ASSESSMENT OF THE POPULATION DYNAMICS OF THE NORTHEASTERN OFFSHORE SPOTTED AND THE EASTERN SPINNER DOLPHIN POPULATIONS THROUGH 2002

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INTRODUCTION

This paper reports the results of assessment modeling conducted as part of the research program established by the International Dolphin Conservation Program Act (IDCPA) of 1997. A primary goal of the research program is to collect, interpret and evaluate data on dolphin populations in the eastern tropical Pacific (ETP) that have been depleted by exploitation in the tuna purse seine fishery. The role of the research program within the larger NMFS effort is to provide scientific advice to the Secretary of Commerce, to contribute to a determination of whether or not the tuna purse seine fishery continues to have a significant adverse impact on the depleted dolphin stocks. The analyses reported here examined existing data for trends in population sizes, estimated average and maximum possible growth rates, compared current abundance levels to estimates of pre-exploitation abundance, and tested for possible changes in growth rates and carrying capacity during the period since the onset of the fishery. Also examined were the effects of including potential proxy measures of unobserved or unreported mortality from the tuna fishery as a covariate of survival. Population abundances from some model runs were projected 200 yrs into the future, given population parameters estimated from the data, to estimate how many years it might take for these depleted stocks to recover, defined as a return to Optimum Sustainable Population levels (between the maximum net productivity level (e.g, 60% of K, the pre-exploitation level) and 100% of K).

Three dolphin stocks are classified as depleted under the terms of the US Marine Mammal Protection Act: the northern offshore spotted dolphin (*Stenella attenuata*), the eastern spinner dolphin (*S. longirostris orientalis*) and the coastal spotted dolphin (*S. attenuata graffmani*). However, there is insufficient information on the historical levels of kill by the fishery, historical abundance, and the stock structure of this sub-species. Consequently, this report addresses only the two other stocks, which are the primary dolphins involved in the industry's capture of tunas in the ETP.

MODELING APPROACH: BACKGROUND

The overall framework of the assessments is to estimate the growth rate of the two depleted populations for which we have sufficient data, the northeastern offshore spotted dolphin and the eastern spinner dolphin. Growth rates are estimated by fitting a population model to available estimates of abundance. Estimates from research vessel surveys using line transect methods are available for three periods: 1979-83 (four estimates), 1986-90 (five estimates), and 1998-2000 (three estimates), for a total of twelve estimates over twenty-one years. Two types of population growth rate will be estimated: (1) the productivity of the population from 1979-2000 and (2) the maximum population growth rate (R_{max} or λ_{max}) under the assumption of a density-dependent model where pre-exploitation population size in 1958 is considered carrying-capacity. Both a simple (aggregated) population model and an age-structured model are used.

The methods used here are similar to other previous analyses (Wade, 1993, 1994; 1999). Following the assessment methodology of Smith (1983), a revised assessment of the depletion level of eastern spinner dolphin was carried out after the completion of abundance surveys from 1986-90. A generalized logistic model was fit to the abundance data, under the assumption that pre-exploitation size was equal to carrying capacity. A bootstrap procedure was used to quantify uncertainty in the estimated depletion level (Wade 1993). A similar analysis was performed for northeast offshore spotted dolphins. Both analyses suggested that each population was depleted, or below its Maximum Net Productivity Level (MNPL). These analyses, combined with other research, led to both populations being designated as "depleted" under the U.S. Marine Mammal Protection Act in 1993.

Subsequently, a method was developed to fit an age-structured population model to abundance data, using Bayesian methods, to estimate the depletion level of both northeastern offshore spotted dolphins and eastern spinner dolphins (Wade 1994). Similar methods have been used to assess the eastern North Pacific Pacific gray whale population (Wade *2002,* Punt and Butterworth *2002*). These assessments using an age-structured model again suggested both populations were depleted. Many papers have used similar age-structured methods to assess the Beaufort –Chukchi-Bering Sea stock of bowhead whales (Givens 1999, Poole *et al.* 1999, Punt and Butterworth 1997, Punt and Butterworth 1999, Raftery et al. 1995. Wade (2002) also introduced the use of the Bayes Factor for model selection and comparison.

Additionally, a similar analysis of northeastern offshore spotted dolphins, but with a non-age-structured model, was done in order to compare and contrast statistical methods for fitting population models to data. A generalized logistic model was fit to the data using (1) maximum likelihood estimation with a non-parametric bootstrap, (2) likelihood inference methods using likelihood profiles, and (3) Bayesian methods using SIR numerical integration (Wade 1999).

MODELING APPROACH: DESCRIPTION

Statistical analyses are performed to assess the populations and the uncertainty in the results. Bayesian statistics, using the SIR numerical integration method, are used to estimate a probability distribution for the quantities of interest, such as the population growth rates. Three main families of population models are used: (1) exponential models to estimate productivity from 1979-2000, (2) generalized logistic models to estimate R_{max} and depletion level (N_{2002}/K), and (3) a density-dependent age-structured model to estimate λ_{max} and depletion level.

Within each family of model, comparisons are made between different varieties of the models using the Bayes Factor (Kass and Raftery 1995). The Bayes Factor is the ratio of the probability of the data under one model to the probability of the data under a second model (assuming equal prior probability of each model, which is the case here). It provides a measure of the probability of one model versus another, and can therefore be used for model selection or model averaging of a parameter of interest.

