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# An expansion of the MSVPA approach for quantifying predator – prey interactions in exploited fish communities

Lance P. Garrison, Jason S. Link, D. Patrick Kilduff, Matthew D. Cieri, Brandon Muffley, Douglas S. Vaughan, Alexei Sharov, Behzad Mahmoudi and Robert J. Latour

Ecosystem-based fisheries management requires tools to place fish-stock dynamics in the broader context of fishery, predator, and competitive removals. Multispecies virtual population analysis (MSVPA) is an approach to quantifying predator–prey interactions and estimating the rates of predation mortality for exploited fish populations. Here, an extended MSVPA (MSVPA-X) is presented as an alternative to existing MSVPA approaches. Notably, MSVPA-X uses index-tuned VPA methods, applies a more flexible feeding model, and includes an alternative functional feeding response. The MSVPA-X model is applied to a western Atlantic fish community, focusing on Atlantic menhaden and its major fish predators, and a sensitivity analysis of major model parameters is presented. The sensitivity analysis highlights the need for adequate diet sampling. The MSVPA-X represents an improvement over previous approaches by increasing the flexibility to model seasonal and interannual dynamics in the strength of predator–prey interactions. Model results demonstrate that, for menhaden in particular, and forage fish in general, quantifying predation mortality is an important part of effective assessments of forage fish, their predators, and the fisheries of both.

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## Introduction

There have been many calls recently to adopt ecosystem-based fisheries management (EBFM). There are many rationales for EBFM, chief of which is the need to evaluate trade-offs among various species or user sectors (Larkin, 1996; Jennings et al., 2001; Link, 2002; Garcia et al., 2003; Garcia, 2005). A key requirement for implementing EBFM is a set of modelling tools analogous to the stock assessment models used in single-species approaches. There is a broad suite of multispecies and ecosystem models that can be applied in a fisheries context (Hollowed et al., 2000; Whipple et al., 2000), ranging from fully coupled biogeochemical system models to multispecies models (Whipple et al., 2000; Link, 2002). As these models continue to be developed and applied for fishery management purposes, their inherent properties, sensitivities, and biases need to be documented fully.

Multispecies virtual population analysis (MSVPA) is one of these approaches, and it focuses on trophic interactions at intermediate levels in a system, with only limited consideration of primary production or other system-wide constraints. The MSVPA approach was developed within ICES as a multispecies extension of cohort analysis or VPA. The basic approach was derived from the model of Andersen and Ursin (1977) and initially described by Pope (1979), Helgason and Gislason (1979), and Gislason and Helgason (1985). The approach is essentially a series of single-species VPA models that are linked by a simple feeding model to calculate natural mortality rates (reviewed in Sparre, 1991; Magnusson, 1995).

The standard (i.e. the ICES-developed 4M Model; Vinther et al., 2002) MSVPA approach, and the associated forecast model MSFOR, has been applied by the ICES Multispecies Working Group for the North Sea ecosystem. The main conclusions from applications to this system, summarized by Pope (1991), are that the rates of natural mortality are higher than typically assumed and are annually variable, and that predation mortality may significantly impact recruitment. In addition,

changes in mesh size to increase the abundance of older, larger fish can result in higher rates of predation and lower fishery yields for forage species. Analysis from subsequent forms of MSVPA for the North Sea supports these general conclusions, such that changes in natural mortality rates attributable to predation can significantly impact fishery yields, whereas the effect of changes in growth as a consequence of declining food availability is relatively small (Collie and Gislason, 2001). The MSVPA approach has also been applied to Georges Bank (Tsou and Collie, 2001), Baltic Sea (Vinther, 2001), and eastern Bering Sea (Livingston and Jurado-Molina, 2000) fish communities.

The MSVPA approach has the advantage of using data inputs (e.g. fishery catch-at-age) that are similar to those used in single-species fishery models. Likewise, model outputs are directly comparable with those of single-species approaches, and their incorporation into fishery management plans is hence simplified. The MSVPA does have limitations (Magnusson, 1995), most obvious of which are concerns over the type of functional feeding response and how prey suitability parameters have been estimated. The ICES Study Group on Multispecies Assessment in the North Sea recently reviewed some of the issues with the MSVPA approach and its application. Notably, the approach of solving for constant suitability coefficients from a single year of data does not account for temporal changes in the size distribution, spatial distribution, and relative abundance of predator and prey species (ICES, 2006). Additionally, MSVPA models typically include only exploited species, and all other components of the ecosystem (e.g. zooplankton, benthic secondary production, apex predators) are either omitted from the model or are included as fixed inputs of biomass (Livingston and Juardo-Molina, 2000).

Here, we present an expanded version of MSVPA, termed MSVPA-X, with which we address some of the limitations of the standard MSVPA. Specifically, we implemented an alternative feeding-selectivity model, modified the functional feeding response, and incorporated tuned VPAs. We describe the MSVPA-X approach and discuss an example application of the MSVPA-X model using US east coast piscivores and their commercially targeted clupeid prey. Considerable additional detail on this application of the model is available in NEFSC (2006). In addition, we describe sensitivity analyses that highlight the properties of the MSVPA-X model.

## Methods
### Standard MSVPA formulation
The MSVPA equations have been previously evaluated by many authors (see Gislason and Helgason, 1985; Magnusson, 1995). Briefly, the model is derived from the basic age-structured VPA approach with the addition of resolving natural mortality ($M$) into components of mortality attributable to predation ($M_2$) and that attributable to other natural causes ($M_1$), e.g. competition, disease, and starvation.

Predation mortality rates are calculated using a simplified feeding model derived from Andersen and Ursin (1977). That model consists of two primary terms, one for the total biomass of food consumed by the predator and a suitability index that determines the predator's diet composition. In its original formulation, the suitability coefficient was resolved into components for spatial overlap, "general vulnerability" of the prey, and size selection as a function of the prey-to-predator weight ratio (Gislason and Helgason, 1985). In practice, the suitability coefficients have

been solved for iteratively by incorporating diet information for all predator and prey age classes for at least 1 year in the MSVPA time-series. The resulting suitability coefficients are assumed to be constant in time and independent of prey abundance (Magnusson, 1995).

## MSVPA-X formulation
The MSVPA-X approach described here builds on the framework of the standard MSVPA by modifying the consumption model, formalizing the selectivity parameters within the framework of general feeding-selectivity literature, and implementing index-tuned single-species VPAs in the form of extended survivors analysis (XSA; Shepherd, 1999). This has been done in an *ad hoc* manner by the ICES Working Group (Vinther, 2001), but tuned VPAs typically have not been employed in other applications of the MSVPA. Both other prey and other predators are included in the MSVPA-X approach to address species where age-structured catch data are not available or are inappropriate. This is consistent with previous applications of MSVPA (e.g. Livingston and Jurado-Molina, 2000; ICES, 2006).

## Food consumption and availability
In the base MSVPA, the total food consumed by a predator is expressed as a constant proportion of body weight across seasons and years. In reality, the rates of food consumption by fish can vary widely between seasons as a function of changing temperature, food availability, and metabolic demand. In the MSVPA-X, the quantity of food consumed by predators varies as a function of water temperature and food availability. We did not include a feedback to predator growth based on varying food availability, though an approach to this has been used in MSVPAs previously (Gislason, 1999). This process may be explored and perhaps included in future implementations of MSVPA-X.

To account for these processes, the Elliot and Persson (1978) evacuation-rate approach was implemented within the MSVPA equations, and a modified functional relationship between food availability and predator consumption rates was included. The constant daily ration is replaced with a consumption rate ($C_{iays}$ in biomass) for predator ($i$), age class ($a$), year ($y$), and season ($s$), given as

$$C_{iays} = 24 E_{ias} \overline{Sc}_{ias} D_s w_{iays} \overline{N}_{iays}, \quad (1)$$

where $\overline{Sc}_{ias}$ is the mean stomach-content weight relative to predator body weight in a season, $D_s$ the number of days in the season, $w_{iays}$ the average weight-at-age for the predator species, and $\overline{N}_{iays}$ the average abundance of the predator age class during the time-interval. The evacuation rate ($E_{ias}$, h$^{-1}$) is given as

$$E_{ias} = \alpha_{ia} \exp(\beta_{ia} t_s), \quad (2)$$

with $t_s$ equal to the seasonal temperature (°C), and $\alpha$ and $\beta$ constants based on laboratory-feeding experiments, field studies, or other sources (Elliot and Persson, 1978; Durbin *et al.*, 1983). The evacuation rate reflects the temperature-dependent metabolic rates of the predator and requires that the MSVPA equations be seasonally resolved. The mean stomach-content weight reflects both the size of the predator and the encounter rates with suitable prey items.

