The Effects of Density Dependent

Population Mechanisms

on Assessment Advice

for the

Northwest Atlantic Mackerel Stock

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October 1988

Recent issues of this series:

The Effects of Density Dependent Population Mechanisms on Assessment Advice for the Northwest Atlantic Mackerel Stock

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SUMMARY

The fishery for Atlantic mackerel has been important in the United States for almost two centuries. More recently, catches have been dominated by foreign fleets, peaking at 430,000 metric tons (mt) in 1973. Several years of overfishing resulted in a collapse of the stock prior to the Magnuson Fishery Conservation Management Act (MFCMA). Since that time, the stock has increased, landings for 1983-86 averaged 52,000 mt, and fishing mortality has remained low. Recent assessment advice based on an $F_{0.1}$ management strategy has indicated that catches in the 300,000 mt range are feasible. Indications are, however, that the stock has increased to the point that compensatory responses are becoming important.

A study of recent trends in growth showed that cohorts since 1980 are growing much more slowly and that average size of fish has declined by 30-40 percent. Predation on young mackerel, primarily ages 1 and 2, has increased; predation mortality rates on large year classes are higher than on smaller ones. Results from modeling exercises suggest that recent assessments have correctly followed new trends in this stock, but advice based on a standard single species model has been too optimistic. Stock rebuilding since 1978 has been very successful and biomass exceeds 1,000,000 mt. However, if recruitment continues to be relatively high, small catches, such as in the last several years, will not insure that annual increases in the stock will continue to occur. If catches were increased to 150,000-200,000 mt, the spawning stock would not be appreciably lowered and trends in growth could be reversed or stablized. Fishery management goals, such as maintenance of a minimum spawning stock and sufficient biomass for a viable recreational fishery, could also be preserved.

INTRODUCTION

Atlantic mackerel (Scomber scombrus) have historically been important to the USA domestic fishery; records from the early 1800s to the 1980s suggest that cumulative landings have been 7 to 8 mt over that time period (Sette and Needler 1934; Hoy and Clark 1967; Anderson 1985). A thriving domestic industry used mackerel well into the 1940s until landings dropped because of declines in abundance, availability, and increased production of fresh and frozen white fish products (haddock, cod, etc) (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 (Anderson 1985). Since many of the important species in the region have declined recently, the US industry has become more interested in mackerel as a volume (low price, high catch) fishery.

Several distinct management regimes have been in effect for mackerel since the early 1970s when the International Commission for the Northwest Atlantic Fisheries (ICNAF) first allocated quotas to various countries. In March of 1977, mackerel were managed under a U.S.Preliminary Management Plan (PMP) under authority provided by the Magnuson FMCA of 1976; later replaced by the Atlantic Mackerel Fishery Management Plan (FMP) in February of 1980. The Mid-Atlantic Fishery Management Council more recently merged the three FMPs for squid, mackerel, and butterfish into one plan originally implemented in September of 1983. Since that time several amendments have followed, specifying a minimum spawning stock biomass for mackerel, annual catch quotas, and moving the fishery reporting period to the calender year. Current management objectives 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.

Landings of mackerel from the Northwest Atlantic were dominated by distant water fleet catches from 1960 to 1986 (Overholtz and Parry 1985). Total catch in 1960 was 10,000 mt, increasing steadily to a peak of 430,000 mt in 1973, dropping precipitously to 78,000 mt in 1977 and averaging about 31,000 mt between 1978 and 1982. Landings have since increased, averaging 52,000 mt during 1983-86, due to an increase in landings from joint venture fisheries and some increases in the Canadian fishery in the Gulf of St Lawrence and along the Newfoundland coast (Overholtz and Parry 1985).

Recent estimates suggest that the size of the stock has increased since the late 1970 collapse. 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 (Anderson 1985; Overholtz and Parry 1985). Assessment advice during the last several years based on an $F_{0.1}$ management strategy, has indicated annual catches in the 300,000 mt range are feasible. Allocations to joint ventures have increased dramatically over the last several years, amounting to about 75,000 mt in 1987. Recent landings, however, have remained well below the 300,000 mt level and fishing mortality has averaged only about 0.07 since 1980 (Overholtz and Parry 1985).

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Pelagic, schooling species such as mackerel are important in the trophic dynamics of fishery ecosystems, supporting populations of fish, birds, and marine mammal predators. Additionally, such stocks may at times increase to densities that inhibit their own population processes (growth, mortality), and those of competitors. Evidence exists that mackerel exhibit strong density dependent growth (McKay 1979, Lett 1980). A negative relationship between mean length of age 1 and 2 fish and respective year class size was detected in another study (Dery and Anderson 1983). Length frequencies of mackerel from Polish trawlers fishing during 1985-87 show that the modal length in the fishery has changed little, from 30 cm in 1985 to 33 cm in 1986 and 34 cm in 1987, indicating that the strong 1982 year class is growing very slowly (Unpublished data, Woods Hole Laboratory 1987). Such data indicate that growth rates have slowed considerably since the late 1970s when the stock size was much smaller. Other important biological factors such as percent mature and fecundity at age are also known to be responsive to major increases or decreases in stock size for other species (Overholtz 1987; Beacham 1983). Natural mortality rates due to predation (M_2) may also change with fluctuating stock size. A preliminary analysis of feeding data of mackerel predators suggested that natural mortality rates (M_2) for this stock were higher during 1973-75 when relatively large numbers of small fish were available, and declined during 1976-80 when the stock was composed of relatively few small fish (NEFC 1987).

This study examines the effect of stock density of the Northwest Atlantic mackerel on growth, sexual maturity, and natural mortality rates. Implications of changes in these factors on catch, stock size, 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. The model should be useful for providing advice on the status of this important ecological and commercial resource.

METHODS

Data on potential density-dependent population regulatory mechanisms were derived from research vessel survey data and commercial catch sources. Data from spring groundfish surveys, conducted by the Northeast Fisheries Center (NEFC) from 1976 to 1985, were examined to ascertain if a relationship existed between mean weight at age and stock size. Plots of age 1 to 14 mean weight vs. VPA stock size (1+ numbers) were examined to see if any age group appeared to show a negative relationship with stock density. The scatter diagrams for ages 1 to 5 indicated that mean weight possibly declined with increasing stock size, consistent with previous studies that suggested a density dependent relationship for young mackerel (Dery and Anderson 1983). To quantify the relationship between mean weights of age 1 to 5 mackerel and stock size, regression analysis was performed on each age group. In addition, regressions of commercial mean weight at age vs. VPA stock size (numbers) for 1967 to 1985 were fit to further examine the relationship between growth and stock size.

Individual fish weights obtained on spring surveys and Polish commercial trawlers for the 1978 to 1982, and 1984 year classes at age 1, 2 and 3 were examined and tested with non-parametric ANOVA (Kruskal-Wallis tests) to determine if there were differences in weight between year classes. Non-parametric measures were chosen because they do not require assumptions about the underlying distributions of the sample populations and they are nearly as powerful as parametric tests. Data obtained on surveys from 1979 to 1986 were assembled, but sample sizes were different (N=30...100); it was decided to randomize the data and provide a set of equal sample sizes for each year class. The sample with the lowest number of observations was chosen as the minimum sample size and the subsamples were picked randomly to equal this minimum number. The sample sizes obtained were 36,30 and 50 for the age 1,2 and 3 analyses respectively. The sample sizes chosen for this analysis are more than adequate for the tests of significance that were performed (Hollander and Wolfe 1973).

Kruskal-Wallis tests were used to determine if significant differences between weights at age of fish from recent year classes were present. Data were available to test age 1 differences for the 78,80,81, and 82 year classes, 78,79,80,81,82,84, year classes at age 2 and the 78,81, and 82 year classes for age 3. Comparison estimators were then calculated to determine which year classes were statistically different for each age group (Hollander and Wolfe 1973). This test is a series of two sample comparisons isolating year class differences and the faster growing cohort. Finally contrast estimators were obtained for each set of two sample comparisons (Hollander and Wolfe 1973), allowing the magnitude of the difference between each two sample pair to be calculated; in this case the difference in weight (grams) between each year class. Regressions for age 1 and 2 mackerel were also completed to determine if there was a relationship between year class size and mean weight at age of a year class. There were not enough age 3 data available to attempt an analysis on this age group.

Maturity data from 1981 to 1986 were evaluated to ascertain if percent maturity at age 2 and 3 changed over the time period. Data were obtained from spring survey cruises and the Polish fishery. Information was summarized by age group and the percent of immature and mature fish at ages 1 to 4 were calculated. Only these age groups were examined since fish older than age 4 are always mature.

Consumption of mackerel by spiny dogfish, Atlantic cod, and silver hake was also estimated. Summaries of the NEFC food habits data base suggested these species are the most important predators of mackerel (Bowman et al. 1976; Maurer and Bowman 1975; Langton and Bowman 1980). Consumption information was then used to determine if natural mortality rates, due to predation (M2), remained constant over a range of stock sizes. 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, availability 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).

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$$C(i) = B(i) \cdot \%BW \cdot \%Rm(i) \cdot Tr \tag{1}$$

$C(i)$ = Consumption 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
i = 1,3

$$CN(ij) = C(i) \cdot F(j)/ Wt(j) \tag{2}$$

$CN(ij)$ = Number of age j mackerel consumed by i
$F(j)$ = Frequency of age j mackerel in the stock
$Wt(j)$ = Mean weight of age j mackerel
j = 1,2

The Northwest Atlantic mackerel stock is concentrated in the Mid-Atlantic region during the late autumn and winter, beginning a northward migration in March. The southern contingent spawns along the New Jersey coast from mid-April to May and the northern contingent traverses Georges Bank in May and moves into the Gulf of St. Lawrence in June to spawn (Figure 1; Sette 1950). Juvenile fish are distributed inshore of the adults until they are about two years of age. The juveniles follow roughly the same migratory pattern as the adults, proceeding up the coast more slowly (Sette 1950). During a portion of the year, the distributions of juvenile fish coincide with those of spiny dogfish, silver hake, and cod (Sette 1950; Almeida et al. 1984). This occurs from September to May for spiny dogfish, March to June and September to December for silver hake, and April to October for cod (Almeida et al. 1984). These overlap times were used to calculate consumption estimates for the three predators.

Research survey food habits data from 1981 to 1985 were examined to determine the size distribution of mackerel as prey items in the three fish predators. These data were chosen since detailed records of predator length 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 (Table 1; Figure 2). These fish were predominantly age 1 and 2 from the 1981 to 1983 year classes (Table 1; Figure 3). Food habits data collected from 1973 to 1980 did not include individual lengths of prey items, but maximum, minimum, and average lengths of fish prey were recorded. Virtually all the mackerel consumed in these years were less than 30 cm long. Our analysis thus centered on predation on age 1 and 2 mackerel. Young-of-the-year mackerel probably comprise a large portion of predator diets, but since the data base is not adequately represented by inshore sampling, the problem cannot be addressed currently. A portion of young-of-year and age 1 fish that origininate from

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spawning by the northern contingent in the Gulf of St. Lawrence remain on the Scotian shelf in the autumn (Stobo 1976; Kulka and Stobo 1981). Our analysis did not attempt to address predation on this component of the stock, but consumption by cod, silver hake, and spiny dogfish undoubtedly also occurs there.

