

Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis

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Tyrrell, M. C., Link, J. S., Moustahfid, H., and Overholtz, W. J. 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis. – *ICES Journal of Marine Science*, 65: 1689–1700.

An expanded version of multispecies virtual population analysis (MSVPA) is used to analyse the effects of predation by 14 key predators on Atlantic herring and Atlantic mackerel in the Northwest Atlantic ecosystem for the period 1982–2002. For herring, MSVPA produced greater abundance estimates than single-species assessments, especially for the youngest age classes. The average rate of predation mortality for herring aged 0 and 1 was also higher than the standard total natural mortality rate (0.2) for the 21-year time frame (0.84–3.2). The same was true for mackerel in this MSVPA (0.37–1.6). Consumptive removals of herring and mackerel generally increased over time. From 1999 to 2001, the biomass removed by predators exceeded each species' commercial landings. The sum of consumption and landings notably exceeded the multispecies maximum sustainable yield for herring for the years 1995–2002 and for mackerel for the period 1999–2002. We highlight the importance of accounting for predation on forage species in the context of changes to the fish community that have taken place in the Northwest Atlantic over the past few decades.

Keywords: Atlantic herring, Atlantic mackerel, forage species, multispecies virtual population analysis, Northwest Atlantic, predation mortality, recruitment, stock assessment.

Received 28 March 2008; accepted 21 October 2008.

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Introduction

The importance of incorporating ecological interactions into fisheries science and management is becoming increasingly apparent (Pope, 1991; Yodzis, 2001; Link, 2002). Several models exist to do this (e.g. Hollowed *et al.*, 2000; Whipple *et al.*, 2000; Plagányi, 2007), and among them are several multispecies models that utilize combined aspects of common fisheries and ecological models. Multispecies virtual population analysis (MSVPA) is well suited to incorporating ecological interactions such as predation, because it is age-structured, utilizes common single-species (SS) approaches, provides familiar outputs commonly used in fisheries management, and importantly, elucidates the influence of predation on various age classes of fish.

Multiple factors can affect the population dynamics of fish, with recruitment in particular having high interannual variability owing to environmental conditions (Hofman and Powell, 1998) and the composition of the fish community (Bax, 1998; Tsou and Collie, 2001b). The role of predation in structuring juvenile stages has long been recognized (Gislason and Helgason, 1985; Pope, 1991; Hollowed *et al.*, 2000; Tsou and Collie, 2001a). MSVPA is a particularly useful tool to examine the relative importance of predation mortality throughout the life history of fish, because predation often disproportionately impacts juvenile life stages.

The Northeast US (NEUS) continental shelf ecosystem has a long history of intense fishing pressure, which has resulted in notable changes to the fish community (Serchuk *et al.*, 1994; Fogarty and Murawski, 1998; Garrison and Link, 2000; Link *et al.*, 2002). Although those changes have been documented in detail elsewhere, briefly, the NEUS ecosystem has experienced a decline in pelagic fish, a decline in groundfish, an increase in elasmobranchs, and a more recent recovery of pelagics over the past 50 years (Serchuk *et al.*, 1994; Fogarty and Murawski, 1998; Garrison and Link, 2000; Link *et al.*, 2002). Owing to the long history and economic importance of fisheries activity in the region, the NEUS ecosystem has an extensive amount of data documenting the environmental conditions, population dynamics, and food habits of its commercially exploited species, permitting the development of an MSVPA. Herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) were chosen as the focal prey species for this MSVPA because they: (i) are important as prey for many predators, (ii) support commercial fisheries, and (iii) have the age-structured data necessary for an MSVPA to be constructed.

The software package used for this application is an expanded version of the original MSVPA developed by the ICES Multispecies Working Group (Gislason and Helgason, 1985). Expanded MSVPA (MSVPA-X; Garrison and Link, 2004) builds on the ICES approach and incorporates additional features to address some limitations of the original model formulation. Briefly,

MSVPA-X modifies the predator consumption equations to incorporate the effects of changing food availability and temperature on predator consumption rates. It also includes a choice of four different SS virtual population analysis models, which allow for greater flexibility to account for differing data availability. The MSVPA-X feeding selectivity model also more explicitly formulates spatial overlap, prey type, and size selectivity than the original MSVPA. Finally, MSVPA-X includes provisions for “biomass predators”; predation by these species affects the mortality of explicitly modelled prey species, but the population dynamics of biomass predators are not modelled explicitly. For more details on the MSVPA-X approach, the reader is advised to consult Garrison and Link (2004).

The main objective of executing this MSVPA was to elucidate the importance of predation and how it may have affected the population dynamics of the focal prey species over a period (1982–2002) when the relative biomass of groundfish was low but pelagic and elasmobranch biomass was relatively high (Fogarty

and Murawski, 1998; Link *et al.*, 2002). Specifically we wanted to: (i) compare SS and MSVPA outputs to ascertain the influence of explicitly modelling predation; (ii) examine trends in predation mortality for herring and mackerel over time; (iii) examine which predators were responsible for the greatest extent of predation on herring and mackerel; (iv) compare the magnitude of predation mortality with fishing mortality and fisheries vs. consumptive removals for these pelagic fish over time; and (v) compare relative changes in reference points in multispecies vs. SS contexts.

Methods

Model structure

In all, 23 species or groups (Table 1) were included in the model, which spanned the time frame 1982–2002 and the entire NEUS continental shelf ecosystem (Figure 1). Three of the species, Atlantic cod (*Gadus morhua*), goosefish (*Lophius americanus*), and silver hake (*Merluccius bilinearis*), were split into two separate stocks to match

Table 1. Species/groups included in the NEUS continental shelf MSVPA.

Common name	Type	Ages (years) or size categories (cm)	Average biomass 1982–2002 (t)	Ranked as prey	Basis of available biomass as a prey species
Georges Bank cod	Age-structured predator	1–10	85 200	Yes	–
Gulf of Maine cod	Age-structured predator	1–7	35 600	Yes	–
Summer flounder	Age-structured predator	1–7	39 000	Yes	–
Spiny dogfish	Biomass predator	<36, >36 to <80, >80	504 000	No	–
Sea raven	Biomass predator	<25, >25 to <50, >50	4 700	No	–
Winter skate	Biomass predator	<30, >30 to <60, >60 to <80, >80	59 300	No	–
Little skate	Biomass predator	<30, >30 to <60, >60 to <80	59 600	No	–
Fourspot flounder	Biomass predator	<20, >20 to <40, >40 to <70	7 200	No	–
Pollock	Biomass predator	<20, >20 to <50, >50 to <80, >80	12 600	No	–
White hake	Biomass predator	<20, >20 to <40, >40	17 400	No	–
Northern goosefish	Biomass predator	<30, >30 to <60, >60 to <90, >90	3 600	Yes	0–30 cm size class of N & S stocks
Southern goosefish	Biomass predator	<30, >30 to <60, >60 to <90, >90	4 600	Yes	0–30 cm size class of N & S stocks
Northern silver hake	Biomass predator	<20, >20 to <40, >40	15 900	Yes	0–20 cm size class of N & S stocks
Southern silver hake	Biomass predator	<20, >20 to <40, >40	6 500	Yes	0–20 cm size class of N & S stocks
Atlantic herring	Age-structured prey	1–10	883 000	Yes	–
Atlantic mackerel	Age-structured prey	1–7	1 662 000	Yes	–
Butterfish	Other prey	NA	28 600	Yes	All size classes
Shortfin squid	Other prey	NA	22 100	Yes	All size classes
Longfin squid	Other prey	NA	41 200	Yes	All size classes
Other fish	Other prey	NA	383 000	Yes	All size classes
Pelagic invertebrates	Other prey	NA	10 250 000	Yes	Link <i>et al.</i> (2006)
Small benthic invertebrates	Other prey	NA	25 260 000	Yes	Link <i>et al.</i> (2006)
Large benthic invertebrates	Other prey	NA	1 870 000	Yes	Link <i>et al.</i> (2006)

NA, not applicable.