The standard formulation of the MSVPA assumes that predator feeding rates are independent of prey availability. 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 such that estimated predation mortality rates on a given prey item increase exponentially at low biomass of prey (Hilden, 1988; Magnusson, 1995). These exponential increases in the values of $M_2$ may result in unrealistic model dynamics, such as extinction of prey by predation, and extremely high values of $M_2$ may prevent unique solutions of the MSVPA equations (Hilden, 1988). In sensitivity runs of the MSPVA−X model with a type II functional response, exponentially increasing values of $M_2$ on early age menhaden (*Brevoortia tyrannus*) were experienced at high, but realistic, predator biomass and consumption rates. In contrast, type III functional responses are compensatory in nature, such that the consumption of a particular prey item declines at low prey abundance, so predation mortality pressure is released. However, Hilden (1988) noted that a type III response may lead to non-unique solutions at elevated values of $M_2$. Accurate parametrization of a type III model typically requires detailed experimental feeding studies or extensive field studies, and these types of study have been rarely conducted for large piscivores. Therefore, we implement a weak type III feeding response in the MSVPA-X model by modifying the consumption equation to incorporate a logarithmic relationship between food availability (measured as total suitable prey biomass) and the quantity of prey consumed by a predator.

Given average stomach contents across years for predator $i$, age class $a$, in season $s$, $\overline{Sc}_{ias}$, as input to the model, the stomach content corrected for food availability in a given year, $y$, is calculated as

$$Sc_{iays} = \overline{Sc}_{ias} + \log\left(\frac{Pb_{iays}}{\overline{Pb}_{ias}}\right)\overline{Sc}_{ias}, \tag{3}$$

where $\overline{Pb}_{ias}$ is the average suitable prey biomass (independent of prey species) available to the predator age group. The proportional stomach-content weight calculated by Equation (3) is substituted for the average value in Equation (1) to calculate total consumption for a predator age, year, and season. The corrected stomach content is further constrained to be $>10\%$ of the input average value and $<3\times$ the input value. These constraints avoid unrealistically small or large feeding rates by predators in extreme cases. This approach avoids the depensatory dynamics of the type II response that can result in extremely high rates of predation mortality, but it does not require experimental parametrization of the type III response. Unlike the results of Hilden (1988), we did not encounter problems of non-unique solutions of the MSVPA equations during either base or sensitivity runs.

## Prey selection and suitability

The base MSVPA equations originally formulated prey suitability as

$$S_{iajb} = O_{iaj}A_{iaj}B_{iajb}, \tag{4}$$

for a given prey species ($j$) and age class ($b$) for predator species ($i$) and age class ($a$), where $O$ is a spatial overlap index, $A$ is a measure of general vulnerability, and $B$ reflects size selection (Gislason and Helgason, 1985). In the initial formulation, the general

vulnerability index was given a somewhat arbitrary definition, and it reflected the extent of overlap between, for example, primarily pelagic vs. primarily benthic species. Index $O$ was likewise developed to express the proportion of predator and prey populations that overlapped horizontally and therefore interacted with each other. The size-selectivity index was expressed as a symmetrical unimodal function of the predator–prey weight ratio. In the implementation of the ICES MSVPA model, these explicit definitions were not used, and the prey-suitability parameters were instead calculated through an iterative process of fitting to a specific year (or years) of comprehensive diet data (Magnusson, 1995). The MSVPA-X model retains the original Gislason and Helgason (1985) formulation, but more explicitly defines the parameters entering the selectivity equation rather than back-calculating constant selectivities from diet information. The suitability equation components are represented by the product of spatial overlap, a type preference or electivity parameter, and a flexible unimodal size-selection parameter that is a function of prey-to-predator length ratios.

Index $O$ may take any form, although it generally ranges between 0 and 1 and reflects the horizontal overlap of the predator and prey populations. The overlap between predator and prey types can be calculated based on available survey data across relevant levels of spatial resolution and extent. As there are seasonal differences in spatial distribution of most fish species, the value of $O$ should generally be resolved seasonally in the MSVPA-X implementation. Potential sources of data include fisheries-independent surveys, tagging studies, and fishery landings. For the species considered here, there is no consistent broad-scale fishery-independent survey that adequately represents the seasonal dynamics (NEFSC, 2006). Seasonal spatial overlap was therefore developed from available spatial information on recreational and commercial fishery catches of the target species. These catch data are expected to be representative of the seasonal spatial distribution owing to the importance of the species for both recreational and commercial fisheries along US Atlantic coast.

The type preference parameter reflects selectivity based on prey species independent of size and follows the definitions of Chesson's (1983) selectivity index as opposed to the *ad hoc* definitions used in the original implementation of the MSVPA. This index expresses the expected diet composition of the predator if all prey were equally available in the environment (Chesson, 1983). Type selection reflects a preference for a particular species relative to all others based on ease of capture, energy content, or other factors that result in a preferred prey type. The type selection index is entered as a proportional rank index, similar to the formulation of Link (2004). Therefore, for each prey type ($j$), a preference rank is assigned for a given predator species ($i$) and age class ($a$) based on both diet information and information on prey abundance. If a prey species is not consumed by that predator age class, then it is given a rank of zero. The proportional rank index ($A_{iaj}$) is calculated from

$$A_{iaj} = \frac{m - r_{iaj}}{\sum_{j=1}^{m} r_{iaj}}, \tag{5}$$

where $m$ is the number of prey species, and $r_{iaj}$ is the preference rank for each prey species. The resulting proportional rank index is equivalent to the expected diet composition (proportion by weight) for the predator, given equal prey abundance and equal prey size. If there is no preference among prey types, then all

prey species are given equal ranks ($1/m$). The development of prey type selection ranks requires a review of available diet information for each predator and associated information on the relative abundance (biomass) of prey in the habitat. Ideally, diet studies would be available over a broad geographic area and would include both the temporal resolution (seasons) and scale (duration) of the model runs.

Size selection as a function of body length is a significant component of prey selection. Type and size selectivity are confounded to some degree because smaller prey types may be more readily consumed by predators than larger prey types. However, the MSVPA-X formulation treats these processes underlying prey selection as independent parameters. The original MSVPA equation for size selectivity was a symmetrical, unimodal function of the ratio of prey and predator weights. However, the feeding literature indicates that prey length relative to predator length, rather than weight, is a better indicator of size selectivity (Scharf *et al.*, 1998; Juanes *et al.*, 2001). In general, this effect results in an asymmetrical dome-shaped relationship between predator−prey length ratios and is reflected as a unimodal distribution of prey size in the diets. To model this pattern effectively, the MSVPA-X model uses a flexible unimodal function (the incomplete beta integral) to describe size selection. The form of this function is consistent with the formulation of Chesson's selectivity index, because it integrates to 1 over the domain of predator-to-prey ratios being considered. The function can be fitted to data on the length distribution of fish prey in stomach data by maximum likelihood estimation. This assumes that the length distribution of prey in the diet reflects selection rather than availability. Therefore, it is important that the diet data used to develop the size-selection parameters is of sufficient temporal and spatial scope to avoid biases attributable to localized availability of certain prey items.

### Index-tuned single species VPA and XSA

Previous MSVPA approaches have used basic cohort analysis to calculate mortality rates and stock sizes using terminal fishing mortality rates derived from independent single-species models. However, single-species assessments and the methods used to calculate terminal mortality rates are contingent on assumptions about natural mortality rates that are calculated within the MSVPA approach. Most VPA assessments currently employ tuning indices such as fishery catch per unit effort (cpue) and/or fishery-independent indices to calculate population sizes in terminal years. For example, XSA (Shepherd, 1999) or the ADAPT−VPA method have become standard tools for single species VPAs. XSA is a tuned VPA that allows the solution of mortality rates in incomplete cohorts based on multiple fishery-dependent and/or fishery-independent abundance indices. The XSA implemented in MSVPA-X is identical with that described in Darby and Flatman (1994), and the approach has been applied previously within the framework of MSVPA by Vinther (2001) and the ICES Multispecies Working Group.

### Other predators and prey

The MSVPA-X, like previous implementations of MSVPA, includes other predators and other prey that are input primarily as bulk biomasses. For other predators, the MSVPA-X differs from previous applications in that it allows the inclusion of a limited degree of size structure in the consumption and prey-selectivity parameters. As there are frequently significant ontogenetic changes in species diets and habitats, this allows the

incorporation of a broader range of dynamics even for data-limited species. Similarly, the MSVPA-X has the capability to include temporal variation (both seasonal and annual) into the biomass vectors for other prey. This is again an important component of the dynamics of some prey that may have either demonstrable trends in biomass or strong seasonality in availability to the modelled predators. Dynamics in the other prey component of MSVPA models has not been typically considered important in previous applications (Jurado-Molina *et al.*, 2004; ICES, 2006), but it is an important aspect of the dynamics of the example system considered here.

