The advantage of explicitly incorporating predation mortality into age-structured stock assessment models: an application for Atlantic mackerel

H. Moustahfid, J. S. Link, W. J. Overholtz, and M. C. Tyrrell

An age-structured assessment programme (ASAP) that explicitly incorporates predation mortality was applied to Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic. Predatory removals were modelled in the same manner as fishing mortality, with a comparable set of time-series, to produce estimates of predation mortality at age and for each year. Results from the analysis showed that incorporating predation into a mackerel stock assessment model notably altered model outputs. When excluding explicitly modelled rates of predation, the model underestimated the magnitude and uncertainty in spawning-stock biomass (SSB) and recruitment. Further, the rates of predation mortality varied across time and were higher for younger fish. Predation mortality was higher than fishing mortality for fish aged 1 year, approximately equal for 2-year-olds, and lower for older fish (3 years and older). Biological reference points for Atlantic mackerel differed considerably when predation mortality was included. For example, SSB_{MSY} was more than twice as high in the model where predation was incorporated than in the fisheries-only model. Although there are several caveats to the predation model outputs, chief of which is that the estimates are conservative because some mackerel predators were excluded, the results demonstrate the feasibility of executing such an approach with an extant tool. The approach presented here ultimately has the advantage of detecting, and upon detection parsing out, the impact of predators relative to fisheries and has the potential to provide useful information to those interested in small pelagic fish and their associated fisheries.

Keywords: age structure, assessment model, biological reference points, Georges Bank, Gulf of Maine, predation mortality, *Scomber scombrus*.

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Introduction

To achieve long-term sustainability in marine fisheries systems, stock assessment scientists need to begin to account for ecosystem considerations (Link, 2002). There has been an increasing interest in accounting for biological interactions (such as predation) via multispecies models (e.g. Sparre, 1991; Livingston and Jurado-Molina, 2000; Tsou and Collie, 2001; Jurado-Molina and Livingston, 2002), or extended single-species stock assessment models (e.g. Livingston and Methot, 1998; Hollowed *et al.*, 2000; Tjelmeland and Lindstrøm, 2005; Overholtz *et al.*, 2008). The ultimate motivation for developing such approaches is to provide more refined and appropriate advice for fisheries management. The results of studies that have incorporated predation into single-species models suggest that traditional stock assessments which assume constant natural mortality generally underestimate the uncertainty in stock biomass (Hollowed *et al.*, 2000), and provide biological reference points, i.e. maximum sustainable yield (MSY), that may be ecologically optimistic and too high (Overholtz *et al.*, 2008).

Atlantic mackerel (*Scomber scombrus*) plays a prominent role in both the fisheries and foodweb of the Northwest Atlantic (Overholtz *et al.*, 1991a, b). It was subject to intense fisheries during the 1970s by foreign and domestic (US) fleets. Total annual landings averaged 350 000 t during the years 1970–1976, but this level was not sustainable and the resource declined (NEFSC, 1996, 1998, 2006). The stock recovered by the mid-1990s (NEFSC, 1998, 2006) because of reduced fishing effort, a bigger spawning stock, and strong recruitment (Overholtz *et al.*, 2000). Mackerel is an important forage species for medium-sized predatory fish such as spiny dogfish (*Squalus acanthias*), silver hake (*Merluccius bilinearis*) and white hake (*Urophycis tenuis*; Link and Almeida, 2000), and is also a common prey of many dolphins, whales, seals, sharks, tunas, billfish, and seabirds in the region (Smith and Gaskin, 1974; Payne and Selzer, 1983; Overholtz and Waring, 1991).

Predation mortality has not usually been accounted for in past and recent assessments of the Atlantic mackerel stock (NEFSC, 1996, 2000, 2006). Natural mortality (M) has also been assumed to be constant over time and ontogeny ($M = 0.2$). Earlier studies suggested that predation likely has a major influence on the dynamics of the species, and that predation mortality is probably the largest component of natural mortality on the stock (Overholtz *et al.*, 1991b). Explicitly accounting for predation mortality in stock assessments of this pelagic species should provide enhanced estimates of biological reference points, such as biomass (B_{MSY}) required to produce MSY.

The main objectives of this study were to incorporate predation mortality into an age-structured model of Atlantic mackerel, to explore the feasibility of such an approach, and to evaluate potential changes to model estimates and outputs (i.e. estimates of biological reference points) by including predation mortality.

Material and methods

Data sources

Atlantic mackerel are distributed in the Northwest Atlantic from North Carolina to the Gulf of St Lawrence (Figure 1; Sette, 1950; Anderson, 1976; MAFMC, 1994) and are subject to seasonal fisheries, commercial and recreational, throughout most of their range. US commercial landings are taken primarily between January and May in southern New England and Mid-Atlantic coastal waters, and between May and December in the Gulf of Maine. US recreational catches are made mainly between April and October. Canadian commercial landings of the species have typically been taken off Nova Scotia, in the Gulf of St Lawrence, and off Newfoundland between May and November (Clark, 1998). Since 1975, all mackerel in the Northwest Atlantic have been assessed as a unit stock (Anderson, 1982), and they are also considered as a unit stock for management purposes (MAFMC, 1994). Here we follow that convention.

We developed a model for the period 1962–2004, and referenced the most recent peer-reviewed assessment of Atlantic mackerel (NEFSC, 2006) for context, comparison, and many of the model inputs. There were three main data types needed for the model: fishery data, survey indices of mackerel abundance,

and predatory removal of mackerel. Fishery data consisted of total catch [including commercial and recreational landings of mackerel for the USA, Canada, and other countries from Northwest Atlantic Fisheries Organization (NAFO) statistical areas 2–6 during the years 1962–2004], fisheries catch-at-age, and mean weights-at-age. Survey data consisted of spring survey log-transformed abundances for the years 1968–2004. Following the most recent Atlantic mackerel stock assessment, we used age classes 1 through 6, and assigned a plus group for ages 7 and older.