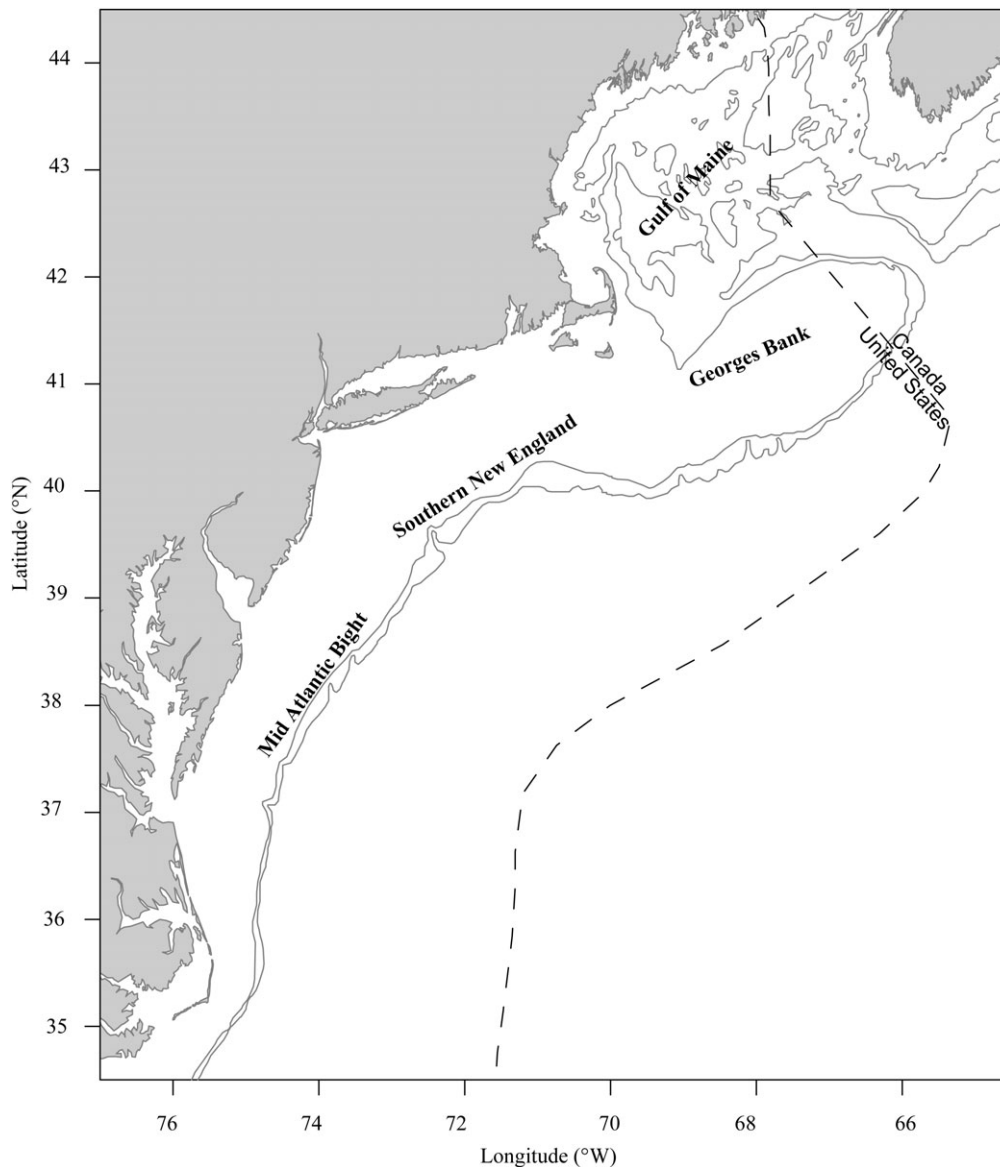


Figure 1. Map of the NEUS continental shelf ecosystem.

the convention for their recent stock assessments. Each stock was put into the model as a separate predator. Five species/stocks had age-structured data available from the latest stock assessment, so their population dynamics were modelled explicitly. Three of these were predators: summer flounder (*Paralichthys dentatus*), Gulf of Maine cod, and Georges Bank cod. The two age-structured prey species were Atlantic herring and Atlantic mackerel. In all, 11 species/stocks were included in the model as biomass predators (Table 1), because their predatory removals of the prey species were important but their most recent stock assessments did not utilize age-structured data. In addition to the two age-structured prey species, we accounted for predation of nine types of “other prey” (Table 1). These groups were chosen because they were important components of the diet of one or more of the predators.

Predator data

Data inputs required for age-structured species in MSVPA-X were: commercial catch, weight, length, and maturity-at-age. We

obtained all inputs for weight, length, and maturity-at-age from the most recent stock assessments (summer flounder—Terceiro, 2006; Gulf of Maine cod—Mayo and Col, 2006; Georges Bank cod—O’Brien *et al.*, 2006). For all three predators, the availability of weight- and length-at-age data was variable through time. For maturity, summer flounder had fixed values through time, but both cod stocks had variable maturity-at-age inputs.

Data inputs for the biomass predators were maximum and minimum sizes, annual biomass, and the portion of biomass in different size classes. Biomass estimates were obtained from the Northeast Fisheries Science Center (NEFSC) bottom-trawl survey. Annual biomass estimates were calculated using an estimate of minimum swept-area for the entire trawl survey region, from Cape Hatteras to the Scotian Shelf. Further details about the bottom-trawl survey design and its protocols are provided by Azarovitz (1981) and NEFC (1988).

Both age-structured and biomass predators also required further data inputs to calculate predator consumption: evacuation

rate parameters, the ratio of stomach contents to predator body weight, prey size selection parameters, ranked prey type preferences, and spatial overlap between predators and prey. For this modelling application, all values of spatial overlap were set to 1, assuming complete overlap between predators and prey.