### Example application of MSVPA-X

The MSVPA-X was tested in an example application focusing on interactions between Atlantic menhaden and three coastal piscivores: striped bass (*Morone saxatilis*), weakfish (*Cynoscion regalis*), and bluefish (*Pomatomus saltatrix*). Atlantic menhaden is a commercially exploited clupeid occupying nearshore coastal waters and estuaries along the US east coast, primarily from North Carolina to New Jersey. It is a critical component of these ecosystems as a forage base for piscivores (Hartman and Brandt, 1995; Walter *et al.*, 2003) and as a consumer of primary production (Luo *et al.*, 2001). It is also heavily exploited commercially and is among the highest volume fisheries along the US east coast (NMFS, 2007).

Menhaden constitute a significant component of the diets of weakfish, bluefish, and striped bass (Hartman and Brandt, 1995; Walter *et al.*, 2003). Additionally, declines in menhaden abundance have been implicated in observed reductions in growth and survival rates and increased disease incidence in striped bass (Uphoff, 2003). The striped bass population has recently rebounded to near historical highs, whereas the bluefish population has been declining over the past two decades (Richards and Rago, 1999). These changes in predator populations may have important implications for menhaden dynamics and fishery yields. The MSVPA-X model was developed specifically to evaluate these issues.

Here, we briefly describe an example application of the MSVPA-X model to Atlantic menhaden and its predators. VPAs for striped bass, weakfish, and menhaden were included in the model using XSA based on age-structured catch, growth, maturity, and abundance indices used in assessments conducted during 2003 and 2004. At the time of model development, age-structured assessment data for bluefish were not available, so it was included as a "biomass" predator resolved into three size categories, corresponding to age classes 0−1, 2−3, and 3+. Seven additional "other food" prey items were included in the model: benthic invertebrates (e.g. amphipods and polychaetes), shrimps and other macrozooplankton, crabs and lobsters, medium-sized forage species (squid and butterfish), bay anchovy, sciaenids (Atlantic spot and croaker), and other clupeids. The "other clupeids" category includes Atlantic herring (*Clupea harengus*) and thread herring (*Opisthonema oglinum*) in particular. The application encompassed the years 1982−2002 and was resolved into four seasons. For greater detail on the data sources, development of other prey abundance, model parameters, and outcomes, the reader is referred to NEFSC (2006). This application is presented strictly as an example to demonstrate the parametrization, performance, and sensitivity of the MSVPA-X model. More recent stock assessments for each of these species have been conducted, and additional data including additional predator and prey types will be incorporated into future MSVPA-X applications.

## Sensitivity analysis

We examined the behaviour and sensitivity of the MSVPA-X model to changes in major parameters, focusing on sensitivity in the estimates of predation mortality rates ($M_2$) for Atlantic menhaden. The sensitivity analysis focused on consumption parameters, spatial overlap indices, type preference ranks, size-selectivity parameters, and the inclusion or exclusion of other prey (Table 1). Although some aspects of the sensitivity analysis are related to the particular predator–prey system modelled here, we focus primarily on the general behaviour of the model. Additional sensitivity analyses and the resulting model outputs can be found in NEFSC (2006).

## Results

### Model output: base run

The mortality rates and biomass trends for striped bass and weakfish modelled within this application were largely consistent with those resulting from their standard stock assessments using the ADAPT–VPA approach. In brief, there was a significant increase in the total biomass of striped bass through the 1990s, although the population biomass appears to have levelled off during the last 3 years of this time-series. Bluefish biomass, in contrast, declined sharply over the same period, then began to recover in the late 1990s. Weakfish biomass remained generally stable (Figure 1a). The major trends in input prey biomass included general declines in the biomass of anchovy and significant increases in the biomass of herring. The increase was dominated by Atlantic herring (Figure 1b). Atlantic menhaden total biomass, modelled by the MSVPA-X, declined steadily during the past decade (Figure 1b), consistent with the outcomes of

single-species assessments for the stock. The decline in total biomass reflects decreases in early age classes (ages 0–1) and age classes that are fully recruited to the fishery (age 2+).

The total prey biomass consumed by striped bass increased during the last decade, driven largely by increasing striped bass biomass (Figure 2a). The total annual prey biomass consumed by striped bass averaged 442 000 t annually during the last 3 years of the time-series, dominated by invertebrates, $\sim$49% of the striped bass consumption when averaged across years and age classes. The primary fish prey included other clupeids (12.4% of total prey on average), bay anchovy (13.5%), and menhaden (15.5%).

For weakfish, the total prey biomass consumed fluctuated across the time-series as the biomass of the older age classes fluctuated. The average estimated total prey consumed annually by weakfish from 2000 to 2002 was 401 000 t, close to that of striped bass, despite the lower total biomass of weakfish, owing to the higher *per capita* consumption rates reflected in input mean stomach-content weights. Weakfish consumption of prey was dominated by bay anchovy (40.0%) and invertebrates (33.5%). Menhaden accounted for 20.2% of the total prey consumed by weakfish on average (Figure 2b).

The trends in bluefish consumption followed that of stock biomass, total consumption exceeded 500 000 t during the early part of the time-series, declined to $\sim$200 000 t through much of the 1990s, and increased to an average of 345 000 t during the last 3 years (Figure 2c). Bluefish diet was more heavily dominated by fish prey than the other two predators, and dominant prey items included other clupeids (41.9% of consumption on average), menhaden (23.3%), medium forage fish and squids (12.0%), and bay anchovy (11.2%). The proportion

**Table 1.** Sensitivity analyses performed to evaluate the MSVPA-X model, examining the effect of changes in input parameters on the estimates of Atlantic menhaden predation mortality ($M_2$).

| Analysis | Parameter value | Description |
|---|---|---|
| Consumption [Equation (2)] | | |
|   Base | $\alpha = 0.004$ and $\beta = 0.115$ | Derived from literature values and set constant for all predator age classes |
|   Vary evacuation rate $\alpha$ | $\alpha = 0.002$ and $\alpha = 0.006$ | Parameter values changed for each predator individually and all predators combined |
|   Vary evacuation rate $\beta$ | $\beta = 0.050$ and $\beta = 0.200$ | Parameter values changed for each predator individually and all predators combined |
| Type selectivity [Equation (5)] | | |
|   Base | Data-derived values | Rank preferences derived from the analysis of available diet and prey abundance information |
|   All ranks equal | All non-zero ranks set equal | All rank preferences tied for all prey consumed by each predator and all predators combined |
|   Fish prey vs. invertebrate prey | Fish vs. invertebrate prey | For each prey type, invertebrate prey items were given equal, tied rank preferences. Fish prey were also given equal, tied rank preferences |
| Spatial overlap | | |
|   Base | Data-derived values | Derived from regional patterns in recreational and commercial catch data |
|   Equal | All non-zero values set to 1 | Assumed uniform distribution and no spatial pattern |
| Size selectivity | | |
|   Base | Data-derived values | Derived from analysis of available data on size frequency of prey in predator diets |
|   Vary median prey size range | Variable by predator | Shift by −20, −10, +10, and +20% for all predators |
| Other prey | | |
|   Base | All prey types included | Includes anchovy, benthic invertebrates, crabs and lobsters, squids and butterfish, other clupeids, and shrimps |
|   Remove anchovy | | |
|   Remove other clupeids | | |
|   Remove squids and butterfish | | |
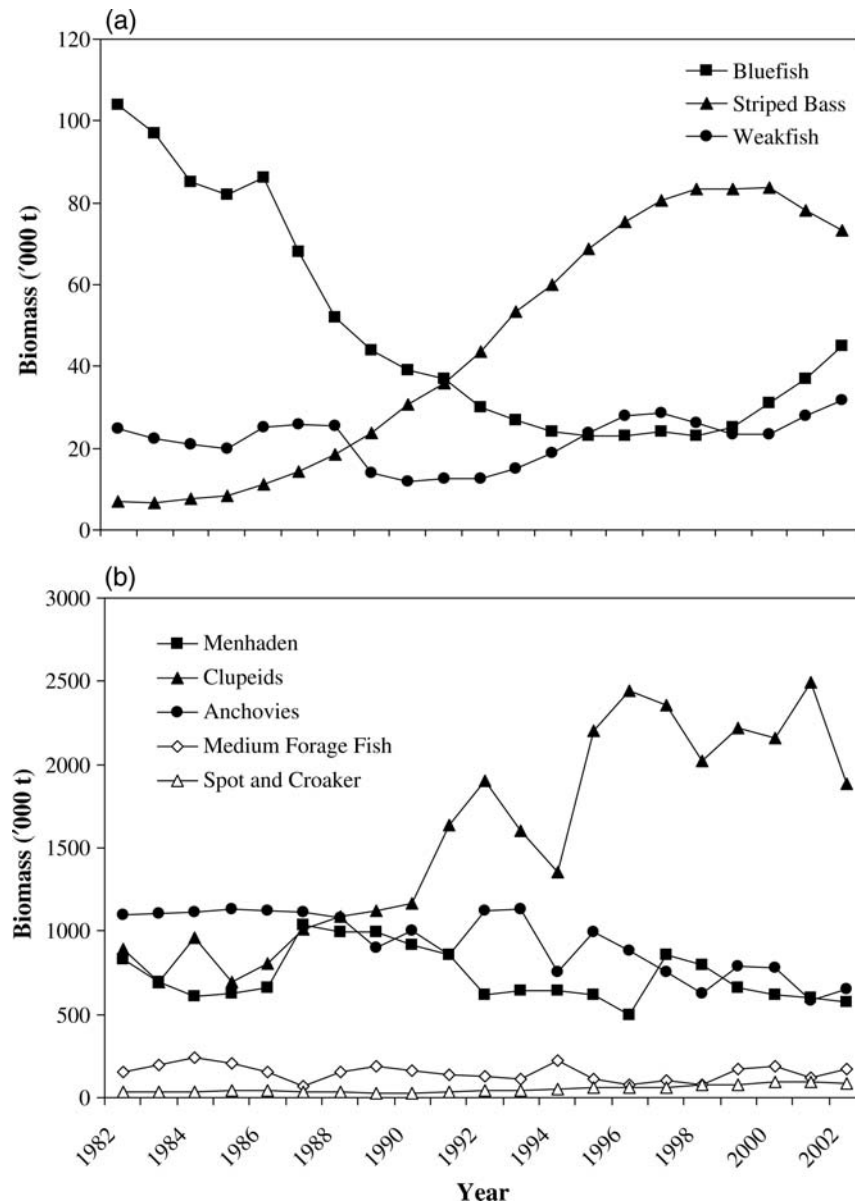
**Figure 1.** Biomass trends for (a) predators and (b) fish prey species from the example MSVPA-X model run. Biomass trends for Atlantic menhaden are derived from calculated fishery and predation mortality rates, and all other parameters were inputs into the model. Note the differences in the *y*-axis scales.