Food habits data collected on various research vessel surveys (Bowman et al. 1976; Maurer and Bowman 1975 for more details), were evaluated for the incidence of mackerel predation by the selected predators. Total food consumed (all species) by each predator was calculated and the percentage of mackerel by weight comprising the diet of each predator was estimated separately for the periods 1973 to 1976 and 1977 to 1980. These two time periods were chosen because the food habits information was collected slightly differently in each period, and because the availability of small mackerel was much different in each of the periods. Large numbers of 1 and 2 year old fish were available during 1973-76, but were sparsely represented from 1977 to 1980 (Figure 4).

Daily ration estimates for each predator were based on those computed in previously reported studies. Silver hake were estimated to consume 1.007 and 0.607 percent of their body weight (BW) per day for spring and autumn respectively (Durbin et al. 1983). Cod consume 0.930 and 0.837 BW per day for spring and autumn respectively (Durbin et al. 1983). Since no seasonal estimates are available for spiny dogfish, an annual estimate of 0.810 BW per day was used in the analysis (Bowman et al. 1984).

Many species that are predators of fish as adults feed on invertebrate prey as juveniles (Maurer and Bowman 1975; Bowman et al. 1976; Hacunda 1981; Cohen and Grosslein 1981). The change to a fish diet occurs at about 50 cm for cod and 30 cm for silver hake (Bowman and Michaels 1984) corresponding to roughly age 3 fish. For these two species 3+ stock biomass from the southern stock of silver hake and the Georges Bank cod stock, were used in the calculations of consumption (Almeida 1987; Serchuk and Wigley 1986). Since VPA stock size was not available for cod over the period 1973 to 1977, a regression of VPA 3+ biomass vs. autumn survey 3+ catch per tow was developed to predict 3+ biomass for the additional years. Spiny dogfish predator biomass was calculated based on a length rather than an age structured model (Waring pers. com. 1987). The transition to a fish diet also occurs at about 50 cm for spiny dogfish (Nammack 1982; Bowman et al. 1984). Available data were previously summarized in 36 to 55 and 56+ cm categories (Waring pers. com. 1987), therefore an estimate of 56+ cm biomass was used to calculate consumption estimates since many of the fish in the 36 to 55 cm range were not predominantly picivorus (Bowman et al. 1984). A three-year moving average of spiny dogfish biomass (derived from expanded trawl survey data) from 1973 to 1980 was used to smooth the variability in the research survey biomass estimates.

Consumption estimates for each species were derived by using 3+ predator biomass to calculate total yearly consumption which when combined with the %BW, and predator-prey co-occurance times, gave the total amount of mackerel consumed annually. Ratios of the numbers of age 1 and 2 fish in the stock were obtained from a previous VPA and used with an estimate of mean weight at age to calculate the total number of age 1 and 2 fish consumed. This method

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assumed that the estimate of 3+ biomass was an appropriate measure of the average standing stock present during the year, that the ratios from the previous VPA were valid relative proportions, and that mackerel consumed were only age 1 and 2 fish. The estimates were made for 1973 to 1980 for each species and the total number of age 1 and 2 fish consumed annually was estimated.

Consumption estimates were combined with landings at age for 1973 to 1980 and a new VPA was completed for these years. A residual natural mortality rate (M1) of 0.20 was used in this analysis to account for other sources of mortality at age 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 to 1980. These values and the new stock size at age estimates were used in regressions to ascertain the relationship between M2 and year class strength. Using the results of this analysis a functional model relating M2 to year class strength at age was fitted and used to predict predation mortalities.

RESULTS OF DATA ANALYSES

Regressions of survey mean weight at age vs. stock size suggested that at ages 1 to 3 a significant negative relationship existed, and for age 4 a similar but non significant (P=.195) relation was present (Table 2). For age 5 there was no relationship or a weak positive relationship between these two variables. These results agree closely with a previous study indicating a similar negative relationship for age 1 and 2 mackerel (Dery and Anderson 1983). Since the mean weights used in this analysis were calculated from a length weight equation, some of the subtle and important annual differences that might be present may have been obscured. If in fact mackerel under crowded conditions weigh less at a given length than under less dense concentrations, then the slope of the relationship would be underestimated. Results from analysis of the commercial mean weight data suggest a negative relationship between weight and stock size for ages 1 to 9 (Table 3). The results are significant at P=0.05 for ages 2 to 4 and nearly so for ages 1 and 5 (Table 3). Beyond age 5 the relationships were not significant at the 0.05 level.

Mean size at age was much different for the various year classes (Figure 5). Growth analyses based on individual weights of fish from different year classes (1978 to 1982, 1984) indicated very different annual growth patterns in the stock from 1979 to 1985. The Kruskal-Wallis tests showed that significant differences exist among age 1 to 3 fish for all the year classes investigated (Tables 4,5,6). Multiple comparison estimators for age 1 fish showed that the 1980 year class attained the largest size of all the cohorts sampled. The 1978 and 1980 year classes both grew faster than the 1981 and

1982 cohorts (Table 4). Contrast estimators for this age group showed that on average the 1980 cohort was almost 37 and 50 g larger than the 1981 and 1982 cohorts, respectively (Table 4; Figure 6).

Several more year classes were available for analysis of relationships at age 2. The 1978 to 1980 year classes all grew faster in the second year of life than the 1981, 1982 and 1984 cohorts (Table 5). The results indicate that the 1979 year class was about 81, 110 and 91 g larger than the 1981, 1982 and 1984 cohorts respectively (Table 5; Figure 6). In all cases the 1982 year class showed the slowest growth of any cohort, followed by the 1984 and 1981 cohorts. The 1984 year class, although similar in size to the 1981 year class, appears to have grown more slowly (Figure 6).

Information for the analysis of growth patterns for age 3 fish were only available for the 1978, 1981, and 1982 year classes. This was because other cohorts were not sampled adequately in the NEFC survey and Polish commercial fishery. The three year classes were significantly different in average weight at age (Table 6). Comparison estimators show that the 1978 year class was significantly different and larger than the 1981 and 1982 year classes and that the 1981 year class fish were larger at age 3 than the 1982 year class (Table 6). Contrast estimators further indicated that the 1978 year class averaged 70 and 119 g larger than the 1981 and 1982 year classes, respectively (Table 6; Figure 6).

When mean weights at age 1 and 2 were used in regressions with year class size at age from VPA, correlation coefficients were relatively high (R= -.77, -.75, respectively). The relationships were not significant at P=0.05 for age 1 and 2 (P=0.226, 0.082) respectively, but this is not surprising since there were only a few data points. Analysis of the age 3 data was not attempted since only three data points were available.

Analysis of maturity data indicated the percent mature at age 2 and 3 fluctuated from 1981 to 1986, but without obvious trend. No fish were mature at age 1 and virtually all fish were mature at age 4. Percent maturity at age 2 ranged from 17 % in 1984 to 53 % in 1983. Percent mature at age 3 ranged from 67 % in 1986 to 98 % in 1983 (Table 7). Sample sizes were relatively small in some years; the data had been collected in conjunction with age sampling, and during the critical time of gonadal development in middle to late April, maturity samples were sparse because age sampling requirements had been fulfilled and no additional maturity samples were processed. The assumption of a 50 % and 100 % maturity ogive at ages 2 and 3 respectively is probably unrealistic. There was an apparent negative relationship with increased stock size and no consistent pattern at age 3. A good statistical design and sampling program for collecting maturity data for mackerel would allow for hypothesis testing to determine if percent maturity at age declines with increased density. 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.

Percentage of mackerel in the diets of predators was quite different in each of the two time periods (1973 to 1976 and 1977 to 1980; Table 8).

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Estimates for spiny dogfish during the 1973 to 1976 period were from Bowman et al. (1984). No occurrences of mackerel predation by cod or spiny dogfish were recorded for 1977 to 1980; an arbitrary value of 0.10 % (by weight) was used however, based on the assumption that at least some small level of predation had occurred during these years (Table 8). These percentages were used to compute the total annual consumption of mackerel by the three predators.

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 9). A VPA that included consumption and landings was completed. Results indicate that consumption of mackerel from 1973 to 1976 was significant. Sizes of incoming year classes increased from one- to twofold in the revised VPA over the 1973-80 period (Tables 10,11). Mortality rates of age 1 and 2 fish (F+M2) also increased markedly (Tables 10,11). When mortality rates from the VPA were apportioned by consumption estimates and landings it was apparent that natural mortality rates (M=M1+M2) were much higher in the 1973-76 period, when mackerel were abundant, than in 1977-80 (Table 12).

The predation mortality rates from this analysis were used in a regression analysis to examine the relationship between M2 and year class size. 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. An examination of the scatter plots from these two regressions revealed that the M2 value from 1976 was high relative to the number of age 1 and 2 fish in the stock. There were few age 1 fish available in 1976 (Figure 4); 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). This analysis suggests that natural mortality rates may change with year class size, large cohorts attracting a disproportionate increase in mortality. A positive relationship between stock 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 natural mortality rates was constructed to evaluate the potential impact of these population regulation 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; Overholtz et al. 1986). 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. 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. 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 with available empirical data, such that size at age 1 varied from 48 g for slow growing fish to 122 g for fast growing fish (Table 13).

$$Wt(1) = a - b(N1) \qquad (3)$$

$Wt(1)$ = Average weight (grams) at age
$N1$ = Year class size at age 1 (numbers)
a,b = Parameters

Age 2 to 5 growth was determined by relationships between adult stock size (numbers) and growth at age.

$$Wt(i) = Wt(i-1) + G(i) \qquad (4)$$

$Wt(i)$ = Average weight at age i, i=2,5
$G(i)$ = Annual age specific growth increment (grams)

$$G(i) = a(i) - b(i)SS \qquad (5)$$

SS = Total adult stock size (numbers)
a,b = Age specific parameters

Growth increments (ranges) for age 2 to 5 fish are shown in Table 13. The increment from ages 2 to 5 was smaller the larger the adult stock. Fish weight at ages 1 to 5 was the result of growth in the first year and subsequent increments at ages 2 to 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 been sufficient to reduce a cohort to low levels. Beyond age 5, the negative relationship between mean weight and stock size was less intense.

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

$$PM(i) = a - b(SSB) \qquad (6)$$

$PM(i)$ = Percent mature at age i, i=2,3
SSB = Spawning stock biomass
a,b = Parameters

The maturity of age 2 fish can vary from 20 to 50% while maturities for age 3 fish range from 70 to 100%.

