

Abstract.— Annual assessments of the Northwest Atlantic mackerel stock have occurred every year since 1973, providing useful advice to fishery managers involved in the decision making process for this important pelagic resource. Since 1985, assessment advice based on an $F_{0.1}$ management strategy has indicated that catches in the 300,000 mt range are feasible because stock biomass has increased greatly after the collapse of the fishery in the mid-1970s. However, indications from previous research are that compensatory processes are very important, so a stochastic simulation model with density-dependent growth, maturity, and natural mortality was constructed to study how these mechanisms might affect our ability to provide short- and long-term advice for this important stock. Model results suggest that our present assessments may be too optimistic relative to yield projections and that minimum spawning-stock biomass levels may be difficult to maintain even with an $F_{0.1}$ fishing strategy. Model results also reveal that natural mortality rates are probably much higher than previously thought and are important in determining trends in abundance in this stock.

Impact of Compensatory Responses on Assessment Advice for the Northwest Atlantic Mackerel Stock

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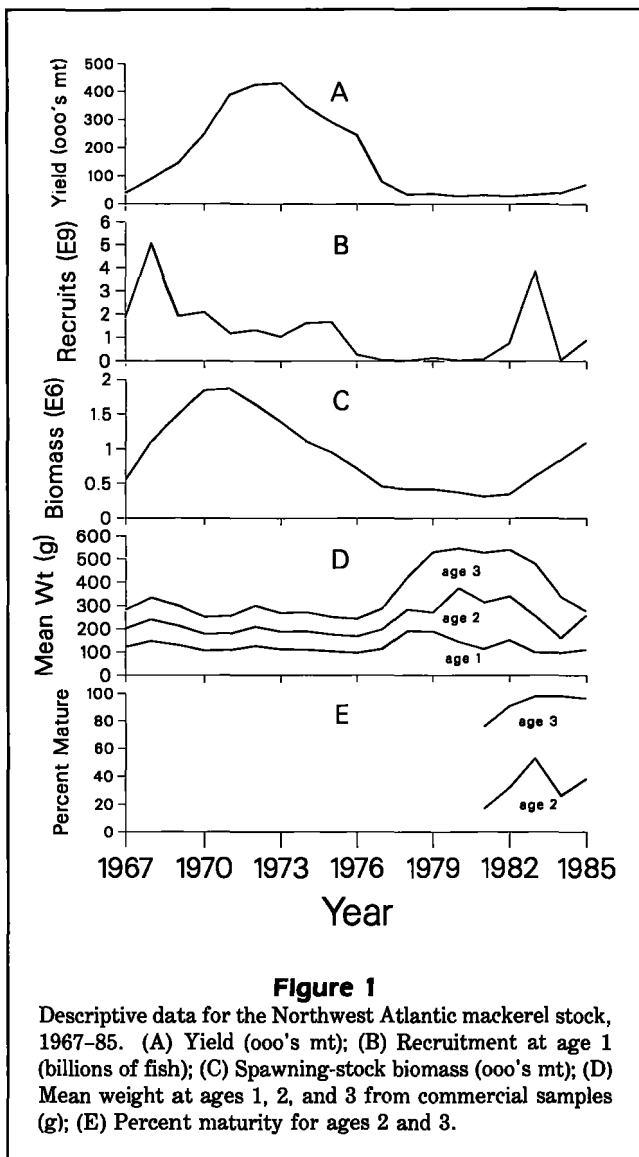
The Northwest Atlantic stock of Atlantic mackerel *Scomber scombrus* has historically been important to the U.S. domestic fishery; records from the early 1800s to the 1980s suggest that cumulative landings have been 7–8 million mt over that time-period (Sette and Needler 1934, Hoy and Clark 1967, Anderson 1985). A thriving domestic industry utilized mackerel well into the 1940s until landings dropped because of declines in abundance, availability, and increased production of fresh and frozen white fish products (e.g., haddock, cod) (Hoy and Clark 1967, Jenson 1967). A resurgence of the fishery occurred in the 1970s when distant water fleets from eastern Europe and the Soviet Union landed an average of 310,000 mt annually from 1970 to 1976 (Fig. 1A). Since many of the important groundfish species in the region have declined recently, the U.S. industry has become more interested in mackerel as a volume (high-catch, low-price) fishery.

The fishery has been managed under the auspices of the Mid-Atlantic Fishery Management Council since 1977. Current management objectives for this stock include maintenance of a minimum spawning stock (600,000 mt), annual quotas based on an $F_{0.1}$ catch strategy and a recognition of the necessity for keeping the total stock at some reasonably high level

to insure that the recreational fishery remains viable.

Recent assessments suggest that the stock has increased since collapsing in the late 1970s. A succession of moderate to good year-classes from 1981 to 1985 promoted rapid recovery of the stock to levels observed in the early 1970s (Fig. 1B, C). Assessment advice during the last several years based on an $F_{0.1}$ management strategy has indicated that annual catches in the 300,000 mt range are feasible in the short term. Allocations to joint ventures have increased over the last several years, amounting to about 75,000 mt in 1987, but recent landings have remained well below the 300,000 mt level and fishing mortality has averaged only about 0.07 since 1980 (Overholtz and Parry 1985).

Pelagic fishes such as mackerel are important in the trophic dynamics of fishery ecosystems, supporting populations of predatory fish, birds, and marine mammals. Additionally, these species may also increase to densities that inhibit their own population processes (e.g., growth, reproduction) and those of competitors. Evidence exists that Atlantic mackerel exhibit density-dependent growth (McKay 1979, Lett 1980, Overholtz 1989). Other factors such as maturation rates, fecundity-at-age, and predation mortality rates may also vary



with stock size. An analysis of the food habits of mackerel predators suggested that natural mortality rates (M_2) for this stock were higher during 1973-75 when relatively large numbers of juvenile mackerel were available, and declined during 1976-80 when there were few small fish (NEFC 1987).

This study examines the impact that compensatory changes in growth, sexual maturity, and natural mortality rates may have on the Northwest Atlantic mackerel stock. Implications of responses in these factors on catch and spawning-stock biomass are evaluated using a simulation model. The model was designed so that changes in these compensatory factors as well as the influence of fishing mortality patterns and strategies could be assessed.