of other clupeids in the diets increased in recent years owing to the increases in total biomass of that prey (Figure 2c).

The total estimated biomass of menhaden consumed by these predators averaged 185 000 t annually over the time-series. The total biomass consumed was high in the 1980s and dominated by bluefish predation, declined through the early 1990s, then increased during the late 1990s with increased biomass of both weakfish and striped bass (Figure 2). The trend in estimated $M_2$ followed these patterns, and different predators were responsible for most of the natural mortality of each age class of menhaden. The $M_2$ of age-0 menhaden was dominated by weakfish predation, but the contribution of striped bass predation increased in recent years (Figure 3a). In contrast, age-1 and age-2 menhaden mortality was dominated by bluefish and striped bass, and the relative contribution between these predators varied with changes in

their biomass across the time-series (Figure 3b and c). The predation mortality on menhaden age-3+ was minimal.

The total $M_2$ on age-0 menhaden varied, with a low of ~0.4 during the early 1990s and highs of 0.8–1.0 in the most recent years. Predation mortality on age-0 menhaden far exceeded fishing mortality, *F*, as would be expected (Figure 4a). In contrast, $M_2$ and *F* were of similar magnitude for age-1 menhaden, with average values of $M_2$ for the most recent years being 0.23 (Figure 4b). The relatively high values of *F*, approaching 1.0 for fully recruited age-2+ menhaden, far exceeded the estimated values of $M_2$ (Figure 4c).
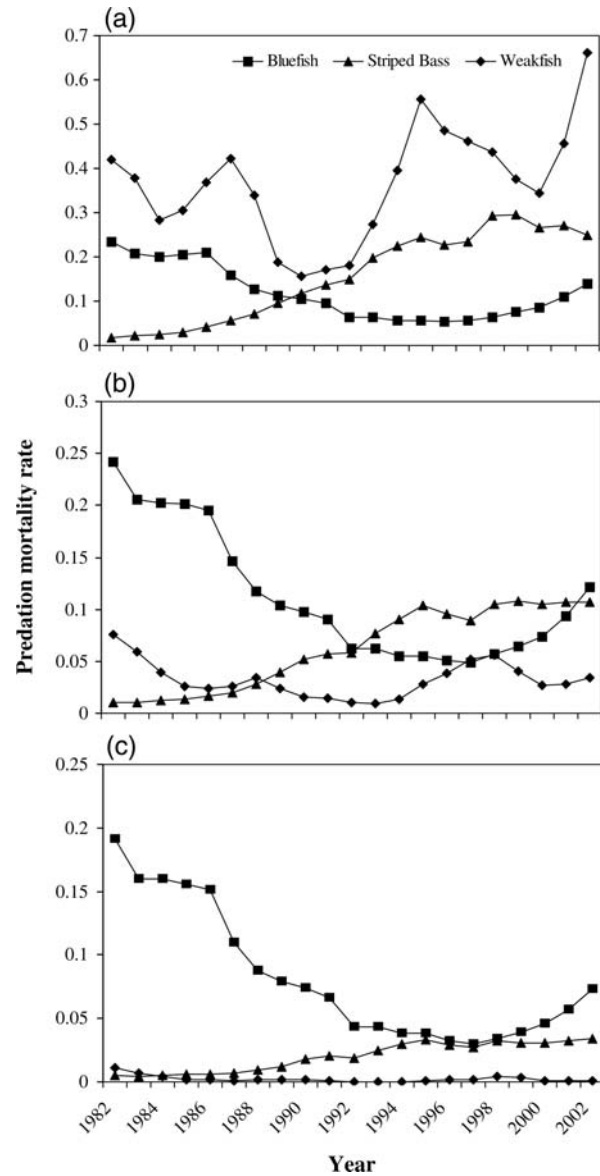
**Sensitivity analyses**