Evacuation rate, E , is a component of the MSVPA-X consumption equation and a function of temperature (Eggers, 1977; Elliott and Persson, 1978):

$$E = \alpha e^{\beta T}, \quad (1)$$

where T is the average seasonal temperature in each year and α and β the empirically derived parameters based on laboratory and field experiments. We used 0.04 for α and 0.115 for β , values similar to those utilized by Tsou and Collie (2001b). To evaluate how changes in α influence model outcomes, we executed an analysis of the sensitivity of herring and mackerel predation mortality rates to 10 and 25% changes in the evacuation rate, α , of the five most important predators.

The consumption equation in MSVPA-X includes a modified Holling Type III functional response (Garrison and Link, 2004) to avoid the depensatory dynamics of the Type II functional response (Magnusson, 1995). Average stomach contents across years, SC , for predator i , age class a , in season s , are input to the model. To modify the feeding rate of predators in response to changing prey availability, a logarithmic relationship between total suitable prey biomass, SB , and the amount of prey consumed by a predator is implemented in MSVPA-X as

$$SC_{ys}^{ia} = \overline{SC_s^{ia}} + \log\left(\frac{SB_{ys}^{ia}}{\overline{SB_s^{ia}}}\right) SC_s^{ia}. \quad (2)$$

For more details on the MSVPA-X approach to feeding, see Garrison and Link (2004). The NEFSC food habits database was used to examine predator species and size preferences, and diet compositions, and to calculate seasonal values for the stomach weight of each predator relative to its body weight. A detailed description of the food habits database and sampling protocols is given in Link and Almeida (2000).

MSVPA-X requires two parameters for the size-selectivity components of the consumption equation. To approximate the size selectivity of predators selecting their prey, MSVPA-X uses a flexible unimodal function, the incomplete beta integral, to model the ratio of predator to prey body lengths (Garrison and Link, 2004). The size selectivity a and b values, the two derived parameters of the incomplete beta function, were found by maximizing the log-likelihood between the observed frequencies of prey/predator body lengths in the stomachs with expected values. These are estimated before the execution of the MSVPA model run as part of the MSVPA-X package (Garrison and Link, 2004).

Electivity-based prey type preference rankings were calculated as the ratio of the weight of a food item in the predator's stomach to its availability in the environment (Ivlev, 1961; Manly *et al.*, 1993). In all, 13 prey types were ranked, including the nine "other prey" types and four of the five age-structured species (the two cod stocks were combined for preference rankings). For four of the age-structured stocks, small size classes of goosfish and silver hake were also included as prey species. We used the average biomass from 1982 to 2002 for the extra small and small size (Table 1) classes from the spring and autumn

NEFSC annual bottom-trawl survey as a basis for their available biomass as prey. For shortfin squid (*Illex illecebrosus*), longfin squid (*Loligo pealeii*), butterfish (*Peprilus triacanthus*), and other fish, the average biomass from 1982 to 2002 for all size classes from the NEFSC trawl surveys was calculated. Biomass estimates for the other groups of invertebrate prey were obtained from a recent energy budget analysis for the northeast shelf ecosystem (Link *et al.*, 2006).

Prey data

For herring and mackerel, size- and maturity-at-age data were fixed for the study time frame; catch- and weight-at-age were variable through time and were obtained from Northeast Fisheries Science Center Reference Documents (herring—Overholtz *et al.*, 2004; mackerel—NEFSC, 2006a).

Data inputs for the category other prey included annual seasonal biomass, minimum and maximum lengths, and size structure parameter values from the beta function. Values for the size structure were obtained in a similar manner as the predator size selectivity values, by maximizing the log-likelihood between expected (based on stomach contents data) and observed values from the beta function. For longfin squid, shortfin squid, butterfish, and other fish, we used the NEFSC survey database to obtain the annual seasonal biomass, the distribution of biomass by size category, and the maximum and minimum sizes. For small benthic invertebrates, large benthic invertebrates, and pelagic invertebrates, we obtained biomass estimates from a recent energy budget analysis for the NEUS Continental shelf ecosystem (Link *et al.*, 2006). We approximated the size distributions and maximum and minimum sizes for these three prey types based on our knowledge of the NEUS ecosystem.

SS virtual population analyses

The MSVPA-X approach offers four SS virtual population analysis (SSVPA) options. Extended survivors analysis (XSA) is a tuned VPA developed by Shepherd (1999) that is conceptually similar to the ADAPT VPA used for the stock assessments of all age-structured species in the model except mackerel and herring. The most recent stock assessments for mackerel and herring utilized an age-structured forward projection model (NEFSC, 2006a; O'Boyle and Overholtz, 2006). The XSA approach constrains estimates of the fishing mortality rates (F) in terminal age classes and years using a method termed "shrinkage to the mean F ". For all age-structured species, we examined the sensitivity of various configurations of XSA to the estimates of fishing mortality rates and population abundances published in the most recent stock assessments. The final XSA configuration yielded similar values of F and abundance to those assessments.

MSVPA implementation

Two 6-month seasons, spring (spring + winter) and autumn (autumn + summer), were utilized for this MSVPA application. Data inputs that were resolved seasonally were: relative stomach weights of all predators, biomass of other prey and biomass predators, and seasonal bottom temperatures for the NEUS shelf calculated using Holzwarth and Mountain's method (1992) to interpolate temperatures between trawl stations. Following Gislason and Helgason (1985) and Daan (1987), residual natural mortality M_1 (for instance through disease, senescence, or starvation) rates for herring and mackerel were set at 0.1 to implement the MSVPA.

Biological reference points

We followed Overholtz *et al.* (2008) in using the Fox (1975) surplus production model to calculate maximum sustainable yield (MSY) reference points for herring and mackerel. The Fox model can be written as (Quinn and Deriso, 1999)

$$S = -\exp \text{MSY} \frac{B}{k} \ln \left(\frac{B}{k} \right), \quad (3)$$

where S is the surplus production, B the biomass estimated by the model, and k the carrying capacity. The only two parameters that need to be estimated by the Fox model are MSY and k . Under the Fox model, biomass at MSY, $B_{\text{MSY}} = k \cdot 0.368$, and fishing mortality at MSY, $F_{\text{MSY}} = \text{MSY}/B_{\text{MSY}}$. Biological reference points in an SS context were generated using inputs from the SSVPA (abundance converted to biomass), but for the multispecies biological reference points, we used estimates for herring and mackerel from MSVPA.

Model outputs

The outputs from an MSVPA encompass a wide range of information, but in keeping with our original objectives, we present results focused on herring and mackerel.

Abundance estimates produced by MSVPA-X and SS methods for various age classes and total abundance were compared over time for both herring and mackerel. Temporal variation in predation mortality (M_2) for young ages of herring and mackerel derived from MSVPA was also compared with the standard total natural mortality estimate for SS models.

The most important predators for each age class of herring and mackerel were identified by calculating the average predation mortality from 1982 to 2002 attributable to each predator. We summed these predation mortalities over all age classes of prey and ranked the importance of each predator based on these sums (data not shown). The annual consumption by these five most important predators on their major prey types is presented.

The annual biomasses of herring and mackerel in the youngest age classes were calculated and compared with the average predation mortality experienced by young prey. A comparison of the relative magnitudes of predation and fishing mortality for each age class of herring and mackerel was also executed. In addition, we compared the annual fishing mortality for fully recruited age classes with the biomass of those age classes.