Model background

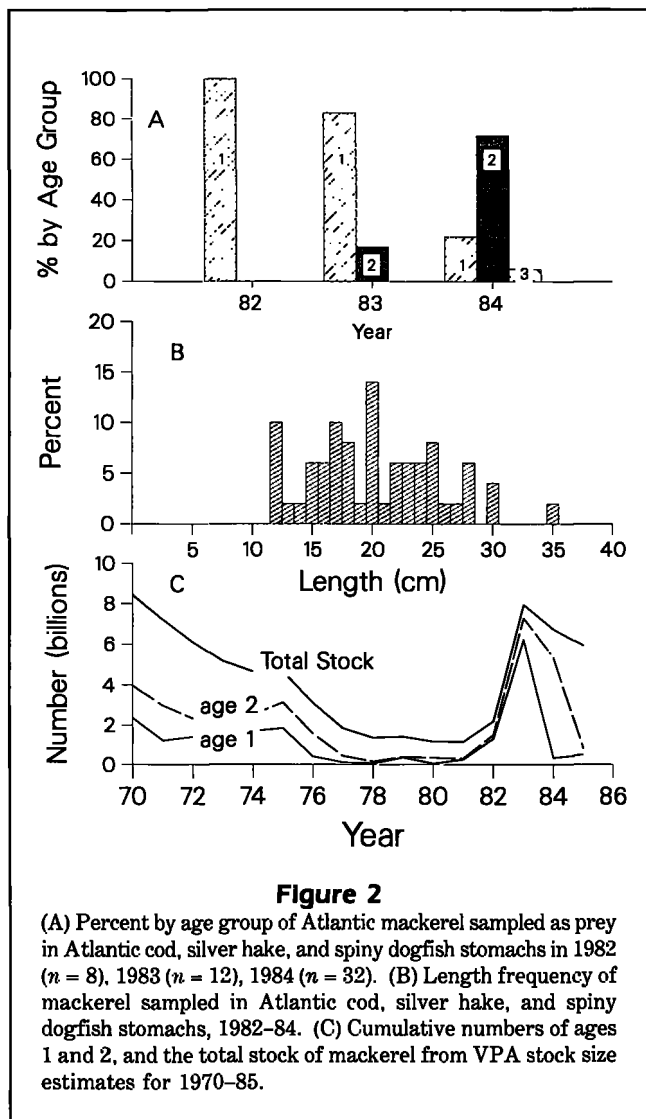
Data on potential density-dependent population regulatory mechanisms were obtained from research vessel survey cruises and commercial fishing operations conducted on the U.S. eastern coast. Information from spring groundfish surveys conducted by the Northeast Fisheries Center (NEFC) during 1973-85 and a commercial fishery conducted by Poland during 1981-86 were examined to quantify compensatory relationships. Analyses were performed to study changes in growth, maturation rates, and natural mortality (Overholtz et al. 1988, Overholtz 1989).

Significant negative relationships between mean weight-at-age and stock size were confirmed for both research and commercial data sources (Overholtz et al. 1988, Overholtz 1989). Mean size-at-age for recent year-classes was also found to be significantly different; large year-classes grew more slowly (Overholtz 1989). In addition mean weight-at-age was also negatively related to year-class size, indicating that large cohorts may depress growth rates of individuals from that particular year (Overholtz 1989) (Fig. 1D). These analyses helped us to quantify the relationship between growth and density for this stock in our modeling exercises.

Maturity data from 1981-86 were evaluated to ascertain if percent maturity at age 2 and 3 changed over the time period. No fish were mature at age 1, and all fish were mature at age 4+ (Overholtz et al. 1988). Percent maturity at age 2 ranged from 17% in 1981 to 53% in 1983 (Fig. 1E). Percent mature at age 3 ranged from 67% in 1986 to 98% in 1983 and 1984 (Overholtz et al. 1988) (Fig. 1E).

The maturity data were collected in conjunction with age sampling and were not a priority item. During the critical time of gonadal development in mid- to late April, maturity samples were often sparse because age sampling requirements had been fulfilled; no additional maturity samples were collected because of this. A cursory examination of the data revealed that there was an apparent negative relationship with increased stock size at age 2 and no consistent pattern at age 3 (Overholtz et al. 1988) (Fig. 1). The null hypothesis of no impact of density on maturity rates could not be accepted or rejected with the data at hand; we therefore included this potential mechanism in our modeling studies to ascertain its overall importance.

During 1967-85 the northwest Atlantic mackerel stock underwent profound changes in recruitment with a subsequent decline in biomass (Fig. 1B, C). We considered this a good time period to study changes in predation on mackerel and associated possible changes in natural mortality rates (M). For the purposes of discussion in this paper we define natural mortality rate ($M = M_1 + M_2$), where M_1 = sources of natural mortal-



ity other than predation, and $M2 =$ predation mortality (ICES 1987). Since there was no multispecies virtual population analysis (MSVPA) available to examine annual trends in predation mortality rates ($M2$), we decided to use another method to examine possible changes in $M2$. We wanted to investigate possible predation mortality models for mackerel for this period of time.

Summaries of NEFC food habits data indicate that spiny dogfish *Squalus acanthias*, Atlantic cod *Gadus morhua*, and silver hake *Merluccius bilinearis* are the most important fish predators on mackerel (Langton and Bowman 1980, Bowman and Michaels 1984, Bowman et al. 1984). Food habits data were collected from 1973 to 1980, but did not include individual lengths of prey items from these predators. However, maximum, minimum, and average lengths of fish prey were re-

Table 1
Percentage of mackerel by weight in stomach samples of silver hake, Atlantic cod, and spiny dogfish, and number of stomachs collected for 1973-76 and 1977-80.

Species	1973-76		1977-80	
	%	N	%	N
Silver hake	4.21	2622	0.82	1657
Cod	11.50	1009	0.10	457
Spiny dogfish	3.30	389	0.10	2662

corded. Almost all the mackerel consumed in these years were less than 30 cm (Overholtz et al. 1988).

To study the problem in more detail, food habits data from 1982-84 were examined to determine the size and age distribution of mackerel as prey items in the three fish predators. These data were chosen since detailed records of predator and prey length were available. Mackerel up to 35 cm were taken as prey by the three species, but fish 30 cm or less composed the bulk of the prey. These fish were predominantly ages 1 and 2 from the 1981-83 year-classes (Fig. 2A, B). Mackerel appeared to be consumed roughly in proportion to their abundance in the sea during 1982-84 (Fig. 2A, C).

Our analysis thus centered on predation by these three predators on age-1 and -2 mackerel. Total food consumed (all species) by each predator was calculated and the average percentage of mackerel by weight comprising the diet of each predator was estimated separately for the periods 1973-76 and 1977-80 (Table 1). A period average was used because there was not enough information available for annual estimates. These two time-periods were chosen because the design of the food-habits sampling regime was different in each period, and because the abundance of small mackerel was much different in each of the periods (Fig. 2C).