The estimated values of $M_2$ for age-0 and age-1 menhaden were sensitive to the input consumption parameters. Generally, the
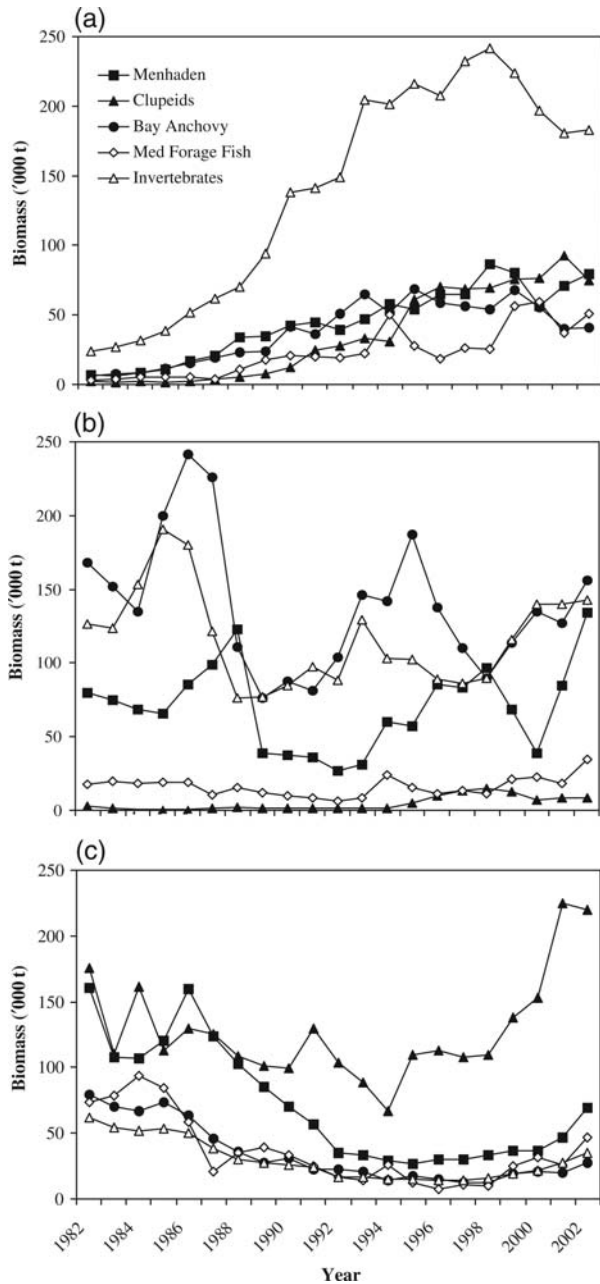
**Figure 2.** Biomass consumed by prey type for (a) striped bass, (b) weakfish, and (c) bluefish from the example MSVPA-X model run. Sciaenids (spot and croaker) are not included, and all invertebrate prey (benthic crustaceans, benthic invertebrates, and macrozooplankton) are combined into the invertebrate category.
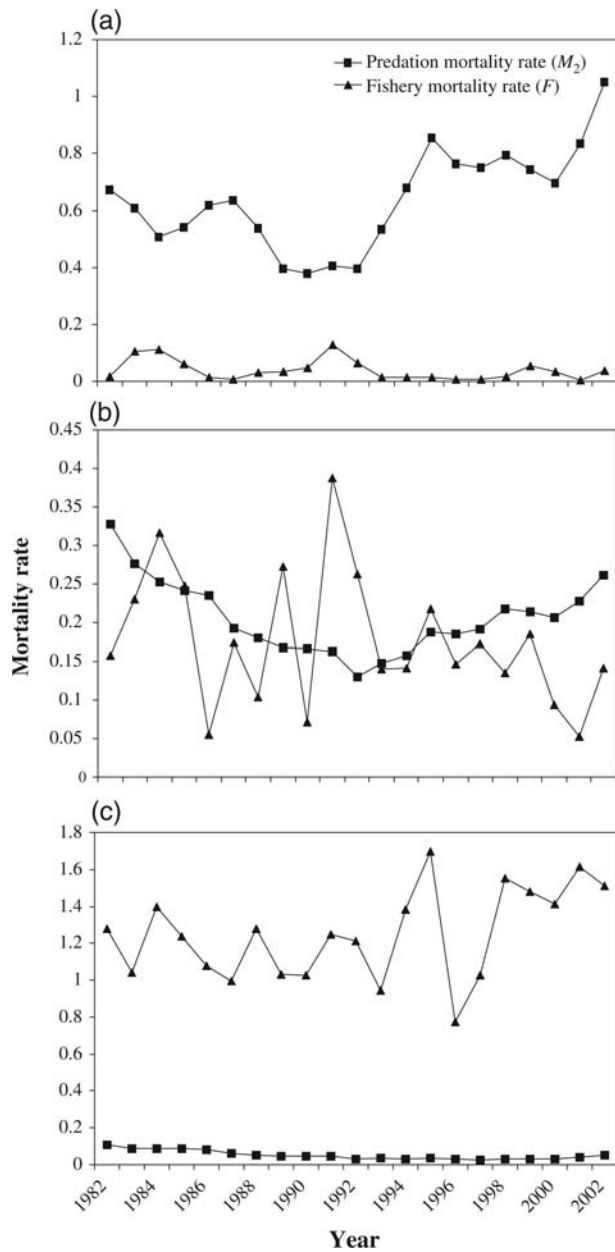


**Figure 3.** Estimated predation mortality rate ($M_2$) by predator type for Atlantic menhaden (a) age-0, (b) age-1, and (c) age-2. Note the differences in the y-axis scales.

$M_2$ of age-0 menhaden was most sensitive to the input parameters for weakfish. For age-1 menhaden, the sensitivity depended on the dominant predator species, so it varied through the time-series, with bluefish being more important during the early period and striped bass later (Figure 5). The sensitivity to the $\alpha$ parameter in the evacuation rate equation was almost linear. When this parameter was decreased by 50% ($\alpha = 0.002$) for all predators, the estimated values of $M_2$ decreased by an average of 44% (Figure 5a and b). When the parameter was increased by 50% ($\alpha = 0.006$), the values of $M_2$ increased by an average of 37%

(Figure 5c and d). The sensitivity to the $\beta$ parameter was non-linear, with greater sensitivity in estimates of $M_2$ at high values of $\beta$. For all predators combined, a 56% reduction in this parameter ($\beta = 0.05$ vs. 0.115) resulted in an average of 59% reduction in the estimated values of $M_2$ (Figure 5e and f). A 73% increase ($\beta = 0.200$ vs. 0.115) resulted in a 164% increase in the values of $M_2$ (Figure 5g and h).

Estimated values of $M_2$ were less sensitive to spatial overlap, and the direction of the sensitivity varied with predator and age class. The sensitivity runs included changing the values of spatial overlap to 1 for each predator individually, then for all predators (Table 1). Compared with base-run values with spatial overlap derived from surveys or fishery-dependent data, the mortalities of age-0 menhaden were lower and most strongly influenced by the overlap with weakfish (Figure 6a). However, the reduction was relatively small, with estimated $M_2$ values ~10% lower than

**Figure 4.** Predation ($M_2$) and fishing ($F$) mortality rates for Atlantic menhaden (a) age-0, (b) age-1, and (c) age-2+, estimated from the example MSVPA-X run. Note the differences in the $y$-axis scales.

those in the base runs with all predators. For older age classes, changing the spatial overlap to 1 increased the estimated rates of predation mortality, the impact being greatest for bluefish during the early portion of the time-series and for striped bass later (Figure 6b). Estimates for age-1 menhaden were more sensitive to spatial overlap than those for age-0 menhaden, with increases of up to 30% in sensitivity runs for all predators compared with base values.

Sensitivity to the type preference ranks was tested by (i) setting all type preference ranks to be equal and (ii) setting equal preference ranks among all fish prey and among all invertebrate prey (Table 1). In the model runs with all rank preferences equal, the predation mortality rates of age-0 menhaden were most sensitive

to changes in weakfish type preferences, resulting in an average of 30% reduction relative to the base run (Figure 7a). In contrast, $M_2$ values for age-1 menhaden were largely insensitive to type preference, with slight increases of ~1% on average (Figure 7b). Setting the rank preferences equal for all fish and invertebrate prey resulted in a 17% average decrease in estimated values of $M_2$ for age-0 menhaden, and an average increase of 9% for age-1 menhaden (Figure 7c and d). Overall, changing the type preference ranks for weakfish was more important in determining menhaden consumption than changing it for either bluefish or striped bass.

The size-selection parameters were modified to result in 10 and 20% increases or decreases in the median prey sizes for all predators. Estimates of $M_2$ rates for age-0 menhaden were largely insensitive to these changes in size selection, with a maximum increase of 11% on average for a 20% increase in median prey size (Figure 8a). Although estimates for age-1 menhaden were insensitive to decreases in median prey size, they were highly sensitive to increases in median prey size (Figure 8b). An increase in median prey size of 20% resulted in an average of 49% increase in estimated $M_2$, an increase driven primarily by increased consumption of older menhaden by weakfish.

Sensitivity to the inclusion of other prey in the model was evaluated by removing each prey type and examining the effect on menhaden $M_2$. For age-0 menhaden, the estimated values of $M_2$ were highly sensitive to the inclusion of bay anchovy (42% average increase in $M_2$ with removal of bay anchovy) and benthic invertebrates (34% average increase; Figure 9a). These are the primary alternative prey to menhaden for weakfish and striped bass, respectively. For age-1 menhaden, the estimated values of $M_2$ were extremely sensitive to the inclusion of other clupeid prey, and removing that prey type from the model resulted in an 80% average increase in estimated $M_2$ (Figure 9b). Herring are the primary prey item for larger striped bass and bluefish, particularly during summer, when age-1 menhaden are both outside the estuaries and farther north. Therefore, their removal significantly increases the predation pressure on menhaden as the only other prey available.

## Discussion

The predation mortalities ($M_2$) for menhaden vary across the time-series in response to changes in predator (and prey) population sizes. Since the mid-1990s as striped bass, weakfish, and bluefish populations increased, the $M_2$ values of age-0 and age-1 menhaden also increased. This is a key aspect of incorporating variable values of $M_2$ into the assessments of stock productivity for forage species. As exploited piscivore populations recover through fisheries management actions, it is critical to evaluate and account for the effects on the forage fish species needed to support piscivore productivity.