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Natural mortality due to predation (M2) for ages 1 and 2 fish was estimated from a relationship between M2 and year class size at age.

$$M2(i) = a\{1-\exp[-b(N(i))]\} \tag{7}$$

$M2(i)$ = Natural mortality due to predation on age i, i=1,2
$N(i)$ = Year class size at age i, i=1,2
a,b = Parameters

M2 mortalities on age 1 and 2 fish could reach 0.9 and 0.5, respectively at high stock sizes. An asymptotic relationship was used since it meets the criterion of being an increasing function over the initial range of stock sizes, thus matching our regression results. Another property of this relationship is that it levels off at higher stock sizes, perhaps mimicking predator satiation when abundance is high.

The model was constructed to investigate the impact of different levels of fishing mortality, management strategies, and hypotheses concerning the role of compensatory responses in regulating this stock. Several different recruitment patterns were simulated in the model runs to assess the effect of annual recruitment trends. Runs with constant and variable recruitment based on the recent pattern of recruitment to the stock were accomplished. Results from the model were compared to forecasts from the 1986 assessment or standard model (Table 14).

MODEL SENSITIVITY AND VALIDATION

A series of runs with different combinations of density dependent growth, percent maturity and M2 mortality rates were performed to examine the sensitivity of catch in 1987 and spawning stock in 1988 and 1991 to these mechanisms. In runs where only a single variable was examined, catch was most affected by changes in the growth pattern (mean weights) of the stock (Table 15). Spawning stock in 1988 on the other hand was sensitive to changes in percent maturity while M2 influenced 1991 spawning stock to the greatest degree. 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. 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 (Table 15). These runs suggest that advice based on the static parameters in Table 14 would have over-predicted catch by about 7% in 1987 and spawning stock size in 1988 by about 11%. Furthermore, if the standard model were used to project more than a few years into the future with some estimate of recruitment, the estimate of spawning stock would be too large; the 1991 estimate would be lower by 35% (Table 15).

Other model runs were designed to give some indication of how sensitive the model was to changes in the values that were used to parameterize the various mechanisms. Only selected mechanisms were studied since there were

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many possible combinations and it would be difficult to examine all the alternatives. The sensitivity of age 1 growth in the model to changes in parameters was studied by observing changes in catch, stock biomass, and spawning stock (SSB). Parameters were varied by 25% in a positive and negative direction and were systematically changed so that all eight combinations of two parameters could be studied. The experiments were completed with all three density dependent factors in operation because this was the model of interest. Since growth is modeled with linear functions, the changes that were observed in model outputs were symmetrical; for instance a 25% increase in the 'a' parameter in equation 3 produced a positive change in catch, stock and SSB and a 25% reduction in this parameter produced a negative response of equal magnitude. The maximum response occurred when both parameters were varied in opposite directions; stock biomass showed the greatest change (Table 16). In general, catch and SSB showed little variation over all eight model runs, while stock biomass levels fluctuated more, to a maximum of 9.4%. The model did not appear to be very sensitive to changes in growth alone.

Another similar experiment was used to study the response of the three variables to changes in the natural mortality model. The runs were structured exactly as in the above example, but the results were not symmetrical since this model is not linear. The maximum range in values was again obtained when the parameters were varied in opposite directions. Changes in catch were small except when 'a' was decreased and 'b' increased, resulting in a 12.4% increase (Table 17). Changes in stock size and SSB were greatest when both parameters were manipulated and the maximum response also occurred with decreasing 'a' and increasing 'b', up to 17.1% and 16.3% respectively. The model, under some circumstances, appears to be sensitive to changes in the parameters in the natural mortality model.

Since the maturity data used to parameterize the percent maturity vs. spawning stock relationship in equation 6 was rather scanty, several sets of parameter values were used to assess the impact on the size of the spawning stock. Parameters were changed according to an arbitrary increase of 50% resulting in values hereafter referred to as high, medium, and low. The high option values for age 2 and 3 parameters correspond to the base model, while the medium and low runs are successive 50% increases in percent maturity respectively. The high option resulted in a 4% decrease in SSB, while each successive increase in percent maturity at age resulted in a 50% reduction to 1% for the low option. The model does not appear to be very sensitive to changes in the percent maturity at age.

The model was validated by comparing the different outputs produced by the various mechanisms to available empirical data. In some cases relationships were re-parameterized or tuned to produce results in the same ranges as observed in the empirical data base. The model was used to investigate a variety of different problems. Runs from the 1986 assessment (key runs) were compared to 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. Key runs were parameterized with the same data as that used in the 1986 assessment (Table 14; NEFC 1987).

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MODEL RESULTS

An attempt was made to compare the results of further stockpiling of fish on expected catches and spawning stock size. Over the last several years the stock has increased dramatically, growth has slowed, and natural mortality (M2) has increased. To address this problem a series of 10-year projections with three different recruitment patterns were used to compare the density dependent model results with projections from the traditional model. Recruitment was scaled upward by a factor of 1.6 to account for the results of the new VPA when using the density dependent model. Fishing mortality was set at 0.05, a value close to the average rate over the last several years.

Option 1 is based on constant recruitment, the mean of the 1981-84 year classes. This option suggests that on average catch and standing stock would be expected to be about 16% lower, and spawning stock 25% lower than the static model projection (Table 18). Option 2, based on the actual pattern of recruitment observed during 1981-84, shows that the standard model again overestimates stock performance. Catch would be about 24% lower, stock size 29% lower, and spawning stock about 33% lower than the dynamic model (Table 18). Option 3 used about the same perspective, but recruitment levels equal to those observed in 1981,1982, and 1984 were used in the projection. This simulates a sequence where a very large year class is proceeded and followed by ones of moderate size over a 10 year period (Table 18). In this case catch is about 29%, standing stock 34% and spawning stock 39% below the expected responses from the traditional projections (Table 18).

To address the impact that different rates of fishing mortality would have on the stock, a series of projections over a range of F values from 0.05 to 1.00 were performed with the density dependent model. These simulations were completed under the same assumptions of recruitment as the previous example. Mean catch, standing stock, and spawning stock over a 10 year projection were calculated. The results of Option 1 suggest that an average catch of 170,000 to 223,000 mt could be removed annually over the long term and still keep the spawning stock at the 900,000 to 1,000,000 mt level (Table 19). Fishing mortality could be increased to as high as 0.60 and an average catch of 299,000 mt taken annually. This level of catch however, would drive the spawning stock down to near the 600,000 mt level (Table 19).

Option 2 suggests that in order to keep the spawning stock at roughly 1,000,000 mt an average catch of about 158,000 mt would be appropriate (Table 19). An F of 0.45 would cause the spawning stock to approach the 600,000 mt level and an F of 0.60 would lower the spawning stock to an average of 541,000 mt. Keeping F at near the present level of 0.05 would maintain the stock at near present levels over the long term, but the impacts of this strategy on growth and natural mortality have already been suggested (Table 18,19).

The third option shows that increasing F to between 0.15 and 0.25 would provide a catch of 169,000 to 220,000 mt and keep the spawning stock at somewhere near an average of 900,000 to 1,000,000 mt (Table 19). As in the first example F could be increased to 0.60 and an average catch of 293,000 mt removed annually, but the spawning stock would decline from present levels of over 1,000,000 mt to near 600,000 mt.

Applying different rates of fishing mortality will cause the standing stock to decrease as F increases and growth should respond by an increasing because the stock is thinned. Growth responses at different fishing mortality levels were examined to assess the changes that might be expected with changes in F. Recruitment options were the same as in the previous examples. The percentage change in growth at selected F values (0.15, 0.20, 0.30, 0.60) was calculated by comparing the growth at that fishing mortality to the growth pattern at F=0.05, near the present average F (Table 20). The results suggest that as F increased, the positive impact on growth increased. The response was similar for all three options except that higher positive increases were noted for Option 3 (Table 20).

DISCUSSION

There is evidence for the important role of biological interactions in regulating marine systems (Sherman et al. 1981; Walters et al. 1986; Overholtz and Tyler 1986). Species interactions are becoming an important fishery management issue and assessment advice is increasingly contingent on the effect of these mechanisms (Anderson and Ursin 1978; Pope 1976, 1979; Shephard 1984; ICES 1987). 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 affecting our traditional methodologies for short-term yield forecasting and perhaps altering management advice.

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. This study is in agreement with others that suggested a density-dependent link to growth in this stock (McKay 1979; Lett 1980; Dery and Anderson 1983). The magnitude of the difference between growth rates in some of the cohorts from the late 1970s and early 1980s was quantified in these analyses. The 1982 year class is one of the largest on record and its growth pattern one of the slowest. Survey and catch data suggest that the 1984 and 1985 year classes are at least moderate in size and the growth analysis from this study showed that the 1984 year class grew slower than the 1981, although similar in abundance. Recently aged samples show that there is considerable overlap in age at length for the 1981 to 1985 year classes (Figure 7).

Predation mortality rate has not been fully accounted for in the past, but recent studies have shown the importance of including this mechanism to enhance stock assessments (Anderson and Ursin 1978; Shephard 1984; ICES 1987). Our analysis suggests that predation has a major influence on the dynamics of Northwest Atlantic mackerel. Strong year classes attract elevated levels of predation, in contrast with the usual assumption of constant natural mortality. Other studies have suggested that M2 should decline or remain constant as abundance increases (Sparre 1984), but this analysis suggests that an increasing function is more appropriate; an asymptotic relationship was used in this study since it is reasonable to assume that predation mortality

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rates should stabilize as year class size becomes larger and larger because of predator swamping or satiation.

Size preference of fish predators was shown to be an important factor in evaluating the impacts of predation on mackerel. Few mackerel greater than 30 cm were eaten by fish predators examined. An interesting aspect of this finding that was not addressed in this analysis was the impact of reduced growth on predation. Since predation is by size rather than age and older slower growing age groups (3+) may remain within the predation window longer than normal if the stock is large. These fish would remain vulnerable to predation for a longer time and the adult stock of 3+ fish remains subject to fish predation (see Table 1). If predation tended to occur only on the youngest age groups and density dependence was not strong, then fishing will have little or no effect on this process since these young fish are only sparsely recruited. However, if the growth-predation hypothesis is operating in the stock then fishing mortality may also partially substitute for natural mortality. Larger mackerel are preyed upon by marine mammals, large pelagic fishes, and sea birds (Waring pers com. 1987, Stillwell and Kohler 1982, 1985; Payne and Selzer 1983; Payne et al. 1984). The impact of these predators was not evaluated in this study.

The results of the model projections show that unless the impacts of these compensatory mechanisms are accounted for, evaluations of the current stock status may in fact be optimistic. 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 this new information. Stock rebuilding since 1978 was successful and biomass is now in excess of 1,000,000 mt, however, continued small catches will not insure incremental annual increases in stock biomass. Removals that average 150,000 to 200,000 mt could occur annually without appreciably lowering the spawning stock and to possibly reversing the declining trend in growth. This would not be at the expense of council management objectives such as maintaining a minimum spawning stock size or sufficient biomass for a viable recreational fishery.