The method used to calculate consumption was based on residence times of the predator and prey, percent by weight of mackerel in the predator diet, daily ration estimates for the predator by season, if available, abundance of 1- and 2-year-old mackerel in the sea, and biomass of predators of the correct size distribution (Bowman et al. 1984, Rexstad and Pikitch 1986). This method assumed that the estimate of predator biomass was an appropriate measure of the average standing stock present during the year, that mackerel consumed were only age-1 and -2 fish, and that predators consumed mackerel relative to their abundance in the sea. The estimates were made for 1973-80 for each predator species and the total number of age 1- and -2 fish consumed annually was estimated (Table 2).

Total consumption of mackerel by each predator was calculated as

$$C_i = B_i \cdot \%BW \cdot \%Rm_i \cdot Tr \quad (1)$$

where

C_i = consumption of mackerel by predator i ,

B_i = biomass of predator i ,

$\%BW$ = daily ration estimate,

$\%Rm$ = percent of total ration composed of mackerel for predator i ,

Tr = residence time of predator and prey (days), and

$i = 1, 3$.

The estimated consumption in weight was then converted to numbers eaten on the basis of information on the abundance of age-1 and -2 mackerel in the sea and the mean weights of each age group. Consumption estimates were combined with landings-at-age for 1973–80 and a new VPA was completed for these years (Overholtz et al. 1988). A residual natural mortality rate ($M1$) of 0.20 was used in this analysis to account for other sources of mortality at ages 1 and 2 and for all the other age groups (3–14) in the analysis. A similar assumption has been used by ICES in the multispecies VPA model of the North Sea (ICES 1987). The mortality rates from the VPA were a proxy for F and $M2$ and were apportioned by using the ratios of consumption and landings to total deaths (numbers). This gave an estimate of F and $M2$ mortalities for 1973–80 (Table 3). Consumption (numbers) of age-1 mackerel exceeded landings of that age group in all years from 1973 to 1980 and was generally smaller than landings at age 2 (Table 2). Sizes of incoming year-classes increased up to a factor of two in the revised VPA over the 1973–80 period (Overholtz et al. 1988). When mortality rates from the VPA were apportioned by consumption estimates and landings, natural mortality rates ($M = M1 + M2$) were generally higher in the 1973–76 period, when mackerel were abundant, than in 1977–80 (Table 3).

These values and the new VPA stock size-at-age estimates were used in regressions to study the relationship between $M2$ and year-class strength. The results of this analysis suggest a positive relationship between $M2$ for ages 1 and 2 and year-class size ($R = 0.37, 0.78, P = 0.363, 0.0234$), respectively (Fig. 3A, B). An examination of the scatter plots from these two regressions revealed that the $M2$ value from 1976 was

Table 2

Annual consumption of age-1 and -2 Atlantic mackerel by spiny dogfish, silver hake, and Atlantic cod, landings of mackerel for 1973–80, and total for both categories (millions of fish).

Year	Consumption		Landings		Total	
	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2
1973	590.0	224.1	161.8	288.2	751.8	507.3
1974	823.0	135.1	95.9	242.2	918.9	377.3
1975	616.0	170.0	373.7	431.4	989.7	601.4
1976	202.8	278.3	12.5	353.5	215.3	631.8
1977	8.4	15.1	2.0	27.0	10.4	42.1
1978	11.1	6.6	0.1	0.2	11.2	6.8
1979	14.1	1.2	0.4	0.6	14.5	1.8
1980	6.1	8.4	1.2	10.9	7.3	19.3

Table 3

Mortality rates of age-1 and -2 Atlantic mackerel for 1973–80.

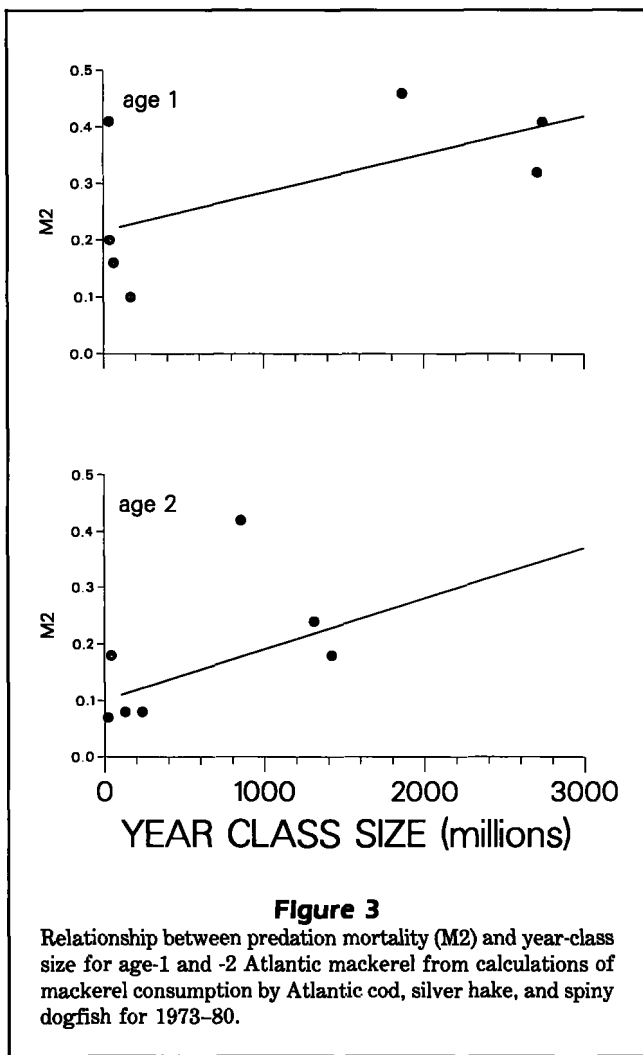
Year	Age 1				Age 2			
	Z	F	M2	M1	Z	F	M2	M1
1973	0.78	0.12	0.46	0.20	0.75	0.31	0.24	0.20
1974	0.66	0.05	0.41	0.20	0.86	0.42	0.24	0.20
1975	0.71	0.19	0.32	0.20	0.83	0.45	0.18	0.20
1976	0.81	0.04	0.57	0.20	0.93	0.41	0.32	0.20
1977	0.40	0.04	0.16	0.20	0.42	0.14	0.08	0.20
1978	0.61	0.00	0.41	0.20	0.39	0.01	0.18	0.20
1979	0.30	0.00	0.10	0.20	0.31	0.04	0.07	0.20
1980	0.44	0.04	0.20	0.20	0.38	0.10	0.08	0.20

high relative to the number of age-1 and -2 fish in the stock. There were fewer age-1 fish in the stock in 1976 (Fig. 2C); furthermore, food habits data indicated that mackerel was not present in the diet of the three predators in 1976. The 1976 data point was dropped and a new regression was fitted for age 1 ($R = 0.60, P = 0.157$, Fig. 3A).