Predation mortality rates also vary across the age structure of menhaden, consistent with the results of previous work in other systems that demonstrated the importance of predation mortality on the recruitment dynamics of forage species (e.g. Livingston and Jurado-Molina, 2000; Collie and Gislason, 2001; Tsou and Collie, 2001; ICES, 2006; Tyrrell *et al.*, 2008). There is also an important change in the primary predators by age class. At age 0, some 50% of menhaden predation mortality is attributable to weakfish, whereas at age 1 and older, the $M_2$ is largely attributable to striped bass and bluefish. These patterns are heavily influenced by the input parameters. In particular, weakfish have a greater preference for small pelagic fish prey (e.g. bay anchovy and
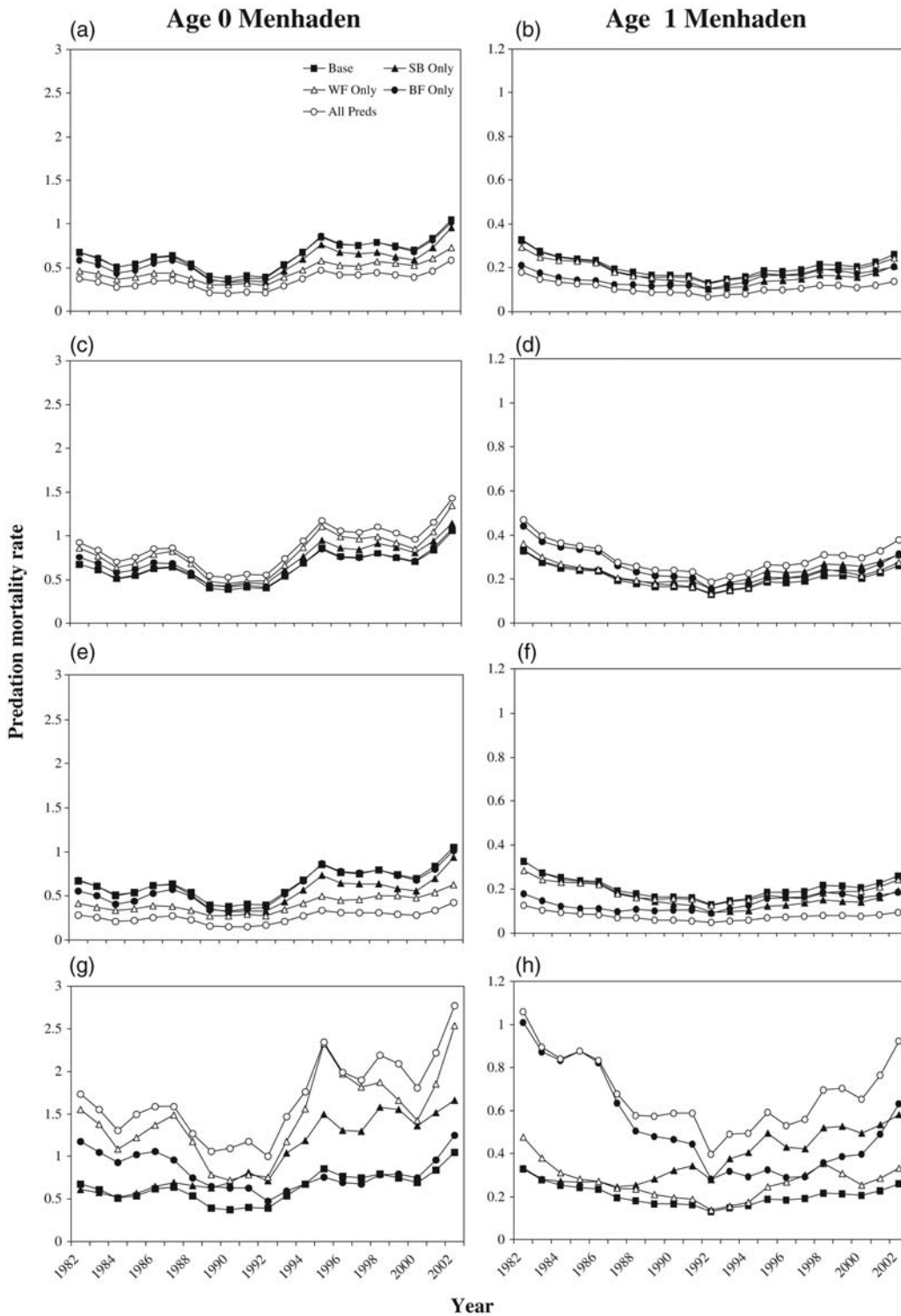
**Figure 5.** Predation mortality rates on age-0 and age-1 Atlantic menhaden as a result of changing evacuation rate parameters. Sensitivity runs were conducted by changing parameters for each predator species individually and all predators. Default parameter values ($\alpha = 0.004$, $\beta = 0.115$) were used for the base run. Parameter values were set to (a and b) $\alpha = 0.002$, (c and d) $\alpha = 0.006$, (e and f) $\beta = 0.050$, and (g and h) $\beta = 0.200$. SB, striped base; WF, weakfish; BF, bluefish. Note the differences in the y-axis scales.

