

APPENDIX 4

SAW 47 Working Paper 10 (TOR 4) – Surplus Production Model

Re-evaluation of Summer Flounder (*Paralichthys dentatus*) Stock Status Following Adjustments for Retrospective Bias and Inclusion of Trophic Effects

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SUMMARY

In this report, a time series (1982-2006) of age aggregated (ages 1+) F and stock size estimates was derived for summer flounder from 1982 to 2006. A subset of tuning indices that significantly ($P < 0.01$) predicted the converged portion of the flounder time series (1982-2000) was used to project stock sizes for the non-converged portion (2001-2006) where the presence of retrospective bias from ADAPT was shown to systematically overestimate stock size. In addition, overfishing thresholds (F_{msy} , B_{msy}) were estimated for flounder by dynamic surplus production models. Finally, I examined the hypothesis that flounder stock rebuilding has been recently halted due mainly to enhanced predation and shifts in environmental factors. The stepwise regression analyses revealed that the recreational cpue index and the NEFSC spring trawl index were selected as the best predictors of mean ages 1+ numbers, biomass and SSB from 1982 to 2000. These regression models accounted for 62 to 89% of the variation in abundance over three converged periods (1982-1998, 1982-1999, 1982-2000), and were then used to project recent (2001-2006) ages 1+ abundance in an effort to address systematic retrospective bias during those years. The ADAPT model overestimated ages 1+ abundance by 35 to 50% in most years after 2000. Based on these analyses, the most reliable time series (1982-2006) of flounder abundance and SSB consisted of the converged portion (1982-2000) from ADAPT plus the predicted abundance and SSB estimates from 2001 to 2006 based on the predictive equations. This time series of stock size estimates was used in all subsequent analyses.

Biomass weighted fishing mortality (F) on ages 1+ flounder was high and variable before 1995, ranging from a low of 0.74 in 1994 to a high of 1.88 in 1988. After 1994, ages 1+ fishing mortality rates dropped considerably and remained relatively stable between 0.38 and 0.54. Ages 1+ flounder biomass (mt) based on ADAPT was relatively high and stable from 1982 to 1987 at around 25 thousand mt, than flounder biomass dropped quickly to below 16 thousand mt from 1988 to 1994. Thereafter stock biomass began to rise and eventually reached about 30 thousand mt by 2001. Ages 1+ stock biomass remained relatively steady at around 30 thousand mt from 2001 to 2005, but the 2006 biomass level fell by 30% to 23 thousand mt. The dynamic Gompertz production model was a good fit to flounder surplus production data, but the model generated an anomalous residual pattern. As a result, several candidate predators (striped bass, bluefish and spiny dogfish) and

environmental variables (mean annual water temperatures and deviations in the winter NAO index) were added to the Gompertz model in a stepwise regression. Striped bass was the only additional variable selected to the Gompertz model at the $P < 0.02$ level. The extended Gompertz model with striped bass predatory effects explained over 83% of the variability in surplus production and, more importantly, removed the serial residual pattern noted from the original Gompertz model. This extended Gompertz production model was then used to estimate flounder overfishing thresholds (F_{msy} , B_{msy}). The resulting overfishing threshold (F_{msy}) for flounder was 0.64 (80% C.I.: 0.51 to 0.77) and the biomass threshold was 32,500 mt (80% C. I: 25,900-39,200 mt). All of the ages 1+ fishing mortality (FW) rates (biomass weighted) on flounder from 1982 to 1994 exceeded the F_{msy} threshold of 0.64, indicating that overfishing had occurred on flounder from 1982 to 1994. However, all subsequent FW estimates were below the F_{msy} threshold, suggesting that overfishing was corrected by additional management measures imposed during the early to mid 1990's. Recent (2002-2005) biomass (mt) levels have approached my B_{msy} threshold, but the 2006 biomass level of 22,900 mt represented a 30% drop and was well below the B_{msy} threshold of 32,500 mt. Since fishing mortality rates (FW) have stabilized below F_{msy} since 1995, the recent lack of stock rebuilding is likely due to enhanced striped bass predation and not overfishing. When the dome-shaped Ricker S-R model was fitted to the flounder S-R data, the model converged and the parameter estimates (A , K_p) were highly significant ($P < 0.0001$). However, the residual pattern from the Ricker Model looked almost exactly like the atypical residual pattern exhibited by the asymptotic Beverton-Holt S-R model. When striped bass abundance from 1982 to 2006 was added as a second explanatory variable, the extended Ricker model explained 91% of the recruitment variability, all three parameter estimates (A , K_p , c) were highly significant ($P < 0.0001$), and most importantly, the anomalous residual pattern observed in the basic Beverton-Holt and Ricker S-R models virtually disappeared. These findings are consistent with the Predation Hypothesis, indicating that surplus production and the transmission of age 0 recruits to the adult stock has been recently impeded due to a recent rise in striped bass predation. The management implications of successful stock rebuilding of summer flounder in the presence of rising predatory mortality are discussed.

INTRODUCTION

The most recent stock assessment for summer flounder (Terceiro 2006) concluded that overfishing on the coast-wide stock has occurred since at least 1982. Current (2006) spawning stock biomass based on the 2007 ADAPT (Terceiro 2007) run is about 6% below the biomass threshold, and the current fully recruited fishing mortality rate (F) is about 25% above the current F_{max} threshold of 0.28. As indicated by Terceiro (2006), all ADAPT model runs conducted thus far have exhibited a pronounced and systematic retrospective bias for the terminal (most recent year) F and stock size estimates. Although the exact origin of retrospective bias is still unclear (ICES 2002), this problem occurs at some level in nearly all catch-at-age models. The ADAPT model for summer flounder almost always underestimated F and overestimated stock size for fully recruited fish in the last three to five years of the time series by a sizeable amount. Such a large systematic bias greatly confounds our ability to establish conservative quotas on the commercial fisheries and, more importantly, over-inflates the true pace of flounder stock rebuilding toward the SSB threshold of 44,760 mt. Given that the most recent (2002-2006)

biomass estimates from ADAPT have been consistently overestimated, the rate of stock rebuilding since 2002 may be much slower than previously suggested based on output from ADAPT.

The current target and overfishing thresholds for summer flounder are both expressed by an F_{max} value of 0.28 based on the Thompson-Bell yield-per-recruit (YPR) model (Terceiro 2006). The threshold F_{max} is assumed to be a suitable proxy for F_{msy} when the shape of the stock-recruitment relationship is indeterminate. The YPR model assumes no density-dependence and constant age-specific somatic growth and natural mortality rates (M). The notion that F_{max} closely approximates F_{msy} under most conditions was challenged recently during a review of reference points for summer flounder conducted by the Mid Atlantic Fishery Management Council (MAFMC). Three reports (Gibson 2000; Crecco 2000; Armstrong 2000) from this meeting estimated F_{msy} for summer flounder based on stock-recruitment and dynamic surplus production models that assume the presence of density-dependent mortality. All of their findings indicated that the range of F_{msy} thresholds (F_{msy} : 0.58-0.82) for summer flounder always exceeded the F_{max} level of 0.28 used in the current assessment as did the range of F_{msy} levels (F_{msy} range: 0.45-0.69) reported earlier by Chang and Pacheco (1976). These findings strongly suggest that summer flounder are under some density-dependent control and are thus more resilient to fishing pressure than previously thought.

Over the last seven years, the stock-recruitment (S-R) relationship for flounder has been extensively examined (Terceiro 2000, 2006; Gibson 2000; Crecco 2000). Terceiro (2006) has shown that the residuals from all Beverton-Holt S-R model runs have exhibited a pronounced and consistent serial correlation over time. The residuals were all large and positive from 1983 to 1987, after which nearly all residuals switched to a negative direction. Gibson (2000) also noted a similar residual pattern for the dome-shaped form of the Shepherd (1982) S-R model, indicating that this serial correlation in residuals over time is widespread and not related to the shape of the S-R curve. The other potential cause for serial residuals is that the basic S-R model lacks an additional important explanatory variable such as an environmental or trophic factor. Given the uncertainty and controversy surrounding the effects of retrospective bias in ADAPT on current F and stock biomass, as well as the persistent occurrence of serial residuals from all current flounder S-R models, I argue here that a thorough examination of these issues are needed even if it occurs outside the normal Peer Review process. The need for such a review may appear unwarranted since the last eight flounder assessments have been upheld by Peer Review (Terceiro 2006). Nevertheless, the ramifications of persistent retrospective bias from ADAPT and residual anomalies from S-R models require more attention here and in future Peer Reviews.

In this report, a time series (1982-2006) of age aggregated (ages 1+) F and stock size estimates was derived from 1982 to 2006. The F and stock size estimates were expressed annually as ratios of landings and discards to ages 1+ abundance from the converged portion of the 2007 ADAPT run (Terceiro 2007). A subset of tuning indices that significantly ($P < 0.01$) predicted the converged numbers and biomass time series was then used to project stock sizes estimates for the non-converged portion (2001-2006) of the biomass, stock numbers and spawning stock biomass (SSB) time series. In addition, overfishing thresholds (F_{msy} , B_{msy}) were estimated for flounder by dynamic surplus production models. Finally, I examined the hypothesis that flounder surplus production and recruitment have recently fallen mainly due to enhanced predation and shifts in environmental factors.

METHODS

Method to Adjust Recent Stock Size for Retrospective Bias

Retrospective bias has been persistent in the most recent (> 2001) flounder abundance estimates from the ADAPT model (Terceiro 2006). In an effort to reduce the impact of retrospective bias, I developed a number of linear least squares predictive models based on the tuning indices and the mean ages 1+ biomass, mean ages 1+stock numbers and spawning stock biomass (SSB) values from the converged portion of the 2007 ADAPT run (Terceiro 2007), where retrospective bias was minimal. Annual mean ages 1+ biomass and SSB are direct outputs from ADAPT, but mean ages 1+ stock numbers are not. To estimate mean stock numbers according to the VPA manual (Alan Seaver, NEFSC pers. comm.), ages 1+ stock size estimates at the beginning of each year from ADAPT was multiplied by the quantity $(1 - \exp(-Z_t)/Z_t)$, where Z_t is the instantaneous total mortality estimate (numbers weighted) from ADAPT.

My approach involved the use of the Pearson correlation and stepwise regression analyses to relate all ages 1+ tuning indices in weight and number against average ages 1+ biomass, spawning stock biomass (SSB) and average ages 1+ numbers from the converged portion (1982-2000) of the VPA (Tables 1-3). Both the Pearson correlation and Stepwise regression methods were conducted in the Statistical Analysis System (SAS 2002). A subset of tuning indices was selected from this analysis that best predicted (maximum rsquare) stock size within the converged portion of the VPA. Before the predictive equation was accepted, residual diagnostics was performed on each model to determine whether or not serial correlations were evident between model residuals and time (1982-2000). The residuals from each predictive model were linearly regressed against time (years) and a significant serial correlation coefficient ($P < 0.05$) would indicate an abnormal residual pattern. This would indicate that the current model configuration was either incorrect or an additional explanatory variable was missing from the model. In addition, the partial correlation coefficients were examined for each explanatory variable from the stepwise model. If the model accurately predicted ($P < 0.01$) abundance trends over the converged portion and passed the residual test, it was then used to estimate ages 1+ abundance in number, biomass (mt) and SSB for the non-converged portion (from 2001 to 2006) of the time series.

Since the degree of retrospective bias declines backwards in time from the terminal stock estimate, the exact cutoff for the most recent value in the converged time series is somewhat subjective. It is clear that the degree of retrospective bias in the abundance time series diminished sharply prior to 2001. Thus, the time series of ages 1+ abundance and SSB from 1982-2000 was defined as the converged portion. This converged portion was therefore considered to be the most reliable time series of flounder abundance. This allowed the converged portion to be used as an unbiased dependent variable in the stepwise model, against which the tuning indices can be regressed in the stepwise model. The stepwise model was designed to screen out tuning indices that were poorly correlated ($P > 0.05$) to ages 1+abundance. The definition of the 1982-2000 time series of ages 1+ abundance as a time frame with which to ground truth the tuning indices is arbitrary. Retrospective bias in ages 1+ F and stock size was still discernible albeit at a low level as far back as 1998 (Terceiro 2007). As a result, to further examine how the 1982-2000 time frame might affect the choice of informative indices, the Pearson correlation and stepwise analyses were repeated for ages 1+ abundance and SSB from ADAPT for an additional two periods 1982-1998 and 1982-1999.

The theoretical foundation of this regression approach could be questioned by the fact that trawl survey indices were used to directly tune the 2007 ADAPT run. The potential influence of the tuning indices on the trend in ages 1+ abundance over the converged portion of ADAPT should be minimal. The overall trend in flounder abundance within the converged portion (1982-2000) is mainly influenced by the catch-at-age matrix, whereas more recent abundance estimates are mainly affected by trends in the tuning indices (Mohn 1999). The candidate abundance indices used in the Pearson correlation and stepwise regression analyses included 10 trawl survey indices and one additional recreational cpue index that has not been previously used to tune ADAPT (Tables 1 and 2). The trawl indices included ages 1+ number/tow from the 1982-2006 Massachusetts (MA) spring trawl survey, ages 1+ number/tow in the 1982-2006 Rhode Island fall trawl survey, ages 1+ number/tow in the 1990-2006 Rhode Island fixed station trawl survey, ages 1+ number from the 1984-2006 Connecticut spring and fall trawl surveys, both ages 1+ number and kg/tow from the 1982-2006 NEFSC spring and fall indices, both ages 1+ number and kg /tow from the 1992-2006 NEFSC winter trawl survey, ages 1+ number /tow from the 1989-2006 New Jersey trawl survey, ages 1+ number/tow from 1990 to 2006 for the Delaware trawl survey. A shorter (1990-2006) time series of flounder kg/tow data are also available for the Connecticut spring and fall surveys. At this time, there are no reported biomass (kg/tow) time series for trawl surveys in Massachusetts, Rhode Island, New Jersey and Delaware. A more extensive description of these 10 trawl survey indices is found in the 2006 assessment report (Terceiro 2007).

The new coast-wide recreational cpue index was derived based on a coast-wide recreational catch-effort ratio from 1982 to 2006:

$$\text{RelNt} = \text{ATLN} / \text{Et}. \quad (1)$$

The coast-wide recreational catch (ATLN) (type A, B1 and B2) in numbers and recreational fishing effort (Et, trips) in equation (1) were based on the private boat sector of the MRFSS annual surveys (Table 1). Flounder catch and fishing effort data were confined to the private boat sector for two reasons. First, the flounder total catch and total effort estimates each year were derived with relatively high precision (proportional CV < 5% of the mean). Second, the private boat sector of the fishery is highly mobile and capable of catching flounder of all sizes throughout their range.

A second time series (1982-2006) of relative abundance indices in weight (RelWt) was also derived as a ratio of recreational catches (A, B1, B2) in weight (RelWt) to fishing effort (Et) (Table 2). The MRFSS has monitored weight (kg) data from only the harvest (A, B1) so weight data from released fish (B2) are not available. As a result, average weight for A, B1 and B2 catches was estimated indirectly as the average weight (kg) per flounder taken from the NEFSC spring and fall surveys from 1982-2006. The average weight (avwt) of a flounder was derived annually from the NEFSC spring and fall surveys as the average kg/tow index divided by the average number/tow index. The resulting weight index (RelWt) for the recreational fishery was expressed annually as the product of the relative abundance index in number (RelNt) and the average weight (avwt) from the spring and fall NEFSC trawl surveys.

The proposed recreational indices for flounder (RelNt and RelWt) are fishery dependent and thus not entirely independent of the total (sport, commercial and discards) coast-wide landings. However, the problem of colinearity between recreational indices and total coast wide landings should be relatively minor for two reasons. First, auto-correlation between the relative abundance

indices (RelNt and RelWt) and total harvest is minimized by the fact that private boat recreational catches (type A, B1 and B2) were used here rather than harvest (type A and B1) to derive the RelNt. The recreational catches are usually three to four times higher each year than the harvest after 1993. Second, in order to derive the recreational indices, the private boat catches (A, B1, B2) in the MRFSS were further divided by private boat fishing effort (Et). Note that the trend in Et from 1982 to 2006 was inversely related ($r = -0.53$, $P < 0.01$) to total coast-wide flounder harvest.

RESULTS

Each of the ages 1+ abundance indices for the three converged periods 1982-1998, 1982-1999 and 1982-2000 was correlated to the corresponding ages 1+ abundance in number and weight (mt) based on ADAPT (Tables 4 and 5). Regardless of the converged time frames (1982-1998, 1982-1999, 1982-2000), ages 1+ number/tow from the NEFSC spring and winter surveys, as well as the Massachusetts, Rhode Island and Delaware surveys were poorly ($P > 0.05$) correlated to ages 1+ stock size in number from the three converged portions (Table 4). The Rhode Island fixed station survey and Connecticut fall survey of ages 1+ abundance were significantly correlated ($P < 0.03$) to the 1982-2000 and 1982-1999 abundance estimates but not to ages 1+ abundance from the 1982-1998 period. All of the other surveys (NEFSC fall, Connecticut spring, New Jersey and the coast-wide recreational cpue (RelNt) were significantly ($P < 0.05$) correlated to ages 1+ abundance across the three converged periods. However, recreational cpue in number was consistently the most highly ($P < 0.0001$) correlated index to ages 1+ abundance across the three converged periods.