We were cognizant of the fact that results of this analysis may have been influenced by the assumption of proportional feeding. However, the suggestion that natural mortality rates may change with year-class size is an interesting research question. A positive relationship between year-class size and predation mortality rate has obvious implications for assessment and management, and thus the potential impacts of density-dependent predation mortality were a major focus of our modeling studies.

Model structure

A simulation model addressing changes in growth, percent maturity-at-age, and predation mortality rates



(M2) was constructed to evaluate the potential impact of these population regulatory mechanisms in the context of single-species assessment advice. The model was a basic fishery simulator much in the same style as many other common fishery models (Walters 1969, Sissenwine 1977). An age-structured Baranov catch equation was used to compute annual fishery yields, and the negative exponential relationship was used to update stock size for 14 age groups.

A stochastic recruitment function was used to model recruitment for the mackerel stock. A three-parameter model (Shephard 1982; Table 4) with a lognormal white-noise multiplier was used to generate an annual estimate of recruitment as:

$$R = (a * SSB) / [1 + (SSB/K)^b] * \lnm \quad (2)$$

where R = recruitment at age 1,
SSB = spawning-stock biomass,

Table 4
Parameters used in stochastic simulations of the Atlantic mackerel stock; e-4 = 10⁻⁴, e-5 = 10⁻⁵, e-6 = 10⁻⁶.

	age	a	b	K
Weight (Wt _i)	1	0.122	-1.24e-5	—
Growth (G _i)	2	0.187	-1.42e-5	—
increment	3	0.154	-1.08e-5	—
	4	0.132	-1.03e-5	—
	5	0.102	-8.62e-6	—
Recruitment (R)	1	5.800	1.7	600.0
Maturity (PM)	2	0.543	-2.14e-4	—
	3	1.043	-2.14e-4	—
Predation	1	0.600	3.00	2.5
mortality (M2)	2	0.500	2.00	2.5

a, b, K = parameters,
lnm = lognormal multiplier with u and s from the SR data.

Recruitment estimates were scaled upward by a factor of 1.5 to account for the fact that the original VPA age-1 stock size estimates do not reflect higher natural mortality rates due to predation (Overholtz et al 1988).

Growth-at-age was based on a two-stage model that related life-history characteristics and year-class size to growth increment for a year-class (Overholtz 1989). Since age-1 fish maintain a separate distribution from the adult stock (Sette 1950) a relationship between age-1 growth and corresponding age-1 year-class size was used to predict weight at age 1. The relationship was parameterized (Table 4) with available empirical data, such that size at age 1 varied from 48g for slow-growing fish to 122g for fast-growing fish (Overholtz 1989). Weight of age-1 mackerel was calculated as

$$Wt_1 = a - bN_1 \quad (3)$$

where Wt = average weight (g) at age,
N₁ = year-class size at age 1 (numbers),
a, b = parameters.

Age 2-5 growth was determined by relationships between adult stock size (numbers) and growth-at-age (Table 4) calculated as

$$Wt_i = Wt_{i-1} + G_i \quad (4)$$

where Wt_i = average weight at age i, i = 2,5,
G_i = annual age-specific growth increment (g),

and

$$G_i = a_i - b_i SS \quad (5)$$

where SS = total adult stock size (numbers),
 a, b = age specific parameters.

The increment from ages 2 to 5 was smaller the larger the adult stock. Fish weight at ages 1–5 was the result of growth in the first year and subsequent increments at ages 2–5; thus, age-1 growth partially determined the average weight of a fish throughout its lifetime. If the stock was reduced in any given year, the cohort could recover and grow faster. Growth at ages 6+ was assumed to follow trends in the recent data, since by this time cumulative mortality has usually been sufficient to reduce a cohort to lower levels.

Percent maturity at ages 2 and 3 was assumed to vary based on a relationship between the fraction mature and spawning stock size calculated as

$$PM_i = a - b(SSB) \quad (6)$$

where PM_i = percent mature at age i , $i = 2, 3$,
 SSB = spawning-stock biomass,
 a, b = parameters.

This submodel was parameterized (Table 4) so that the maturity of age-2 fish can vary from 20 to 50%, while maturities for age-3 fish range from 70 to 100%.

Natural mortality due to predation (M_2) for ages 1 and 2 fish was estimated from a relationship between M_2 and year-class size-at-age (Fig. 4; Table 4) calculated as

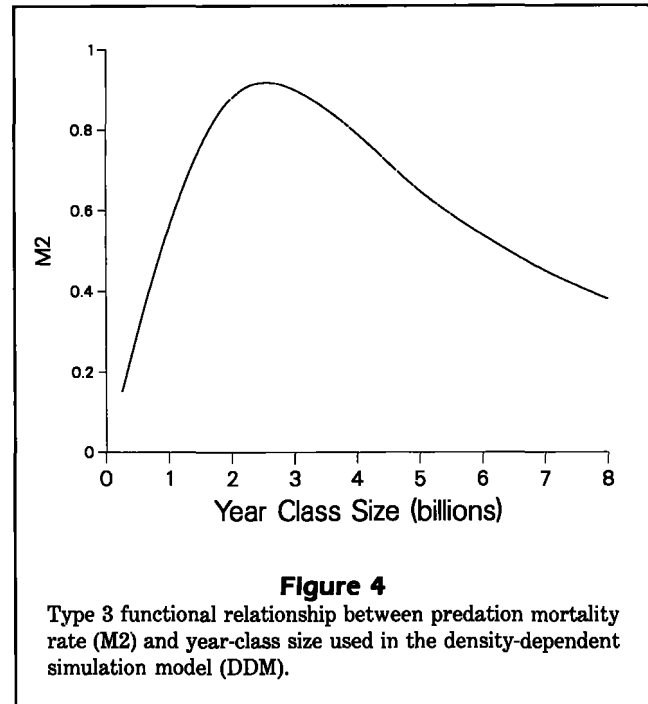
$$M_{2i} = (a * YC_i) / [1 + (Y C_i / K)^b] \quad (7)$$

where M_{2i} = natural mortality due to predation on age i , $i = 1, 2$,
 $Y C_i$ = year-class size at age i , $i = 1, 2$,
 a, b, K = parameters.

M_2 mortalities on age-1 and -2 fish could reach approximately 1.0 and 0.6, respectively, with this model.

This relationship was used since it approximates the findings of our mortality study over an initial range of stock size (Fig. 3A, B), and since it appears to be an appropriate predator-prey response model (Holling 1965, Murdoch 1973). Although this model does not produce a typical type-3 response (Holling 1965) exactly, since there is no inflection point over the initial stock sizes (Fig. 4), it serves as a sufficient functional model to study the natural mortality mechanism.