menhaden) and a more consistent spatial overlap with age-0 menhaden, particularly in estuaries. Adult bluefish and striped bass migrate north during summer, and this reduces the extent of spatial overlap with recruiting menhaden and increases the overlap with more northern prey, such as herring. The MSVPA-X formulation uses seasonal spatial overlap to model these patterns, and this is a critical aspect of capturing the dynamics of this system.
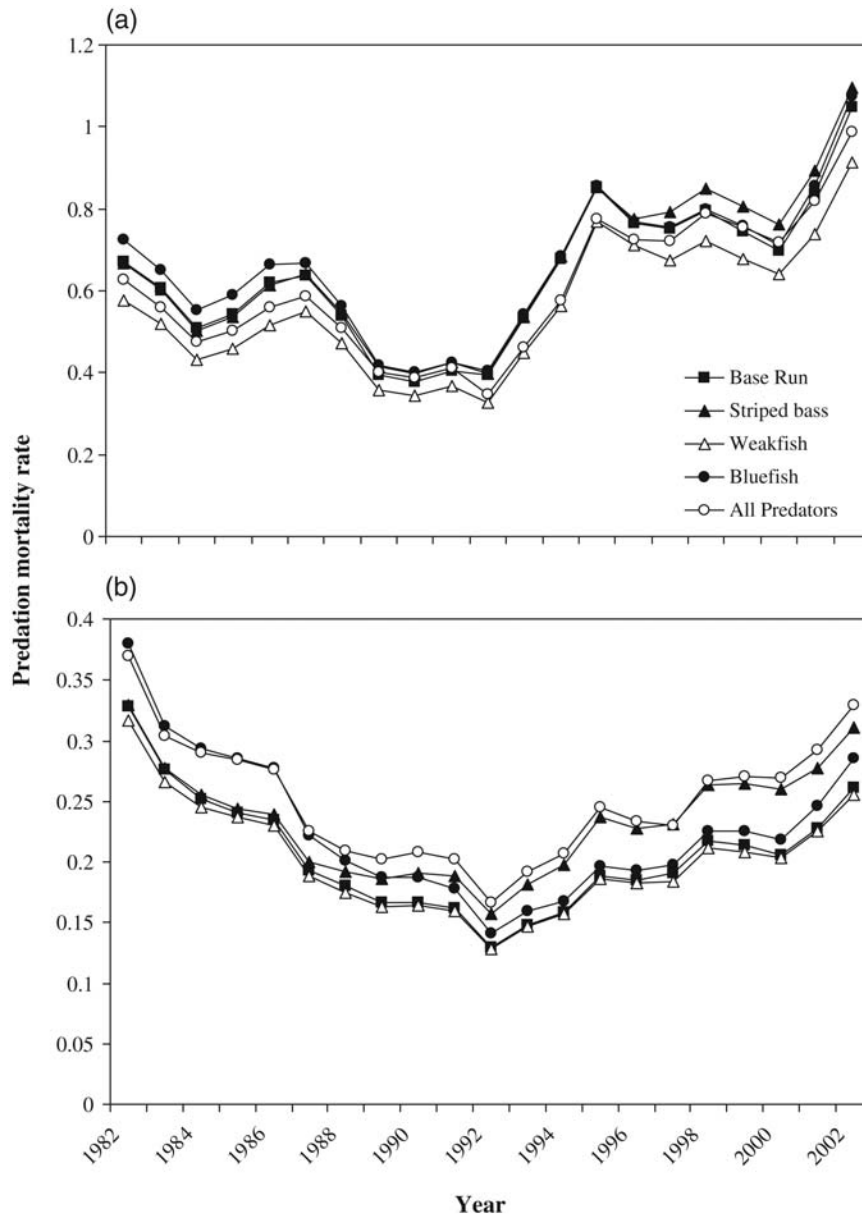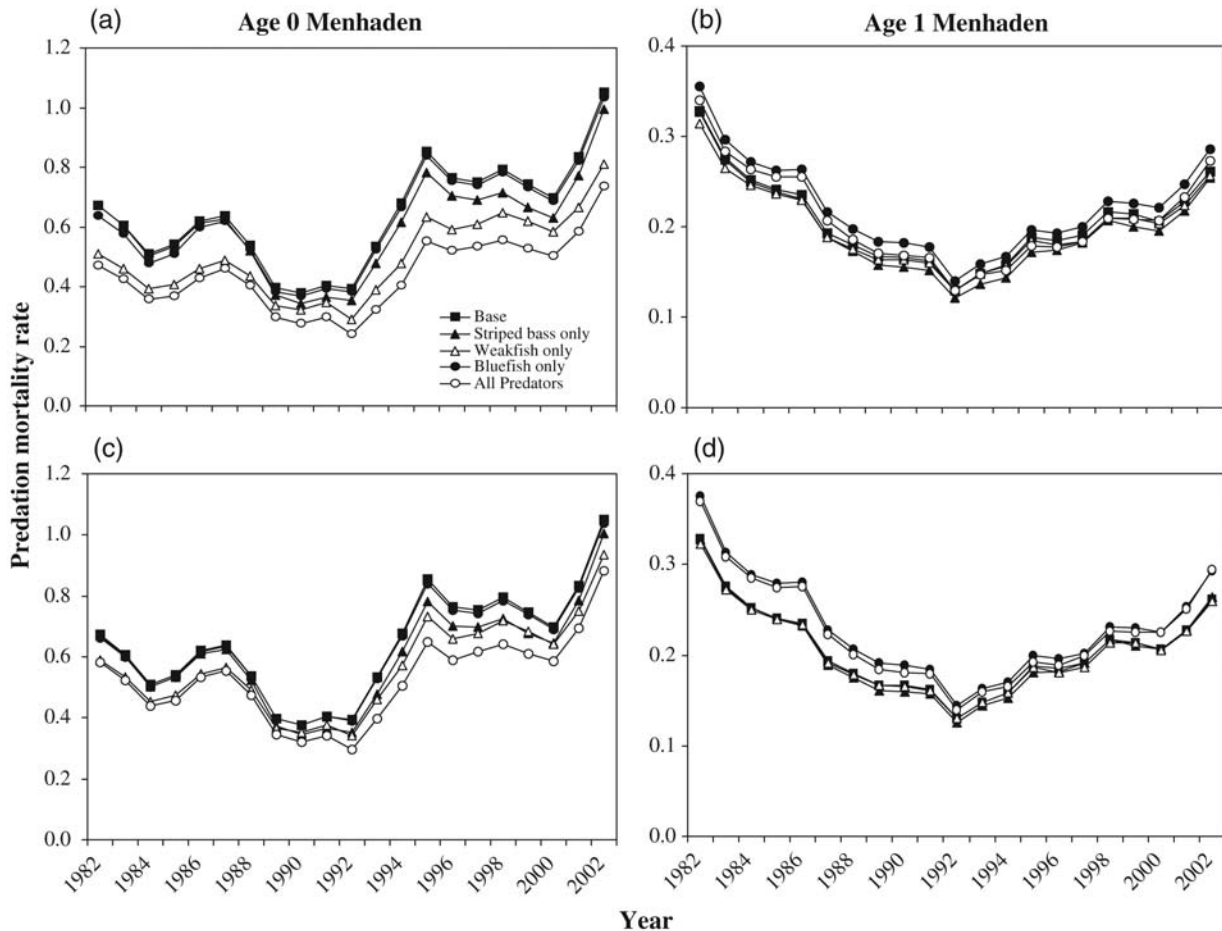
**Figure 6.** Predation mortality rates on Atlantic menhaden (a) age-0 and (b) age-1 as a result of changing spatial overlap values. Sensitivity runs were conducted by setting all spatial overlap values equal to 1 for each predator species individually and all predators. Note the differences in the *y*-axis scales.

The predicted diets of striped bass, bluefish, and weakfish are consistent with available stomach content data from these predators (Hartman and Brandt, 1995; Walter *et al.*, 2003), and *per capita* consumption rates are likewise similar to those derived using other approaches (e.g. Hartman and Brandt, 1995; Buckel *et al.*, 1999). Unfortunately, there is no large-scale, long-term, seasonal, diet dataset to compare directly with the model result. Clearly, more consistent stomach sampling will help in this or any other MSVPA application. Moreover, for many systems, there is a variety of available diet studies of varying scales (e.g. various theses and project reports), and summarizing the results of these studies into a synthetic view of seasonal and spatial variation in diets would be a useful exercise to both parametrize models and identify data gaps (Walter *et al.*, 2003). Predator

diet composition is temporally dynamic in response to seasonal movements of predators and prey and changes in prey abundance. This general approach of estimating prey selectivity has been tested and field-validated for other species (Link, 2004), so likely represents a credible depiction of what these predators eat and is a reasonable way to account for these dynamics. Therefore, the formulation of the MSVPA-X allows a high degree of flexibility to model feeding dynamics and to estimate the impacts on predation mortality rates.

There are general implications of this example analysis for forage fish in marine and aquatic ecosystems. The trophic linkages within an ecosystem are especially important for early age classes of top predators and small forage species that are important prey items for multiple predators and are heavily exploited by

**Figure 7.** Predation mortality rates on Atlantic menhaden age-0 and age-1 as a result of changing type preference values. Type preferences were (a and b) set equal among all prey items for each predator individually and all predators, or (c and d) given tied ranks for all fish and invertebrate prey. Note the differences in the y-axis scales between graphs depicting age-0 and age-1 mortality rates.

fisheries. The relative size of predator and prey is an important factor limiting capture probability and other aspects of the predation process (Scharf *et al.*, 1998; Hartman, 2000; Juanes *et al.*, 2001). As a result, nearly all predation is on early age classes of a particular forage species. Significant changes in predator abundance can therefore affect the survival of new recruits and the overall productivity of a forage species. As fisheries generally target the larger members of a given population, fishery removals of top predators may result in important changes in the rates of predation mortality on prey populations. Likewise, fishery removals of prey species spawning-stock biomass may indirectly reduce the availability of young fish and hence the quantities of preferred prey for top piscivores.

The developments presented in the MSVPA-X approach represent improvements over the standard MSVPA. Strengths of the MSVPA-X approach are that it incorporates a weak type III functional feeding response, has an explicit prey-selection model, and incorporates a more dynamic consumption model. The factors evaluated in the sensitivity analysis highlight some of the distinctiveness of the MSVPA-X. The changes improve the estimation procedure for consumption. As such, they represent a departure from the standard MSVPA and address some of the underlying concerns voiced in previous reviews (Magnusson, 1995). The elements of prey selectivity (spatial overlap, type preference, size

preference) were more explicitly derived here than the suitability parameter from the ICES MSVPA. By providing a more explicit and decoupled method to model prey selectivity, and therefore diet composition, the MSVPA-X better allows for situations with less data on food preference. However, there is a clear link between the derivation of these parameters and available data, and the model behaves predictably relative to the variability in input parameters. Estimated predator diet composition and the resulting estimated $M_2$ on age-0 and age-1 menhaden are sensitive to the rank preferences assigned to specific prey types. Therefore, a thorough understanding of predator diet composition and prey preferences throughout the spatial and temporal range of the model is an important component of developing an accurate estimate of predation mortality.