Results of the correlation analyses for biomass (Table 5) revealed that the NEFSC winter biomass indices were poorly correlated to ages 1+ biomass from the converged portions, whereas the Connecticut spring and fall indices were significantly ($P < 0.05$) correlated to ADAPT biomass from 1982 to 1999 and 1982-2000, but not for the period 1982-1998. The NEFSC spring and fall biomass (kg/tow) indices and the recreational cpue index in kg (RelWt) were highly correlated ($P < 0.05$) to ages 1+ biomass across the three converged periods (Table 4). The recreational index (RelWt) always exhibited the highest correlation ($P < 0.0001$) to ages 1+ abundance across the three converged periods.

Ages 1+ biomass (mt) from the converged portion (1982-2000) was highly correlated ($P < 0.0001$) to spawning stock biomass (SSB). The correlation matrix (Table 5) indicated that all biomass indices except the NEFSC winter survey were significantly correlated to SSB levels from 1982 to 2000. As in the other comparisons, the recreational cpue (RelWt) was the most highly correlated ($P < 0.0001$) time series to the SSB for the converged portion (1982-2000).

Results from the stepwise regression that related ages 1+ abundance from the converged portion to the tuning indices revealed that the recreational cpue index was the only index selected as the best predictor of mean ages 1+ numbers, accounting for 62 to 68% of the variation in abundance over the three converged periods (1982-1998, 1982-1999, 1982-2000) (Table 6). None of the ten trawl survey indices were selected as a second predictor variable from the stepwise regression. The predictive equation that explained 68% of the variation in abundance from 1982-2000 (Figure 1) was:

$$\text{PredN} = 5.28 + 26.38 * \text{RelNt} . \quad (2)$$

The resulting residual pattern from equation (2) was random over time ($P < 0.15$) (Figure 2), indicating that this predictive model was unbiased and a reliable predictor of abundance at least from 1982-2000. As a result, this model was used to predict ages 1+ flounder abundance from 2001 to 2006 in an effort to adjust recent ages 1+ abundance for systematic retrospective bias. Severe overestimation of ages 1+ stock size from ADAPT was clearly evident in recent years (2001-2006) (Figure 3). The lowest systematic bias occurred in 2001 (23.7%) and highest took place in 2003 (53.9%). The percentage bias for ages 1+ abundance was 50.5% in the terminal (2006) year. The most reliable time series (1982-2006) of ages 1+ abundance was considered to be the converged portion (1982-2000) of ages 1+ abundance from ADAPT plus the predicted ages 1+ abundance estimates from 2001 to 2006 based on equation (2).

Results from the stepwise regression of ages 1+ biomass (mt) from the converged portion and the tuning indices revealed that the recreational cpue index in weight (RelWt) and the NEFSC spring index (kg/tow) were together the best predictors of ages 1+ biomass for the three converged periods (1982-1998, 1982-1999, 1982-2000), each accounting for 87 to 88% of the variation (Table 6). The partial correlation coefficients were always much higher for the recreational cpue (0.77-0.80) than for the NEFSC spring indices (0.09-0.11). The predictive equation for the converged period 1982-2000 was:

$$\text{PredW} = 4.30 + 4.94 * \text{NEFSC} + 23.10 * \text{RelWt}, \quad (3)$$

which explained 88% of the variation in ages 1+ stock biomass from 1982-2000 (Figure 4). A plot of residuals was random ($P < 0.60$) across the time series (Figure 5), indicating that the predictive model (equation 3) was unbiased. As a result, this model was used to predict ages 1+ flounder biomass from 2001 to 2006 in an effort to adjust ages 1+ biomass for retrospective bias (Figure 6). The percentage bias between the ADAPT stock biomass and the predicted (PredW) biomass from equation (3) was relatively low (1.5%) in 2001, but the bias generally increased in magnitude over time to the highest (45.5%) level in 2006, indicating that the terminal stock biomass estimate is severely overestimated by ADAPT. The most reliable time series (1982-2006) of ages 1+ biomass for further analyses was the converged portion (1982-2000) of ages 1+ biomass from ADAPT plus the predicted ages 1+ biomass estimates from 2001 to 2006 based on equation (3). This biomass time series was used in all subsequent surplus production modeling.

Stepwise regression analyses of SSB (mt) relating the converged portion of ADAPT to the tuning indices also revealed that the recreational cpue index in weight (RelWt) and the NEFSC spring index (kg/tow) were the best predictors of flounder SSB for the 1982-2000 period (Table 6), accounting for 79% of the variation in SSB (Figure 7). The partial correlation coefficient was much higher for the recreational cpue (0.67) than for the NEFSC spring indices (0.11). The predictive equation for SSB over the converged period 1982-2000 was:

$$\text{PredSSB} = 4.40 + 5.90 * \text{NEFSC} + 19.26 * \text{RelWt}. \quad (4)$$

The residuals based on the difference between observed and predicted SSB (PredSSB) were random ($P < 0.17$) across the time series (Figure 8), indicating that the predictive model (equation 4) was unbiased. As a result, this model was used to predict flounder SSB from 2001 to 2006 in an effort to adjust SSB for retrospective bias (Figure 9). The percentage bias between the ADAPT stock biomass and the predicted (PredW) biomass from equation (4) was relatively low (-5.8%) in 2001, but the bias generally rose in magnitude over time to the highest (47.3%)

level in 2006. Based on this analysis, the most reliable time series (1982-2006) of flounder SSB for further analyses was the converged portion (1982-2000) of SSB from ADAPT plus the predicted SSB estimates from 2001 to 2006 based on equation (4) (Table 3). This SSB time series was used in all subsequent stock-recruitment analyses.

Approach to Estimate ages 1+ F and Surplus Production

In this analysis, age aggregated (ages 1+) fishing mortality (F_t) was derived annually on summer flounder from 1982 to 2006. The theoretical underpinnings of our approach is based on a simple re-arrangement of the Baranov catch equation (Ricker 1975, page 13, equation 1.17) with respect to F :

$$F = \text{Catch} / \text{Mean Stock Size}, \quad (5)$$

where: mean stock size is typically expressed as the average stock size in years t and $t+1$. The ages 1+ F_t estimates were based on the ratio of ages 1+ coast-wide (commercial and sport plus discards) landings (numbers) of flounder in year t (Catch $_t$) to the corresponding ages 1+ abundance estimates (N_t , N_{t+1}) in year t and $t+1$:

$$F_t = \text{Catch}_t / [(N_t + N_{t+1})/2], \quad (6)$$

where: N_t and N_{t+1} are the flounder ages 1+ abundance estimates from the converged portion (1982-2000) of ADAPT whereas N_t values from 2001 to 2006 represent the predictive values (equation 2). The landings and discards (Catch $_t$, $n \times 1000$) of ages 1+ flounder (Table 2) in the numerator of equation (6) were derived earlier in the 2007 stock assessment (Terceiro 2007). Equation (6) is very similar to the equation introduced earlier by Sinclair (1998) except that he estimated relative exploitation:

$$\text{Relu} = \text{Catch} / \text{Rel}N_t \quad (7)$$

instead of F . Because the 2007 abundance estimate (N_t) is not yet available, the N_{t+1} value a year later in 2006 was assumed to be the same as the 2006 N_t abundance estimate. Ages 1+ F estimates via equation (6) do not consider temporal and spatial shifts in the age structure, so this approach is designed only to monitor age aggregated F values across time (1982-2006). Thus, the F_t values are uninformative about year-class and age-specific changes in F over the time series. However, since F_t estimates from equation (6) are expressed as a ratio of annual harvest to average abundance, the trend in ages 1+ F is not confounded by the assumption of constant natural mortality ($M = 0.2$) used explicitly to derive F estimates ($F = Z - 0.2$) in ADAPT and in other catch-age models.

Another time series (1982-2006) of biomass weighted F estimates for ages 1+ flounder was estimated from 1982 to 2006 as a ratio of ages 1+ landings and discards (mt) to the average ages 1+ biomass estimates in year t (Biot) and $t+1$ (Biot+1). As with the other analysis, Biot and Biot+1 represent the flounder ages 1+ biomass estimates from the converged portion (1982-2000) of ADAPT whereas the Biot estimates from 2001 to 2006 were derived from the predictive equation (equation 3).

A time series (1982-2006) of surplus production estimates in year t (SURPt) was also derived for flounder. As in Jacobson et al (2002), the SURPt values were expressed each year by subtracting flounder biomass in year t (BIOt) from the biomass in year t+1 (BIOt+1), and then adding the coast-wide harvest and discards (mt) (catcht):

$$\text{SURPt} = \text{BIOt+1} - \text{BIOt} + \text{Catcht}. \quad (8)$$

Overfishing Thresholds (Fmsy, Bmsy)

Surplus production estimates have been used to monitor trends in per capita stock productivity for many exploited finfish populations (Jacobson et al 2002). Having a time series (1982-2006) of flounder surplus production (SURPt) (Table 7) and stock biomass estimates in year t (Biot) (Table 7), updated Fmsy and Nmsy thresholds were estimated for flounder using the dynamic version of the Gompertz external surplus production model (Quinn and Deriso 1999; Jacobson et al 2002). Like stock-recruitment models, the theoretical foundation of production models assumes the existence of compensatory density-dependent mortality for finfish populations, a position widely held by most fish population ecologists (Wahle 2003). We selected the Gompertz form over the more widely used logistics equation because Yoshimoto and Clarke (1993) reported that under simulation conditions, the Gompertz model produced more realistic (positive) and stable overfishing thresholds than the logistics model. In the asymmetrical Gompertz model, surplus production estimates (SURPt) from 1982-2006 were regressed against biomass (Biot) and the product of the log flounder biomass and biomass (LogBiot*Biot) in a two variable linear regression model without a y-axis intercept:

$$\text{SURPt} = a * \text{Biot} + b * ((\text{LogBiot}) * \text{Biot}), \quad (9)$$

where: K – theoretical carrying capacity (mt) = $\exp(a/b)$;
 MSY- maximum sustainable yield (mt) = $(-b * K)/2.72$;
 Bmsy – stock size (mt) at MSY = $K / 2.72$;
 Fmsy – instantaneous fishing mortality at MSY = MSY / Bmsy ;
 Fcoll – instantaneous fishing mortality at stock collapse = $\text{Fmsy} * 2.72$.

Our ability to estimate precise Fmsy and Bmsy values in surplus production models are often plagued by the presence of outliers caused by moderate to high measurement errors. To minimize the effects of outliers, the Gompertz model (equation 9) was fitted as a linear robust regression model using the least trimmed squares regression (LTS) objective function as recommended by Rousseeuw and Van Driessen (2000). The parameter estimates (a, b) and resulting reference points (Fmsy, Bmsy, Fcoll) from the dynamic production model (equation 9) were derived from the ROBUSTREG procedure contained in the Statistical Analysis System (SAS 2002). The parameter estimates (a, b) and their standard errors based on least squares (LS) are highly prone to the presence of outliers. With robust linear regression like LTS, outlying observations are identified and automatically down-weighted, resulting in higher precision and greater overall stability of the parameter estimates (a, b) over those derived from ordinary least squares.

Before the overfishing thresholds (F_{msy} , B_{msy}) were estimated via equation (9), the pattern of residuals was examined for the presence of serial correlations over time. The residuals from an unbiased model should be distributed randomly over time. By contrast, a significant ($P < 0.05$) correlation between residuals and time (1982-2006) would indicate model misspecification. A serial correlation occurs when the residuals are all in one direction during say the first half of the time series then they switch abruptly in the opposite direction thereafter. This anomalous residual pattern could be due to an incorrect configuration of the production model (i. e. Logistics versus Gompertz), or perhaps, the model lacks an important explanatory variable. If the parameter estimates (a , b) of the model are statistically significant ($P < 0.05$), and if the residual pattern from the model exhibited no serial correlation, the model was considered unbiased and used to estimate overfishing (F_{msy} , B_{msy}) thresholds.

To examine the hypothesis that flounder surplus production has recently been eroded by trophic and environmental factors, candidate predators such as striped bass, bluefish and spiny dogfish abundance (pred term) were included in the production model as an extra independent variable (Table 3). In addition, environmental variables such as annual mean water temperature and deviations in the winter North Atlantic Oscillation (NAO) index (environ term) from 1981 to 2006 (Table 3) were also added to the external production model:

$$SURPt = a*Biot + b * ((LogBiot)*Biot) + c*(Pred of Environ), \quad (10)$$

in a stepwise regression fashion. Since all female flounder reach sexual maturity by age 2 (Almeida et al 1992), water temperature and winter NAO values were lagged $t-1$ and $t-2$ years to coincide with flounder recruitment to the adult stock. Environmental disturbances have been proposed as a major process structuring ecological systems (Hollowed et al 2000), both by causing direct mortality and by changing the carrying capacity of the ecosystem. Bluefish, striped bass and spiny dogfish are major inshore finfish predators that have recently risen sharply in abundance along the Atlantic coast. Moreover, these finfish predators overlap the spatial and temporal distribution of flounder, and all are considered, to some extent, as potential candidate predators on flounder (Rountree 1999). Striped bass is regarded as a voracious predator from the Mid and North Atlantic on menhaden, gizzard shad and herring (Hartman 1993). Larger (> 70 cm) striped bass, however, have been reported to switch their prey preference from herring and small menhaden to spot, flounder and weakfish in Chesapeake Bay (Hartman and Brandt 1995; Walter and Austin 2003). Bluefish (*Pomatomous saltatrix*) also prey upon a variety of finfishes including flounder throughout the Atlantic coast (Bowman et al 2000). Dogfish (*Squalus acanthias*) are found coast-wide and are regarded as a primary finfish predator of juvenile summer flounder (Rountree 1999).

Statistical evidence consistent with the predation hypothesis would be evident if the slope (c) for predation effects in equation (10) was negative and statistically significant ($P < 0.05$). This would imply that enhanced predation has eroded flounder surplus production independent of fishery effects. Moreover, if the slope for predation effects is significant, the inclusion of the extra predation term in the model can greatly enhance the precision around the (a) and (b) parameters of equation (10), thus allowing more precise estimates of F_{msy} and B_{msy} thresholds. To test for potential joint effects of fishing (F) and trophic interactions on flounder productivity, residual plots against time were examined for the presence of serial correlations. Further statistical support for the predation hypothesis would exist, if the pronounced serial correlation

evident in the basic production model (equation 9) should disappear following the addition of predation effects to the model (equation 10).

Annual changes in coast-wide striped bass abundance (ages 7+) in numbers (Table 3) have been monitored annually from 1988 to 2006 by the ratio of ages 7+ harvest to the tag-based F derived from the catch equation approach (Versak 2007). In addition, a time series (1982-2006) of ages 8+ striped bass abundance has been derived recently from the Statistical Catch-at-Age model (Nelson 2007). Annual changes in spiny dogfish and bluefish from 1982 to 2006 were indexed here as cpue based on the coast-wide recreational catches in number (A, B1, B2) and coast-wide effort (trips) from the private boat fishery in the MRFSS surveys (Table 3). These trends in coast-wide recreational cpue of dogfish and bluefish were assumed to be informative about coast-wide changes in these stocks from 1982 to 2006. A time series (1982-2006) of average annual surface water temperatures was taken from a continuous temperature recorder in Long Island Sound located at the Millstone Nuclear Power Station, Waterford CT. Annual deviations in the winter NAO indices from 1982 to 2006 were taken from the NOAA web site.

Stock-Recruitment Effects

Over the last seven years, the stock-recruitment (S-R) relationship for flounder has been extensively examined (Terceiro 2000, 2006; Gibson 2000; Crecco 2000). Terceiro (2006) has argued that the asymptotic Beverton-Holt S-R model should be chosen over the parabolic Ricker S-R model based on theoretical grounds, despite the fact that the parabolic model was a better fit to stock-recruitment data (Gibson 2000). Terceiro (2006, 2007) has repeatedly shown that the residuals from all Beverton-Holt S-R model runs have exhibited a persistent serial correlation over time. The residuals were all high and positive from 1983 to 1987, then nearly all subsequent residuals switched to a negative direction. Since Gibson (2000) noted a similar anomalous residual pattern when flounder S-R data were fitted to the dome-shaped form of the Shepherd (1982) S-R model, this serial residual pattern is widespread and not related directly to the shape of the S-R curve. The other potential cause for the serial correlation in residuals is that the basic S-R model may lack an additional important explanatory variable such as environmental or predatory effects.

In this report, the shape and residual pattern of the flounder stock-recruitment relationship was further explored with the flexible Shepherd (1982) S-R model:

$$\text{Rec} = A * \text{SSB} / (1 + (\text{SSB} / K_p)^b), \quad (11)$$

where: A = the magnitude of compensatory reserve;

K_p = the flounder spawning stock biomass (mt) at which compensatory effects dominate;

b = the degree of compensatory density-dependent mortality;

Rec = estimated age 0 recruits from the most recent ADAPT run (Terceiro 2007) (Table 3);

SSB = estimated SSB from the converged portion (1982-2000) of ADAPT plus predicted SSB from the stepwise model from 2001-2006 (Table 3).