The data required to incorporate predation consisted of total annual consumption-at-age of mackerel by demersal fish. Diet composition data from spring and autumn Northeast Fisheries Science Center (NEFSC) bottom-trawl survey cruises for the years 1977–2004 were examined to identify the most important demersal fish preying on Atlantic mackerel in the Northwest Atlantic. A detailed description of the methods for the NEFSC food habitats programme, sampling and analytical protocols can be found in Link and Almeida (2000). We identified 13 demersal species that consistently prey on Atlantic mackerel (i.e. where mackerel constitute >5% of the diet by weight for most of the time-series): spiny dogfish, silver hake, Atlantic cod (*Gadus morhua*), goosefish (*Lophius americanus*), white hake, spotted hake (*Urophycis regia*), pollock (*Pollachius bilinearis*), bluefish (*Pomatomus saltatrix*), winter skate (*Raja ocellata*), red hake (*Urophycis chuss*), summer flounder (*Paralichthys dentatus*), smooth dogfish (*Mustelus canis*), and sea raven (*Hemitripterus virens*).

Seasonal estimates of predator relative abundance (N) were calculated using swept-area from the bottom-trawl surveys
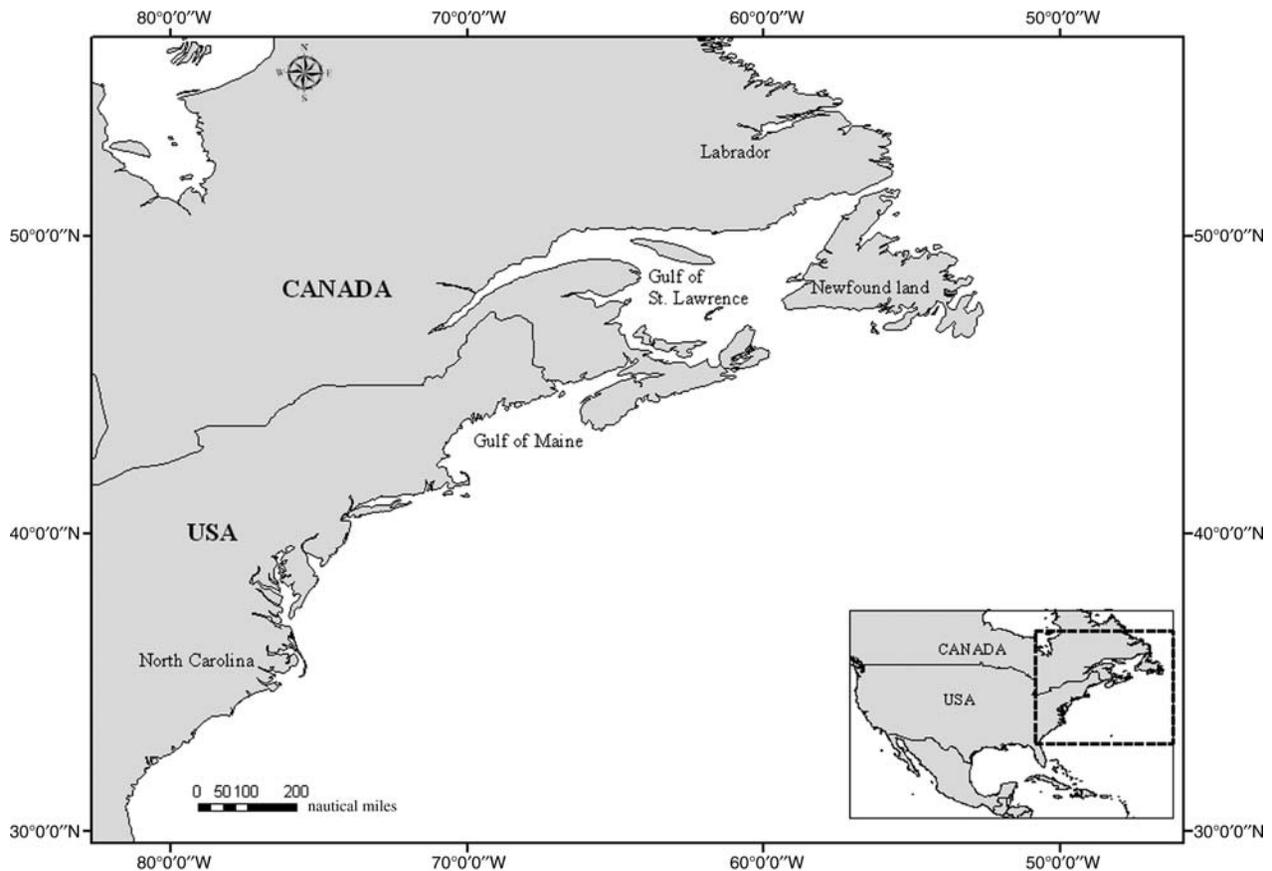
Figure 1. Map of the area inhabited by Atlantic mackerel (*Scomber scombrus*) in the Northwest Atlantic.
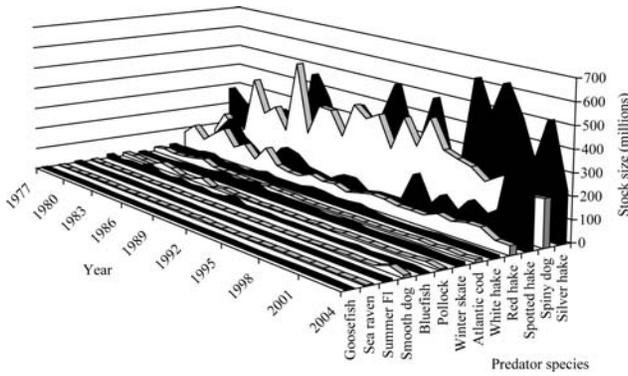
Figure 2. Population sizes (millions) of predatory fish species used to estimate consumption during the period 1977–2004.