One of the major observations to emerge from the MSVPA-X approach was the importance of other prey. In other recent applications of MSVPA models, the sensitivity of $M_2$ estimates to other prey has been limited (Jurado-Molina *et al.*, 2004). However, for our application, excluding or including other prey had direct impacts on the estimates of menhaden $M_2$. Some of this modelled behaviour is a characteristic of the current system. In particular, the piscivores considered here have diverse diets that include benthic invertebrates and other alternative prey. However, it is likely that in cases where there is strong seasonal variability in
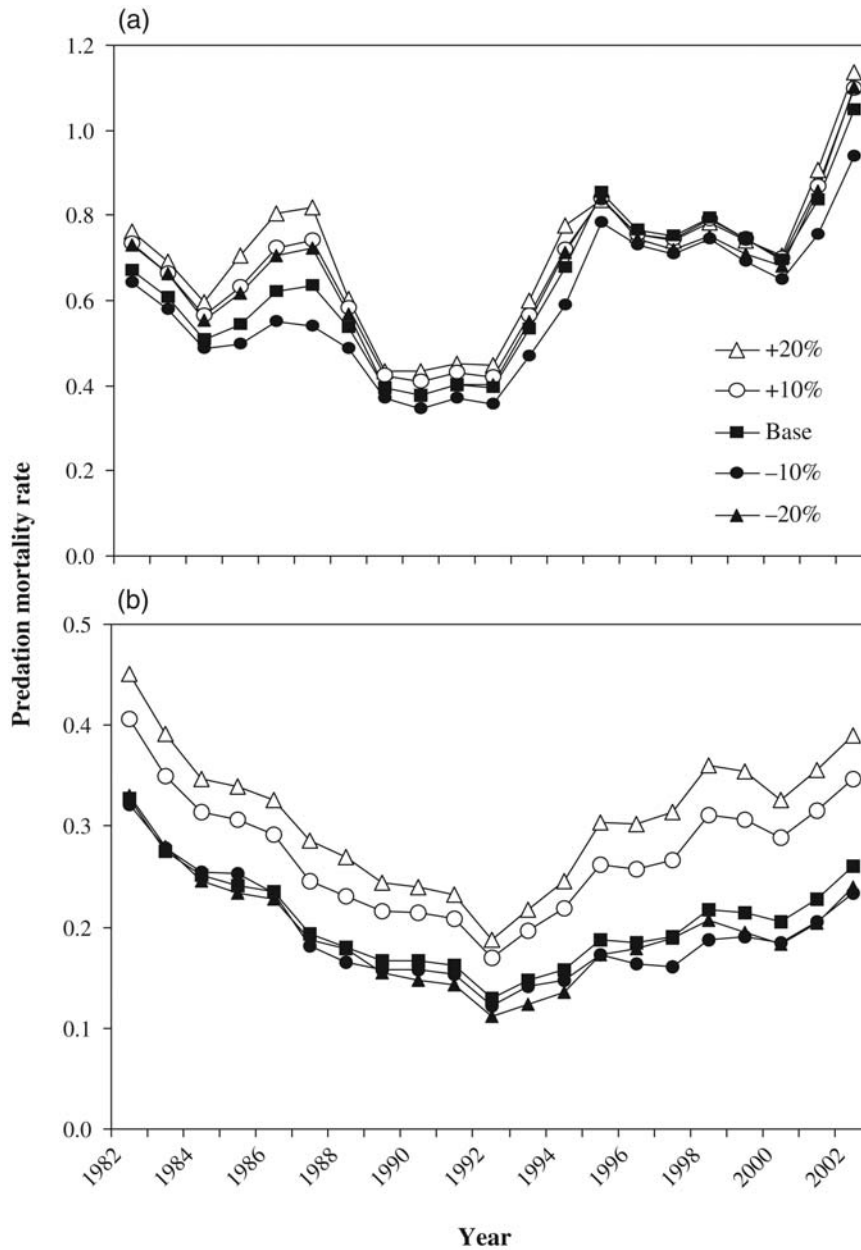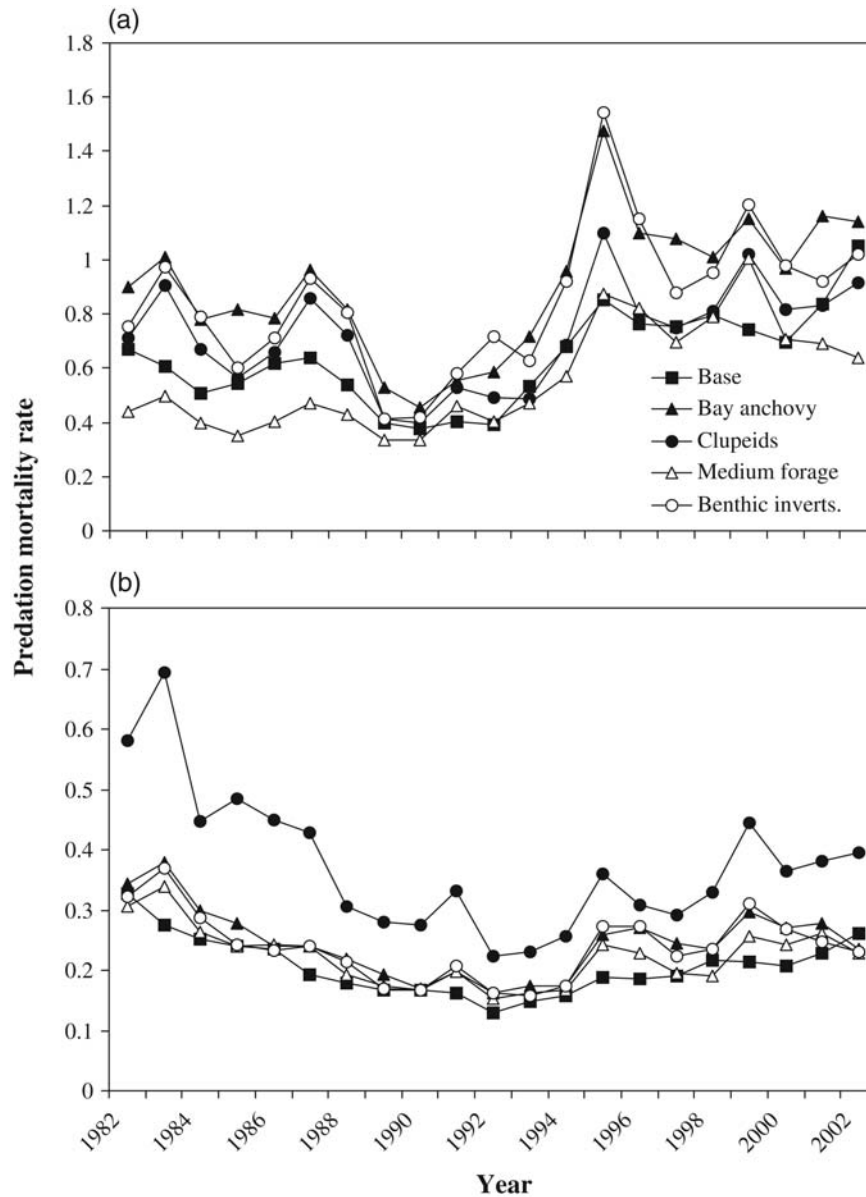
**Figure 8.** Predation mortality rates for Atlantic menhaden (a) age-0 and (b) age-1 as a result of changing size-selectivity curves. For all predators, size-selection curves were adjusted so as to reduce or increase the median prey size by 20 and 10%. Note the differences in the *y*-axis scales.

predator and prey spatial overlap, or where there are significant temporal changes in the biomass of other prey, then one could expect strong impacts on the estimated values of $M_2$ of other forage species.

Incorporating other predators that were not explicitly modelled is a strength of the MSVPA-X approach and is also critical in other applications of MSVPA models. For example, the inclusion of bluefish is a critical part of capturing the dynamics of menhaden predation mortality. Other studies have similarly incorporated biomass predators into an MSVPA framework. Livingston and Jurado-Molina (2000) developed an MSVPA model of the Bering Sea ecosystem involving six prey species and six predators and included northern fur seals (*Callorhinus ursinus*) and arrowtooth

flounders (*Atheresthes stomias*) as "other predators" using a similar approach. The ICES Multispecies Working Group implemented an MSVPA model for the entire North Sea, involving a large number of fish prey species and their predators. Estimates of species- and size-specific fish consumption by grey seals (*Halichoerus grypus*), seabirds, and cetaceans were included in that analysis. In both instances, the mortality of emphasized forage species was higher when including other predators. Like other prey, the inclusion of these other predators is a critical aspect of applying MSVPA approaches in these systems. Future applications of MSVPA-X to this system could likewise include other apex predators (e.g. sharks and billfish) to enhance our understanding of menhaden dynamics.

**Figure 9.** Predation mortality rates for Atlantic menhaden (a) age-0 and (b) age-1 as a result of removing individual other prey types from the model for all predators. Note the differences in the *y*-axis scales.

A weakness of the MSVPA approach relative to other models 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 omitted from the model or are included as fixed inputs of biomass. Therefore, such important processes as system-level changes in primary production, climate variation that may influence recruitment, and losses to other predators are ignored. Hence, 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 assessments. Our and other MSVPA approaches are merely a step along the gradient from single-species stock assessment models to major ecosystem models (Link, 2002).

Ultimately, when should an MSVPA be used? Situations where there are a concentrated number of early age classes of top predators and small forage prey species, which are also heavily exploited by fisheries, are particularly germane for MSVPA analysis. Fisheries agencies with the requisite data to conduct routine age-structured single-species stock assessments, augmented by some food habits data, should be able to explore an MSVPA approach. The MSVPA-X presented here represents enhancements to the standard MSVPA that help to mitigate the requirement for comprehensive diet information to support this approach.

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