If the b parameter estimate in equation (11) is less than 1.0, the curve approximates a power function. If (b) is equal to 1.0, the S-R curve is consistent with the asymptotic Beverton-Holt model, whereas a (b) estimate greater than 1.0 is consistent with the parabolic Ricker type S-R curve. The entire time series (1982-2006) of flounder recruitment (Rec) based on the 2007

ADAPT run (Terceiro 2007) was fitted to equation (11) because Terceiro (2006) has shown that the degree of retrospective bias on recent recruitment estimates from ADAPT was relatively small. In order to explore the residual patterns from the Beverton-Holt and Ricker type S-R models, the S-R data were fitted to equation 11 holding the (b) parameter constant at 1.0 and 2.0, respectively. The remaining parameter estimates (A, Kp) from the S-R model (equation 11) were derived from the NLIN procedure (marquardt algorithm) contained in the Statistical Analysis System (SAS 2002).

Given the likely presence of outliers in the S-R data, the Shepherd S-R model was fitted as a nonlinear robust regression using the iterative reweighted least squares method outlined by Holland and Welsch (1978). The algorithm and rationale for this approach is described in SAS (2002). This re-weighting scheme is designed to detect outliers, thereby allowing the down weighting of S-R data from certain years in the model where model residuals, regardless of direction, exceeded a previously defined threshold level. As indicated by Holland and Welsch (1978), the choice of a threshold is subjective and always represents a trade-off between minimizing the variances around the parameters (A, Kp) and at the same time generating globally converged parameter estimates. As suggested by Holland and Welsch (1978), a range of threshold estimates was used initially and the final threshold value was selected that satisfied the trade-off between global convergence of all parameter estimates and parameter estimates with maximum precision and minimum variance. The two-step re-weighting approach always produced converged estimates (global estimates) that were within 10% of the parameter estimates (A, Kp) derived by the nonlinear least squares approach. However, the standard errors about the estimates based on iterative re-weighting were always 30 to 45% lower than the standard errors from the least squares method.

To examine for potential predatory and environmental effects on flounder recruitment and on the residuals from the S-R model, the Shepherd S-R model (equation 11) included an extra exponent (c) reflecting potential predation (pred) and environmental (environ) effects:

$$\text{Rec} = A * \text{SSB} / (1 + (\text{SSB} / \text{Kp})^{**b}) * \exp(c * \text{pred}, \text{environ}). \quad (12)$$

As in the surplus production analyses, candidate predators (pred) included striped bass, bluefish and spiny dogfish abundance (Table 3) were added separately to the model. Potential environmental variables (environ) included annual water temperature and deviations in the winter North Atlantic Oscillation (NAO) index. Statistical evidence consistent with the predation and environmental hypotheses would exist if the additional exponent (c) for predation and environmental effects in equation (12) was negative and statistically significant ($P < 0.05$). This would imply that biotic and abiotic factors external to the fishery have reduced recent age 0 recruitment over time. Further statistical support for the predation and environmental hypotheses would be evident, if the serial correlation in residuals evident in the basic Shepherd S-R model (equation 11) disappeared following the addition of predation or environmental effects to the S-R model (equation 12).

RESULTS

Ages 1+ Fishing Mortality (F) and Surplus Production (SURPt)

Ages 1+ fishing mortality estimates (FN) (catch weighted) were derived from 1982 to 2006 as the ratio of total annual landings (including discards) to average (t, t+1) ages 1+ abundance (Table 7). These FN estimates on ages 1+ flounder were high and variable before 1995, ranging from a low of 0.74 in 1982 to a high of 2.22 in 1988 (Figure 10). After 1994, ages 1+ fishing mortality rates dropped considerably and remained relatively stable at around 0.50 thereafter.

Ages 1+ abundance in number from ADAPT was relatively high from 1982 to 1984, then flounder abundance fell quickly to the lowest level in the time series at 9.5 million fish in 1989 (Table 7, Figure 10). Ages 1+ abundance rose steadily after 1988 to a peak abundance of 33 million fish in 2000. Note that ages 1+ flounder stock sizes from 2001 to 2006 were predicted from equation 2 in order to adjust for retrospective bias from ADAPT. These predicted biomass levels fell slightly after 2000 and remained relatively stable thereafter at around 25 million fish.

Ages 1+ fishing mortality (FW) (biomass weighted) on flounder were again high and variable before 1995 (Table 7), ranging from a low of 0.74 in 1994 to a high of 1.88 in 1988 (Figure 11). Biomass weighted FW levels on ages 1+ flounder dropped steadily from 1994 through 2002 to below 0.38, but FW levels rose slightly thereafter to a peak of 0.54 in 2006.

Ages 1+ flounder biomass (mt) based on ADAPT was relatively high and stable from 1982 to 1987 at around 25 thousand mt, then flounder biomass dropped quickly to below 16 thousand mt from 1988 to 1994 (Table 7, Figure 11). Thereafter stock biomass began to rise and eventually reached about 30 thousand mt by 2001. Ages 1+ stock biomass remained relatively steady at around 30 thousand mt from 2001 to 2005, but the 2006 biomass level fell by 30% to 23 thousand mt. Note that stock biomass from 2001 to 2006 was predicted by equation 3 in order to adjust for severe retrospective bias from ADAPT.

Surplus production (SURPt) estimates (mt) for flounder were derived via equation 8 from 1982-2006 (Table 7, Figure 12). Surplus production was highest during the early to mid-1980's despite the presence of high fishing mortality (F) rates (Figures 10 and 11). SURPt levels did fall steadily after 1986, presumably due to high fishing mortality, to the lowest level in the time series in 1990. SURPt levels for flounder increased by 20 to 30% after 1991 but never recovered to the pre 1987 levels despite the presence of relatively low and steady fishing mortality from 1997 to 2006 (Figures 10 and 11).

Overfishing Thresholds (Fmsy, Bmsy)

To estimate overfishing thresholds (Fmsy, Bmsy), flounder surplus production estimates from 1982 to 2006 (Figure 12) were fitted to flounder biomass via the Gompertz dynamic production model (equation 9). The Gompertz model accounted for 80% of the variation in surplus production and the parameter estimates (a, b) were determined with high precision (Table 8). However, the plot of model residuals indicated a severe ($P < 0.01$) serial correlation over time (Figure 13), indicating model misspecification. The residuals were large and positive from 1982 to 1986, then the residuals for most years shifted in the opposite direction. Even when the Logistics form of the surplus production model was used instead of Gompertz, the same serial residual pattern persisted over time, indicating that the residual problem was not due to the

configuration of the production model. Due to the clear residual problem with the basic Gompertz and Logistics models, they were not used to estimate overfishing thresholds for flounder.

Since a serial residual pattern persisted in the basic (equation 9) production model, the environmental-dependent form of the Gompertz model (equation 10) was used in the linear stepwise regression model with potential explanatory variables such as striped bass, bluefish and spiny dogfish, mean annual water temperature and winter NAO. The stepwise model selected striped bass abundance (either tag-based or SCAM estimates) as the only negative and significant ($P < 0.01$) explanatory variable (Table 9). No other variables were chosen at the $P < 0.05$ level.

When this extended production model was fitted to the robust regression procedure, all parameters (a, b, c) estimates were highly significant ($P < 0.0001$) (Table 8). This production model with striped bass effects explained 83% of the variation in flounder surplus production from 1982-2006. Moreover, the serial residual pattern present in the basic production model virtually disappeared (Figure 14) ($P < 0.49$) when striped bass abundance was added as a second variable to the production model. These findings are consistent with the Predation Hypothesis, indicating that flounder productivity has recently been eroded by enhanced striped bass predation.

This extended production model with striped bass predatory effects was then used to estimate flounder overfishing thresholds (F_{msy} , B_{msy}). The resulting overfishing threshold (F_{msy}) for flounder was 0.64 (80% C.I.: 0.51 to 0.77) and the biomass threshold was 32,500 mt (80% C. I: 25,900-39,200 mt) (Table 8). All of the ages 1+ fishing mortality (FW) rates (biomass weighted) on flounder from 1982 to 1994 exceeded the F_{msy} threshold of 0.64 (Figure 16), indicating that overfishing had occurred on flounder from 1982 to 1994. However, all subsequent FW estimates were below the F_{msy} threshold, suggesting that overfishing was corrected by additional management measures imposed during the early to mid 1990's. By contrast, although ages 1+ biomass (mt) has risen steadily since 1989 (Figure 15), except for the 2001 ages 1+ stock biomass of 33,900 mt, all other ages 1+ biomass estimates have remained below the estimated B_{msy} threshold of 32,500 mt (Figure 16). Recent (2002-2005) biomass levels have approached the B_{msy} threshold, but the 2006 biomass level of 22,900 mt represented a 30% drop and is well below the B_{msy} threshold of 32,500 mt. Since fishing mortality rates (FW) have stabilized below the F_{msy} threshold since 1995, the recent lack of stock biomass growth is likely due largely to enhanced striped bass predation and not overfishing.

Stock –Recruitment Effects

The Beverton-Holt version ($b = 1.0$) of the Shepherd S-R (equation 11) model was fitted to age 0 recruitment and spawning stock biomass (mt) estimates (Table 3) from 1982-2006 using iterative reweighted least squares regression. The S-R model converged but the parameter estimates (A , K_p) did not differ significantly ($P < 0.05$) from zero (Table 10, Figure 17). Moreover, the residual plot over time indicated the presence of significant ($P < 0.0005$) serial correlation in the residuals (Figure 18). The residuals were large and positive from 1982 to 1987 then the residuals became smaller and mostly negative (Figure 17), indicating model misspecification.

When the Ricker version ($b = 2.0$) of the S-R model was fitted to the S-R data (Table 3), the model converged and the parameter estimates (A , K_p) were highly significant ($P < 0.0001$)

(Table 10, Figure 19). However, the residual pattern from the Ricker Model (Figure 20) looked almost exactly like the atypical residual pattern from the Beverton-Holt S-R model. When bluefish and dogfish abundance, as well as lagged (t-1, t-2) mean annual temperature and lagged winter NAO were added separately to the extended Ricker model (equation 12), the resulting exponent (c) for each of these variables did not differ significantly ($P < 0.05$) from zero. However, when striped bass abundance was added as a second explanatory variable, the model explained 91% of the recruitment variation, all three parameter estimates (A, K_p , c) were highly significant ($P < 0.0001$) (Table 10, Figure 21) and, most importantly, the anomalous residual pattern seen in the basic Beverton-Holt and Ricker S-R models virtually disappeared (Figure 22). These findings are consistent with the Predation Hypothesis, indicating that the transmission of age 0 recruits to the adult stock has been recently impeded due to enhanced striped bass predation.

Management Implications and Scientific Advice

My results indicate that density-dependent processes play a much greater role in stabilizing flounder abundance than is assumed in the current stock assessment (Terceiro 2006). The main conclusion from the last stock assessment (Terceiro 2006) is that flounder have been overfished since at least 1982 despite the implementation of catch quotas on commercial fisheries beginning in 1990 and a steady decline in fishing mortality (F) since 1995. The current assessment results show that flounder stock biomass has not yet reached the biomass threshold of 44,760 mt because F has remained too high. The important conclusion from the last assessment that summer flounder have remained overfished for at least 25 years largely depends on the degree of compensatory density-dependent mortality inherent to the flounder stock. It is widely recognized that the magnitude of F_{msy} and the level of resilience to exploitation depends on the degree of density-dependent compensation (Quinn and Deriso 1999). The current assessment has assumed that little if any compensation occurs for flounder and therefore used an F_{max} of 0.28 from the YPR model as a proxy for F_{msy} . In this report, F_{msy} was estimated directly to be 0.64 based on the extended Gompertz model that assumes moderate to high density-dependent compensation. My findings indicate that the flounder were overfished before 1995 when ages 1+ F estimates exceeded my F_{msy} , but that extensive management measures imposed during the early to mid 1990's enabled F to drop below the overfishing threshold. The very strong fit of both the production and dome-shaped Ricker models suggests that moderate to strong density-dependent mortality is evident in the summer flounder stock, allowing the flounder stock to absorb the effects of relatively high ($F < 0.64$) fishing mortality. My findings of moderate to high density-dependent compensation for summer flounder is consistent with their suite of life history traits that include early female maturation (age 2) (Almeida et al 1992), relatively rapid somatic growth and a relatively short lifespan (12 years) (Dery 1988). My F_{msy} threshold of 0.64 is well within the range of F_{msy} levels reported from four earlier studies (Chang and Pacheco 1976; Gibson 2000; Crecco 2000; Armstrong 2000). They reported F_{msy} thresholds (F_{msy} : 0.45-0.82) for summer flounder that always exceeded the F_{max} level of 0.28 used in the current assessment, and were clearly closer to my F_{msy} estimate of 0.64 based on the Gompertz production model. These earlier findings are consistent with my results, suggesting that summer flounder are under at least partial density-dependent control and are thus more resilient to fishing pressure than previously thought.

The possibility for further rebuilding of summer flounder biomass beyond the B_{msy} level of 32,500 mt over the next five years is more uncertain due to the recent rise in predatory mortality. My findings indicate that the rapid build-up in stock biomass inferred from 2001 to 2006 based on ADAPT is overstated due to persistent retrospective bias. When the recent (2001-2006) abundance estimates from ADAPT were adjusted downward by 20 to 50% to account for retrospective bias, the rate of stock rebuilding after 2000 was minimal. My results suggest that enhanced predation by striped bass on young flounder provides the most plausible explanation for the recent stagnation of flounder population growth and age 0 recruitment to the adult stock. Moreover, the inclusion of striped bass effects in both the extended Ricker S-R and Gompertz models was the only variable examined thus far that removed the recurring residual problem that constantly plagued the Beverton-Holt S-R model in previous assessments (Terceiro 2006). The fact that the exponent for striped bass predation was negative and highly significant ($P < 0.0001$) in both the extended Ricker S-R and Gompertz surplus production models is not surprising, given that annual changes in age 0 recruitment largely govern the net changes in fish surplus production (Walters and Martell 2004).

It is widely recognized that statistical evidence (regression and production models) alone does not demonstrate causality, but recent empirical evidence is wholly consistent with the Predation Hypothesis involving striped bass. Due to the success of striped bass management, striped bass abundance has risen steadily to record levels in mid and north Atlantic coastal waters from 1993 to 2006 (Crecco 1994; Nelson 2007). The results of coast-wide tagging of striped bass since 1987 indicate that abundance of ages 7+ stripers has risen nearly four-fold coast-wide from 1998 to 2006 (Versak 2007). Moreover, coast-wide tag returns from Maine to North Carolina indicate that striped bass are found mostly in state waters (Versak 2007) that clearly overlap the temporal and spatial distribution of summer flounder. Since striped bass are known to consume finfish prey up to 60% of their own body length (Manooch 1973), it is reasonable to hypothesize that striped bass abundance has reached such high abundance that flounder population growth would be severely impeded by enhanced striped bass predation. Larger (> 70 cm) striped bass have been reported to switch their prey preference from herring and small menhaden to spot, flounder and weakfish in Chesapeake Bay (Hartman and Brandt 1995; Walter and Austin 2003). Striped bass grow rapidly to a large size (>90 cm) that can easily prey on smaller adult flounder, are highly piscivorous (Hartman 1993), and are efficient diurnal and nocturnal predators along inshore waters (Nelson et al 2006). Recent studies on river herring and American shad in the Connecticut River (Savoy and Crecco 2004), as well as the coast-wide weakfish stock assessment (Kahn et al 2005; Uphoff 2005) concluded that enhanced striped bass predation was the most reasonable hypothesis to explain the unexpected declines of these finfishes under low exploitation. Nelson et al (2006) reported that the average consumption level (mt) of Atlantic menhaden by striped bass along the Massachusetts coast from 1997 to 2000 was 12 times greater than the total menhaden commercial landings (mt) from Massachusetts. Finally, Bax (1998), in a comprehensive review of finfish predatory effects, noted that finfish predation accounts for between 2 and 35 times the finfish losses (mt) reported annually to commercial fisheries throughout the world.