The magnitude of consumption was compared with commercial fisheries landings for each year in the model. Landings for herring were obtained from Overholtz *et al.* (2004) and for mackerel from NEFSC (2006a). MSY calculated in an SS context was compared with the sum of landings plus consumption for each age-structured prey species. The ratio of MSVPA vs. SSVPA biological reference points was also calculated.

Results

MSVPA vs. SS abundance and predation mortality

MSVPA produced markedly higher abundance-at-age estimates than SSVPA, and the difference was especially notable for the youngest age classes of herring and mackerel (Figure 2). When the abundance of fully recruited age classes of each species was examined through time, MSVPA produced consistently higher estimates for both herring and mackerel (Figure 3). The trends in abundance of fully recruited herring and mackerel were also similar between MSVPA and SSVPA.

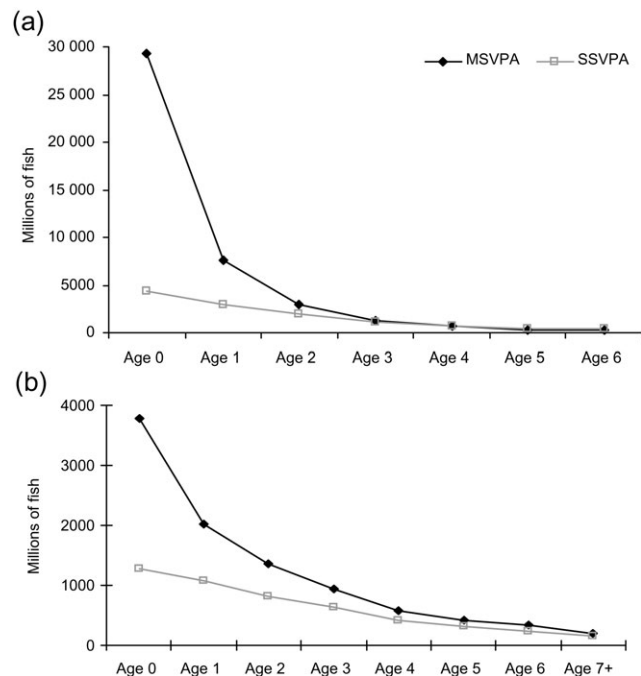


Figure 2. Estimates of abundance-at-age produced by MSVPA and SSVPA (XSA) averaged over the period 1982–2002 for (a) herring and (b) mackerel.

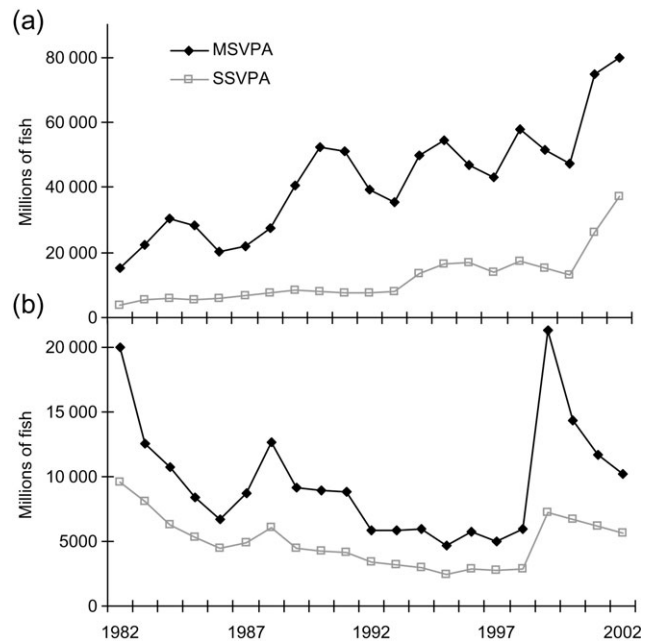


Figure 3. Abundance estimates derived from SSVPA (XSA) and MSVPA, 1982–2002, for (a) herring and (b) mackerel.

Figure 4 is a comparison of the temporal variability in predation mortality for herring and mackerel aged 0 and 1 plotted against the time-age invariant standard total natural mortality rate ($M = 0.2$) used in SSVPA (and more generally other conventional stock assessment models). The average predation mortality rate for herring was more than five times higher than the standard total natural mortality rate and predation mortality combined

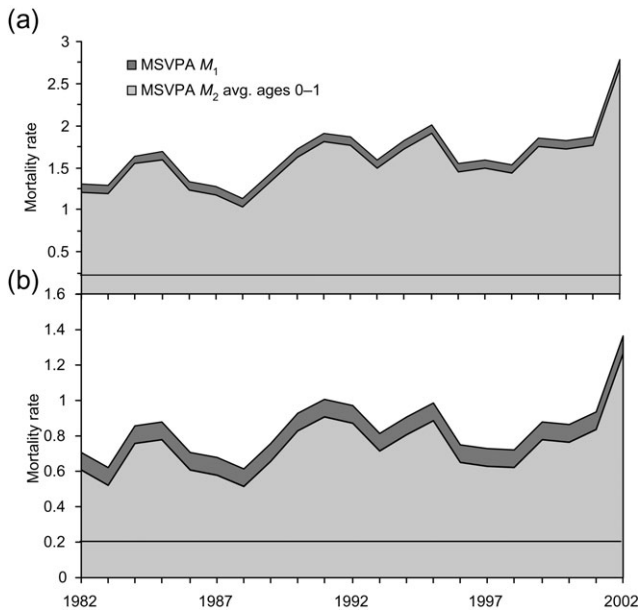


Figure 4. Temporal variability in natural mortality on young age classes of (a) herring and (b) mackerel estimated by MSVPA, and showing the standard total natural mortality (0.2; line on each panel) for traditional SSVPA.

with M_1 , yielding an average total natural mortality rate well over seven times higher than the traditional value of 0.2. For mackerel, predation mortality was lower than that of herring, but the MSVPA average predation mortality rate was still more than three times higher than the traditional 0.2.

Table 2. Average predation mortality (M_2) and percentage change from base-run values when the evacuation rate α was changed by ± 10 and $\pm 25\%$.

Species	Base run	25% decrease		10% decrease		10% increase		25% increase	
	M_2	M_2	% change	M_2	% change	M_2	% change	M_2	% change
Herring	0.80	0.64	-20.3	0.74	-7.7	0.91	14.3	0.97	21.6
Mackerel	0.36	0.28	-22.2	0.32	-8.7	0.39	8.9	0.44	22.5

Table 3. Each predator's average annual consumption (as a percentage) of herring, mackerel, and all prey types.