The density-dependent simulation model (DDM) was used to study the impact of different levels of fishing mortality, management strategies, and to investigate hypotheses concerning the role of compensatory re-



sponses in regulating this stock. Monte Carlo simulations were produced for a variety of different scenarios, and average results from 1000 annual data points were summarized. Results from the model were compared with forecasts from the current standard assessment model (STD).

Model sensitivity and validation

The sensitivity of model results to the different density-dependent mechanisms was investigated by comparing catch in 1987 and spawning stock in 1988 and 1991 for all the different combinations of growth, maturity, and natural mortality at a reference fishing mortality of 0.05. In runs where only a single mechanism was examined, 1987 catch was most affected by changes in the growth pattern (mean weights) of the stock (Fig. 5-B). Spawning stock in 1988, on the other hand, was almost equally sensitive to maturity and natural mortality. Density-dependent natural mortality influenced 1991 spawning stock to the greatest degree (Fig. 5-C).

When the results of pairing the mechanisms were examined, weight and natural mortality had the greatest effect on catch, percent maturity, and natural mortality on SSB in 1988 and weight and natural mortality on SSB in 1991 (Fig. 5-D, E, F). When the three mechanisms were all operating there was no change in the impact on 1987 catch, but spawning stock in 1988 and 1991 was several percentage points lower (Fig. 5-G).

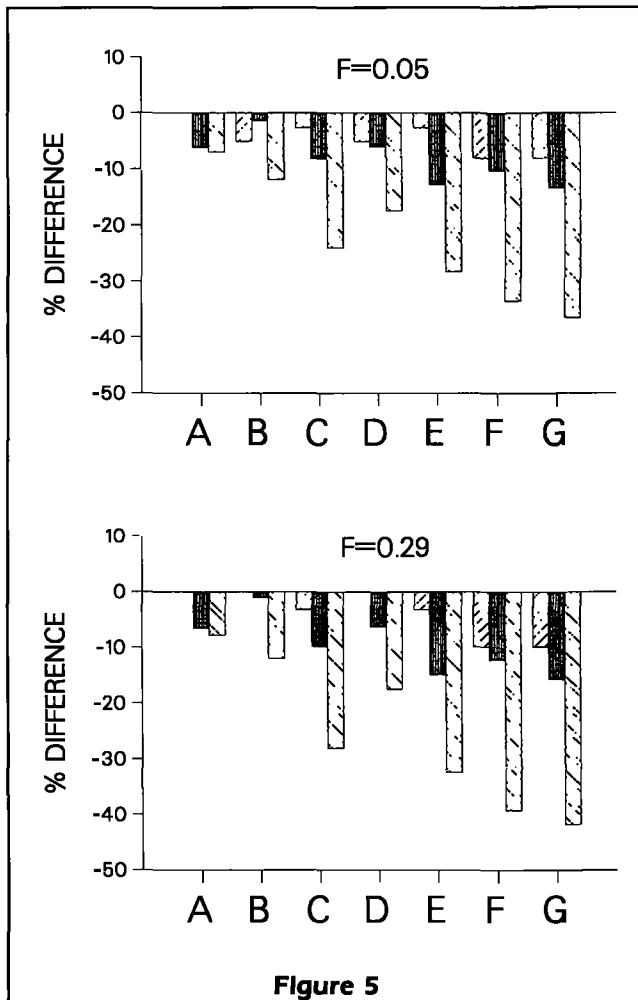


Figure 5
Impact on 1987 catch, 1988 spawning-stock biomass (SSB), and 1991 SSB of running the density-dependent simulation (DDM) model with all possible combinations of growth, maturity, and predation mortality. (A) maturity; (B) growth; (C) predation mortality; (D) growth, maturity; (E) maturity, predation mortality; (F) growth, predation mortality; (G) maturity, growth, predation mortality.

A validation run of the density-dependent model was produced for comparison with the observed time-series of catch and VPA biomass for 1967–85 (Fig. 6). The simulated series was produced by using the same fishing mortality series as in the VPA, recruitment scaled upward by a factor of 1.5, and density-dependent growth, maturity, and natural mortality. The pattern of simulated versus observed catch and biomass is quite comparable in terms of trend and magnitude, except for a few years in the early 1970s. This occurs even though the density-dependent model has greatly different natural mortality rates at ages 1 and 2 and much higher recruitment. Another run with the same F pat-