The current management regime relies on catch and stock size projections based on an $F_{0.1}$ strategy. The use of a biological reference point such as $F_{0.1}$ is probably not very useful for mackerel since growth and natural mortality 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 an average catch or maintain constant effort over several years, preserve a reasonable level of spawning stock biomass, and monitor the results. This method would be keyed more to the productive capabilities of the stock rather than a target level of fishing mortality.

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 to 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

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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 that were found in this analysis. Defining the incidence of mackerel predation on the Scotian Shelf and in the Gulf of Maine in summer would also be helpful. Obtaining some information on predation mortality on age 0 fish 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 populations may increase M2 mortality on mackerel. 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 more accurate predictions of the impacts of these important factors and better management advice could be provided (Livingston 1986).

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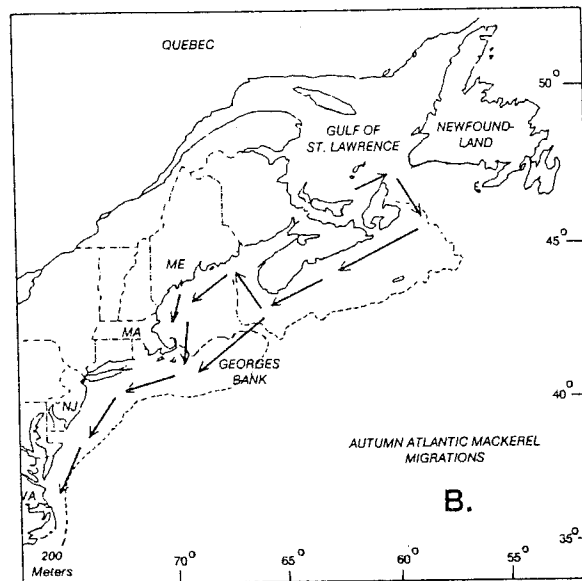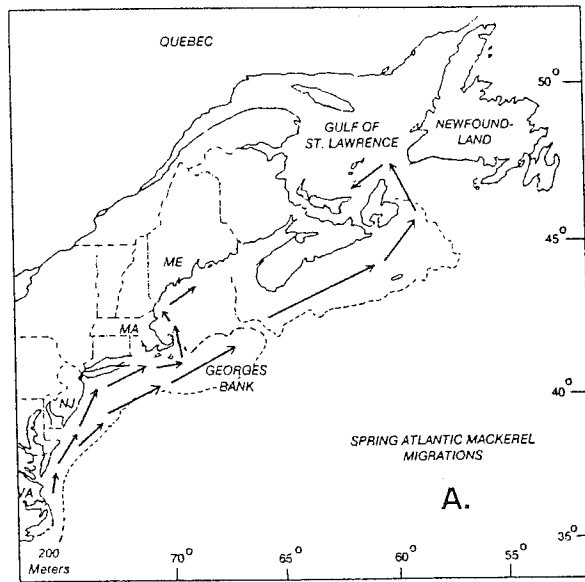
Figure 1. Migration routes of the Northwest Atlantic mackerel stock during the spring (A) and autumn (B) (from Sette(1950)).
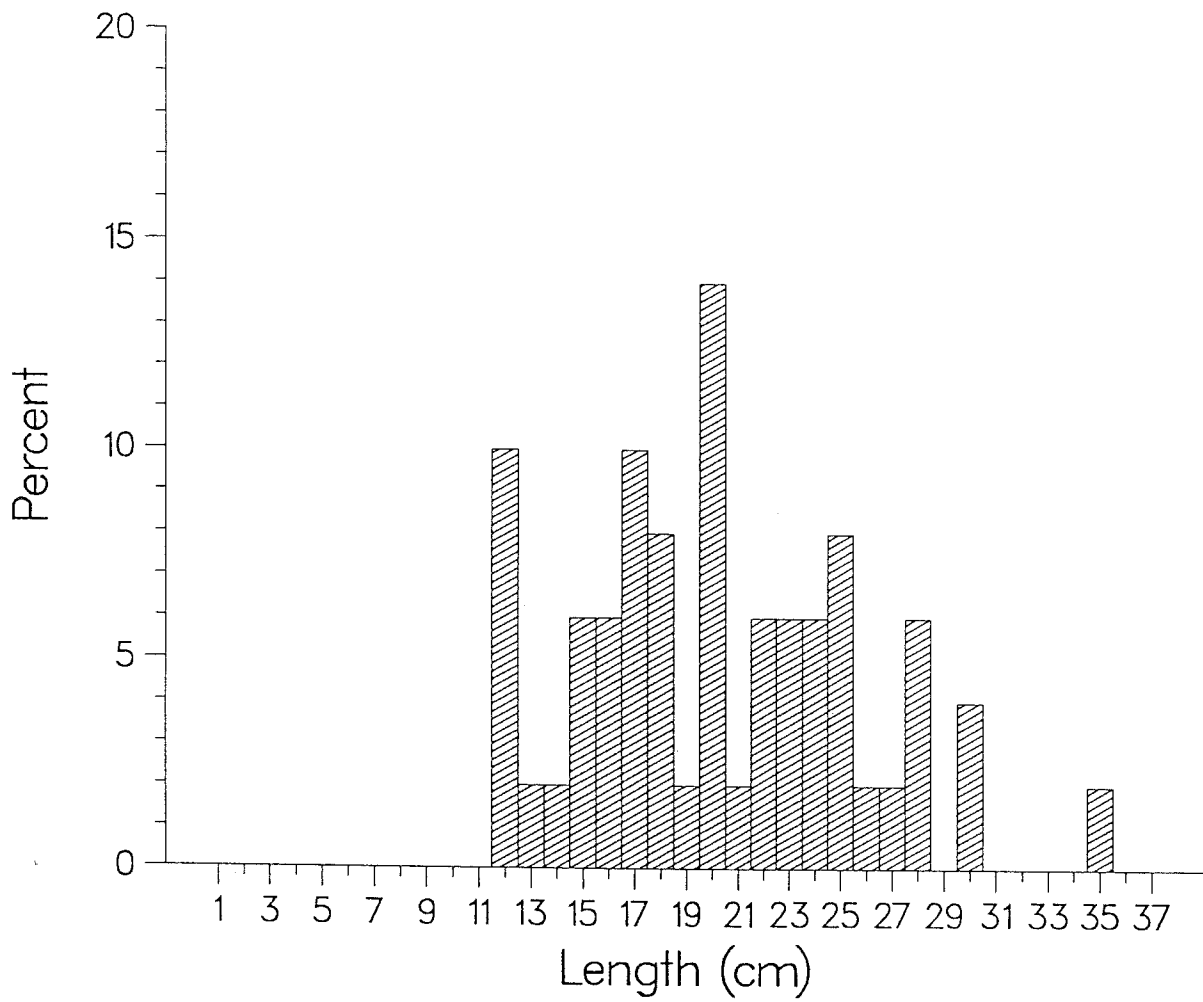
Figure 2. Length frequency of Atlantic mackerel obtained in stomachs of
silver hake, Atlantic cod, and spiny dogfish from 1982 to 1984
collected on NEFC cruises.

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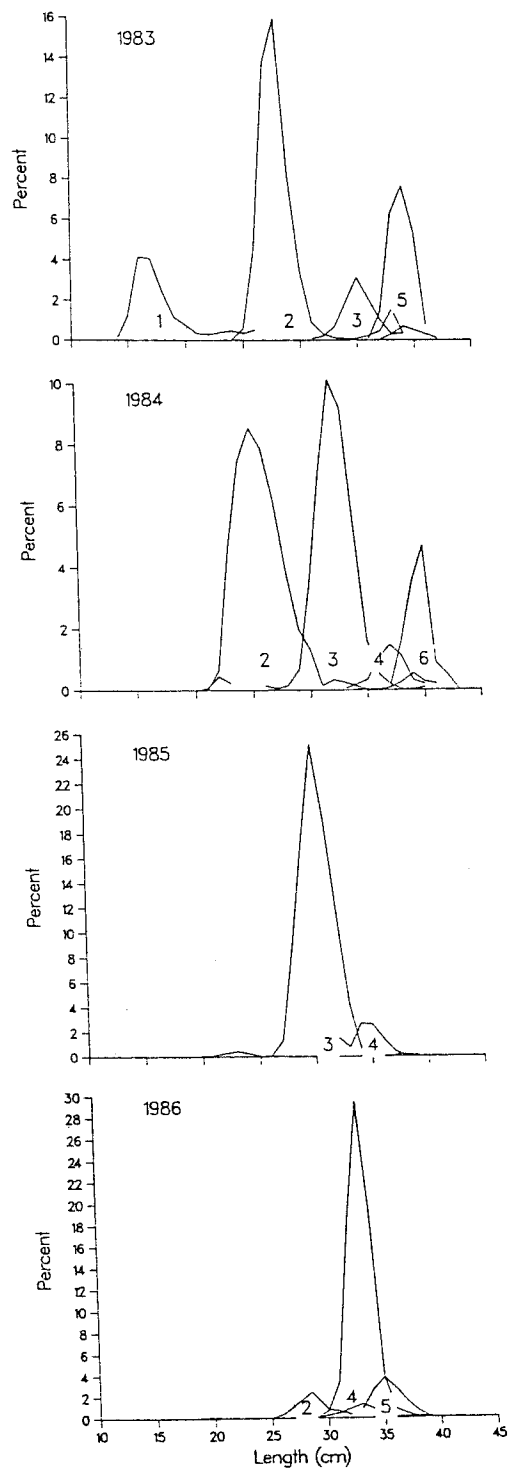
Figure 3. Length frequencies of Atlantic mackerel by age group for 1983 to
1986 from Polish catches.