Predator species	% of herring consumed	% of mackerel consumed	% of all prey consumed
Spiny dogfish	54	45	56
Georges Bank cod	3	4	13
Little skate	0	0	6
Gulf of Maine cod	2	1	5
White hake	12	19	4
Northern silver hake	4	7	4
Winter skate	4	6	3
Summer flounder	7	0	3
Pollock	2	5	1
Southern silver hake	3	4	1
Southern goosefish	4	7	1
Sea raven	1	0	1
Northern goosefish	5	2	1
Fourspot flounder	0	0	1
Average annual consumption (t)	401 234	141 628	

Predation mortalities for the two youngest age classes of mackerel were consistently lower than those of the corresponding herring age classes in the same year (Figure 4). In the last five years of the model, the average predation mortality for herring aged 0 and 1 was more than two times higher than for mackerel. The average predation mortality for herring aged 0 and 1 from 1982 to 2002 was 1.57, whereas for mackerel it was 0.74. The sensitivity analyses of the evacuation rate α produced changes in predation mortality that were proportional to the changes in that input parameter (Table 2). Therefore, the results are largely reflective of patterns in predator consumption.

Important predators of herring and mackerel

When the total consumptive removal of all 13 prey types was considered, spiny dogfish was the most important predator in the model (Table 3). Elasmobranchs in general had high consumptive removals; aside from spiny dogfish, little skate (*Leucoraja erinacea*) had the third highest total annual consumption, and winter skate (*Leucoraja ocellata*) had the seventh highest consumption (Table 3).

For herring, the most important predators in descending order were spiny dogfish, white hake, summer flounder, northern goosefish, and southern goosefish. For mackerel, the five most important predators were spiny dogfish, white hake, southern goosefish, northern silver hake, and winter skate. When the average predation mortalities for herring and mackerel by each predator were summed, the five most important predators for herring and mackerel combined were spiny dogfish, white hake, northern silver hake, winter skate, and southern goosefish. These five predators accounted for 79% of all herring and 84% of all mackerel consumed (Table 3). Importantly, all five most important predators of herring and mackerel were input to the model as biomass predators.

For the five most important predators, there was high annual variability in the total amount of food consumed; this was especially apparent for prey (e.g. pelagic and small benthic invertebrates in addition to herring) that experienced the highest biomass loss (Figure 5). The biomass consumed by spiny dogfish was substantially higher than that of the other predators, even among the top five most important predators. For example, over the 21-year time frame, spiny dogfish consumed 4.5 million tonnes of herring and 1.3 million tonnes of mackerel, and white hake consumption was substantially less, at a million tonnes of herring and 568 000 t of mackerel.

Herring, and to a lesser extent mackerel, generally became increasingly important in the diets of the top five predators through time (Figure 5). Additionally, for spiny dogfish, white hake, winter skate, and southern goosefish, peak consumption of herring coincided with peak biomass of ages 0 and 1 of the species. For mackerel, the timing of maximum consumption by

spiny dogfish, northern silver hake, and southern goosefish corresponded to maximum biomass of ages 0 and 1 of mackerel.

Overall average annual consumption of all prey types by the 14 predators exceeded 10 million tonnes. The five most important predators accounted for 68% of the average annual consumption. Average annual consumption by these five predators on prey groups that support commercial fisheries (all prey types except small and large benthic invertebrates, pelagic invertebrates, and unspecified other fish) was >500 000 t.

Mortality over time and ontogeny

The relationships between predation mortality and biomass of young age classes were similar for the two age-structured fish prey species. The biomass of herring aged 0 and 1 peaked later in the time-series (Figure 6), but fluctuations in the biomass of those age classes increased dramatically in 1995 and continued to vary, with a generally increasing trend, until 2002. The fluctuations in the predation

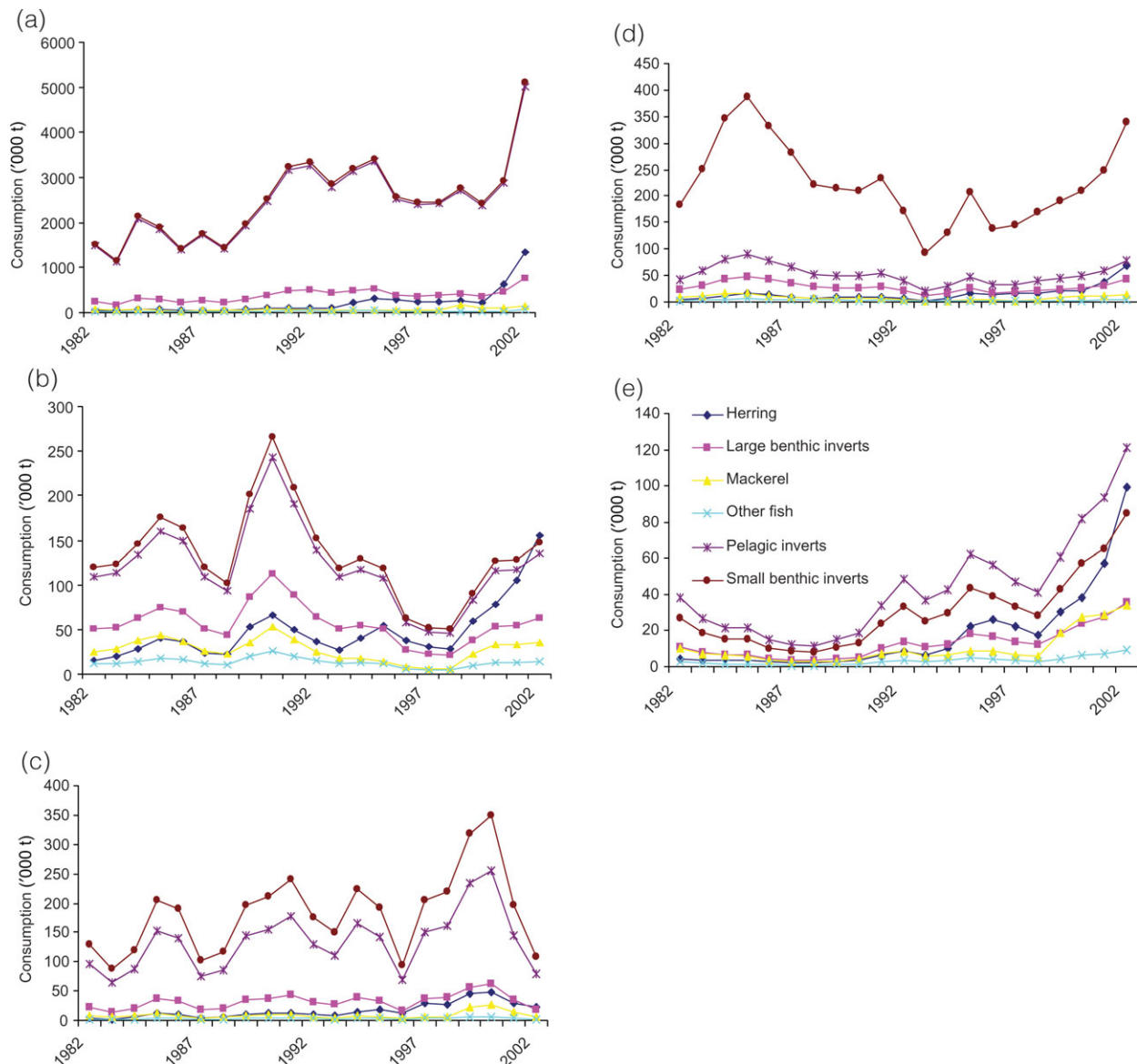


Figure 5. Annual biomass of prey types consumed by (a) spiny dogfish, (b) northern silver hake, (c) winter skate, (d) northern goosefish, and (e) white hake.