(Azarovitz, 1981). All calculations of diet composition, predator abundance, and bottom temperature were based on a half-year basis; autumn survey data were used as a proxy for both autumn and winter, and spring survey data encompassed spring and summer. Abundance estimates for predators were considered conservative because corrections for catchability (q) were not incorporated into the swept-area calculations, although gear corrections were made (Sissenwine and Bowman, 1978). The demersal predators considered in this analysis, especially spiny dogfish, silver hake, and red hake, have relatively large populations in the Northwest Atlantic (Figure 2).

To calculate annual predation of mackerel by demersal fish, we followed the method of estimating evacuation rate used in previous studies (Overholtz *et al.*, 2000; Link *et al.*, 2002; Overholtz and Link, 2007). Diet composition data were aggregated into 5-year time-blocks for all 13 predators except spiny dogfish and silver hake, which were aggregated into 2-year time-blocks. Total daily consumption was based on the average weight of the predator's stomach contents and an hourly gastric evacuation rate (Eggers, 1977; Elliott and Persson, 1978; Pennington, 1985):

$$C_{it} = 24R_{it}\overline{S_{it}^{\gamma}}, \qquad (1)$$

where C_{it} is the daily consumption (g) for each predator species i and period t (season and year), 24 the number of hours in a day, S_{it} the mean stomach content weight (g), γ a shape function assumed to equal 1 (Gerking, 1994), and R_{it} is the evacuation rate. The parameter R_{it} is calculated from

$$R_{it} = \alpha e^{\beta T}, \qquad (2)$$

where α and β are fitted constants, and T the seasonal bottom temperature (°C) obtained from NEFSC bottom-trawl surveys (Holzwarth and Mountain, 1992). The values of α and β were set as 0.004 and 0.115, respectively (Durbin *et al.*, 1983; Overholtz *et al.*, 2000; Overholtz and Link, 2007); such values yield conservative estimates of consumption. Daily consumption estimates were scaled up to half-year estimates by multiplying the number of days in each half year:

$$C'_{it} = C_{it} \times 182.5. \qquad (3)$$

These were then multiplied by seasonal estimates of predator abundance (N) to calculate a total quantity of Atlantic mackerel

removed by each predator species i for each half year:

$$C''_{it} = C'_{it}N_{it}D_{it}, \qquad (4)$$

where D_{it} is each predator's diet composition of mackerel during time t.

Total consumptive removal of mackerel by all 13 predators was then the sum of C''_{it} across all i predators,

$$C_t = \sum_i C''_{it}. \qquad (5)$$

This calculated consumption was apportioned by age using aggregated size compositions of mackerel for all predators (collected from stomach contents of the demersal fish predators) and age–length keys for mackerel (obtained from NEFSC bottom-trawl surveys). Data on food habits were not available before 1977, so consumption-at-age of mackerel for the years 1962–1976 was estimated using a linear relationship between predator biomass and consumption of mackerel from 1977 to 2004 ($r^2 = 0.75$).

Population model

An age-structured assessment programme (ASAP; Legault and Restrepo, 1999) was used to model the dynamics of Atlantic mackerel. The model has been used extensively as an assessment tool for many similar species (e.g. Pacific sardine, *Sardinops sagax*, and Pacific mackerel, *Scomber japonicus*), and recently for Atlantic mackerel (NEFSC, 2006). The general estimation approach used in the ASAP is that of a flexible forward projection that allows for efficient and reliable estimation of a large number of parameters. The population dynamics and statistical foundations of ASAP are well established and follow those of Fournier and Archibald (1982), Deriso *et al.* (1985), Methot (1998), and Ianelli and Fournier (1998).

The ASAP model offers a framework to incorporate predation. In the analysis, predators were considered as a type of fishing fleet and entered into the model via a time-series of consumption-at-age. In this approach, predation mortality is explicitly modelled in the same manner as fishing mortality, with an input selectivity pattern and a multiplier to produce predation mortality-at-age and mortality-per-year.

The population model begins in 1962 with an estimate of the population abundance-at-age. The spawning stock for that year is calculated and the associated recruitment for the next year is determined using a Beverton–Holt (B–H) stock–recruitment relationship (Beverton and Holt, 1957). Each cohort estimated in the initial population abundance-at-age is then reduced by the total mortality (Z) and subsequently projected into the next year/age combination. This process of estimating recruitment and projecting the population forward continues until the final year of data (2004) is reached. Total mortality rates used to decrease cohort abundances over time represent the sum of residual natural mortality [assumed to be 0.10, and constant over time in this application; confirmed by sensitivity analyses which showed minimal change in overall results with changes in this parameter (NEFSC, unpublished data), and which is a common approach when estimating M2 directly (Livingston and Methot, 1998; Hollowed *et al.*, 2000; Overholtz *et al.*, 2008)], fishing mortality (F), and predation mortality ($M2$). The values of F (or $M2$) were assumed to be separable into age (commonly referred to as selectivity) and year [commonly referred to as F

(or $M2$) multipliers] components. The product of selectivity-at-age and the year-specific F (or $M2$) multiplier equals the F (or $M2$) by year and age combination. Predicted catch in weight and catch-at-age were estimated using Baranov's catch equation. Maximum-likelihood calculations were the foundation of the overall numerical estimation. The ASAP model includes nine likelihood components and a few penalties (for more detail, see Legault and Restrepo, 1999).