The management implications and long-term prognosis for flounder in the presence of enhanced striped bass predation are challenging and somewhat ambiguous. In the current assessment (Terceiro 2006), natural mortality (M) in both the ADAPT and YPR models was assumed constant at 0.20 for all ages and years. It is widely recognized from recent multispecies models (Hollowed et al 2000; Walters et al 2005) that the scientific foundation supporting the

constant M assumption in single species assessments is highly questionable, particularly for younger fish. Moreover, unless long-term tagging studies are conducted, there is no other way to scientifically verify the assumption of a fixed M estimate. Despite the lack of scientific foundation around the fixed M assumption, the constant M approach is used in nearly all single species assessments conducted along the Atlantic coast. The wide acceptance of constant M occurs because time varying M is often difficult to estimate with confidence, and because a constant M assumption greatly reduces the number of parameters to be estimated in age structured VPA models. The constant M assumption implies that no systematic shifts in finfish mortality and productivity associated with predation, inter-specific competition and environmental effects are possible. Thus, the constant M assumption greatly limits our ability to explore for enhanced predation effects that may result in a systematic rise in M particularly among younger and smaller prey, as well as temporal shifts in environmental factors that can adversely affect recruitment, somatic growth and maturation. Since the choice of a fixed M value can greatly affect the magnitude of the F_{max} reference point, more detailed analyses are therefore required to determine whether or not M has change systematically over time due to enhanced predation and shifts in environmental variables. In future flounder stock assessments, the assumption that trophic and environmental effects are constant over time should be critically examined. The potential impacts of trophic and environmental effects on summer flounder should also be integrated into fisheries models and rigorously tested as a potential alternative hypothesis to the Overfishing Hypothesis.

The highly significant exponent (c) for striped bass predation from the extended Ricker S-R and Gompertz models is consistent with the presence of enhanced density-independent mortality although, under certain conditions, enhanced finfish predation can give rise to compensatory or even depensatory density-dependent mortality (Tsou and Collie 2001). In any event, increased predation should result in a systematic rise in M , particularly for smaller flounder. This phenomenon plus the apparent emergence of a flounder recruitment bottleneck between ages 0 and 1 makes stock rebuilding of flounder via further management measures an exceedingly difficult task. As indicated by Spencer and Collie (1997), fish stocks that are subject to moderate to severe predatory mortality, often undergo a sudden and persistent drop or prolonged stagnation in recruitment and surplus production over time even when fishing mortality rates have remained low for several years. Note that biomass weighted fishing mortality (F_W) on ages 1+ flounder reported here have been below my estimated F_{msy} threshold of 0.64 since 1995. If density-independent predation remains high, flounder recruitment and biomass may remain unresponsive to favorable climatic events and to further fishery management restrictions. The phenomenon of enhanced predation mortality could lead to a persistent stagnation in future flounder rebuilding unless predation pressure reverts back to pre 1998 levels.

There is a prevailing consensus that overfishing has had an adverse effect on many fish stocks throughout the world (Myers et al 1997; Hutchings and Reynolds 2004; Scheffer et al. 2001). However, the catch-at-age models traditionally used to estimate fishing mortality over time have almost always assumed a low and constant ($M = 0.20$) natural mortality rate. Under the assumption of low and constant M , a rise in total mortality (Z) over time is always construed as a rise in fishing mortality (F). Thus in nearly all single species assessments, projection models always predict rapid stock rebuilding following sizeable reductions in F . But if the wide-spread assumption of constant M is violated and M actually rises systematically over time due to enhanced predatory mortality, the results from projection models of rapid stock rebuilding would

be highly misleading. Clearly there are finfish stocks throughout the world where natural mortality (M) approximates 0.20 for some period of time or can otherwise vary without trend. But as shown here for flounder and elsewhere for American shad (Savoy and Crecco 2004) and weakfish (Kahn et al 2005; Uphoff 2005), a systematic rise in predatory mortality on age 0 flounder coupled with relatively low and stable fishing mortality (F) can either greatly extend the timetable for rebuilding, or can simply eliminate the likelihood of any stock rebuilding even after the imposition of stringent conservation measures. A similar case study linking a rise in natural mortality to the lack of stock rebuilding has been recently addressed for Northern cod stocks (Shelton et al 2006). Several cod stocks on the Grand Banks have been under a landings moratorium since 1996, but stock rebuilding of these depleted stocks has, as of 2006, not been realized. Shelton et al (2006) reported that the lack of stock rebuilding of eight cod stocks was attributed to a recent rise in natural mortality from 0.2 prior to 1990 to 0.4 to 0.8 due mainly to enhanced gray seal (*Halichoerus grypus*) predation. In the case of summer flounder, the probability of successful stock rebuilding via management intervention is reduced further by the emergence of a recruitment bottleneck at age 0 as indicated by results from the extended Ricker S-R model. Due to recent increases in the minimum size on flounder, age 0 flounder are now only slightly susceptible to direct harvest, so a coast-wide moratorium would have little if any impact on the recently emergent recruitment bottleneck.

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Table 1 Flounder Ages 1+ mean stock size (NAV, millions) from ADAPT and predicted stock size (PREDNAV), ten trawl surveys and the recreational cpue in numbers (RelNt) from 1982-2006. Trawl survey indices include the federal spring (NMFSS), federal fall (NMFSF), federal winter (NMFSW), Massachusetts spring (MA), Connecticut Long Island Sound spring (CTS) and fall (CTF), Rhode Island fall (RIF) and fixed station (RIFIX), New Jersey (NJ) and Delaware (DE).

YEAR	nav	prednav	NMFSS	NMFSF	NMFSW	MA	CTS	CTF	RIF	RIFIX	NJ	DE	RelNt
1982	41.70	25.86	2.27	1.95		2.03			0.81				0.78
1983	42.20	37.20	0.95	1.94		2.12			0.68				1.21
1984	43.40	41.16	0.66	1.91		0.30	0.63	1.00	1.24				1.36
1985	31.80	22.95	2.38	1.33		1.41	0.44	1.19	0.61				0.67
1986	26.80	31.40	2.14	1.05		1.64	0.95	1.72	2.89				0.99
1987	33.90	28.76	0.93	0.83		1.22	1.06	1.40	1.22				0.89
1988	24.70	22.95	1.50	0.83		1.24	0.50	1.42	0.56		4.09		0.67
1989	9.50	8.45	0.32	0.26		0.43	0.10	0.14	0.07		0.69		0.12
1990	14.00	16.62	0.72	0.45		0.36	0.35	0.87	0.78	0.27	1.58	1.40	0.43
1991	18.30	22.69	1.08	0.94		0.09	0.64	1.26	0.23	0.15	2.98	1.35	0.66
1992	13.20	20.84	1.20	1.33	12.29	0.70	0.56	1.02	1.30	0.34	3.65	0.36	0.59
1993	21.20	31.13	1.27	0.84	13.60	0.68	0.51	1.11	0.72	0.25	5.91	2.36	0.98
1994	22.90	24.01	0.93	0.78	12.05	3.02	0.86	0.55	0.18	0.13	1.17	0.44	0.71
1995	24.00	23.22	1.09	1.47	10.93	1.38	0.28	0.54	0.73	0.05	3.42	1.47	0.68
1996	30.30	27.18	1.76	1.85	31.25	0.84	0.96	2.19	2.24	0.94	8.03	1.33	0.83
1997	28.70	25.33	1.06	2.76	10.28	2.01	1.00	2.50	1.80	0.69	14.70	1.24	0.76
1998	28.30	30.60	1.19	4.14	7.76	2.00	1.31	1.72	0.54	0.43	8.80	1.55	0.96
1999	32.50	32.19	1.60	3.58	11.06	2.26	1.44	2.68	3.10	0.87	10.41	1.49	1.02
2000	33.20	27.18	2.14	3.10	15.76	3.49	1.79	1.91	2.55	2.52	6.40	1.05	0.83
2001	38.40	29.29	2.69	2.88	18.59	2.09	1.75	4.42	2.14	0.97	5.06	2.30	0.91
2002	44.80	21.64	2.47	2.57	22.68	2.12	3.19	6.12	4.70	1.92	15.33	0.32	0.62
2003	51.00	23.48	2.91	2.80	35.62	2.41	3.42	3.39	5.47	3.73	9.24	0.58	0.69
2004	49.70	24.01	3.03	3.88	17.77	0.78	1.84	1.95	2.86	2.07	9.76	0.14	0.71
2005	55.30	27.70	1.81	2.59	12.89	2.02	0.80	2.41	3.29	2.46	8.08	0.43	0.85
2006	46.90	23.22	1.77	2.25	21.04	2.00	0.86	2.19	3.00			0.40	0.68

Table 2. Flounder ages 1+ stock biomass (BAV, mt*1000) from ADAPT and predicted biomass (PREDBAV), five trawl surveys and the recreational cpue in kg/effort (RelWt) from 1982-2006 trawl survey indices include the federal spring (NMFSSK), federal fall (NMFSFK), federal winter (NMFSWK) and spring and fall CT (CTSK, CTFK),

YEAR	bav	predbav	nmfssk	nmfsfk	nmfswk	ctsk	ctfk	RelWt
1982	21.20	19.25	1.11	0.90				0.41
1983	25.00	21.93	0.53	0.47				0.65
1984	25.30	25.58	0.38	0.65				0.84
1985	20.80	19.47	1.20	0.87				0.40
1986	19.70	20.13	0.82	0.45				0.51
1987	20.60	21.65	0.38	0.28				0.67
1988	16.30	18.98	0.68	0.11				0.49
1989	7.67	7.10	0.24	0.08				0.07
1990	9.40	10.72	0.27	0.19				0.22
1991	10.00	11.11	0.35	0.17				0.22
1992	10.40	13.04	0.46	0.49	4.90	0.35	0.87	0.28
1993	12.40	14.99	0.48	0.04	5.50	0.27	0.85	0.36
1994	14.90	15.35	0.46	0.35	6.03	0.48	0.47	0.38
1995	18.20	15.58	0.46	0.83	4.81	0.16	0.43	0.39
1996	21.30	17.31	0.67	0.45	12.35	0.53	1.61	0.42
1997	21.00	18.63	0.61	0.92	5.54	0.60	1.84	0.49
1998	23.30	22.61	0.76	1.58	5.13	1.15	1.77	0.63
1999	22.50	24.77	1.01	1.66	7.99	1.09	2.27	0.67
2000	27.80	29.56	1.70	1.82	12.59	1.35	1.77	0.73
2001	33.40	33.91	2.16	1.55	15.68	1.21	3.19	0.82
2002	36.30	29.93	2.29	1.40	18.43	2.38	4.41	0.62
2003	44.80	30.58	2.42	1.93	27.48	2.45	3.27	0.62
2004	44.70	31.32	2.43	3.06	15.25	1.69	1.74	0.65
2005	45.70	32.48	1.59	1.83	10.32	0.67	1.93	0.88
2006	42.00	22.93	1.34		15.93	0.61	1.35	0.52

Table 3. Flounder recruitment (REC) from ADAPT, spawning stock biomass (SSB2, mt) and various environmental predictors, note that SSB2 from 1982-2000 from ADAPT and 2001-2006 from predicted model. Ages 7+ striped bass (STRIP) abundance from tagging (STRIP) and ages 8+ striper abundance from VPA.

YRC	REC	SSB2	temp	nao	blue	STRIP	stripvpa	DGFISH
1982	74300	22600.0	11.10	2.00	0.68		463	1.31
1983	80300	24400.0	12.00	0.74	0.69		333	3.33
1984	48400	21900.0	12.00	-0.38	0.48		245	0.92
1985	48600	19900.0	12.00	-0.03	0.52		232	0.35
1986	53400	18400.0	11.90	0.34	0.68		337	10.59
1987	43900	19100.0	11.80	0.10	0.78		412	5.58
1988	13000	10900.0	11.10	2.86	0.43	1770	495	5.74
1989	27300	7000.0	11.30	2.37	0.46	2830	628	10.19
1990	30400	9900.0	12.10	0.21	0.55	1996	1375	6.78
1991	28700	8700.0	12.60	1.68	0.38	1526	1918	14.21
1992	32300	9900.0	11.50	1.43	0.40	1715	2329	11.06
1993	33200	12300.0	11.70	1.80	0.27	2177	2621	8.94
1994	35300	15100.0	11.60	2.44	0.28	3728	3052	10.22
1995	38700	19000.0	12.50	-2.32	0.28	3308	3496	5.91
1996	28200	20000.0	10.60	0.18	0.26	4869	3865	3.40
1997	28900	20300.0	10.90	0.80	0.30	4397	4498	6.68
1998	31000	22000.0	12.10	0.98	0.24	3739	4372	6.72
1999	29200	22300.0	12.90	1.85	0.26	3921	4421	6.61
2000	33200	25400.0	12.20	-0.50	0.33	7454	4982	2.49
2001	33400	32945.4	12.50	0.79	0.38	9339	6934	18.14
2002	36600	29858.4	12.70	0.40	0.35	11371	7133	16.34
2003	27900	30625.4	11.50	-0.20	0.38	12168	7669	20.80
2004	38000	31262.5	11.70	-0.11	0.48	14727	8028	27.28
2005	17000	30738.6	11.80	-0.82	0.42	11865	6927	26.07
2006	30300	22326.4	13.00	1.83	0.39	12852	5915	33.76

Table 4. Pearson Correlation (r) Analyses between relative abundance (catch/tow) of each of the 11 candidate tuning indices and ages 1+ flounder abundance over the converged portion from ADAPT. This analysis was conducted on ages 1+ abundance over three converged time periods (1982-1998, 1982-1999, 1982-2000). An asterisk (*) indicates a statistically significant ($P < 0.05$) correlation between the ages 1+ tuning index and ages 1+ abundance.

Index	Time Periods (Years)					
	82-98		82-99		82-00	
	r	P	r	P	r	P
NMFSS	0.34	0.18	0.35	0.15	0.38	0.11
NMFSF	0.48	0.05*	0.48	0.04*	0.50	0.03*
NMFSW	0.31	0.49	0.20	0.63	0.23	0.56
MA	0.39	0.13	0.41	0.09	0.42	0.08
CTS	0.51	0.05*	0.54	0.03*	0.56	0.02*
CTF	0.46	0.09	0.50	0.05*	0.52	0.03*
RIF	0.24	0.35	0.27	0.27	0.31	0.20
RIFIX	0.58	0.10	0.68	0.03*	0.65	0.03*
NJ	0.72	0.01*	0.76	0.004*	0.72	0.005*
DE	0.25	0.52	0.28	0.44	0.19	0.58
RelNt	0.79	0.0001*	0.79	0.0001	0.79	0.0001*

Table 5. Pearson Correlation (r) Analyses between relative abundance (kg/effort) of each of the 6 candidate tuning indices and ages 1+ flounder biomass (mt) and SSB over the converged portion from ADAPT. This analysis was conducted on ages 1+ biomass and SSB over three converged time periods (1982-1998, 1982-1999, 1982-2000). An asterisk (*) indicates a statistically significant ($P < 0.05$) correlation between the ages 1+ tuning index and ages 1+ biomass and SSB.

Index	Time Periods (Years)							
	82-00		82-98		82-99		82-00	
	SSB				Biomass			
	R	P	r	P	r	P	r	P
NMFSSk	0.66	0.002*	0.51	0.04*	0.54	0.02	0.63	0.004*
NMFSFk	0.66	0.002*	0.63	0.007*	0.62	0.006*	0.69	0.001*
NMFSWk	0.57	0.11	0.34	0.45	0.40	0.33	0.62	0.07
CTSk	0.85	0.004*	0.66	0.10	0.72	0.04*	0.82	0.007*
CTFk	0.82	0.007*	0.70	0.08	0.75	0.03*	0.73	0.02*
RelWt	0.82	0.0001*	0.88	0.0001*	0.88	0.0001*	0.89	0.0001*

Table 6. STEPWISE REGRESSION MODEL relating the 11 tuning indices to ages 1+ numbers, ages 1+ biomass and SSB for the three converged time periods (1982-1998, 1982-1999, 1982-2000). Flounder ages 1+ abundance, biomass and SSB from ADAPT were used as dependent variables. Independent variables selected by the stepwise model at the $P < 0.05$ level were the recreational cpue in number (RelNt) and weight (RelWt) and the NEFSC spring index in kg/tow (NMFSSk). The parameter estimates (Est) and their standard error (SE) are give as well as the coefficient of determination (r^{**2}).

Parameter	Time Periods (Years)							
	82-00		82-00		82-99		82-98	
	SSB				Ages +Biomass			
	Est	SE	Est	SE	Est	SE	Est	SE
Intercept	4.40	1.76	4.30	1.40	3.46	1.58	2.68	1.57
NMFSSk	5.90	1.93	4.94	1.54	6.32	1.96	7.28	1.96
RelWt	19.26	3.63	23.10	2.89	23.32	2.87	24.25	2.79
r^{**2}	0.79		0.88		0.88		0.88	

	Ages 1+ numbers							
Intercept			5.28	3.80	5.15	4.46	5.08	4.63
RelNt			26.28	4.66	27.58	5.30	27.72	5.58
r^{**2}			0.68		0.63		0.62	

Table 7. Combination of estimated and predicted ages 1+ abundance, coast-wide landings (#), catch weighted F ages 1+ biomass, landings biomass and biomass weighted F and surplus production, 1982-2006.