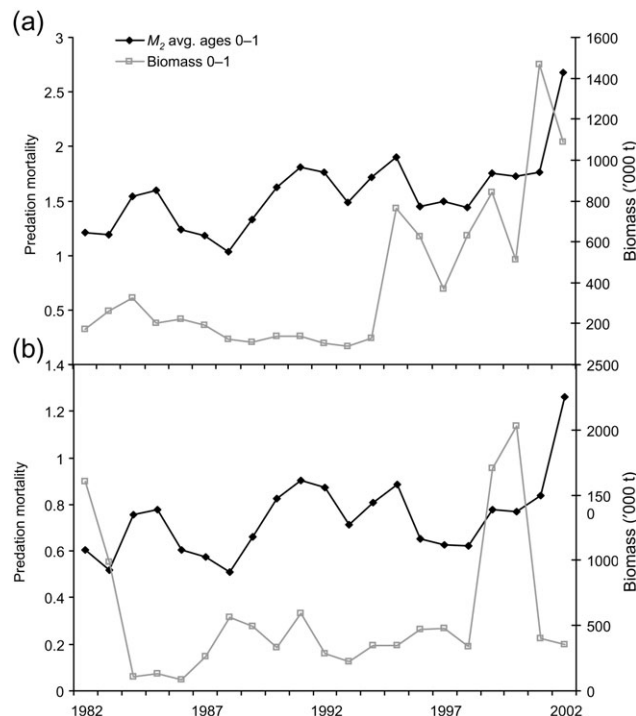


Figure 6. Comparison of the relationship between predation mortality (M_2) and the biomass of young (a) herring and (b) mackerel, 1982–2002.

mortality of young herring generally coincided with the fluctuations in the pattern, but not the magnitude, of biomass of the same age classes for the years 1995–2002. The biomass fluctuations of mackerel aged 0 and 1 were similar to those of herring, with biomass peaking in 1999 and 2000, but then declining notably. Throughout the time-series, there was relatively good correspondence between the biomass of young mackerel and its predation mortality.

A comparison of the relative importance of fishing and predation mortality over ontogeny for herring and mackerel showed that predation mortality declined with increasing age, and for both species this decline was especially pronounced between ages 0 and 1 (Figure 7). For both herring and mackerel older than 3 years, F remained relatively constant. Herring recruit to the fishery at age 2, but before that experience peak rates of F while they are still subject to relatively high predation mortality. For herring 5+ years old, the average level of F was greater than that of predation mortality. Mackerel experienced substantially less predation and fishing mortality than herring, so predation mortality values exceeded F for every age class. Starting at age 1, mackerel predation mortality was approximately two times lower than that of the corresponding age class of herring, until age 5. Mackerel fishing and predation mortalities stabilized to low and relatively consistent levels for every age class after age 3.

For fully recruited age classes, the relationship between F and biomass was inconsistent for both herring and mackerel. From 1983 to 1991, herring fishing mortality as estimated by MSVPA was variable, with an average across ages 2–6 of 0.45 (Figure 8). Since 1992, F on herring has generally declined, and in the final 6 years of the model, average F was 0.23. In contrast, the biomass of the same age classes of herring was relatively constant from 1982 to 1994, but then increased at the time when F was stabilizing. The magnitude of F for mackerel was much lower than for

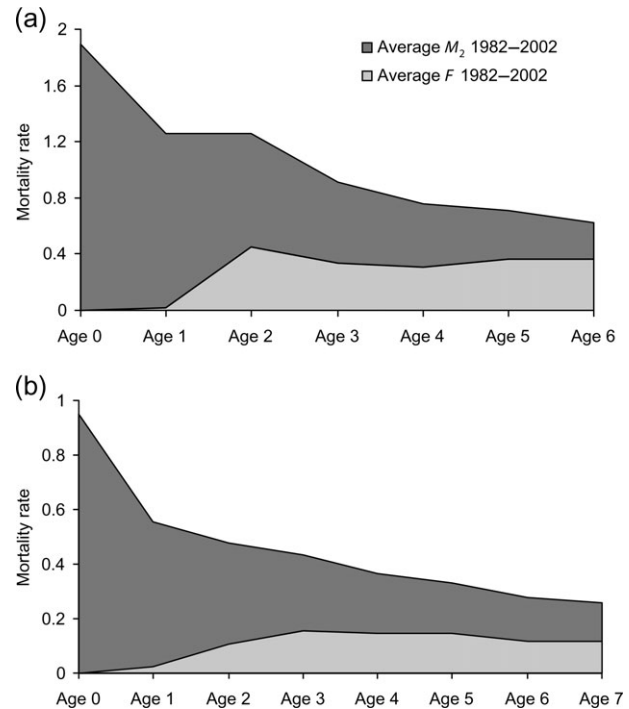


Figure 7. Stacked area graph of average fishing and predation mortality by age class for (a) herring and (b) mackerel, averaged over the period 1982–2002.

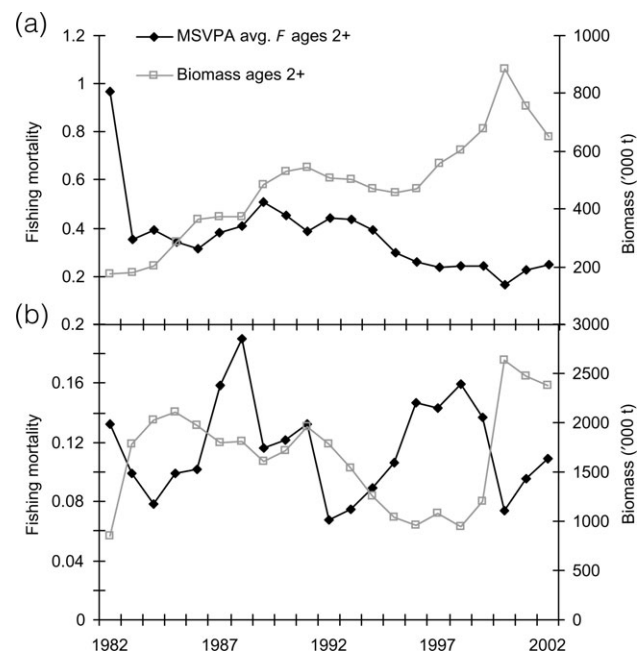


Figure 8. Average fishing mortality and biomass for fully recruited fish, 1982–2002: (a) herring and (b) mackerel.

herring. The MSVPA estimate of mackerel F peaked in 1988 at 0.19. Similar to herring, however, there appears little temporal concordance between fishing mortality and the biomass of mackerel's susceptible age classes.