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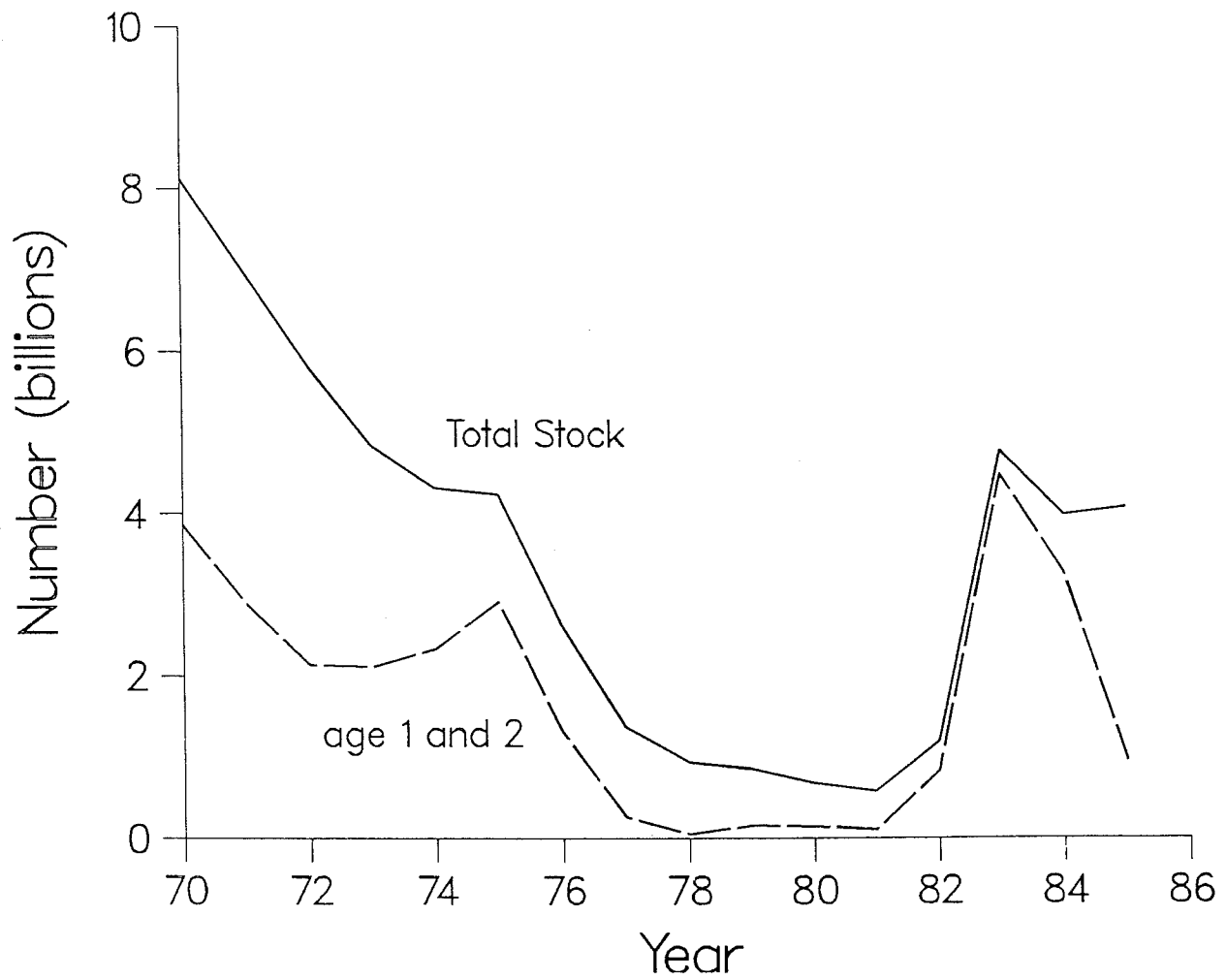
Figure 4. Atlantic mackerel stock sizes and numbers of 1- and 2-year-old fish from 1970 to 1985.

AGE 1

AGE 2

AGE 3
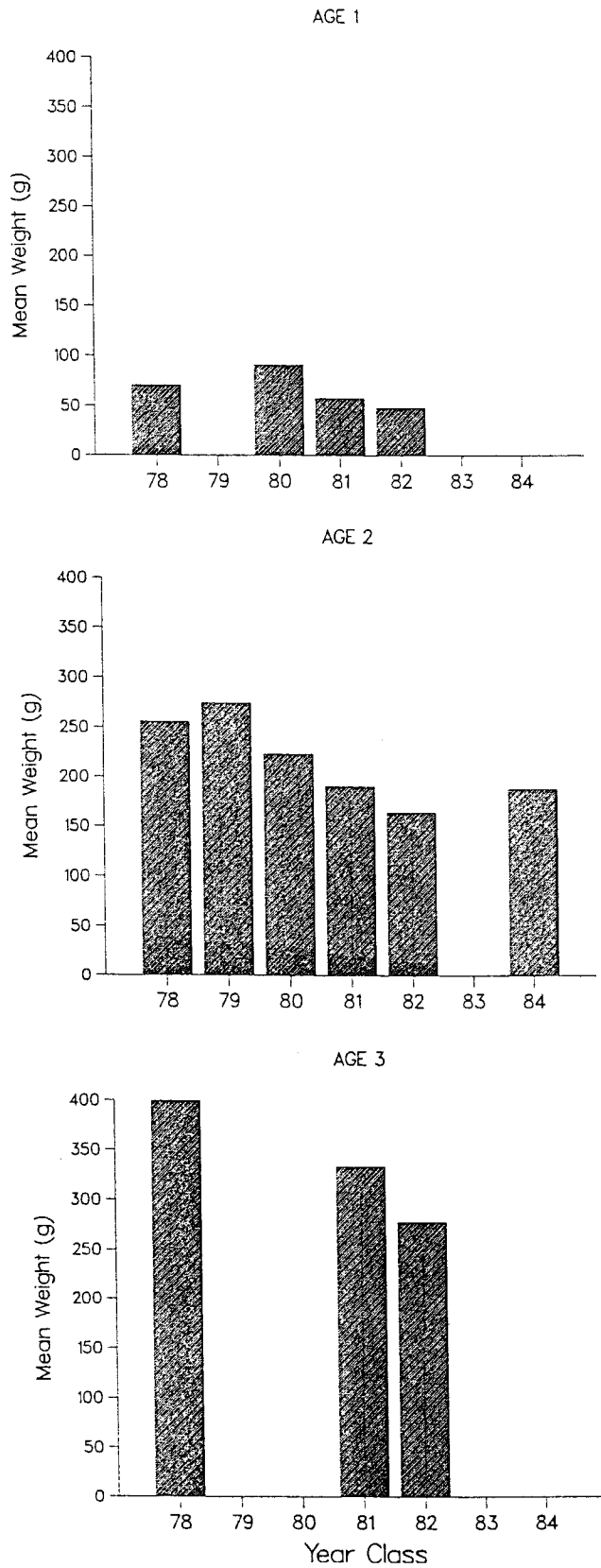
Year Class

Figure 5.   Mean weights by age group for Atlantic mackerel from the 1978- to
1984-year classes.

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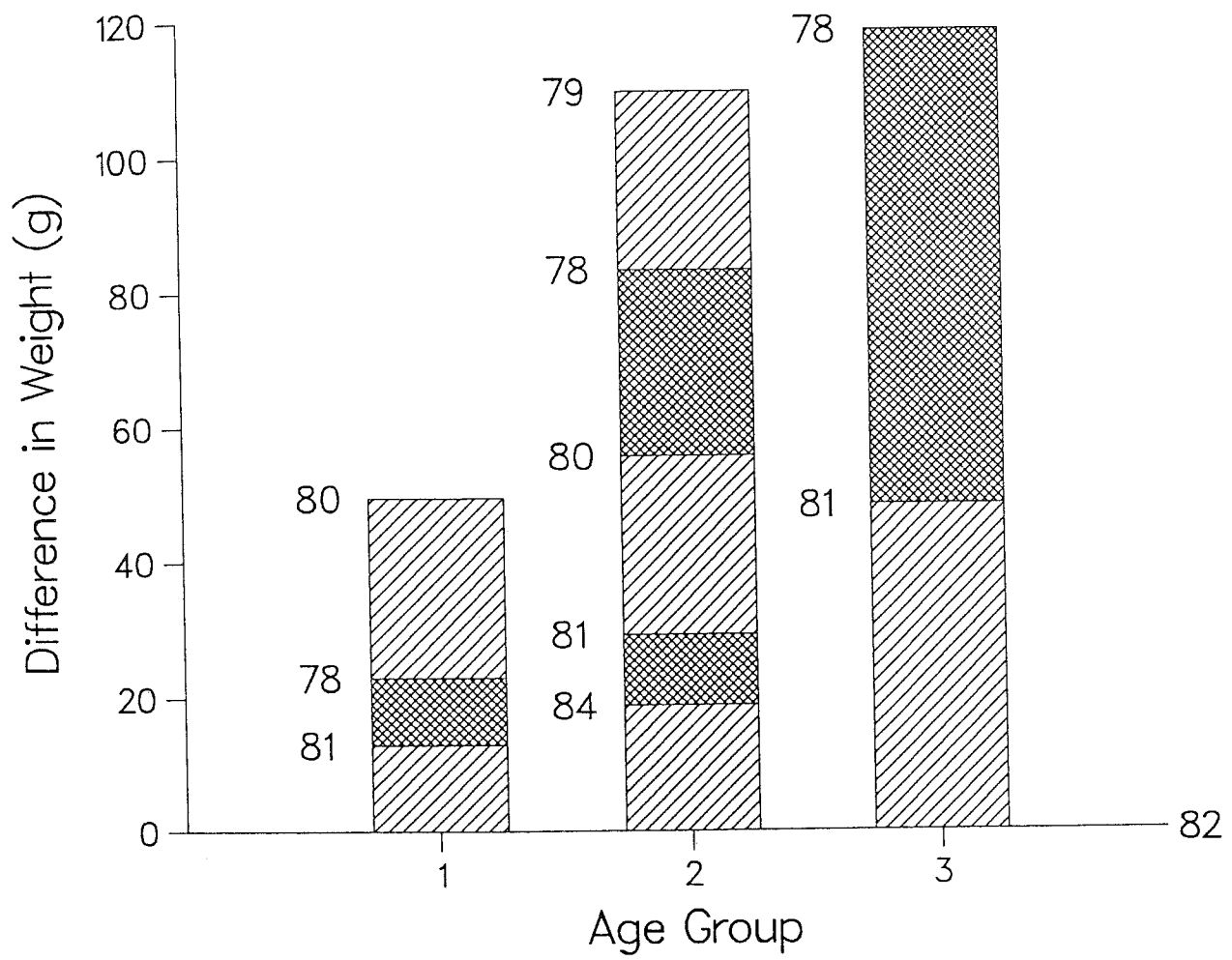
Figure 6. Differences in weight (grams) among the 1978- to 1984-year classes of Atlantic mackerel from results of Kruskal-Wallis tests, with the 1982 year class as the standard year of comparison for age groups 1 to 3.
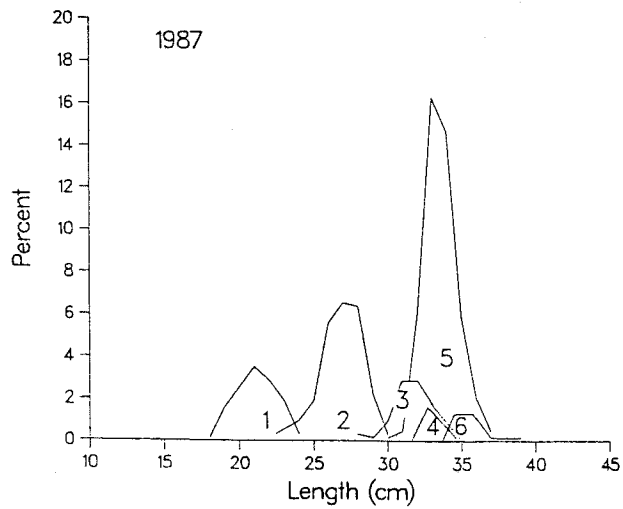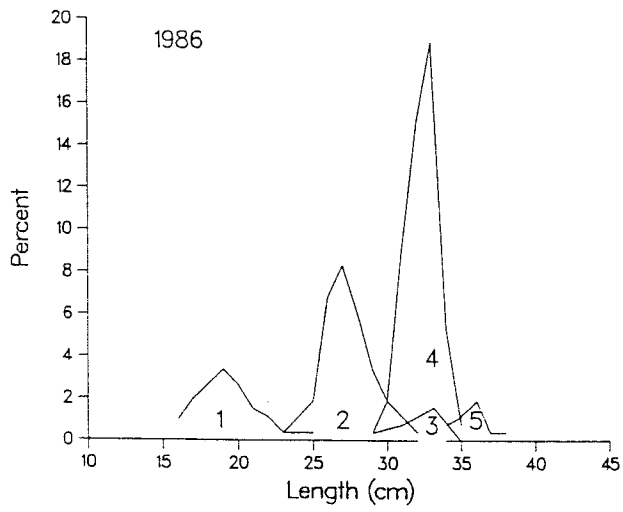
Figure 7.   Length frequencies of Atlantic mackerel by age group for 1986 and
1987 from NEFC spring bottom trawl surveys.