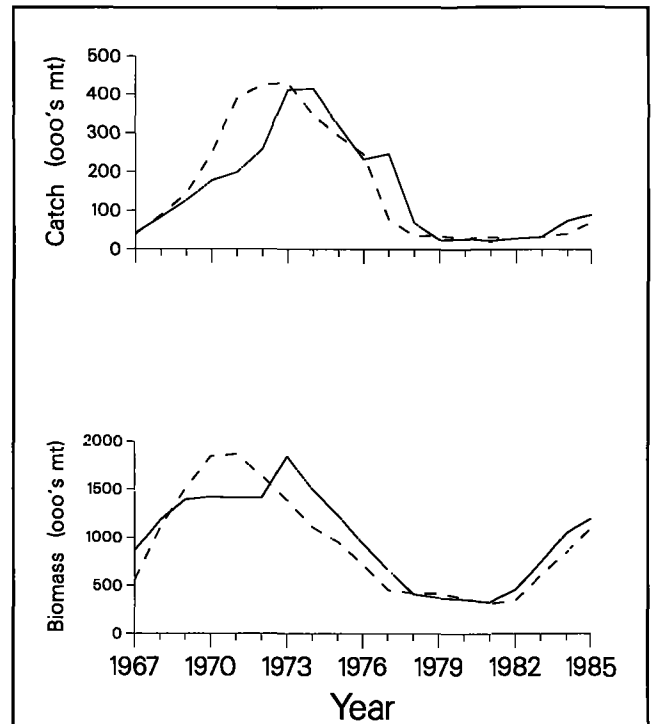
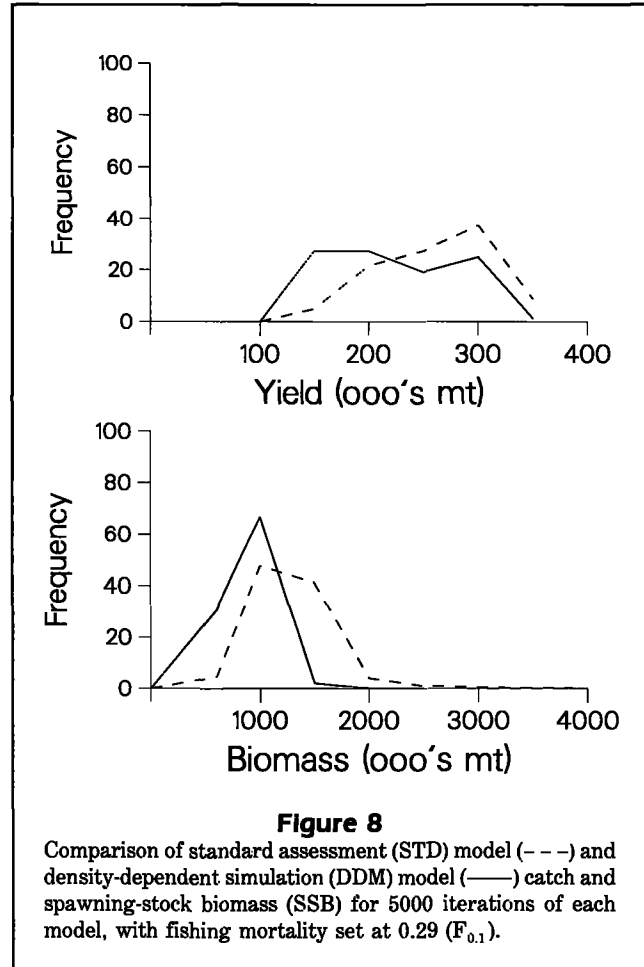
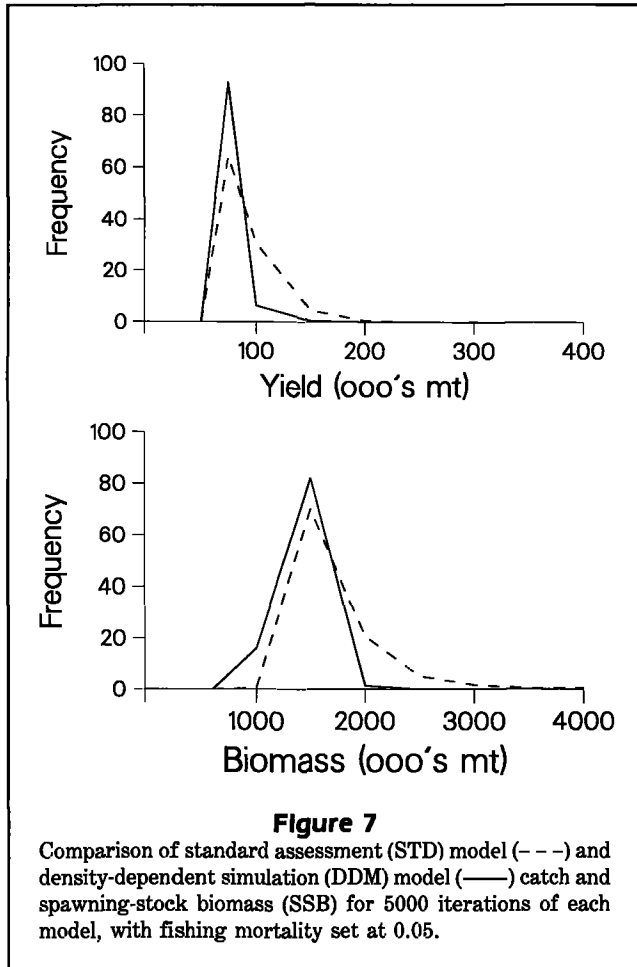


Figure 6
Comparison of observed (---) catch and biomass versus simulated (—) catch and biomass obtained from running the density-dependent simulation (DDM) model with historic estimates of fishing mortality, historic recruitment estimates scaled by a factor of 1.5, and density-dependent growth, maturity, and predation mortality.

tern, recruitment scaled by 1.5, and no density dependence produced the same trend in catch and biomass for 1967–85, but the values were approximately a factor of two larger than the observed series. Thus, not including the density-dependent component resulted in values of catch and SSB that were greatly different than the observed series.

The model components were validated by comparing the different outputs produced by the various mechanisms with available empirical data. In some cases, relationships were re-parameterized or tuned to produce results in the same ranges as observed in the empirical database. The model was used to investigate a variety of different problems. Runs from the STD model were compared with the results of the different density-dependent model outputs to gauge the changes that occurred in catch, total stock, spawning stock, mean weights, and other factors. STD runs were parameterized with the same data as that used in the 1986 assessment (Overholtz et al 1988).