The annual average biomass consumed by the 14 predators in the 21-year model time frame was some 3–5 times higher than the

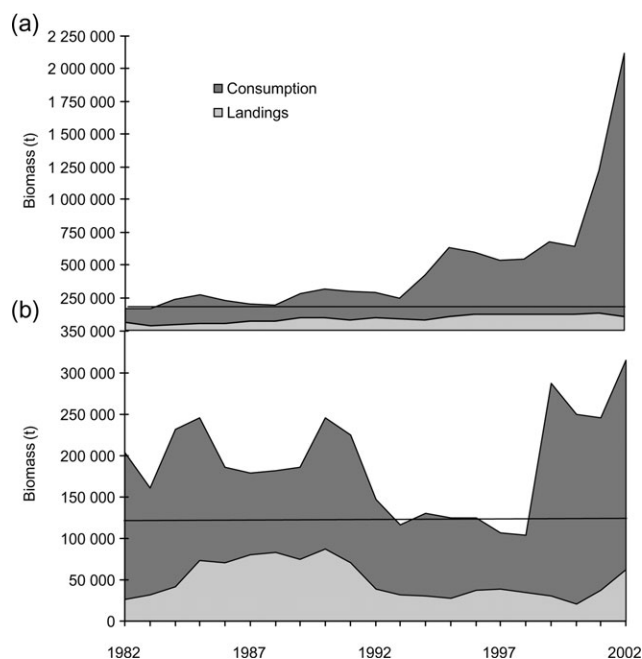


Figure 9. Landings and total consumption by all predators in the model of (a) herring and (b) mackerel. The horizontal line indicates the MSY calculated in an SS context.

average annual landings of herring and mackerel (Figure 9). In every year, the consumption of each age-structured prey species exceeded the landings of that species. The total consumption of herring by demersal fish generally increased through time, and landings also increased, but to a lesser degree. For mackerel, both fisheries landings and consumption by all predators were highly variable through time, but with an increase in recent years. Despite the increase in the mackerel consumed from 1999 to 2002, the coefficient of variation between years in the total herring biomass consumed (108%) was more than twice as high as for mackerel (42%). For herring, the interannual variation in the biomass landed was substantially less than the variation in the amount consumed.

As would be expected, the MSY for herring in a SS context was lower than the MSY calculated using multispecies biomass considerations (Table 4). Similarly, the mackerel SS MSY was also lower than the MSY calculated in a multispecies context (Table 4). These results were expected because there is less mortality in the SS model, implying that prior (backward) estimates of biomass and abundance would be lower than if a greater mortality had been accounted for, as in the multispecies model. Therefore, the multispecies model predicted that there had been more fish than in the SS model, and calculations of these reference points are conditioned on that observation.

The trends in B_{MSY} for both prey species were also similar. The values of F_{MSY} for both species were comparable (not shown) in an SS and a multispecies context, but would need to be further

partitioned to account for fishing and predation in the multispecies version (*sensu* Overholtz *et al.*, 2008).

Discussion

The results from this MSVPA of the NEUS fish community demonstrate that predation mortality for herring and mackerel was variable over time and that the youngest age classes experienced the highest rates of predation mortality. That the MSVPA produced higher rates of predation mortality and abundance estimates for young herring and mackerel than SS techniques is supported by applications of MSVPA for other ecosystems, including Daan (1987) for six species in the North Sea, Sparholt (1994) for three species in the Baltic Sea, Livingston and Jurado-Molina (2000) for walleye pollock (*Theragra chalcogramma*) in the Bering Sea, NEFSC (2006b) for menhaden (*Brevoortia tyrannus*) on the US Atlantic coast, and Tsou and Collie (2001a) for five species on Georges Bank. Our results should be evaluated strictly for the demonstrative value of incorporating multispecies considerations in age-structured abundance estimates of forage species. In addition, the time-series for this MSVPA is shorter than those of the recent formal stock assessments of herring and mackerel. Therefore, these MSVPA results should not be considered as alternative stock assessments for either herring or mackerel, but rather for their heuristic value of explicitly formulating predation mortality estimates. The dynamic predation mortality rates for these forage species in this MSVPA context when compared with the standard value of 0.2 used in SSVPA illustrate the utility of examining predation mortality individually for each forage species.

Several different MSVPAs that have examined herring and mackerel predation mortality produced similar estimates to ours, but not without differences between various MSVPA applications. For example, Tsou and Collie's (2001b) MSVPA of the Georges Bank fish community estimated mackerel predation mortality as <0.05 for all age classes. We obtained similar, but slightly higher results for just older age classes of mackerel. Gislason and Helgason's (1985) estimates of herring predation mortality were similar to ours for ages 1 and older, but for mackerel, our estimates of predation mortality for ages 2 and older were similar but slightly higher than theirs. Daan's (1987) age 0 and 1 herring predation mortalities for the North Sea were similar to, though slightly higher than, our corresponding estimates. Finally, Sparholt's (1994) trend of decreasing predation mortalities with age for herring in Subdivision 25–27 of the Baltic Sea was similar to ours, and the discrepancy between our estimates and his for corresponding age classes steadily declined with increasing age classes.

In our MSVPA, herring were more affected by both predation and fishing mortality than mackerel. Herring were preferred over mackerel by almost every predator in the model, but the biomass of herring was much lower than that of mackerel, so predation mortality rates were higher than for mackerel. Tsou and Collie's (2001b) Georges Bank MSVPA also reported lower predation mortality estimates for all age classes of mackerel than for herring. Similarly, Overholtz *et al.* (1999) found that mackerel were less important in the diets of piscivorous fish than herring. Mackerel reach larger maximum size at a faster growth rate than herring (Wigley *et al.*, 2003), which may allow them to reach sizes less vulnerable to predation more quickly than herring.

The results from this MSVPA highlight the importance of the relationship between elasmobranchs, particularly spiny dogfish, and these two forage prey species. Spiny dogfish population fluctuations and consumption strongly influenced herring and mackerel

Table 4. Ratio of multispecies (fishing and predation) to SS reference points (fishing only) for the two main prey species.

Species	MSY	B_{MSY}
Herring	1.38	1.25
Mackerel	1.11	1.57

population dynamics. The spiny dogfish assessment shows a trend of increasing overall biomass since 2000, and although there are very few spiny dogfish recruits (NEFSC, 2006c), the abundance of young pelagic fish could be expected to continue to be impacted through predation by large spiny dogfish and other predators. Factors that could contribute to the strong influence of elasmobranch consumption on predation mortality include: (i) the average biomass of spiny dogfish, little skate, and winter skate, which were respectively the first, third, and fourth highest of all the predators in the model (Table 1); and (ii) the elasmobranchs, especially spiny dogfish and winter skate, were some of the largest predators and therefore were able to consume a wider size range of prey. Link *et al.* (2002) also found that piscivory by elasmobranchs was concentrated on pelagic fish such as herring and mackerel rather than on groundfish. The switch in biomass dominance from demersal groundfish to piscivorous elasmobranchs in the NEUS (Fogarty and Murawski, 1998; Garrison and Link, 2000; Link and Garrison, 2002; Overholtz and Link, 2007) indicates greater rates of predation mortality on a wider range of age classes of pelagic fish as the biomass of larger predators such as spiny dogfish increases. Our results contrast with those of Tsou and Collie (2001b), who found that silver hake was the most important herring predator in the Georges Bank fish community, although they also found that predation by elasmobranchs on fish became more important in the early 1990s. There have been a wide range and changing group of small pelagic predators, with recent population increases of some predators contributing to changes in the value of M_2 for these pelagic fish prey.