YEAR	nav2	nav2l	catchn	FN2	bav2	bav2l	catchw	Fw2	surpbb
1982	41741.99	42186.33	31100	0.7411	21200.0	25000.0	18960	0.8208	22760.0
1983	42186.33	43434.67	42600	0.9951	25000.0	25300.0	26500	1.0537	26800.0
1984	43434.67	31760.21	46200	1.2288	25300.0	20800.0	26100	1.1323	21600.0
1985	31760.21	26774.55	35300	1.2061	20800.0	19700.0	20400	1.0074	19300.0
1986	26774.55	33900.41	32500	1.0713	19700.0	20600.0	20900	1.0372	21800.0
1987	33900.41	24732.20	30200	1.0301	20600.0	16300.0	18300	0.9919	14000.0
1988	24732.20	9517.85	38000	2.2190	16300.0	7600.0	21800	1.8243	13100.0
1989	9517.85	14033.94	14300	1.2144	7600.0	9400.0	10300	1.2118	12100.0
1990	14033.94	18316.34	12200	0.7542	9400.0	10000.0	8000	0.8247	8600.0
1991	18316.34	13185.28	20100	1.2761	10000.0	10400.0	11300	1.1078	11700.0
1992	13185.28	21166.18	18600	1.0829	10400.0	12400.0	11800	1.0351	13800.0
1993	21166.18	22903.52	17600	0.7987	12400.0	14900.0	10800	0.7912	13300.0
1994	22903.52	23991.90	18700	0.7975	14900.0	18200.0	12200	0.7372	15500.0
1995	23991.90	30334.12	14800	0.5449	18200.0	21300.0	10500	0.5317	13600.0
1996	30334.12	28649.71	18500	0.6273	21300.0	21000.0	11600	0.5485	11300.0
1997	28649.71	28259.64	14500	0.5096	21000.0	23300.0	10300	0.4650	12600.0
1998	28259.64	32531.04	15000	0.4935	23300.0	22500.0	11600	0.5066	10800.0
1999	32531.04	33174.50	14100	0.4292	22500.0	27800.0	10900	0.4334	16200.0
2000	33174.50	29285.80	15700	0.5027	27800.0	33912.4	13800	0.4472	19912.4
2001	29285.80	21635.60	13200	0.5185	33912.4	29934.6	11900	0.3728	7922.2
2002	21635.60	23482.20	12200	0.5408	29934.6	30576.8	11300	0.3735	11942.2
2003	23482.20	24009.80	13000	0.5475	30576.8	31319.2	12900	0.4168	13642.4
2004	24009.80	27703.00	14300	0.5531	31319.2	32482.6	13800	0.4326	14963.4
2005	27703.00	23218.40	13900	0.5459	32482.6	22931.6	13400	0.4836	3849.0
2006	23218.40	23218.00	12635	0.5442	22931.6	22932.0	12300	0.5364	12300.4

Table 8. Parameter estimates (a, b, c) for summer flounder derived from the Gompertz external production model with and without striped bass predation. The overfishing thresholds (F_{msy} , B_{msy}) were derived from the Gompertz model with striped bass effects. The models were fitted to the LTS Robust regression model. The standard error (SE) is given for each parameter estimate (a, b, Strip), as well as the coefficient of determination (r^2). Overfishing thresholds (F_{msy} , B_{msy}) are presented with 80% CI.

LTS Robust Regression Model Without Striped Bass

Parameter	Mean	SE	P
a	8.05	1.08	< 0.0001
b	-0.74	0.11	< 0.0001
r^2	0.80		

LTS Robust Regression With Striped Bass Effects

Parameter	Mean	SE	P
a	7.29	1.01	< 0.0001
b	-0.64	0.10	< 0.0001
c**	-1.36	0.34	<0.0001
r^2	0.83		

Threshold	Mean	80% Confidence Limit
F_{msy}	0.64	0.51 – 0.77
Fcoll	1.74	1.39 – 2.09
B_{msy}	32,500 mt	29,900 – 39,200 mt

** c is the slope estimate for striped bass effects

TABLE 9. Stepwise model relating the abundance of three candidate predators (bluefish, striped bass and spiny dogfish) and two environmental variables (t and t-1 lagged mean annual water temperature and deviations in the winter NAO) to surplus production from the Gompertz Production model. The stepwise model selected striped bass abundance (SCAM based) as the only significant ($P < 0.02$) explanatory variable. The standard error (SE) is given for each parameter estimate (a, b, c), as well as the coefficient of determination (r^2).

Least Squares Fit

Parameter	Mean	SE	P
a	7.84	1.20	< 0.0001
b	-0.70	0.12	< 0.0001
c**	-1.04	0.42	< 0.02
r^2	0.85		

** c is the slope estimate for striped bass effects

Table 10. Shepherd S-R Parameter estimates (A, Kp, c) for summer flounder with and without striped bass predation. The S-R models were fitted by nonlinear iterative re-weighted least squares regression. The shape parameter (b) was fixed at 1.0 for the Beverton-Holt model and at 2.0 for the dome-shaped Ricker model. The approximate standard error (SE) is given for each parameter estimate (a, Kp, Strip), as well as the coefficient of determination (r^2).

Parameter	Beverton-Holt			Ricker		
	Mean	SE	P	Mean	SE	P
A	23.65	15.45	<0.34	4.16	0.51	<0.0001
Kp	1488.3	1056.5	< 0.47	17532.0	1903.3	< 0.0001
r^2	0.85			0.81		

Ricker S-R With Striped Bass Effects

Parameter	Mean	SE	P
a	4.46	0.31	< 0.0001
Kp	22171.6	1948.5	< 0.0001
c **	-0.000092	0.000012	<0.0001
r^2	0.91		

** c is the exponent for striped bass effects

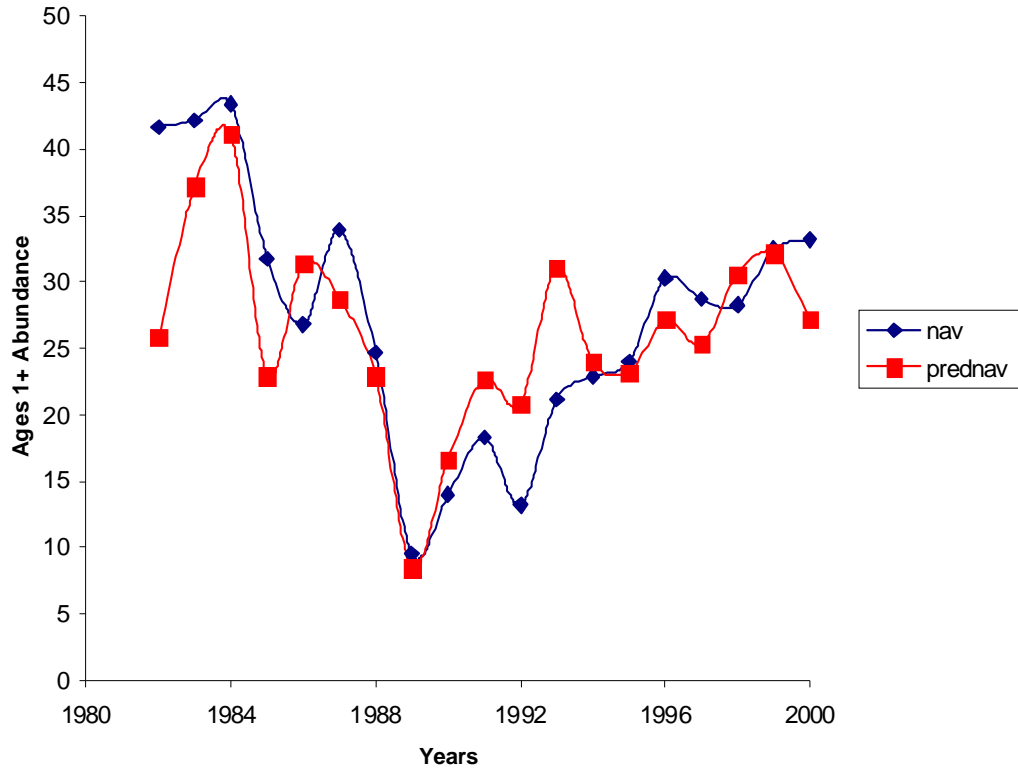


Figure 1. Plot of estimated and predicted ages 1+ flounder numbers over the converged portion (1982-2000) of ADAPT.

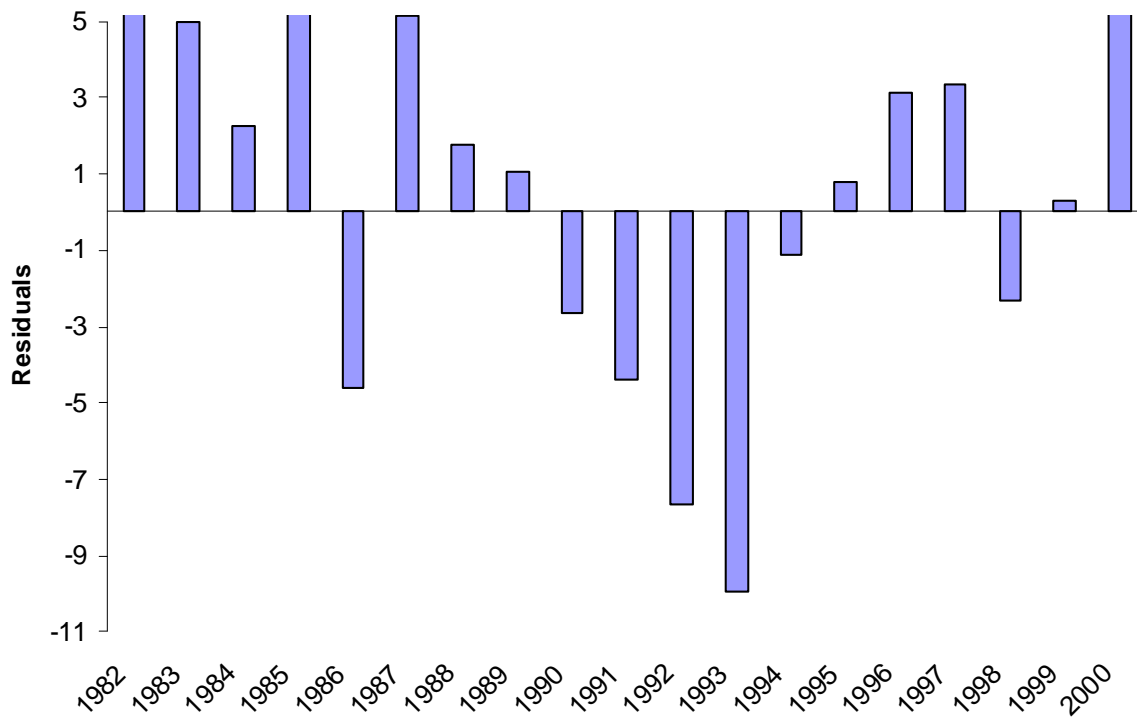


Figure 2. Residual plot for estimated and predicted ages 1+ numbers over time 1982-2000.

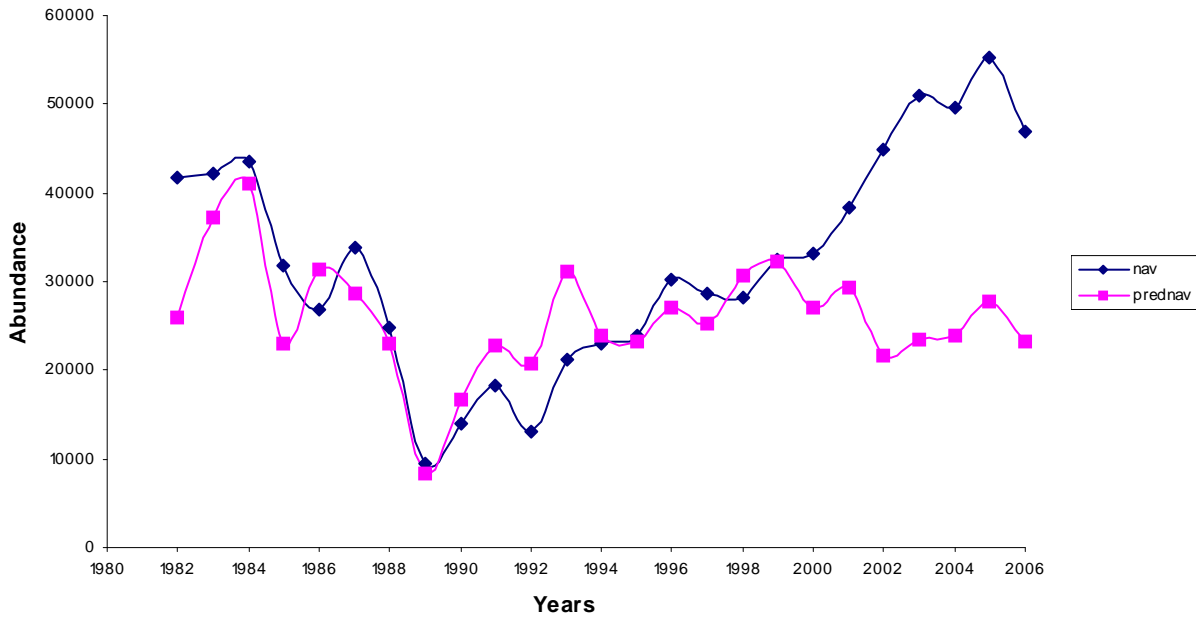


Figure 3. Estimated and predicted ages 1+ flounder abundance, 1982-2006.

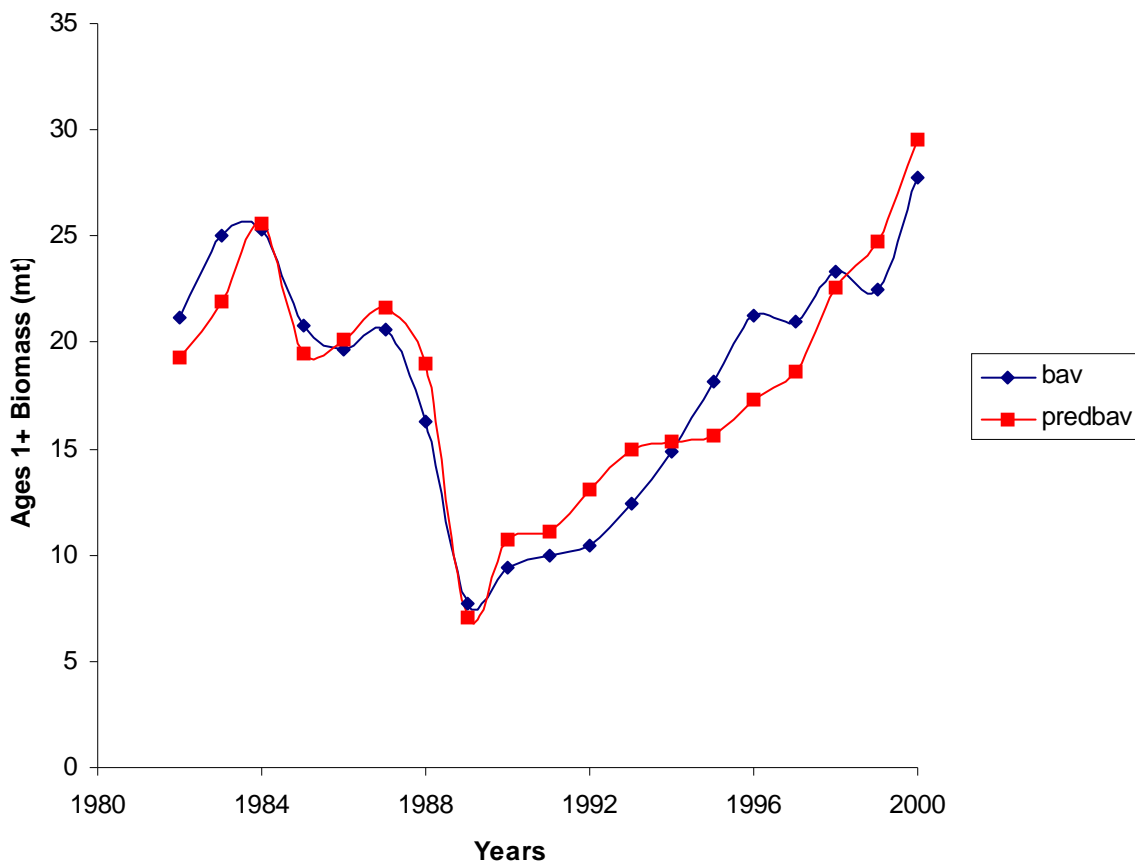


Figure 4. Plot of Estimate and predicted ages 1+ flounder biomass over the converged portion (1982-2000) of ADAPT.

