch per tow in each region for each season (Figure D.33) was used to calculate the seasonal spatial distribution of each size class.

2.7.5 Menhaden

The seasonal spatial distribution of Atlantic menhaden was derived from the time series of purse seine landings. The relative distribution of landings of ages 0-2 menhaden were used since this size range is the primary component of predator diets. Menhaden landings occurred exclusively in the North Carolina region during winter months. During spring, landings were concentrated in the mid-Atlantic region and southern New England. In the summer, landings are concentrated in the Chesapeake Bay and then again in the North Carolina and Chesapeake Bay in the fall (Figure D.34).

2.7.6 Other Fish Prey

For medium forage fish (primarily butterfish and squid) and herrings (primarily Atlantic herring), seasonal spatial distribution was derived from the mean catch per tow in each region from NMFS bottom trawl survey data. Since the survey does not sample inside the Chesapeake Bay, stations from offshore waters of Virginia and Maryland were used as a proxy. The spring survey was used as a proxy for seasons 1 and 2, and the fall survey for seasons 3 and 4. The relative distribution of medium forage species was highest in the North Carolina and Gulf of Maine regions during the colder seasons (Seasons 1 and 2), and highest in the Gulf of Maine for summer and fall (Figure D.35a). The herrings were distributed throughout the region during the colder months, but were highest in the Gulf of Maine. In the warmer months, nearly all of the clupeid biomass was in the Gulf of Maine region (Figure D.35b).

The spatial distribution of the sciaenids (croaker and spot) was derived from commercial landings data, similar to the approach used for the predator species. Sciaenid landings were concentrated in the North Carolina region during the winter, then further north in the Chesapeake

Bay region during spring and summer, and again in North Carolina during the fall (Figure D.35c).

2.7.7 Anchovy and Invertebrate Prey

For the remaining other prey there was no seasonal data on spatial distribution available. Therefore, the regional spatial distributions are constant across seasons. For the benthic invertebrates, crustaceans, and macrozooplankton the relative spatial distribution is based upon the regional densities used to develop biomass estimates (see Section 2.5, Figure D.36). For anchovy, there is no coast wide measure of relative abundance. Therefore, arbitrary values were used centering the majority of the biomass in the North Carolina and Chesapeake Bay regions (Figure D.36).

2.7.8 Spatial Overlap Indices

The seasonal and age-specific relative distribution of biomasses was used to calculate spatial overlap values for each predator age class and prey type. These values are input into the MSVPA-X model as a component of the feeding selectivity equations (Tables D.29-D.31).