The results from this and other MSVPAs lead to a refined understanding of the effects of predator stock-rebuilding efforts on total prey biomass, and importantly, the specific age classes of prey that are most strongly affected by these actions. Predation disproportionately affects the smallest size classes of fish (Sissenwine, 1986; Sparholt, 1991; Overholtz *et al.*, 1999; Livingston and Jurado-Molina, 2000; Tsou and Collie, 2001b; this study), so for many species, recruitment will likely be underestimated by assessments that use an age-class-invariant rate of natural mortality. That MSVPAs emphasize age 0 and 1 prey, whereas SSVPA often neglect age 0 groups (prerecruits), is important, and distinguishes the outputs of MSVPAs. MSVPA quantification of predation against fishing mortality for each age class permits improved predictions of how various age classes will be depleted through time. In addition to the predator type preferences, the high rates of predation on the youngest herring in this MSVPA may be due to their smaller size than mackerel.

Our calculations were affected by factors that may have led to both underestimation and overestimation of herring and mackerel predation mortality for this period. A factor that may have led to slightly higher rates of predation mortality for some of our predators was that spatial overlap for all our predators and prey was set to 1. Portions of herring and mackerel populations have distinct seasonal migration patterns. Various methods have been unsuccessful in discriminating between the major spawning contingents of mackerel (Studholme *et al.*, 1999) and herring (Reid *et al.*, 1999), so both species are currently assessed as unit stocks. As more information about the seasonal spatial distribution of different portions of the herring and mackerel populations becomes available, the predators' spatial overlap with these two prey species could be refined.

Our model parameterization included several factors that may have led to over- or underestimates of predation mortality. For

example, although the evacuation rate parameters we used were similar to others from this region (Durbin *et al.*, 1983; Tsou and Collie, 2001b) and our sensitivity results showed a proportional response, the use of different values could alter the results (linearly proportional, positively, or negatively). Moreover, our method of calculating abundance using a minimum swept-area estimate may have led to conservative estimates of abundance for some important predator species. Catchability estimates vary widely for species such as spiny dogfish (Edwards, 1968; NEFSC, 2006b). Because of the discrepancies in catchability estimates from different studies and the fact that they were not available for all species, we chose to use an abundance calculation method that was likely conservative for many predators (Harley and Myers, 2001). Additionally, predation by marine mammals was not included in this study, which may have led to an underestimate of predation mortality for both herring (Overholtz and Link, 2007) and mackerel (Overholtz *et al.*, 1991). Hence, we stress that the results of this study are only preliminary estimates for the impact of demersal fish predation on herring and mackerel, so future applications of the model might explore the feasibility of incorporating enhancements to these caveats.

Predation is an important influence on forage species abundance in the NEUS (Sissenwine, 1986; Overholtz *et al.*, 1999, 2008; Tsou and Collie, 2001a, b), and the fact that consumption exceeded landings of herring and mackerel shows that predator consumption rates and diet composition have had increasingly stronger influences on the population dynamics of these species than commercial fisheries. Elasmobranch biomass has been increasing since the low levels of the mid-1990s (NEFSC, 2006c, 2007) and the quantity of herring and mackerel consumed could continue to exceed commercial fisheries landings if the trend of augmented abundance of these demersal fish predators continues. Both herring (Overholtz *et al.*, 2004) and mackerel (NEFSC, 2006a) stocks were above their SS reference point thresholds in their most recent assessments, and both appear to be in continued recovery from their historically low abundances in the mid- to late 1970s (Overholtz *et al.*, 2000). Continued investigation of the interactions of forage species with their predators is warranted, to provide improved information regarding the effects of different management scenarios on predator and prey population dynamics.

Some of the distinctive features of MSVPA-X, particularly those that affect consumption estimates, had important contributions to the results of this MSVPA of the NEUS. For example, the importance of the allowance in MSVPA-X for biomass predators in addition to age-structured predators is underscored by the fact that the five dominant predators all lacked age-structured data in their latest stock assessments, so were input to the model as biomass predators. Our empirically derived abundance estimates for nine other prey types in addition to the two age-structured prey species resulted in more accurate estimates of the relative availability of a diverse array of prey types for this MSVPA application than previous analyses. The feature of MSVPA-X in allowing for predator diet compositions to adjust in response to changes in prey population sizes (confirmed in our food habits data; Link and Almeida, 2000) contributed to the high interannual variability in the quantity of each prey type consumed by each predator. All these features of MSVPA-X, in combination with the more precise formulation of prey availability, contribute to the utility of this application in estimating rates of predation mortality for herring and mackerel in the NEUS.

Although they have larger and more complex data requirements, multispecies models are a substantial improvement over SS models because they help quantify the trade-offs between predator and prey biomass (Gislason, 1999). MSVPA has been demonstrated to be a reliable method for quantifying how the population dynamics of predators, in addition to the availability of other food, affects the abundance of forage species. Incorporating these temporally varying factors into population assessment models of species that are especially susceptible to predation is difficult without access to substantial amounts of data regarding prey consumption by predators, the age-structure of prey populations, and the age or size structure of predator populations. Nevertheless, the accumulation of MSVPAs for diverse ecosystems (e.g. Gislason and Helgason, 1985; Daan, 1987; Sparholt, 1991; Livingston and Jurado-Molina, 2000; Tsou and Collie, 2001a, b; Vinther, 2001; NEFSC, 2006b) suggest that these efforts are worthwhile and helpful for improving the ecological realism of fisheries population assessments.

Fish consumption of commercially valuable prey species is an important removal that should be considered. Bax (1991, 1998) noted that piscivory is high on Georges Bank compared with other ecosystems, and several other studies conducted for the larger NEUS ecosystem (Overholtz *et al.*, 1999; Link *et al.*, 2006; Overholtz and Link, 2007) have demonstrated that piscivory is one of the more important ecological interactions in the region. Accounting for shifts in species composition, size structure, and the distribution of predator biomass are important considerations for ecosystem-based fisheries management. As we have demonstrated here for the NEUS, these types of considerations for piscivorous fish are especially influential for herring. Although quantification of predation mortality is an important contribution from MSVPA, it is only one of many factors, e.g. competition, environmental effects, physical disturbance, to be considered in implementing ecosystem-based fisheries management. Nevertheless, we assert that time- and age-varying predation mortalities can be incorporated into stock assessments while improvements to MSVPA and other multispecies and ecosystem models are made.

Acknowledgements

We thank the present and past members of the Food Web Dynamics Program (NMFS NEFSC) for maintaining the database that supported this work. The content of this paper benefited from comments provided by K. Curti, M. Fogarty, M. Terceiro, and three anonymous referees. The work was supported by Lenfest Ocean Program Grant Number 2004-001492-105.

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doi:10.1093/icesjms/fsn185