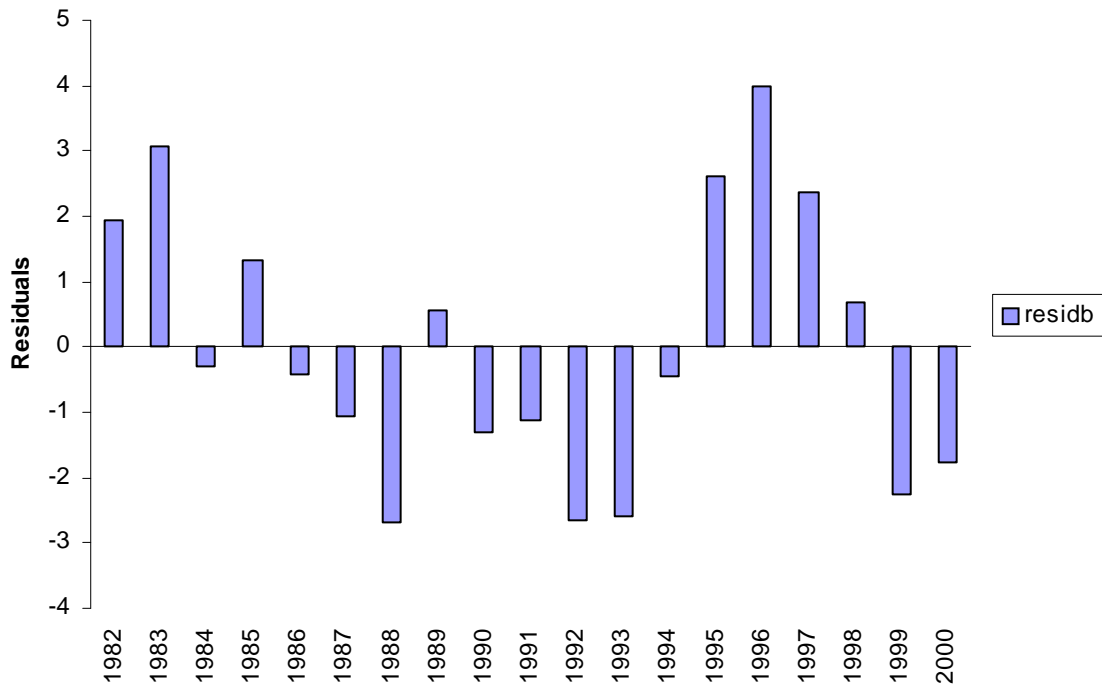


Figure 5. Residual plot for estimated and predicted ages 1+ biomass over time 1982-2000.

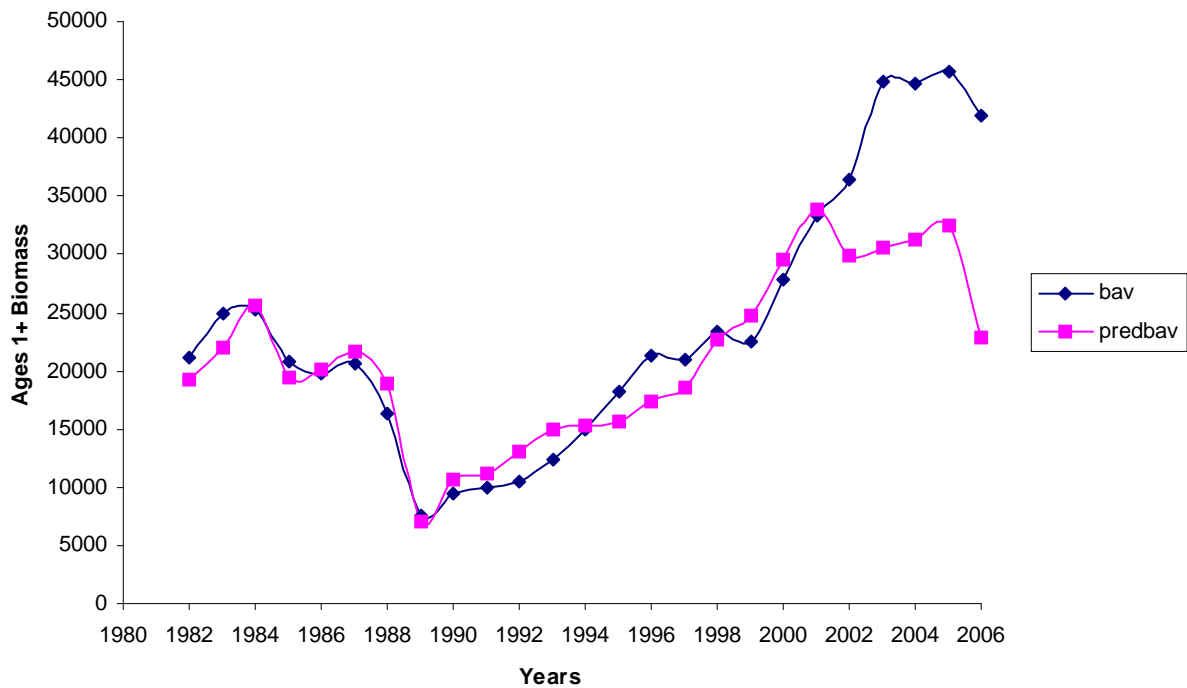


Figure 6. Estimated and predicted ages 1+ flounder biomass, 1982-2006.

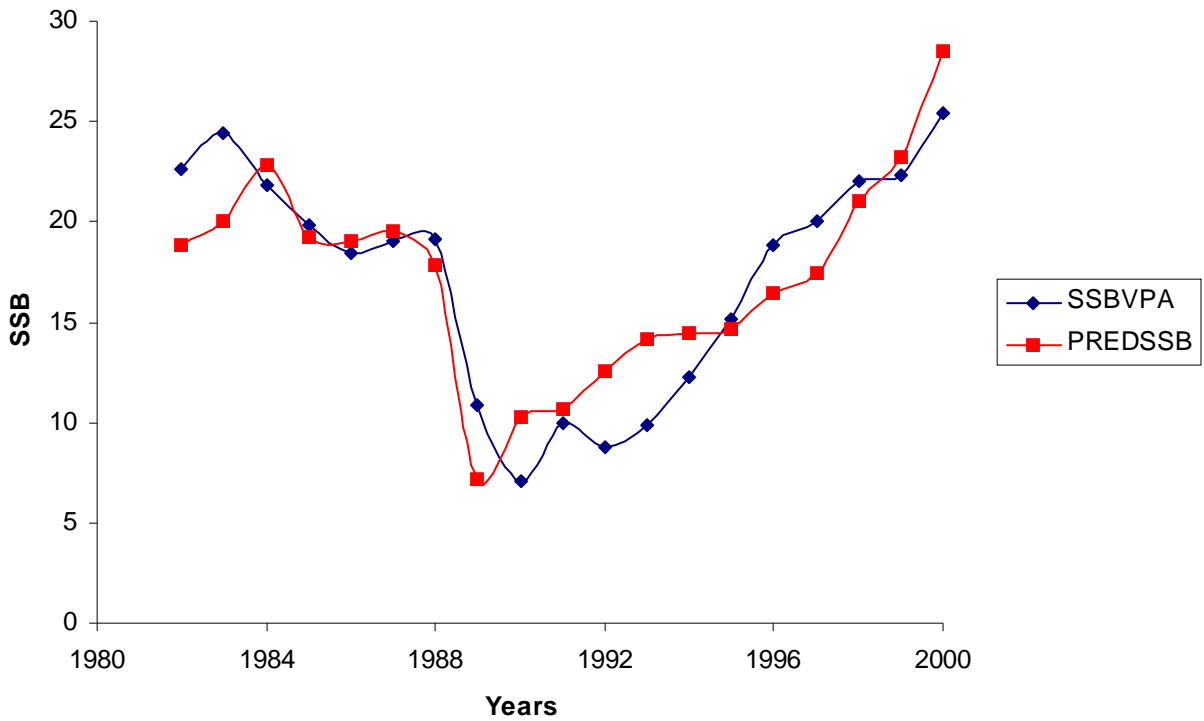


Figure 7. Plot of estimated and predicted ages 1+ flounder ssb over the converged portion (1982-2000) of ADAPT

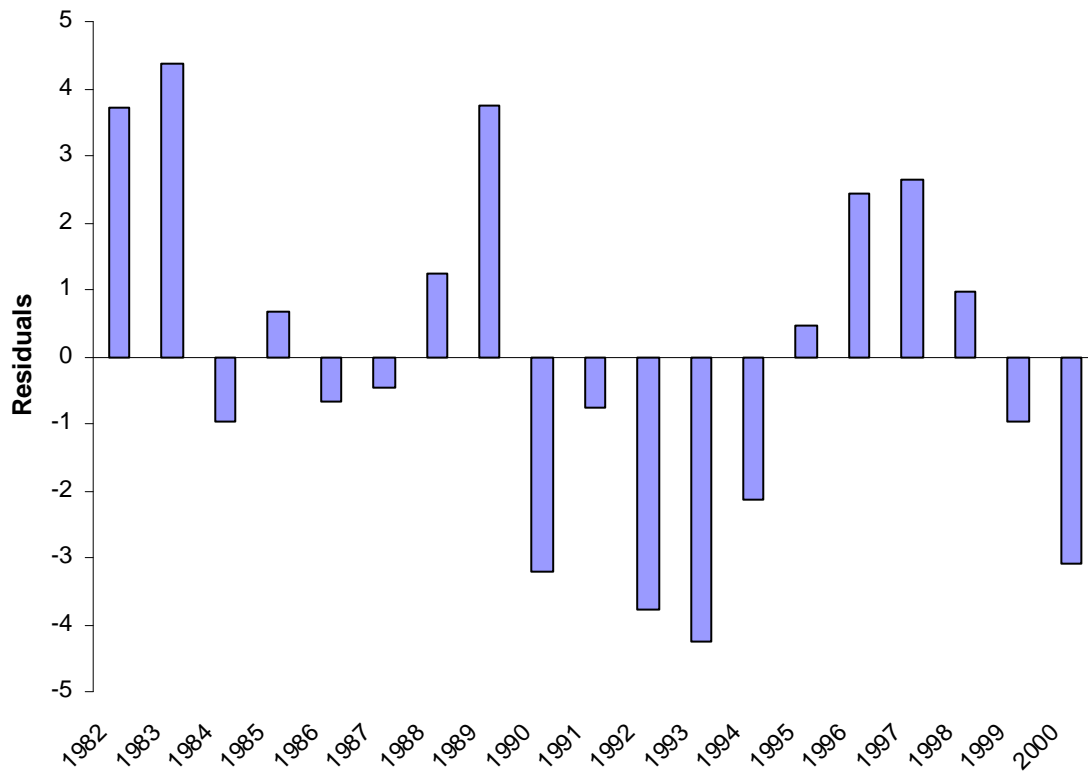


Figure 8. Residual plot for estimated and predicted SSB over time 1982-2000.

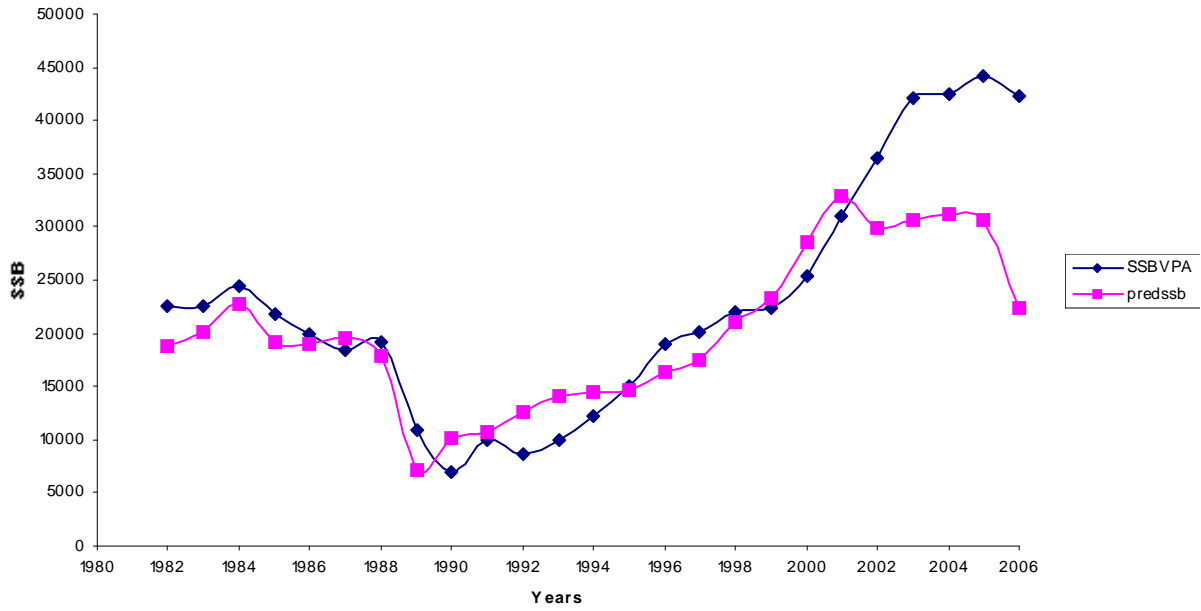


Figure 9. Estimated and predicted flounder SSB, 1982-2006.

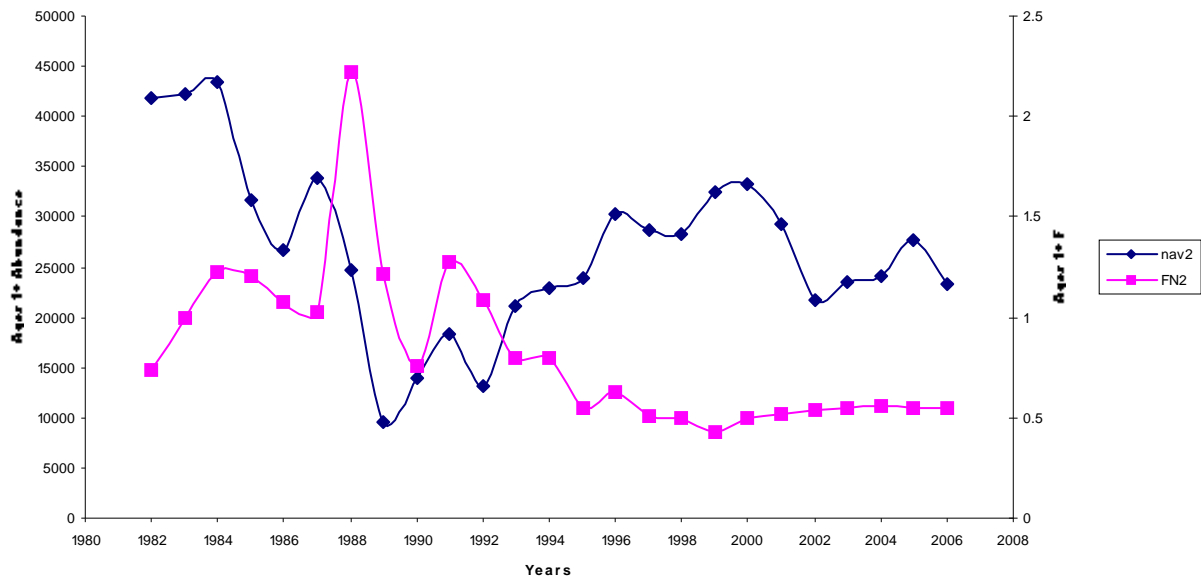


Figure 10. Relationship between ages 1+ fishing mortality and ages 1+ abundance, 1982-2006.

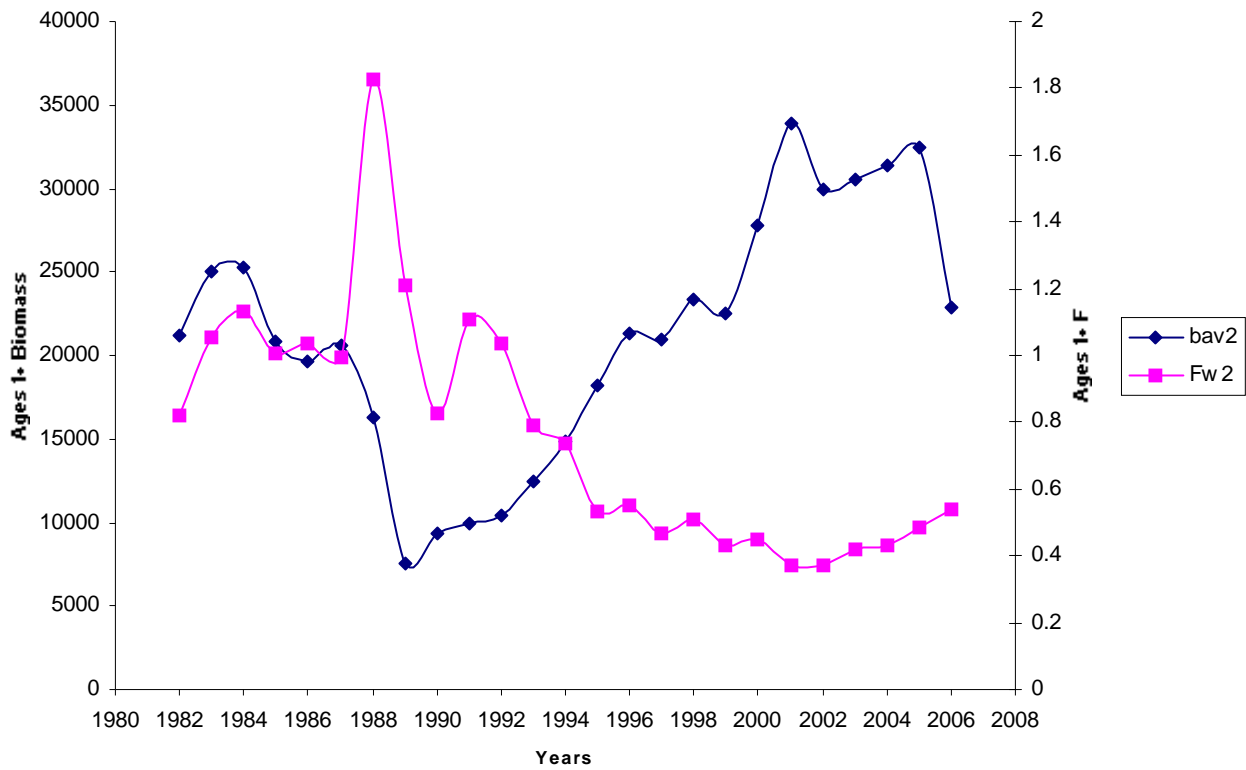


Figure 11. Relationship between biomass weighted F and ages 1+ flounder biomass 1982-2006.