The likelihood function to be minimized includes the following components. Total catch in weight (Y) by fleet j (fishery or predator) at age a and year y (lognormally distributed):

$$L_1 = \lambda_1 \left[\ln \left(\sum_a Y_{a,y,j} \right) - \ln \left(\sum_a \hat{Y}_{a,y,j} \right) \right]^2, \qquad (6)$$

with catch proportions in numbers of fish (p) by fleet j (fishery or predator; multinormally distributed):

$$L_2 = - \sum_y \sum_j \lambda_{2,y,j} \sum_a P_{a,y,j} \ln(\hat{P}_{a,y,j}) - P_{a,y,j} \ln(P_{a,y,j}), \qquad (7)$$

and indices of abundance (I; lognormally distributed):

$$L_3 = \sum_j \lambda_{3,j} \sum_y \frac{[\ln(I_{y,j}) - \ln(\hat{I}_{y,j})]^2}{2\sigma_{y,j}^2} + \ln(\sigma_{y,j}). \qquad (8)$$

The sigmas (σ) in Equation (8) are input by the user and can optionally be set all equal to 1.0 for equal weighting of all index points. The weights (λ) assigned to each component of the likelihood function correspond to the inverse of the variance assumed to be associated with that component.

For comparative purposes, we developed the following. (i) A conventional stock assessment model by mimicking (to the extent possible) the structure employed in the recent stock assessment base-case model, with spring survey tuning indices split at 1985 (spring 1 designates data from 1968 to 1984, and spring 2 data from 1985 to 2004) to address the survey catchability issue for mackerel that was attributable to a conversion to different survey doors in 1985. After 1984, survey catches of mackerel on average increased dramatically over values before the door change (for more detail, see NEFSC, 2006). Natural mortality was assumed to be 0.2. (ii) A predation-based assessment model that used the same configuration as the conventional assessment model and where the consumption-at-age of mackerel by fish predators was incorporated as a second "fishing fleet". The residual mortality was assumed to be 0.10. Fishery and predator selectivities were estimated by the model. We also executed a model run with estimable predator and flat fishing selectivities (NEFSC, unpublished data), which did not result in substantially different outcomes; as such we do not include those results here.

Estimation of biological reference points
In ASAP, the estimation of biological reference points (MSY, F_{MSY}, and SSB$_{MSY}$) follows standard calculations based on equilibrium conditions, per-recruit analyses, and a B–H stock–recruitment relationship (Legault and Restrepo, 1999). ASAP has a feature that allows the designation of each fleet as either directed or non-directed for projections and fishing mortality reference point calculation. Fleets that are not directed are held at the terminal year F, and

directed fleets have their F vectors combined to produce a directed selectivity pattern. The directed fleets' combined selectivity is multiplied by F (either input or solved for) to match a catch or desired reference level ($F_{MSY} = 0.12$ in this application and equivalent to the level used in the assessment). For the model that included predation, we designated the predator fleet as non-directed. In this case, $M2$ is treated separately from F when deriving the biological reference points. The new reference points now include both predation and fishery effects, so we assigned different names to distinguish them from traditional reference points. The new reference points were named as follows: total MSY (MSYtot), which is analogous to MSY but includes both fishery and predatory removals, total spawning-stock biomass (SSBtot), and total mortality at MSYtot (F_{MSYtot}), which is comparable to F_{MSY} in a conventional assessment but includes both fisheries and predation mortality.

The biomass levels of predatory fish and marine mammals are expected to increase over the next few decades (Overholtz and Link, 2007), so we investigated the effect of varying predation mortality on reference points, particularly the available surplus yield for the fishery. We calculated the surplus yield for the fishery (SF) at different values of predation mortality, and to perform these calculations, we estimated the surplus yield for the fishery. The proportion of total yield attributable to the fishery was calculated by multiplying total yield at age by $F/(F+M2)$ at the same age. SF was estimated by changing the value of F and holding $M2$ constant. We then changed the values of $M2$, holding F constant, to re-estimate a range of SF. We partitioned the source of removals between the fishery and predators by exploring various scenarios across a range of values of F and $M2$.

Results
Atlantic mackerel consumption by the set of demersal fish examined in this study was relatively high in the early 1970s, reaching 69 000 t, then declining during the late 1970s (Figure 3). Consumption then increased into the late 1980s, averaging 89 000 t during that period. Atlantic mackerel consumption and landings were similar during the 1980s and 1990s, and consumptive removals were low compared with landings more recently (Figure 3).

Estimated selectivities for the conventional assessment model and the predation-based assessment indicated that fisheries selectivity had a dome-shaped pattern (Figure 4). In contrast, the selectivity by predators showed a left-skewed selectivity pattern, indicating that demersal fish had a preference for younger mackerel. The summary results of the likelihood components and the diagnostics of the fit of the conventional and predation-based assessment models are listed in Table 1.
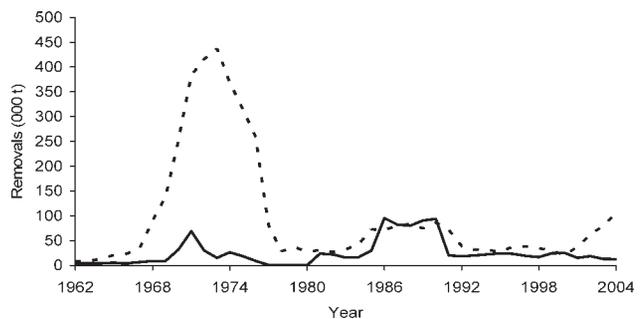
Figure 3. Annual consumption (thick line) and landings (dashed line) of Atlantic mackerel during the years 1962–2004.
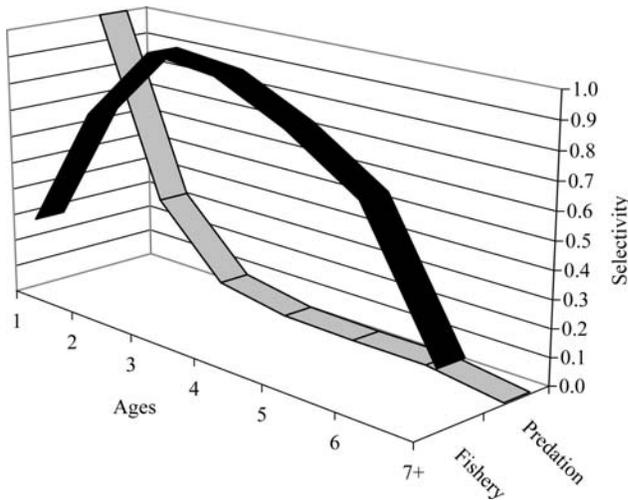
Figure 4. Fishery and predation selectivities estimated by the ASAP model for the predation-based assessment model.