Model results

Short-term perspective

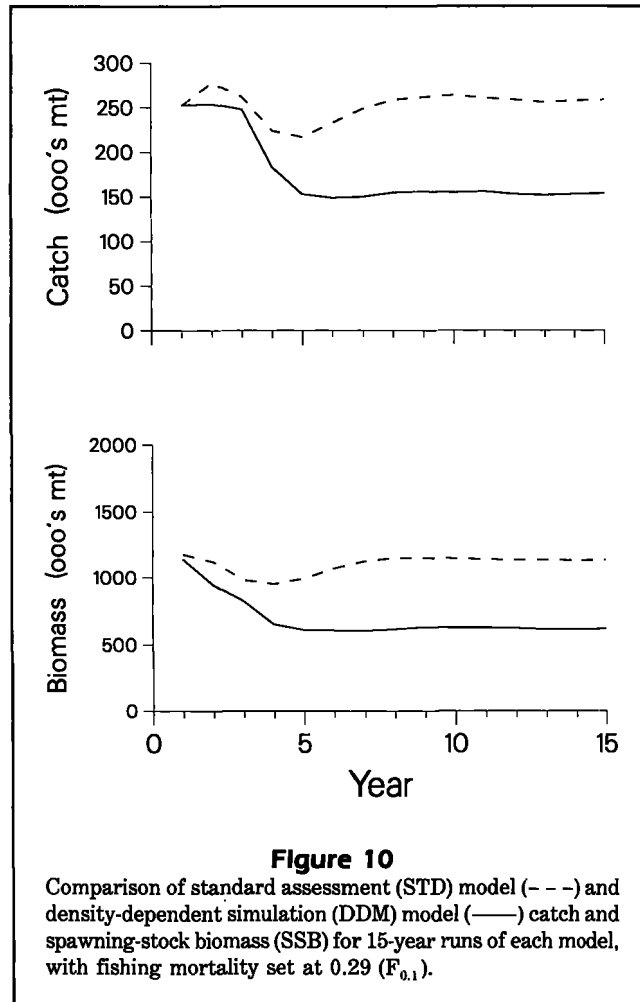
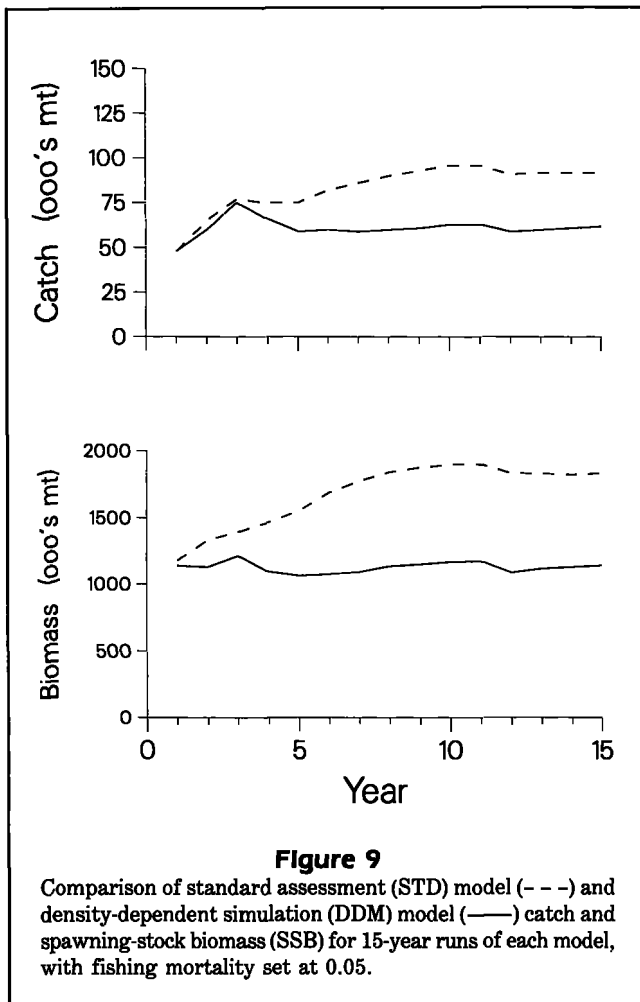
Since fishing mortality has been so low in recent years and the stock has increased, an attempt was made to investigate the effect of further stockpiling of fish on expected catches and spawning stock size. To address this problem, a series of 5-year simulations were used to compare the density-dependent model results with projections from the standard model. Fishing mortality was set at 0.05, a value close to the average rate over the last several years. These runs suggest that advice based on the standard model would have over-predicted catch by about 8% in 1987 and spawning stock size in 1988 by about 13% (Fig. 5-G). Furthermore, if the standard model were used to project more than a few years into the future, the estimate of spawning stock could possibly be too large; the 1991 estimate would be lower by 37% for the DDM model (Fig. 5-G). If the frequency of yields over this 5-year series is calculated, the STD model is more optimistic with a

mean catch of 74,892 mt versus 63,686 mt for the DDM model (Fig. 7). Similarly for spawning-stock biomass (SSB), the STD model suggests a higher mean SSB of 1.5 million mt versus 1.1 million mt for the DDM model (Fig. 7).

Since $F_{0.1}$ is an important benchmark fishing-mortality rate in the present management plan, another 5-year summary with $F = 0.29$ ($F_{0.1}$) was also produced. As with the previous example, mean yield for the STD model was considerably higher, 242,939 mt versus 197,116 mt for the DDM model (Fig. 8). Spawning-stock biomass would be considerably different under the two perspectives with an estimated mean SSB of 1.0 million mt under the STD model and 725,887 mt under the DDM model (Fig. 8).

Long-term perspective

To develop a longer-term perspective, simulations at the same two levels of fishing mortality ($F = 0.05, 0.29$) were produced for 15-year series to allow sufficient



time for the stock to reach an equilibrium point. At $F = 0.05$, and after roughly 7–8 years, catch would be higher under the STD model than for the DDM model (Fig. 9). Spawning-stock biomass would also be considerably higher, about 1.7 million mt for the STD model versus about 1.1 million mt for the DDM model (Fig. 9).

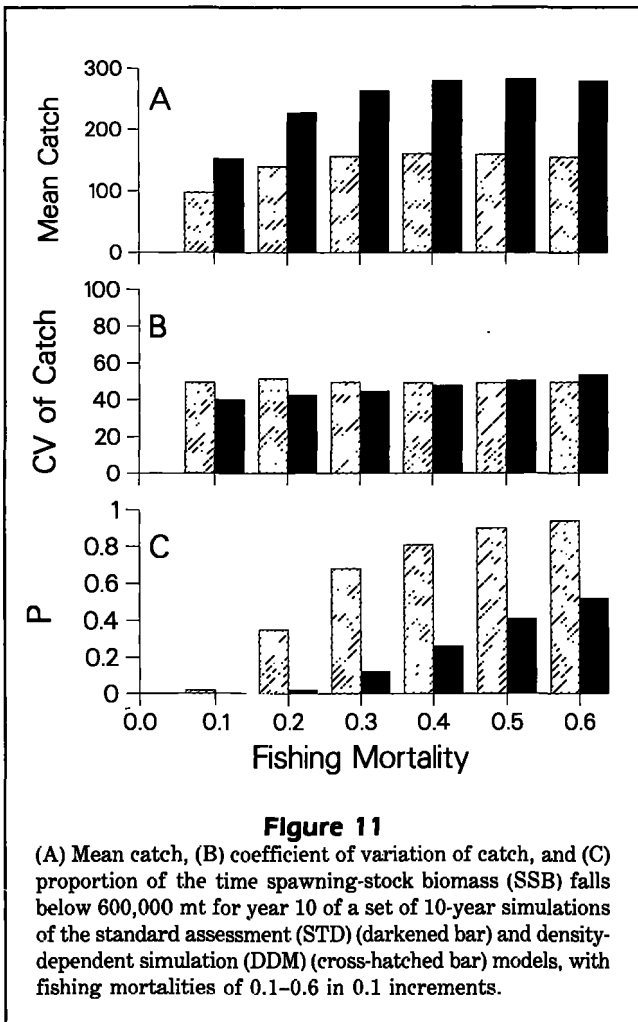
Fishing the stock at $F_{0.1}$ for a 15-year period would result in an equilibrium catch of roughly 250,000 mt (STD) versus 150,000 mt (DDM) after about 7–8 years (Fig. 10). The spawning stock would appear to be much higher, 1.1 million mt versus 615,000 mt, for the STD and DDM models, respectively (Fig. 10).

To evaluate the overall differences between the two models, two measures of performance and one measure of risk were produced for fishing mortality values ranging from 0.1 to 0.6, in 0.1 increments for a total of 1000 runs of each model. Mean catch, coefficient of variation (CV) of catch, and proportion of time the spawning stock fell below 600,000 mt, the management plan

benchmark, were calculated for year 10 of the simulation. Based on the previous model runs, the tenth year of the simulation appeared to be a reasonable choice for a summary year (Figs. 9, 10).