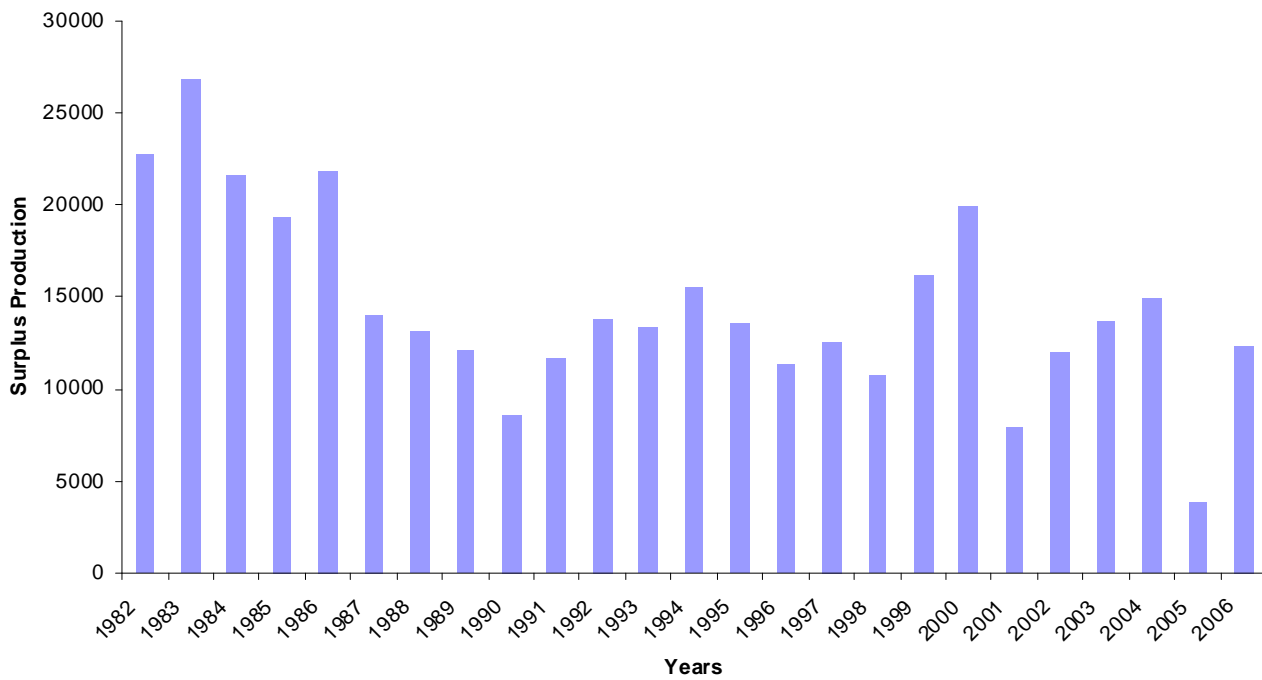


Figure 12. Plot of flounder surplus production, 1982-2006.

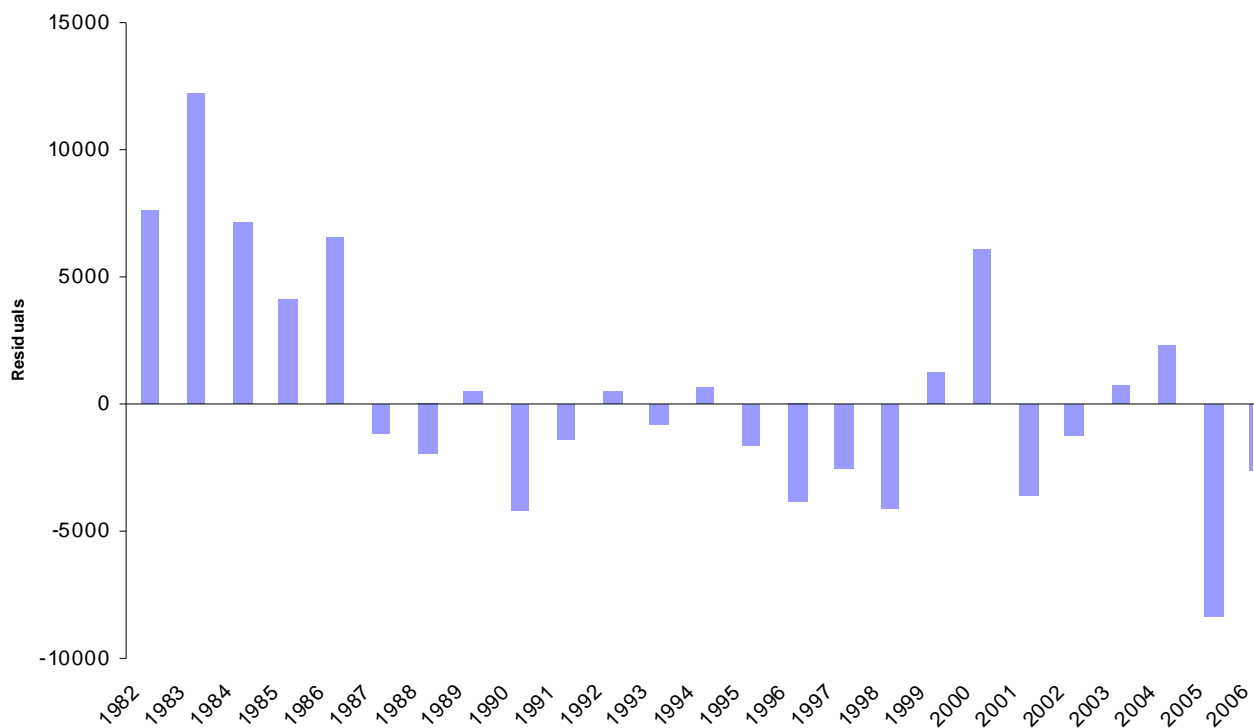


Figure 13. Residual plot for Gompertz Surplus Production Model for flounder without predation, 1982-2006.

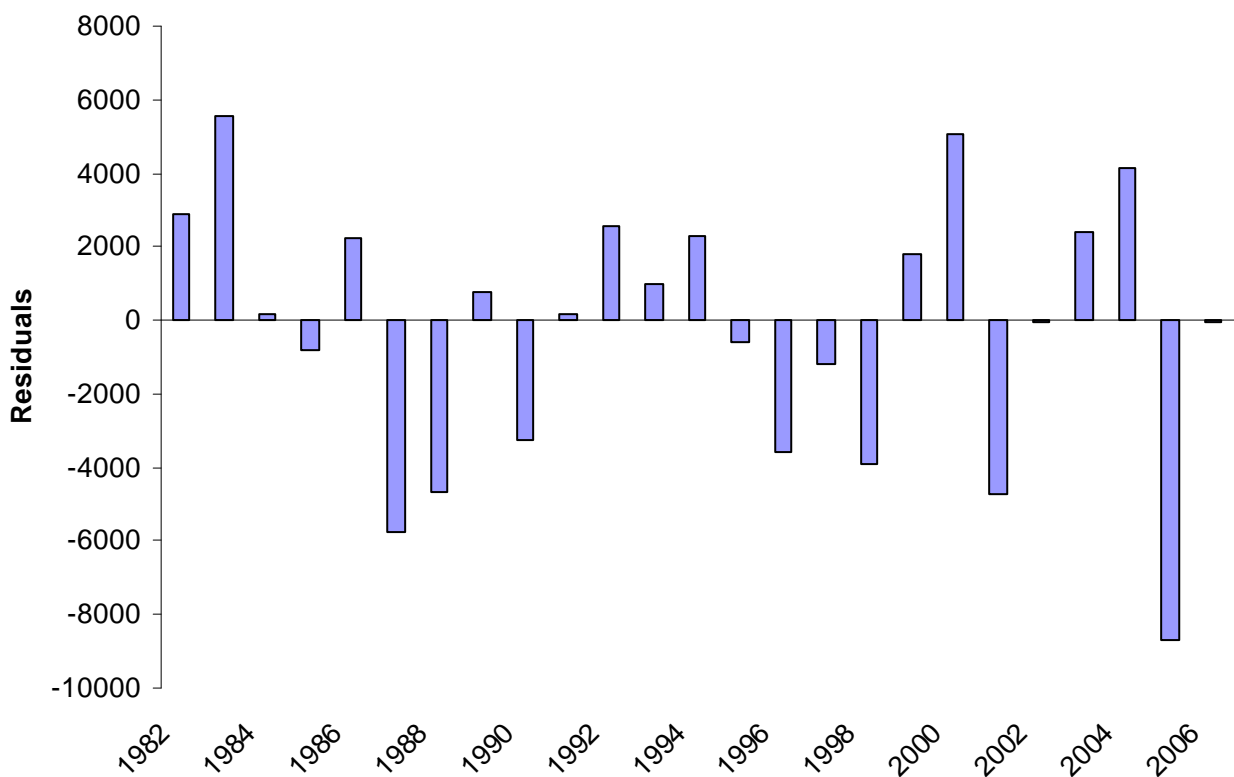


Figure 14. Residual plot from Gompertz model for flounder with striper predation effects, 1982-2006

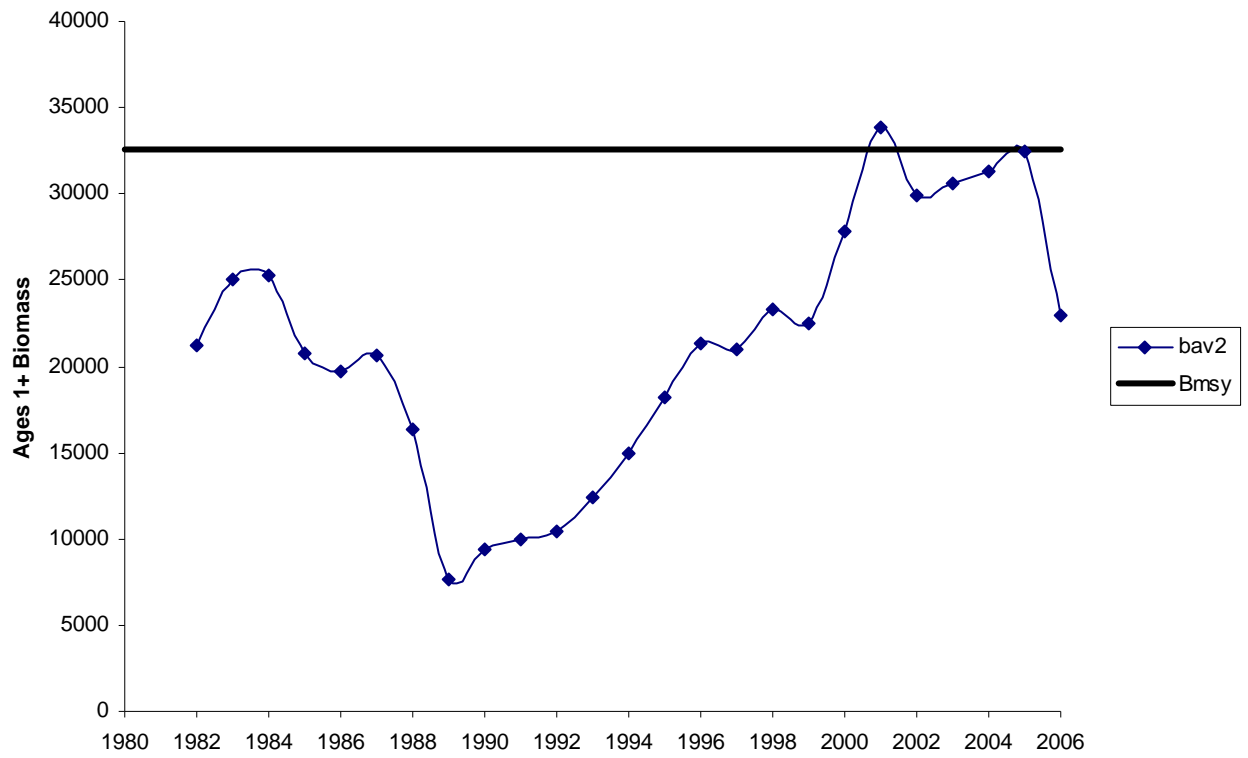


Figure 15. Plot of ages 1+ biomass and Bmsy from Gompertz model with predation 1982-2006.

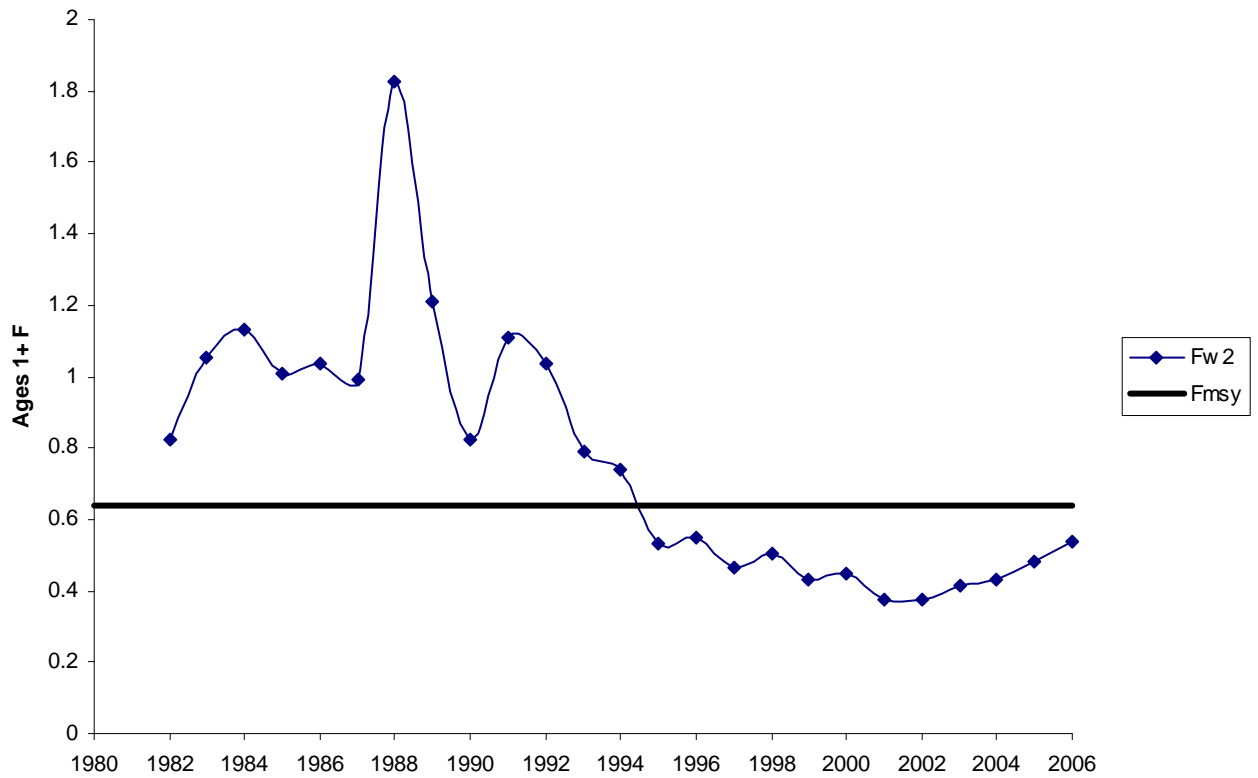


Figure 16. Plot of ages 1+ biomass weighted F and Fmsy from Gompertz model with predation, 1982-2006.