Rates of predation mortality were variable during the years 1962–2004 (Figure 5). They were <0.10 in the 1960s, peaked at 0.23 in 1971, dropped to a series low of 0.003 in 1980, then started to increase again. Predation mortality increased slightly to 0.18 in 1981, but then increased rapidly to peak at 0.6 in 1986. After 1986, the rates of predation mortality dropped to <0.1 in 1991 and averaged just 0.03 during the years 2000–2004.

The combined rates of fishing and predation mortality were relatively small during the early 1960s, an average of ∼0.08 (Figure 5). Then, from 1970 to 1977, the combined rates increased to peak at 0.41 in 1974, and subsequently declined to a series low of 0.025 in 1980. Later, the rates increased to a lower peak of 0.21 in 1981 and to a larger peak of 0.65 in 1986. The combined rates of fishing and predation mortality then declined dramatically to a low of 0.10 in 1991, followed by a stable period during the period 1991–1999. The average of the combined fishing and predation mortality rate from 2000 to 2004 was ∼0.05.

Predation mortality was highest on the youngest age classes (1 and 2 years), compared with fishing mortality that mostly affected older fish (ages 3 and older; Figure 6). Nevertheless, there was some overlap in age composition of mackerel by both mortality components; this overlap was centred on age 2 mackerel.

Estimated natural mortality was relatively high in the early 1970s and very high in the mid-1980s for younger mackerel (Figure 7). In contrast to the assumption of constant natural mortality ($M = 0.2$) used in the conventional assessment models for mackerel, our results showed that natural mortality was not constant at age and also that it was temporally variable.

Table 1. Likelihood function components for conventional and predation-based assessment models.

Component	Conventional assessment model				Predation-based assessment model			
	nobs	Lambda	RSS	Likelihood	*nobs*	Lambda	RSS	Likelihood
Total removals in weight								
Fishery	43	1 000	0.00050	0.49526	43	1 000	0.00019	0.18692
Predation	–	–	–	–	43	1 000	0.00005	0.05457
Total removals	43	1 000	0.00050	0.49526	86	1 000	0.00024	0.24149
Removal at age_proportions	301	–	–	254.81000	602	–	–	329.038
Index_Fit								
Spring 1-age 1	17	6.74	26.63870	89.77250	17	6.74	26.9961	90.9767
Spring 1-age 2	17	6.74	15.35370	51.74210	17	6.74	14.9999	50.5497
Spring 1-age 3	17	6.74	20.50570	69.10420	17	6.74	21.5864	72.7463
Spring 1-age 4	17	6.74	23.67870	79.79710	17	6.74	25.0391	84.3816
Spring 1-age 5	17	6.74	36.79580	124.00200	17	6.74	37.2128	125.407
Spring 1-age 6	16	6.74	29.02750	97.82260	16	6.74	31.4965	106.143
Spring 1-age 7+	16	6.74	41.97900	141.46900	16	6.74	46.323	156.109
Spring 2-age 1	20	6.74	13.35440	45.00440	20	6.74	17.7965	59.9741
Spring 2-age 2	20	6.74	11.74340	39.57520	20	6.74	12.2891	41.4144
Spring 2-age 3	20	6.74	12.11140	40.81530	20	6.74	11.9066	40.1253
Spring 2-age 4	20	6.74	16.38750	55.22580	20	6.74	15.8509	53.4174
Spring 2-age 5	20	6.74	27.37910	92.26760	20	6.74	26.8658	90.5379
Spring 2-age 6	20	6.74	28.27780	95.29630	20	6.74	30.0782	101.364
Spring 2-age 7+	20	6.74	59.37260	200.08600	20	6.74	57.0161	192.144
Total	257	94.36	362.60500	1221.98000	257	94.36	375.457	1265.29
F-mult-deviations								
Fishery	42	0	5.39280	0	42	0	6.09463	0
Predation	–	–	–	–	42	0	42.2366	0
Total	42	0	5.39280	0	84	0	48.3312	0
N in Year 1	6	0	11.94690	0	6	0	5.88893	0
Stock-Recruit_Fit	43	1	36.69500	66.0984	43	1	29.2594	49.4376
Recruitment	43	1	36.39510	36.6951	43	1	29.2595	29.2595
*F*_penalty	301	0.001	0.61835	0.00062	301	0.001	0.140307	0.00014
Objective function value	–	–	1 580	–	–	–	1 673	–