Mean catch would continue to increase dramatically under the STD model until F reached about 0.40 and would remain relatively constant thereafter. Yields would also steadily increase for the DDM model at F 's ranging from 0.1 to 0.3, but would remain constant after that point (Fig. 11A). A comparison of expected yields under the two models suggests that the STD model is always more optimistic, especially at the higher levels of fishing mortality (Fig. 11). Mean catch at $F = 0.5$ would be about 125,000 mt higher under the STD model.

Variability as measured by CV's of the catch increased with increases in fishing mortality for the STD model, but remained relatively constant at about 50% for the DDM model. Thus the STD model is more optimistic at lower levels of fishing mortality and becomes



progressively more variable as fishing mortality increases (Fig. 11B). Both models have relatively high CV's at all levels of fishing mortality, suggesting a large range in possible catches.

The minimum spawning-stock criteria of 600,000 mt is a threshold biomass defined in the present fishery management plan. This value was chosen by managers because a relatively clear demarcation point between low and high recruitment is evident in the 1962–85 stock-recruit data series (Anderson 1985). When the simulation results are expressed relative to the proportion of times the SSB drops below the 600,000 mt level for each model, the STD model appears to be much less prone to risk and, therefore, is much more optimistic than the DDM model results. The proportion ranges from 0.0 at $F = 0.1$ to about 0.52 at $F = 0.6$ for the STD model, while P ranges from 0.01 to 0.94 for the DDM model (Fig. 11C). The STD model results suggest that there is little risk of the SSB dropping below the threshold, even at fishing mortality rates

of 0.4–0.5 (Fig. 11C). The DDM model results are much less optimistic, suggesting the need for some concern at fishing mortality levels of 0.3 and greater (Fig. 11C).

Discussion

Biological interactions may play an important role in regulating marine ecosystems (Sherman et al. 1981, Walters et al. 1986, Overholtz and Tyler 1986, Overholtz et al. In press). Species interactions are becoming an important fishery management issue, and assessment advice is increasingly contingent on these mechanisms (Anderson and Ursin 1977; Pope 1976, 1979; Shephard 1984; ICES 1987, 1988). This study indicates that the stock dynamics of Atlantic mackerel are not only influenced by fishing, but that predation and intraspecific compensatory mechanisms including density-dependent growth are strong influences that probably effect yield forecasts and management advice in the short and long term.

Large differences in mackerel growth suggest that year-class size partially influences the initial pattern of growth during a cohort's first several years. Adult stock size probably plays an important role in regulating growth after a year-class recruits to the adult portion of the population (Overholtz 1989). Declines in growth are probably significant as stock biomass increases (Overholtz 1989). Model results, although not presented in this paper, suggest that mackerel would reach a larger size if the mackerel stock were fished more heavily. Larger catches of Atlantic mackerel would probably cause growth to stabilize at higher rates, and more of the annual production would be available for harvest.

Predation mortality rate has usually not been accounted for in the past in most assessment work, but recent studies have shown the importance of including this mechanism to enhance stock assessments (Anderson and Ursin 1977; Shephard 1984; ICES 1987, 1988; Overholtz et al. 1990). Our analysis suggests that predation probably has a major influence on the dynamics of Northwest Atlantic mackerel. Predation mortality is probably the largest component of natural mortality on this stock, since other sources such as general diseases, parasitism, and epizootics are not thought to be important sources of mortality on most fish stocks on an annual basis (Anderson 1979). Strong year-classes of mackerel may attract elevated levels of predation, in contrast with the usual assumption of constant natural mortality. Other studies have suggested that predation mortality rates should continually decline or remain constant as abundance increases (Sparre 1984). Our model results indicate that preda-

tion mortality rates on Atlantic mackerel are probably much higher than previously thought.

The results of the model projections show that unless the impacts of compensatory mechanisms are accounted for, evaluations of current stock status using the current standard assessment methodology may, in fact, be optimistic and risky if catches are increased to high levels in the future (Fig. 11). The differences in results between the two models are, of course, contingent on the parameterizations of the growth and predation mortality submodels and how recruitment is scaled in the density-dependent model. Two advances in research on mackerel would help to improve our ability to assess the stock: An MSVPA to provide correctly scaled estimates of recruitment, and a general predation mortality model that would provide useful estimates of M_2 's for forecasting purposes. Although recent assessment advice indicates that catches can be increased on the mackerel stock (Overholtz and Parry 1985), it perhaps needs to be modified to accommodate the results of this study.

The current management regime relies on catch and stock size projections based on an $F_{0.1}$ strategy. The use of a reference point such as $F_{0.1}$ is probably not very useful for mackerel since growth, sexual maturity, and natural mortality rates appear to fluctuate considerably. This concept is best applied in situations where these important variables are stable in the long term. A more appropriate approach might be to remove a moderately large sustainable catch annually or apply an appropriate constant effort level over several years, preserve a reasonable amount of spawning-stock biomass, and monitor the results. This method would be keyed to some of the uncertainties in stock dynamics that we have investigated in this study and would provide information on stock responses with a low probability of stock collapse (i.e., $F = 0.2-0.3$; Fig. 11C).

Additional analyses are necessary to confirm the population processes that were modeled in this study. Weights of individual fish should be monitored closely to assess future changes. Sexual maturities of ages 2-3 fish should also be followed annually. Collection of these data would also allow better parameterization of the growth and maturity models. Sufficient samples must be collected at the correct times to assess whether these two variables, particularly percent maturity, are continuing to change with stock density. Additional food habits sampling at critical times and places would help confirm and quantify the relationships found in this analysis. Obtaining some information on predation mortality on age-0 mackerel would be valuable.

Preliminary data suggest that predator preference may play an important role in determining the levels of predation on available prey species. Recent declines in sand lance *Ammodytes dubius* populations may in-

crease predation mortality on mackerel and Atlantic herring *Clupea harengus*. This points to the need for a multispecies VPA where simultaneous impacts of predation may be investigated. Improved predation models that account for predator preference and prey abundance would allow for more accurate predictions of the impacts of these important factors, and better management advice could be provided (Livingston 1986). Larger mackerel are preyed upon by marine mammals, large pelagic fishes, and sea birds (Stillwell and Kohler 1982, 1985; Payne and Selzer 1983; Payne et al. 1984; Overholtz et al. 1990). The impact of these predators is no doubt important, but was not evaluated in this study.

Acknowledgments

We thank the personnel from the Northeast Fisheries Center and other institutions who have collected data on research surveys over the last 25 years. We are grateful to the foreign fishery observers and scientists who collected data from the Polish commercial fishery. Special thanks to Louise Dery who provided the age data for the study. We would also like to thank Brian Rothschild for his guidance and insight in the initial phases of this research.

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