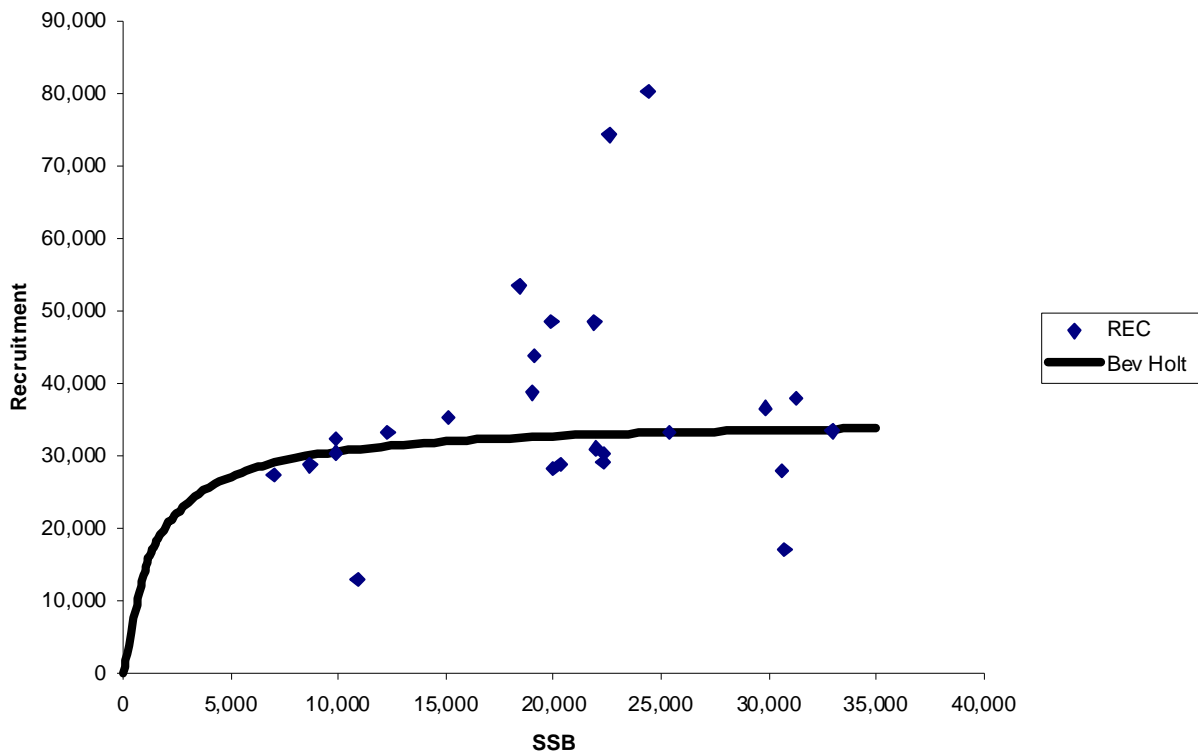


Figure 17. Stock-Recruitment fit to the Beverton-Holt model, 1982-2006.

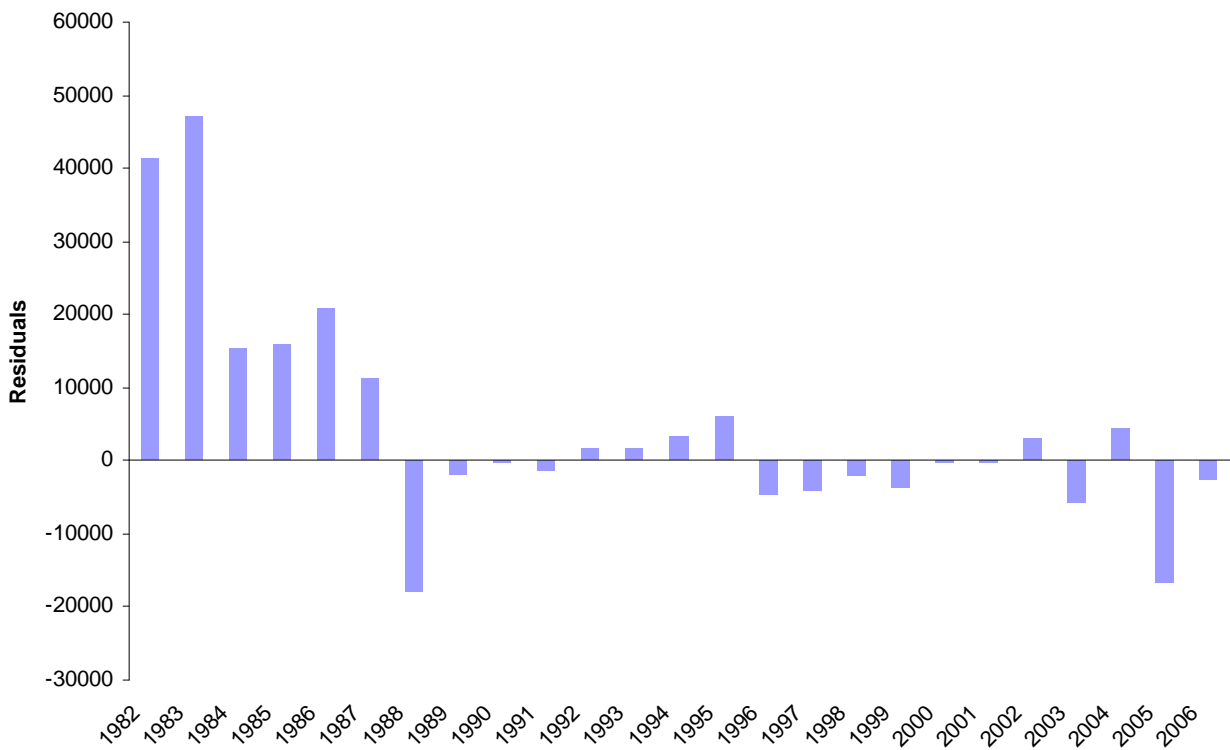


Figure 18. Plot of residuals for Beverton-Holt Model, 1982-2006

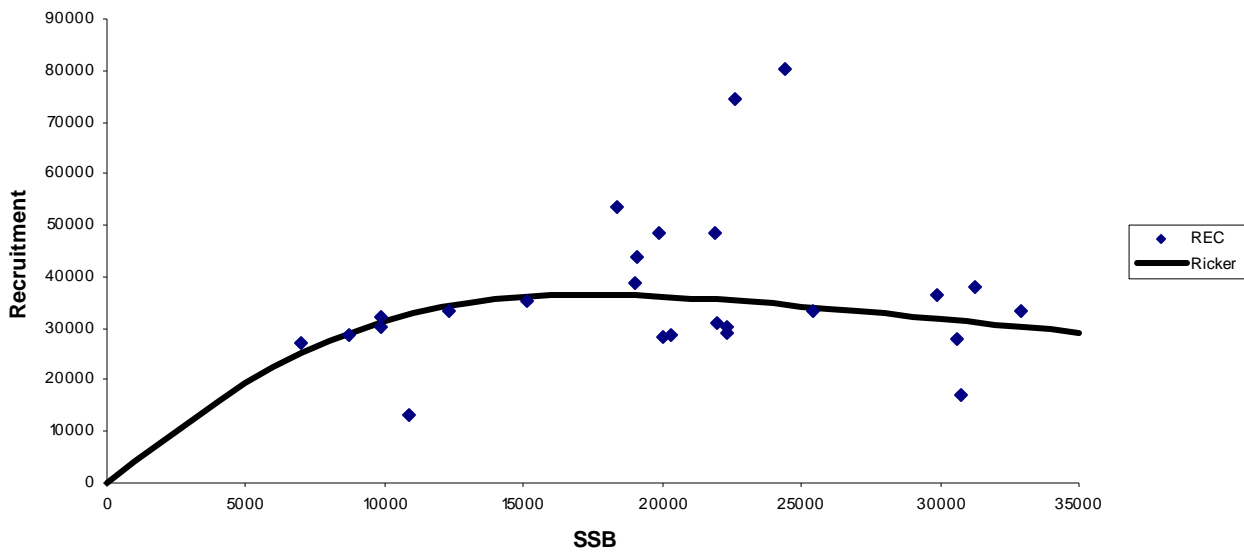


Figure 19. Stock-recruitment fit to the Ricker S-R model, 1982-2006.

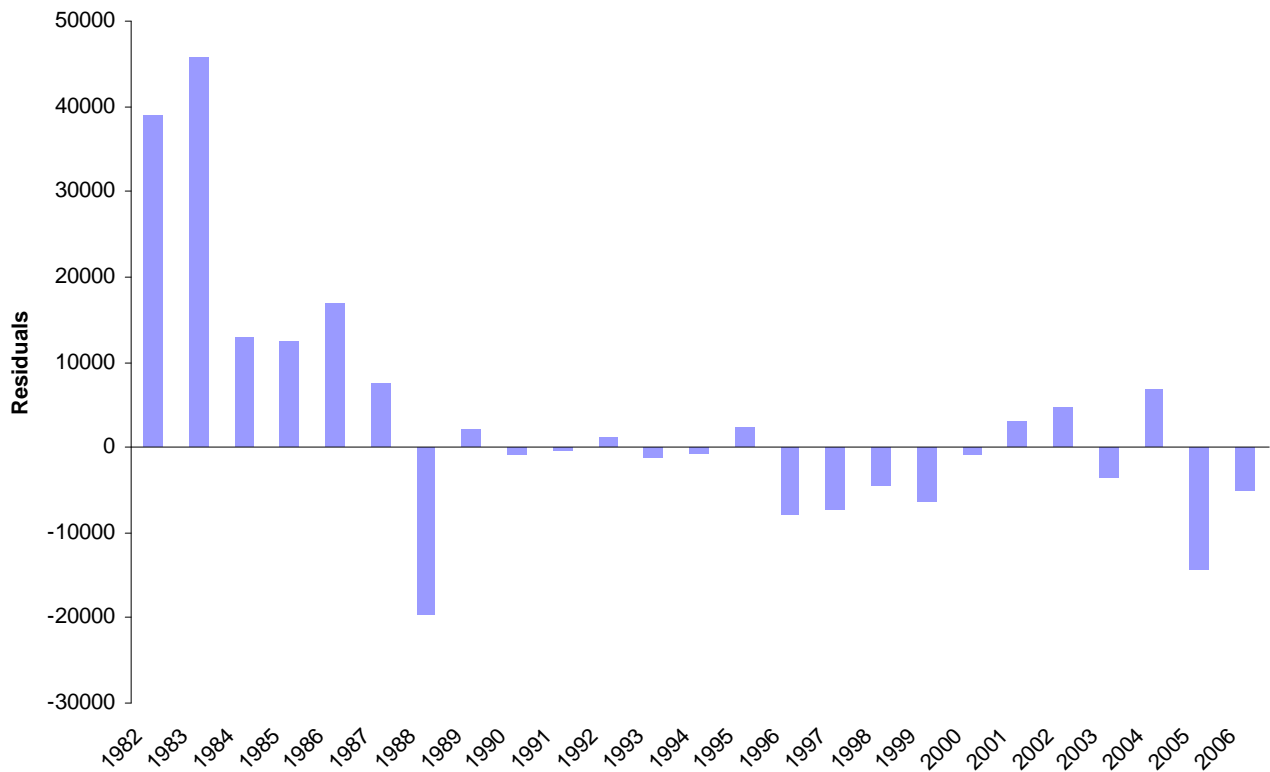


Figure 20. Plot of residuals for the Ricker Type Model, 1982-2006.

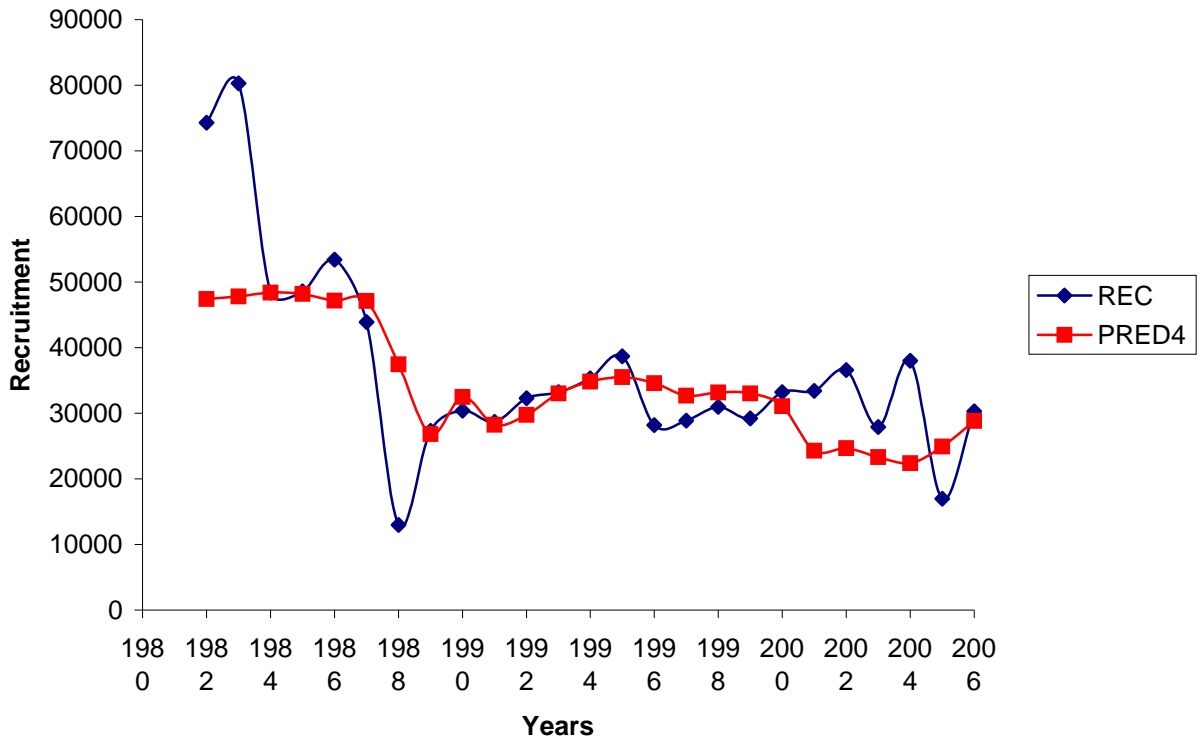


Figure 21. Observed and predicted recruitment from the Ricker Type Model with striped bass predation, 1982-2006.

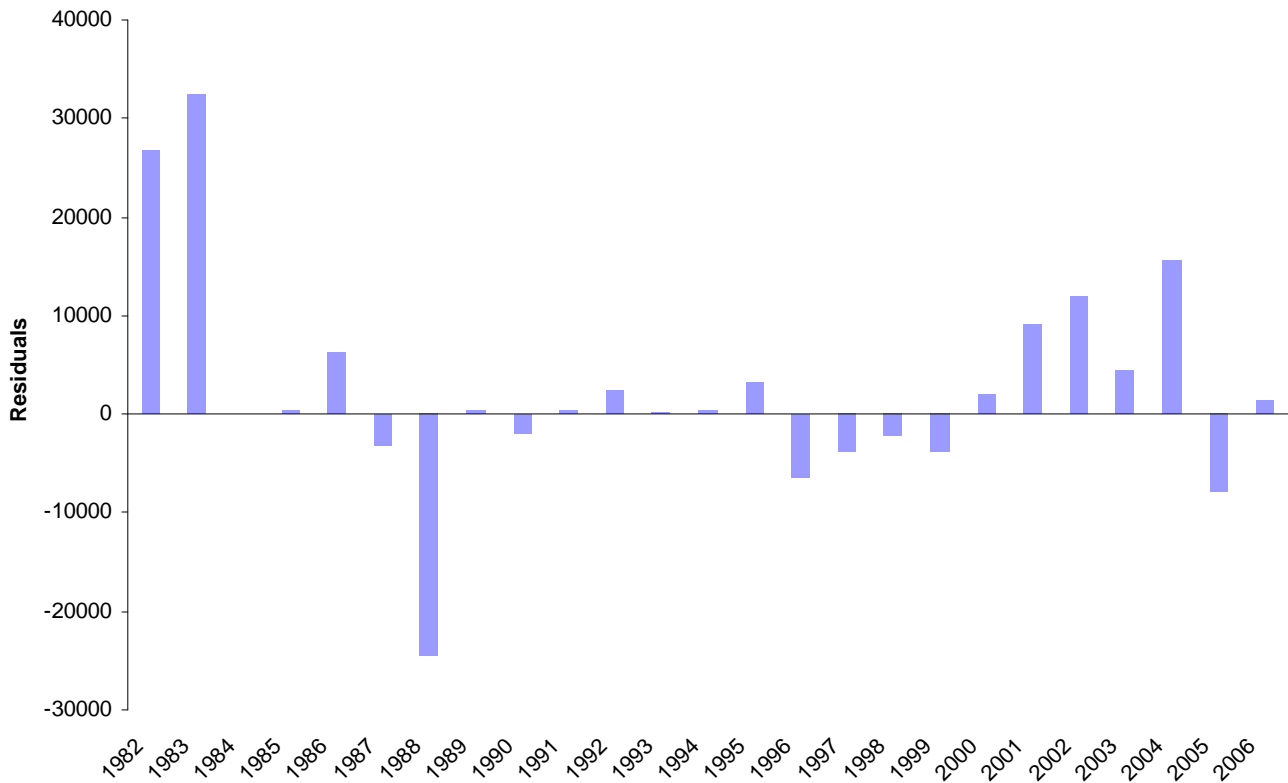


Figure 22. Plot of residuals from the Ricker Type Model with striped bass predation, 1982-2006.