Table 1. Length frequency of Atlantic mackerel as prey
          for spiny dogfish, silver hake, and Atlantic cod.

	Number by year		
Length (cm)	1982	1983	1984
10			
11			
12		1	4 84
13		1	yc
14		1	
15	2		1
16	1	2 82	83
17	3	1 yc	1 yc
18	81 3	1	
19	1 yc		
20		1	6
21			1
22	1		2
23			3 81&82
24			3 yc
25			4
26		1	
27		81 1	
28		1 yc	2
29			
30			2
31			
32			
33			
34			
35			1
36			
Total number	8	12	32
Mean length	17.25	18.00	21.94

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Table 2. Statistics from regressions of mean weights
at ages 1 - 5 from NEFC spring bottom trawl
surveys during 1976-86 versus VPA stock size
as numbers at ages 1+.

	Statistic			
Age	R	R^2	F	P
1	-.779	.608	10.84	.013
2	-.821	.674	12.42	.013
3	-.826	.682	12.88	.012
4	-.476	.227	2.05	.195
5	.062	.004	0.03	.865

Table 3. Statistics from regressions of mean
weights at ages 1 – 9 from commer-
cial catches during 1967-85 versus
VPA stock size as numbers at ages 1+.

Age	Statistic			
	R	R^2	F	P
1	−.417	.174	3.58	.076
2	−.556	.309	7.59	.014
3	−.594	.353	9.27	.007
4	−.501	.251	5.71	.029
5	−.431	.186	3.89	.065
6	−.399	.159	3.22	.091
7	−.361	.130	2.56	.130
8	−.405	.164	3.33	.086
9	−.410	.168	3.44	.081

Table 4. Results of Kruskal-Wallis tests between year classes from individually weighed fish for age 1 Atlantic mackerel with multiple comparisons and contrast estimators.

Year class	N	Rank sum	Mean score	
78	36	2984	82.88	*
80	36	3609	100.24	*
81	36	2291	63.62	*
82	36	1558	43.26	*

Miller large sample multiple comparisons

Treatment	Test statistic	Result	Conclusion	
78vs80	625>18.96	78=80	80>78	**
78vs81	693>18.96	78=81	78>81	**
78vs82	1426>18.96	78=82	78>82	**
80vs81	1318>18.96	80=81	80>81	**
80vs82	2051>18.96	80=82	80>82	**
81vs82	733>18.96	81=82	81>82	**

Hodges-Lehmann contrast estimators

Treatment	Test statistic	Conclusion
78vs80	w7880=26.50	80 is 26.50 g larger than 78
78vs81	w7881=10.01	78 is 10.01 g larger than 81
78vs82	w7882=23.01	78 is 23.01 g larger than 82
80vs81	w8081=36.51	80 is 36.51 g larger than 81
80vs82	w8082=49.51	80 is 49.51 g larger than 82
81vs82	w8182=13.00	81 is 13.00 g larger than 82

* All tests significant; P = 0.0001.
** All tests significant; P = 0.05.

Table 5. Results of Kruskal-Wallis tests between year classes from
individually weighed fish for age 2 Atlantic mackerel with
multiple comparisons and contrast estimators.

Year class	N	Rank sum	Mean score	
78	30	3884	129.47	*
79	30	4373	145.75	*
80	30	3021	100.68	*
81	30	1896	63.18	*
82	30	1335	44.50	*
84	30	1782	59.42	*

Miller large sample multiple comparisons

Treatment	Test statistic	Result	Conclusion	
78vs79	489>45.25	78=79	79>78	**
78vs80	864>45.25	78=80	78>80	**
78vs81	1989>45.25	78=81	78>81	**
78vs82	2549>45.25	78=82	78>82	**
78vs84	2102>45.25	78=84	78>84	**
79vs80	1352>45.25	79=80	79>80	**
79vs81	2477>45.25	79=81	79>81	**
79vs82	3038>45.25	79=82	79>82	**
79vs84	2590>45.25	79=84	79>84	**
80vs81	1125>45.25	80=81	80>81	**
80vs82	1686>45.25	80=82	80>82	**
80vs84	1238>45.25	80=84	80>84	**
81vs82	561>45.25	81=82	81>82	**
81vs84	113>45.25	81=84	81>84	**
82vs84	448>45.25	82=84	84>82	**

Table 5. (continued)

Hodges-Lehmann contrast estimators

Treatment	Test statistic	Conclusion
79vs78	w7978=26.34	79 is 26.34 g larger than 78
78vs80	w7880=27.75	78 is 27.75 g larger than 80
78vs81	w7881=54.08	78 is 54.08 g larger than 81
78vs82	w7882=83.41	78 is 83.41 g larger than 82
78vs84	w7884=64.58	78 is 64.58 g larger than 84
79vs80	w7980=54.09	79 is 54.09 g larger than 80
79vs81	w7981=80.50	79 is 80.50 g larger than 81
79vs82	w7982=109.75	79 is109.75 g larger than 82
79vs84	w7984=90.92	79 is 90.92 g larger than 84
80vs81	w8081=26.33	80 is 26.33 g larger than 81
80vs82	w8082=55.66	80 is 55.66 g larger than 82
80vs84	w8084=36.83	80 is 36.33 g larger than 84
81vs82	w8182=29.33	81 is 29.33 g larger than 82
81vs84	w8184=10.50	81 is 10.50 g larger than 84
84vs82	w8482=18.83	84 is 18.83 g larger than 82

 * All tests significant; P = 0.0001.
** All tests significant; P = 0.05.

Table 6. Results of Kruskal-Wallis tests between year classes from
individually weighed fish for age 3 Atlantic mackerel with
multiple comparison and contrast estimators.

Year class	N	Rank score	Mean score	
78	50	5559	111.18	*
81	50	3679	73.58	*
82	50	2087	41.74	*

Miller large sample multiple comparisons

Treatment	Test statistic	Result	Conclusion	
78vs81	1880>22.61	78=81	78>81	**
78vs82	3472>22.61	78=82	78>82	**
81vs82	1592>22.61	81=82	81>82	**

Hodges-Lehmann contrast estimators

Treatment	Test statistic	Conclusion
78vs81	w7881=70.33	78 is 70.33 g larger than 81
78vs82	w7882=118.67	78 is 118.67 g larger than 82
81vs82	w8182=48.34	81 is 48.34 g larger than 82

 * All tests significant; P = 0.0001.
** All tests significant; P = 0.05.

Table 7. Atlantic mackerel percentage (%) maturity and sample size (N) for 1981-86 from data collected on NEFC spring bottom trawl surveys and Polish commercial trawlers.

Age	81		82		83		84		85		86	
	%	N	%	N	%	N	%	N	%	N	%	N
1	0	5	0	2	0	10	0	2	0	34	0	8
2	17	23	32	107	53	113	26	144	38	8	34	62
3	76	38	91	22	98	97	98	176	96	77	67	3
4	100	1	100	61	100	10	100	52	99	84	100	78

Table 8.   Percentage (%) of mackerel by weight in stomach
            samples of silver hake, Atlantic cod, and spiny
            dogfish, and number (N) 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

Table 9. Annual consumption of ages 1 and 2 Atlantic mackerel by spiny
dogfish, silver hake, and Atlantic cod, landings of mackerel for
1973-80, and total for both catagories (millions of fish).

	Consumption			Landings			Total	
Year	Age 1	Age 2		Age 1	Age 2		Age 1	Age 2
73	590.0	224.1		161.8	283.2		751.8	507.3
74	823.0	135.1		95.9	242.2		918.9	377.3
75	616.0	170.0		373.7	431.4		989.7	601.4
76	202.8	278.3		12.5	353.5		215.3	631.8
77	8.4	15.1		2.0	27.0		10.4	42.1
78	11.1	6.6		0.1	0.2		11.2	6.8
79	14.1	1.2		0.4	0.6		14.5	1.8
80	6.1	8.4		1.2	10.9		7.3	19.3

Table 10. Fishing mortality (F) and stock size (N) (millions) by age and year for Atlantic mackerel in NAFO Subareas 2-6 derived from VPA for the 1986 assessment.

	Year											
Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973

FISHING MORTALITY

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
1	0.053	0.007	0.074	0.036	0.036	0.000	0.031	0.004	0.098	0.072	0.019	0.187
2	0.011	0.018	0.054	0.027	0.059	0.051	0.045	0.075	0.039	0.211	0.111	0.344
3	0.042	0.006	0.021	0.028	0.050	0.137	0.151	0.157	0.209	0.121	0.288	0.643
4	0.142	0.094	0.025	0.026	0.032	0.042	0.419	0.250	0.236	0.361	0.254	0.462
5	0.062	0.346	0.093	0.040	0.039	0.052	0.239	0.100	0.158	0.517	0.462	0.464
6	0.086	0.020	0.423	0.127	0.079	0.054	0.138	0.072	0.172	0.302	0.438	0.449
7	0.069	0.014	0.376	1.056	0.205	0.081	0.009	0.057	0.175	0.344	0.354	0.275
8	0.145	0.013	0.061	0.839	0.323	0.525	0.017	0.052	0.430	0.173	0.271	0.272
9	0.187	0.049	0.063	0.080	0.085	0.327	0.175	0.047	0.233	0.336	0.734	0.462
10	0.050	0.065	0.063	0.000	0.000	0.000	0.172	0.380	0.108	0.301	0.562	0.944
11	0.054	0.065	0.000	0.000	0.000	0.000	0.000	0.000	0.212	0.305	0.351	0.491
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14+	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MEAN F	0.054	0.065	0.063	0.080	0.085	0.145	0.172	0.163	0.212	0.305	0.351	0.491