nobs, number of observations in that component; lambda, weight given to that component; RSS, residual sum of squared deviations.
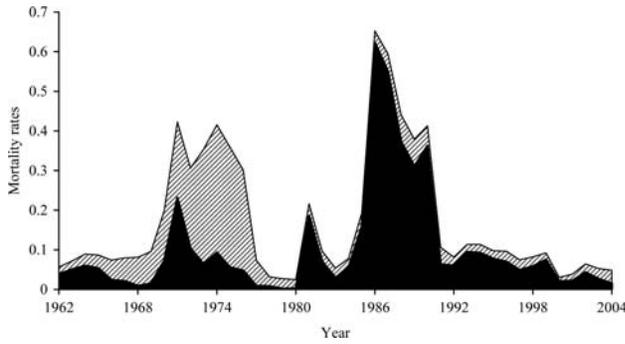
Figure 5. Stacked area graph of the rates of predation (M2) (black) and fishing mortality (F) (hatched area) at age for Atlantic mackerel during the period 1962–2004.
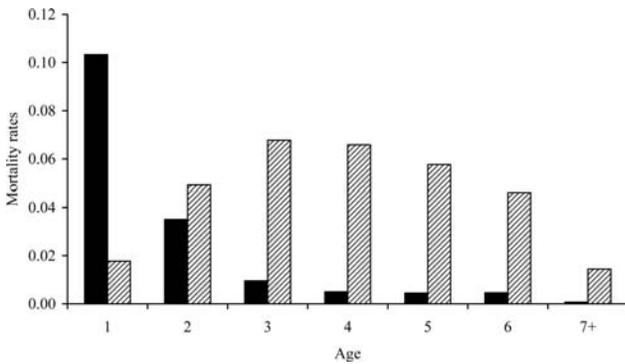
Figure 6. Rates of predation (M2) (black) and fishing mortality (F) (hatched) for Atlantic mackerel during the period 1962–2004.
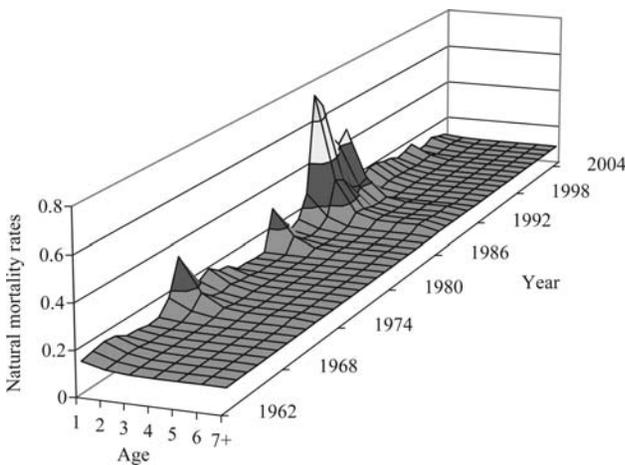
Figure 7. Rates of natural mortality over time and age for Atlantic mackerel during the years 1962–2004.

Figure 8. Total biomass of Atlantic mackerel during the years 1962–2004 estimated by conventional assessment (open circles) and predation-based assessment (dots).
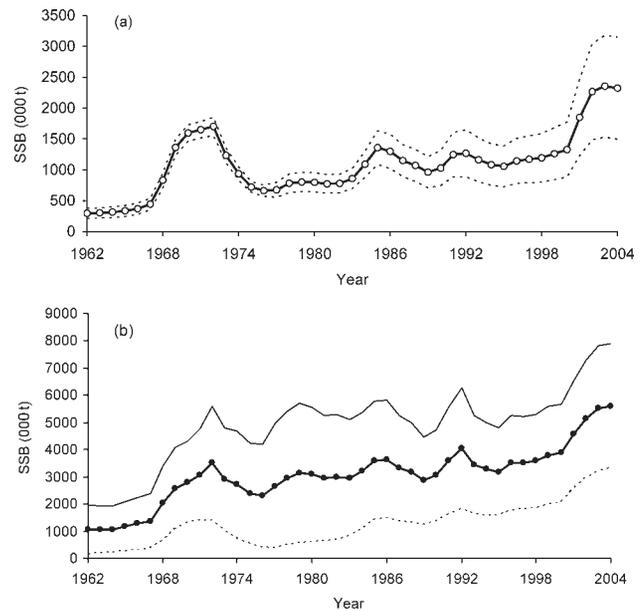
Figure 9. SSB of Atlantic mackerel estimated during the years 1962–2004 from (a) conventional assessment, and (b) predation-based assessment, with associated 95% confidence interval (dotted lines).

Stock biomass estimated from the predation-based assessment was similar in trend but 2–3 times greater in magnitude than the stock biomass estimated from the conventional stock assessment (Figure 8). Stock biomass from the predation-based assessment increased from low levels in the early 1960s to peak at 3.7 million tonnes in 1972, after which it declined until 1976. Thereafter, stock biomass increased steadily to 4.3 million tonnes in 1999 and rapidly to 6.3 million tonnes in 2004.

SSB was also consistently 2–3 times greater for the model that incorporated predation than for the conventional assessment model (Figure 9a and b). Estimated from the predation-based assessment, SSB was relatively high in the early 1970s, peaking at 3.5 million tonnes in 1972. It then declined to 2.3 million tonnes in 1976 before increasing again to peak at 5.6 million tonnes in 2004. The predation-based assessment model also revealed a greater degree of uncertainty surrounding SSB estimates than the conventional assessment model.

In general, the trend in estimated recruitment (age 1 abundance) in the predation-based assessment is similar to that of the conventional stock assessment, with three large year classes in 1967, 1982, and 1999 (Figure 10). The difference between the two assessments is that the 1982 and 1999 year classes estimated by the predation-based assessment were greater in magnitude. Recruitment estimated by the predation-based assessment ranged from 0.16 to 5.8 billion fish from 1962 to 2004, averaging 1.4 billion fish, whereas the conventional assessment averaged just 1.2 billion fish during the same period. B–H model parameters
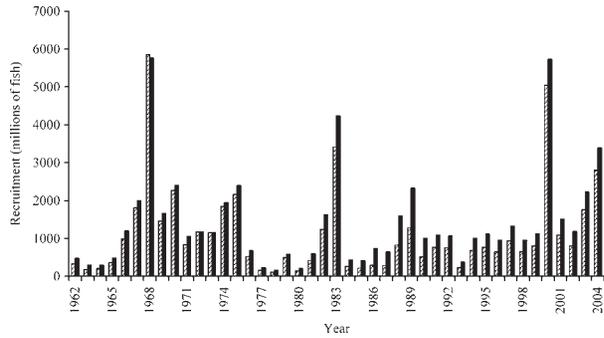
Figure 10. Recruitment (age 1) of Atlantic mackerel estimated for the years 1962–2004 from conventional assessment (cross-hatched) and predation-based assessment (black).
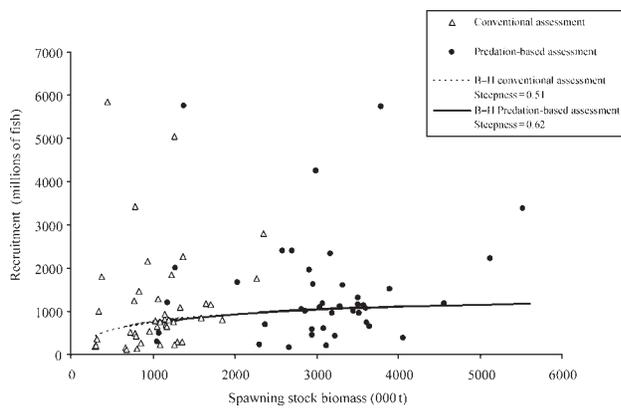
Figure 11. Atlantic mackerel stock–recruitment plot from conventional assessment and predation-based assessment, with estimated Beverton and Holt (B–H) curves.

Table 2. Estimates of the biological reference points MSY, SSB_{MSY}, and F_{MSY} (fishery only), and MSY_{tot}, SSB_{MSYtot}, and F_{MSYtot} (including predation and the fishery) for Atlantic mackerel from conventional and predation-based assessment models.

Biological reference point	Conventional assessment	Biological reference point	Predation-based assessment
MSY	89 000 t	MSY_{tot}	163 000 t
SSB_{MSY}	644 000 t	SSB_{MSYtot}	1 745 000 t
F_{MSY}	0.16	F_{MSYtot}	0.19

for the stock–recruitment relationship for the model that incorporated predation were: $\alpha = 1376.4$; $\beta = 960$; virgin = 5300; steepness $(h) = 0.62$. Relative to the conventional assessment model, the compensatory productivity (the so-called steepness parameter) of the population at low adult stock sizes was higher when predation was included in the model (Figure 11).

Biological reference points for Atlantic mackerel were very different when a predation component was added to the model. Estimates from the predation-based ASAP model were $MSY_{tot} = 163\,000$ t, $SSB_{tot} = 1\,745\,000$ t, and $F_{MSYtot} = 0.19$ (Table 2). These estimates are up to 2–3 times higher than those estimated from the conventional assessment (Table 2). By accounting for another "fishery", the model that explicitly incorporated predation resulted in higher estimates of abundance for mackerel.
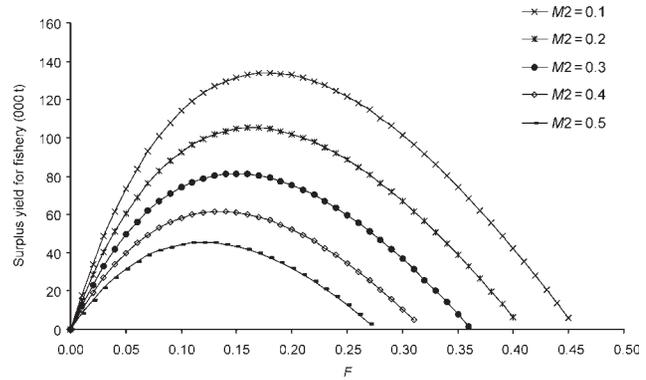
Figure 12. Surplus available to the fishery at several values of predation mortality (*M*2) for fishing mortality (*F*) values from 0 to 0.48.

Projections of available surplus for the fishery at different levels of predation mortality showed that the surplus for the fishery would decrease if predation mortality increased over the next few decades (Figure 12). Clearly, increased predatory demands will result in lower surplus yields for the fishery.

Discussion

Our analysis shows that incorporating predation into a mackerel stock assessment model has clear implications for the resulting fishery management advice. Adding demersal fish predation to the model increased the estimated number of age-1 mackerel, thus changing the stock–recruitment relationship from one with low recruitment compensation to one with high recruitment compensation. Uncertainty in stock biomass also appears to be underestimated in models that do not account for predation. Moreover, biological reference points differed considerably when predation mortality was included, resulting in higher estimates of SSB_{MSY} and lower estimates of an MSY harvest level. These results are consistent with other studies that have incorporated other sources of mortality, particularly predation, into stock assessment models (Livingston and Methot, 1998; Hollowed *et al.*, 2000; Tjelmeland and Lindstrøm, 2005; Overholtz *et al.*, 2008).

In this study, predation mortality was relatively high for the younger ages during the 1970s, a time when mackerel were subject to heavy fishing by foreign and domestic fleets. These fleets removed substantial quantities of young fish (NEFSC, 1996, 1998, 2006). This overlap between predation and fisheries that targeted the same size of fish may explain the sharp decline of mackerel during the 1970s. These observations are similar to those of Overholtz *et al.* (2008) in their explanation of Atlantic herring's contemporaneous decline, so confirming the importance of incorporating predation in the stock dynamics analysis of these pelagic species. Predation on mackerel during the 1980s was high for younger fish, perhaps attributable to the high abundance of several demersal fish species, especially spiny dogfish, and the low abundance of other prey species (Overholtz *et al.*, 2008). This extensive predation on young fish during the 1980s was manifest in relatively low biomass of mackerel then. Demersal fish predation on mackerel declined during the 1990s and continued to be low recently even as mackerel biomass has increased. This reduction is probably related to relative preferences or availability (e.g. spatial overlap of predator and prey) of these prey fish to demersal fish predators (Overholtz *et al.*, 2000). Alternatively,

the reduction in demersal fish predation on mackerel could be accounted for by the recently diminished abundance of demersal fish, especially spiny dogfish.