	Year											
Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985

FISHING MORTALITY

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
1	0.068	0.282	0.051	0.049	0.005	0.003	0.042	0.144	0.005	0.001	0.011	0.004
2	0.468	0.481	0.471	0.147	0.006	0.037	0.107	0.237	0.198	0.025	0.015	0.043
3	0.628	0.419	0.645	0.237	0.034	0.050	0.079	0.117	0.203	0.130	0.068	0.062
4	0.500	0.523	0.649	0.250	0.058	0.067	0.050	0.225	0.158	0.154	0.137	0.102
5	0.433	0.610	0.573	0.171	0.089	0.081	0.085	0.191	0.205	0.186	0.192	0.153
6	0.542	0.497	0.651	0.198	0.174	0.119	0.080	0.133	0.285	0.176	0.185	0.189
7	0.479	0.524	0.633	0.263	0.136	0.188	0.057	0.101	0.102	0.215	0.226	0.189
8	0.384	0.431	0.818	0.185	0.156	0.104	0.085	0.089	0.084	0.154	0.146	0.168
9	0.252	0.326	0.349	0.188	0.195	0.231	0.053	0.159	0.055	0.169	0.156	0.174
10	0.573	0.135	0.695	0.085	0.105	0.145	0.156	0.061	0.107	0.150	0.161	0.157
11	0.522	0.476	0.113	0.028	0.149	0.065	0.142	0.086	0.053	0.136	0.115	0.131
12	0.000	0.000	0.000	0.032	0.072	0.085	0.061	0.048	0.086	0.081	0.126	0.131
13	0.000	0.000	0.000	0.000	0.083	0.096	0.077	0.113	0.110	0.158	0.092	0.131
14+	0.000	0.000	0.000	0.000	0.000	0.096	0.077	0.113	0.110	0.158	0.092	0.071
MEAN F	0.522	0.476	0.623	0.220	0.083	0.096	0.077	0.113	0.110	0.158	0.092	0.071

Table 10. (continued)

						Year						
Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973

STOCK SIZE

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
1	342.4	181.5	199.3	280.0	755.0	1878.4	5053.8	1919.1	2287.3	1175.8	1327.0	1044.6
2	275.4	265.8	147.6	151.5	221.2	596.7	1555.8	4010.6	1564.8	1698.2	895.4	1067.0
3	411.5	223.1	214.0	114.5	120.8	170.7	464.3	1218.5	3047.4	1232.0	1125.5	655.9
4	31.6	323.2	181.5	171.6	91.2	94.2	122.0	326.8	852.9	2025.0	893.7	691.2
5	22.1	22.5	240.9	145.0	136.9	72.3	73.9	65.7	208.3	551.7	1156.1	567.5
6	21.4	17.0	13.0	179.8	114.0	107.8	56.2	47.7	48.6	145.7	269.4	596.5
7	23.2	16.1	13.6	7.0	129.6	86.2	83.7	40.1	36.3	33.5	88.2	142.3
8	6.5	17.7	13.0	7.7	2.0	86.5	65.1	67.9	31.0	25.0	19.4	50.7
9	2.6	4.6	14.4	10.0	2.7	1.2	41.9	52.4	52.8	16.5	17.2	12.1
10	2.2	1.8	3.6	0.0	0.0	0.0	0.7	28.8	40.9	34.2	9.7	6.8
11	6.3	1.8	0.0	0.0	0.0	0.0	0.0	0.0	16.1	30.1	20.7	4.5
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total N	1145.3	1075.0	1040.9	1067.1	1573.5	3094.0	7517.4	7777.4	8186.4	6967.6	5822.4	4839.0
Weight*	248.3	282.9	306.3	315.1	370.7	554.7	1104.8	1507.9	1843.5	1866.8	1639.9	1388.5
Spawning N	665.2	760.6	767.8	711.2	707.8	917.2	1685.7	3853.0	5116.7	4942.7	4047.7	3260.9
Weight*	191.1	241.9	274.1	274.8	278.6	321.6	481.9	968.7	1485.4	1603.7	1433.3	1193.8

						Year						
Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985

STOCK SIZE

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
1	1615.5	1668.9	278.5	45.9	22.4	144.4	31.8	85.6	768.7	3854.1	61.4	904.0
2	709.5	1236.2	1030.4	216.7	35.8	18.3	117.9	25.0	60.7	626.6	3202.7	49.8
3	619.2	363.8	625.5	526.8	153.1	29.2	14.4	86.7	16.1	40.8	500.3	2583.3
4	282.2	270.6	195.9	268.5	340.4	121.2	22.7	10.9	63.2	10.8	29.3	382.8
5	356.5	140.1	131.3	83.8	171.3	263.0	92.8	17.7	7.1	44.1	7.6	20.9
6	292.1	189.3	62.3	60.6	57.8	128.3	198.5	69.8	12.0	4.8	30.0	5.1
7	311.6	139.1	94.3	26.6	40.7	39.7	93.2	150.1	50.0	7.4	3.3	20.4
8	88.5	158.1	67.4	41.0	16.7	29.1	27.0	72.1	111.1	37.0	4.9	2.1
9	31.6	49.4	84.1	24.4	27.9	11.7	21.5	20.3	54.0	83.7	25.9	3.4
10	6.3	20.1	29.2	48.6	16.5	18.8	7.6	16.7	14.2	41.8	57.9	18.2
11	2.2	2.9	14.4	11.9	36.5	12.2	13.3	5.3	12.8	10.4	29.5	40.3
12	0.0	0.0	0.0	10.5	9.5	25.8	9.3	9.4	4.0	10.0	7.5	21.5
13	0.0	0.0	0.0	0.0	8.3	7.2	19.4	7.2	7.4	3.0	7.5	5.4
14+	0.0	0.0	0.0	0.0	0.0	12.0	11.9	8.2	13.7	6.0	20.1	19.3
Total N	4315.1	4238.4	2613.1	1365.3	937.1	860.8	681.4	585.0	1194.9	4780.4	3987.8	4076.7
Weight*	1109.0	955.4	716.4	453.0	419.5	420.4	371.2	310.7	346.3	606.8	847.2	1097.7
Spawning N	2344.8	1951.4	1819.5	1211.0	896.7	707.2	590.6	486.9	395.9	613.0	2325.0	3147.8
Weight*	891.1	685.8	598.4	429.4	412.3	399.3	349.5	299.3	255.4	257.2	581.7	990.9

* Unaudited values.

Table 11. Predation and fishing mortality (M2+F) and stock size (N) (millions) by age and year for Atlantic mackerel in NAFO Subareas 2-6 derived from VPA for the 1986 assessment.

	Year											
Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973

M 2 + F

1	0.053	0.007	0.074	0.036	0.036	0.000	0.031	0.004	0.098	0.072	0.015	0.580
2	0.011	0.018	0.054	0.027	0.059	0.051	0.045	0.075	0.039	0.211	0.111	0.550
3	0.042	0.006	0.021	0.028	0.050	0.137	0.151	0.157	0.209	0.121	0.288	0.643
4	0.142	0.094	0.025	0.026	0.032	0.042	0.419	0.250	0.236	0.361	0.254	0.462
5	0.062	0.346	0.093	0.040	0.039	0.052	0.239	0.100	0.158	0.517	0.462	0.464
6	0.086	0.020	0.423	0.127	0.079	0.054	0.138	0.072	0.172	0.302	0.438	0.449
7	0.069	0.014	0.376	1.056	0.205	0.081	0.009	0.057	0.175	0.344	0.354	0.275
8	0.145	0.013	0.061	0.839	0.323	0.525	0.017	0.052	0.430	0.173	0.271	0.272
9	0.187	0.049	0.063	0.080	0.085	0.327	0.175	0.047	0.233	0.336	0.734	0.462
10	0.050	0.065	0.063	0.000	0.000	0.000	0.172	0.380	0.108	0.301	0.562	0.944
11	0.054	0.065	0.000	0.000	0.000	0.000	0.000	0.000	0.212	0.305	0.351	0.491
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14+	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MEAN F	0.054	0.065	0.063	0.080	0.085	0.145	0.172	0.163	0.212	0.305	0.351	0.491

	Year											
Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985

M 2 + F

1	0.457	0.510	0.602	0.197	0.414	0.098	0.234	0.144	0.005	0.001	0.011	0.004
2	0.656	0.620	0.728	0.221	0.190	0.107	0.183	0.237	0.198	0.025	0.015	0.043
3	0.628	0.419	0.645	0.237	0.034	0.050	0.079	0.117	0.203	0.130	0.068	0.062
4	0.500	0.523	0.649	0.250	0.058	0.067	0.050	0.225	0.158	0.154	0.137	0.102
5	0.433	0.610	0.573	0.171	0.089	0.081	0.085	0.191	0.205	0.186	0.192	0.153
6	0.542	0.497	0.651	0.198	0.174	0.119	0.080	0.133	0.285	0.176	0.185	0.189
7	0.479	0.524	0.633	0.263	0.136	0.188	0.057	0.101	0.102	0.215	0.226	0.189
8	0.384	0.431	0.818	0.185	0.156	0.104	0.085	0.089	0.084	0.154	0.146	0.168
9	0.252	0.326	0.349	0.188	0.195	0.231	0.053	0.159	0.055	0.169	0.156	0.174
10	0.573	0.135	0.695	0.085	0.105	0.145	0.156	0.061	0.107	0.150	0.161	0.157
11	0.522	0.476	0.113	0.028	0.149	0.065	0.142	0.086	0.053	0.136	0.115	0.131
12	0.000	0.000	0.000	0.032	0.072	0.085	0.061	0.048	0.086	0.081	0.126	0.131
13	0.000	0.000	0.000	0.000	0.083	0.096	0.077	0.113	0.110	0.158	0.092	0.131
14+	0.000	0.000	0.000	0.000	0.000	0.096	0.077	0.113	0.110	0.158	0.092	0.071
MEAN F	0.522	0.476	0.623	0.220	0.083	0.096	0.077	0.113	0.110	0.158	0.092	0.071

Table 11. (continued)

						Year						
Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973

STOCK SIZE

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
1	342.4	181.5	199.3	280.0	755.0	1878.4	5053.8	1919.1	2287.3	1175.8	1625.6	1867.3
2	275.4	265.8	147.6	151.5	221.2	596.7	1555.8	4010.6	1564.8	1698.2	895.4	1310.9
3	411.5	223.1	214.0	114.5	120.8	170.7	464.3	1218.5	3047.4	1232.0	1125.5	655.9
4	31.6	323.2	181.5	171.6	91.2	94.2	122.0	326.8	852.9	2025.0	893.7	691.2
5	22.1	22.5	240.9	145.0	136.9	72.3	73.9	65.7	208.3	551.7	1156.1	567.5
6	21.4	17.0	13.0	179.8	114.0	107.8	56.2	47.7	48.6	145.7	269.4	596.5
7	23.2	16.1	13.6	7.0	129.6	86.2	83.7	40.1	36.3	33.5	88.2	142.3
8	6.5	17.7	13.0	7.7	2.0	86.5	65.1	67.9	31.0	25.0	19.4	50.7
9	2.6	4.6	14.4	10.0	2.7	1.2	41.9	52.4	52.8	16.5	17.2	12.1
10	2.2	1.8	3.6	0.0	0.0	0.0	0.7	28.8	40.9	34.2	9.7	6.8
11	6.3	1.8	0.0	0.0	0.0	0.0	0.0	0.0	16.1	30.1	20.7	4.5
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total N	1145.3	1075.0	1040.9	1067.1	1573.5	3094.0	7517.4	7777.4	8186.4	6967.6	6121.0	5905.7
Weight*	248.3	282.9	306.3	315.1	370.7	554.7	1104.8	1507.9	1843.5	1866.8	1668.6	1510.6
Spawning N	665.2	760.6	767.8	711.2	707.8	917.2	1685.7	3853.0	5116.7	4942.7	4047.7	3382.9
Weight*	191.1	241.9	274.1	274.8	278.6	321.6	481.9	968.7	1485.4	1603.7	1433.3	1215.4

						Year						
Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985

STOCK SIZE

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
1	2741.5	2709.9	520.2	64.1	36.2	171.3	38.5	85.6	768.7	3854.1	61.4	904.0
2	856.2	1420.7	1332.2	233.3	43.1	19.6	127.2	25.0	60.7	626.6	3202.7	49.8
3	619.2	363.8	625.5	526.8	153.1	29.2	14.4	86.7	16.1	40.8	500.3	2583.3
4	282.2	270.6	195.9	268.5	340.4	121.2	22.7	10.9	63.2	10.8	29.3	382.8
5	356.5	140.1	131.3	83.8	171.3	263.0	92.8	17.7	7.1	44.1	7.6	20.9
6	292.1	189.3	62.3	60.6	57.8	128.3	198.5	69.8	12.0	4.8	30.0	5.1
7	311.6	139.1	94.3	26.6	40.7	39.7	93.2	150.1	50.0	7.4	3.3	20.4
8	88.5	158.1	67.4	41.0	16.7	29.1	27.0	72.1	111.1	37.0	4.9	2.1
9	31.6	49.4	84.1	24.4	27.9	11.7	21.5	20.3	54.0	83.7	25.9	3.4
10	6.3	20.1	29.2	48.6	16.5	18.8	7.6	16.7	14.2	41.8	57.9	18.2
11	2.2	2.9	14.4	11.9	36.5	12.2	13.3	5.3	12.8	10.4	29.5	40.3
12	0.0	0.0	0.0	10.5	9.5	25.8	9.3	9.4	4.0	10.0	7.5	21.5
13	0.0	0.0	0.0	0.0	8.3	7.2	19.4	7.2	7.4	3.0	7.5	5.4
14+	0.0	0.0	0.0	0.0	0.0	12.0	11.9	8.2	13.7	6.0	20.1	19.3
Total N	5587.7	5464.0	3156.6	1400.0	958.2	889.0	697.3	585.0	1194.9	4780.4	3987.8	4076.7
Weight*	1243.0	1088.0	793.0	457.7	423.1	424.2	374.9	310.7	346.3	606.8	847.2	1097.7
Spawning N	2418.1	2043.7	1970.4	1219.3	900.4	707.9	595.2	486.9	395.9	613.0	2325.0	3147.8
Weight*	904.1	702.1	625.1	430.9	413.1	399.5	350.9	299.3	255.4	257.2	581.7	990.9

*Unaudited values.

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Table 12. Mortality rates of ages 1 and 2 Atlantic mackerel for 1973-80 from Table 11.

Year	Age 1					Age 2			
	Z	F	M2	M1		Z	F	M2	M1
73	0.78	0.12	0.46	0.20		0.75	0.31	0.24	0.20
74	0.66	0.05	0.41	0.20		0.86	0.42	0.24	0.20
75	0.71	0.19	0.32	0.20		0.83	0.45	0.18	0.20
76	0.81	0.04	0.57	0.20		0.93	0.41	0.32	0.20
77	0.40	0.04	0.16	0.20		0.42	0.14	0.08	0.20
78	0.61	0.00	0.41	0.20		0.39	0.01	0.18	0.20
79	0.30	0.00	0.10	0.20		0.31	0.04	0.07	0.20
80	0.44	0.04	0.20	0.20		0.38	0.10	0.08	0.20

Table 13. Growth information used to
parameterize the age 1 and
age 2 models.

Age	Min (g)	Max (g)
1	48	122
2*	85	187
3	89	154
4	70	132
5	50	102

*   Values for ages 2-5 are annual growth
    increments.

Table 14.   Data for forecasts of catch in 1987 and stock in 1988 and 1991 for the
standard Atlantic mackerel model.

Age	Stock size in 1986 (millions)	Exploitation pattern	Mean weight of the catch (kg)	Mean weight of stock on Jan 1 (kg)	Maturity ogive
1	450.0	0.06	0.133	0.111	0.0
2	737.2	0.33	0.309	0.260	0.5
3	39.0	0.47	0.383	0.338	1.0
4	1987.9	0.78	0.454	0.416	1.0
5	283.0	1.17	0.568	0.558	1.0
6	14.7	1.44	0.678	0.644	1.0
7	3.5	1.44	0.708	0.677	1.0
8	13.9	1.28	0.729	0.665	1.0
9	1.5	1.33	0.788	0.737	1.0
10	2.4	1.20	0.775	0.717	1.0
11	12.7	1.00	0.808	0.715	1.0
12	29.0	1.00	0.801	0.739	1.0
13	15.5	1.00	0.806	0.731	1.0
14+	18.6	1.00	0.889	0.782	1.0

Table 15. Comparison of different density dependent model outputs with 1986 assessment results for catch in 1987, and spawning stock in 1988 and 1991 expressed as percentage change of model results versus 1986 assessment results.

Model mechanism	Catch 87	Spawning stock 88	Spawning stock 91
Maturity	0.0	−5.5	−3.6
Weight	−5.1	−1.2	−5.8
Natural mortality	−1.3	−1.9	−26.6
Maturity weight	−5.1	−5.7	−8.7
Maturity natural mortality	−1.3	−7.8	−29.6
Weight natural mortality	−6.5	−6.8	−32.3
Maturity weight natural mortality	−6.5	−10.7	−34.8

Table 16. Results of sensitivity analysis on age 1 growth model
for eight experiments (Ex) where the parameters 'a' and 'b'
were varied by 25% in a positive (+) and negative (-)
direction or held constant (c). The impact on average
catch, stock size, and spawning stock biomass was calculated
relative to the baseline model with all the density
dependent factors operating.

Ex #	a	b	Catch	Stock	SSB
1	+	c	+1.91	+6.95	+3.64
2	-	c	-1.91	-6.95	-3.64
3	c	+	-0.25	-2.45	-1.82
4	c	-	+0.25	+2.45	+1.82
5	+	+	+1.66	+4.50	+1.84
6	-	-	-1.66	-4.50	-1.84
7	+	-	+2.16	+9.40	+5.43
8	-	+	-2.16	-9.40	-5.43

Table 17. Results of sensitivity analysis on the natural mortality model for
eight experiments (Ex) where the parameters 'a' and 'b' were
varied by 25% in a positive (+) and negative (-) direction
or held constant (c). The impact on average catch, stock
size, and spawning stock biomass was calculated relative to the
baseline model with all the density dependent factors operating.

Ex #	a	b	Catch	Stock	SSB
1	+	c	-3.55	-5.19	-4.96
2	-	c	+4.45	+6.29	+5.94
3	c	+	-1.86	-2.49	-2.45
4	c	-	+2.56	+3.45	+3.34
5	+	+	-5.54	-7.88	-7.64
6	-	-	+1.67	+9.21	+8.72
7	+	-	-0.83	-1.42	-1.27
8	-	+	+12.41	+17.07	+16.26

Table 18.   Results of several comparisons of regular prediction model results
             (Key Runs) and Density Dependent Model results (DDM) to assess the
             problem of stockpiling fish at F=0.05 for Atlantic mackerel.
             Option 1 is constant recruitment; the mean of the 1981-84 year
             classes. Option 2 is a series of repeating recruitments equal to the
             same values as the 1981-84 year classes in the same order of
             occurrence. Option 3 is a series of repeating recruitment patterns
             equal to the same values as the 1981, 1982, and 1984 year classes in
             the same order of occurrence.

Option		Mean catch (000's mt)	% change	Mean stock (000's mt)	% change	Mean SS (000's mt)	% change
1	Key Run	91		2,139		1,837	
	DDM	76	-15.9	1,804	-15.7	1,374	-25.2
2	Key Run	94		2,212		1,895	
	DDM	71	-24.4	1,582	-28.5	1,266	-33.2
3	Key Run	107		2,597		2,212	
	DDM	76	-29.3	1,726	-33.5	1,350	-39.0

Table 19. Average catch, stock size, and spawning stock (SS) from several
different recruitment patterns and various levels of fishing
mortality with the density-dependent model over a 10-year
simulated period. Option I is constant recruitment; the mean of
the 1981-84 year classes. Option II is a series of year classes
equal to the same values as the 1981-84 cohorts in the same
order of occurrence. Option III is a series of year classes equal
to the 1981, 1982, and 1984 cohorts in the same order of occurrence.

F	Mean catch (000's mt)	Mean stock (000's mt)	Mean SS (000's mt)
	OPTION I		
0.05	76	1,846	1,402
0.15	170	1,548	1,121
0.20	200	1,443	1,022
0.25	223	1,356	941
0.30	241	1,285	874
0.40	267	1,172	769
0.60	299	1,020	629
1.00	330	849	473
	OPTION II		
0.05	71	1,605	1,279
0.15	158	1,319	1,007
0.20	185	1,219	912
0.25	205	1,138	836
0.30	222	1,070	771
0.45	245	949	672
0.60	273	826	541
1.00	300	672	398
	OPTION III		
0.05	76	1,764	1,372
0.15	169	1,470	1.090
0.20	198	1,365	992
0.25	220	1,280	911
0.30	238	1,210	845
0.45	263	1,110	742
0.60	293	952	605
1.00	323	790	455

Table 20. Percentage change in growth at selected fishing mortalities (F) for three options of recruitment for Atlantic mackerel ages 2 – 5 as compared to growth at F=0.05.

F	Age 2	Age 3	Age 4	Age 5
	OPTION 1			
0.15	+3.8	+3.8	+3.8	+3.7
0.20	+4.9	+5.2	+5.3	+5.1
0.30	+7.0	+7.5	+7.6	+7.4
0.60	+10.8	+11.7	+11.9	+11.6
	OPTION 2			
0.15	+3.2	+3.4	+3.7	+3.5
0.20	+4.4	+4.8	+5.0	+4.8
0.30	+6.3	+6.9	+6.9	+6.9
0.60	+9.7	+10.6	+11.1	+10.8
	OPTION 3			
0.15	+4.3	+4.3	+4.3	+4.2
0.20	+5.8	+6.0	+6.0	+5.8
0.30	+8.4	+8.6	+8.7	+8.5
0.60	+12.9	+13.5	+13.6	+13.4

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