The results of our analysis confirmed that the assumption of constant natural mortality made in conventional mackerel stock assessments is likely inappropriate. Other investigations have executed these types of extended single-species models with similar results (Livingston and Methot, 1998; Hollowed et al., 2000; Tjelmeland and Lindstrøm, 2005; Overholtz et al., 2008), but the advantage of an age-structured approach is that it clearly depicts and quantifies a change in predation mortality throughout ontogeny. The rapid growth rate of mackerel (Wigley et al., 2003) results in a relatively brief period of vulnerability to demersal fish predation, as demonstrated by the sharp decline in predation mortality after age 1.

There are several caveats in interpreting our model results, with some obvious known uncertainties. Here, we considered only demersal fish predators, ignoring other major predators of mackerel. Atlantic mackerel are commonly preyed on by many marine mammals, such as pilot whales (Globicephala spp.), white-sided dolphins (Lagenorhynchus obliquidens), and common dolphins (Delphinus delphis). Overholtz et al. (1991a) estimated that marine mammals consumed ~36 000 t of mackerel annually from the northeastern US continental shelf. This value was estimated for the late 1970s and early 1980s, which was when mackerel abundance was low and marine mammals had a relatively small proportion of mackerel in their diets. The increasing abundance of both mackerel and marine mammals in the past two decades (Waring et al., 2002; NEFSC, 2006) may imply that marine mammal predation currently constitutes a much greater fraction of total mackerel removals. Our results of mackerel consumption may have been more pronounced if we had included marine mammal predation on mackerel. Furthermore, we parameterized the ASAP model in a manner that was consistent with the prior stock assessment, which may have led to conservative results. In addition, our predator abundance calculations were not catchability-corrected and thus should be considered conservative estimates.

In this analysis, we estimated a single selectivity for the predators as a whole. This assumption is justified by the fact that there were only small differences in the selectivity of different demersal fish predators. If, for example, we had considered in our analysis other predator groups such as marine mammals and large pelagic fish, then a separate selectivity curve for each predator group may have been needed.

The assumption that predator consumption patterns of mackerel would remain stable regardless of changes in mackerel abundance, equivalent to a Holling type I (linear) functional response (Holling, 1965), is probably a weak one. There is evidence that mackerel predators may exhibit a Holling type II (hyperbolic, inversely density-dependent) and Holling type III (sigmoid, density-dependent) functional response (NEFSC, unpublished data), so if that is the case then our projections may be altered. We strongly urge investigating the functional feeding responses of demersal fish predators in the region to improve the accuracy of these types of model.

The fishery data were from the northeast US and Canada, which contain both spawning components of the mackerel population (Sette, 1950; MAFMC, 1994). The food habits data, however, were available only from the northeastern US, covering only part of the northern components of the population. In the

Gulf of St Lawrence, mackerel have been reported to be important dietary components of large cod, large demersal fish, and cetaceans (Savenkoff et al., 2005). Adding extra information on the consumptive removals of mackerel by predators in Canadian waters could also improve our estimates.

Certainly, further refinement and validation of this model will be needed. The two salient points are: (i) there are known areas in which the model could be improved given the availability of additional data, and (ii) the interpretation of our model results needs to account for these caveats, likely with the recognition that ours are conservative estimates of predatory removals.

Despite the caveats listed above, we think that our results are generally robust to various model assumptions and parameterizations. In other words, by adding in another source of mortality (predation), regardless of the specific magnitude, we expect the general patterns and magnitudes to hold. One of these general patterns is that biological reference points are more conservative (e.g. a higher SSB_{MSY}) when predation is included. That there were more fish retrospectively is not surprising when adding in another "fleet" (i.e. predators), and equally unsurprising is that there would be more removals in projections when including these predators. We suspect that this general pattern of extra removals will hold true for most small pelagic fish that serve as forage for upper trophic levels. However, the partitioning of removals among various sources remains a key issue (Overholtz et al., 2008). That the other reference points change and are clearly different when including predation is true, but because some of the yield no longer goes to the fishery but rather to predators, there is not a simple, linear or proportional solution with the addition of this predation mortality.

It will be important to consider explicitly incorporating predation mortality if predatory fish stocks recover from overfishing. Over the next few decades, the biomass of demersal fish may continue to increase in the Northwest Atlantic, implying that predation mortality on Atlantic mackerel could increase. If such a scenario occurs, the available fishery yields from Atlantic mackerel will likely decline. If predation mortality increases and is not accounted for in stock assessments, then declines in Atlantic mackerel could result, with seemingly no explanation. By extension, similar considerations are important for small pelagic fish and their associated fisheries worldwide. If, however, demersal predator stocks remain overfished, it would be judicious to evaluate whether there is a sufficient forage base of small pelagic species such as mackerel to support the recovery of those predators.

This work has demonstrated the feasibility of incorporating predation mortality in an age-structured model. Documenting the impact of predators on prey is useful information for decision-makers to consider when managing small pelagic fisheries. An explicit quantification of predation mortality allows managers to make adjustments to estimates of fishery yield based on changes in predator populations. As we continue to move towards implementing an ecosystem approach to fisheries, this and similar approaches will be valuable for evaluating the effects of ecological interactions such as predation.

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