A simple exponential model is compared to an exponential model with 2 slopes (growth rates), with a breakpoint. This latter model has 2 additional parameters to estimate; the second slope and the year in which the population growth rate changes. This comparison is used to assess whether there has been a change in the growth rate of the population through time.

A generalized logistic model is compared to 2 variants of the generalized logistic model: (1) a generalized logistic with 2 R_{max}s (maximum population growth rates), and (2) a generalized logistic with 2 Ks (carrying capacities). These latter 2 models have 2 additional parameters to estimate; the second R_{max} or K and the year in which the parameter changes. This comparison is used to assess whether there has been a change in the growth rate of the population or a change in the carrying capacity.

A density dependent age-structured model is used to incorporate life history data and the observed age distribution of the fisheries mortality. A second version of this model is used which makes survival rates a function of a covariate based on the number of sets on dolphins each year divided by the estimated number of dolphins in each year. This comparison investigates whether the population dynamics can be better explained by changes in the number of dolphin sets per dolphin in the population, which is a proxy for the potential affect the fishery may be having on either population above and beyond the observed direct kill.

Finally, analyses using the exponential model were repeated incorporating Tuna Vessel Observer Data (TVOD) estimates of relative abundance. Wade (1994) performed analyses both with and without the TOVD estimates. The TVOD estimates were assumed to be biased, and were therefore treated as relative estimates, but the bias was hoped to be constant through time. Recently, caution has been expressed about the use of the estimates because of indications of time-varying biases that affect the estimates (Lennert et al. 2001). Trends in the index could be trends in abundance or trends in biases. McAllister (2002) suggested incorporating a linear trend in the bias of the TVOD estimates, based on a roughly linear-looking relationship between TVOD estimates and research vessel abundance estimates. This linear trend in bias of the TVOD estimates was incorporated into all the TVOD analyses presented here.

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewers' comments can be found in Appendix A.

METHODS

Data

Abundance estimates are available from research vessel surveys in twelve years from 1979 to 2000. Fisheries mortality estimates are available for every year from 1959 to 2000. For both stocks, estimates for 1959-72 were from Wade (1995). For the northeastern offshore spotted dolphin, estimates for 1973-2000 were from the IATTC. For the eastern spinner dolphin, estimates for 1973-1978 were from Wahlen (1986), as modified in Wade (1993). Estimates for 1979-2000 were from the IATTC. Estimates of fisheries mortality for 2001 and 2002 are not yet available; therefore, mortality in 2001 and 2002 was assumed to be equal to mortality in 2000. The sampling errors of the mortality estimates were assumed to be log-normal. Additionally, the sampling errors of the mortality estimates from 1959-72 were assumed to be perfectly correlated, because mortality-per-set rates were pooled across that time period (Wade 1995).

Models: overview

All of the models include one of two related measures of population growth: *productivity* (r), defined as the average exponential growth rate during the period for which abundance data are available, or the *maximum or intrinsic growth rate* of the stock (R_{max}), which is the population growth rate that would take place at a low population size where density dependence had no effect on the growth rate. In both cases, a positive value (e.g., 0.02) indicates a net gain of individuals (positive growth), a negative value (e.g. -0.02) indicates a net loss of individuals from the population (negative growth), and zero indicates no change in the number of individuals in the stock. In all cases, the estimates explicitly accounted for the estimated level of fisheries mortality. For example, an estimate of productivity was not based only on the observed change in abundance over time – fisheries mortality was also accounted for (*e.g.*, if the observed change in abundance was 0.03 per year, and the fisheries mortality was on average 0.01 of the population size, then the estimated productivity would be 0.04).

Exponential model

An exponential model was fit to the data to estimate the productivity of the population. Two parameters were estimated: the exponential rate of change of the population (r), and the initial population size (N_{init}) in 1978. The population was projected forwards from 1978 to 2001, subtracting the estimated fishery kills in each year. Because the fishery kills were accounted for in the model, the estimate of r represents the productivity of the population, not just the observed rate of change.

A 2 slope exponential type model was also fit to the data, with two additional parameters, $r2$ and y_{change}, the year in which the population growth rate changes. In other words, this model allows for a change in r through time, and the year in which the change occurs is an estimated parameter.

Generalized logistic model

A generalized logistic model was used with 3 parameters: (1) the maximum population growth rate (R_{max}), carrying capacity (K), and a shape parameter that controls the non-linearity of the density dependent response (z). The shape parameter is what differentiates the generalized logistic model from the logistic model, which is sometimes referred to as the θ-logistic model (where the shape parameter is referred to as θ instead of z). The population was assumed to be at carrying capacity in 1958, and was projected forwards to 2001, subtracting the estimated fishery kills in each year.

Two variants of the generalized logistic model were also fit to the data. A 2-R_{max} model was used that had two additional parameters, a second population growth rate (R_{max2}) and the year in which the growth rate changed (y_{change}). A 2-K generalized logistic model was also used that had two additional parameters, a second carrying capacity ($K2$) and y_{change}, the year in which the carrying capacity changes.

The generalized logistic model was also used to test for effects of possible additional mortality as a result of the fishery, in addition to reported numbers. This was done by simply multiplying estimated mortality (recorded mortality in the last years) by 1.5 and 2.0, to examine model results for situations where true mortality was 50% and 100% higher than reported mortality. This was done with just the base-level model (single K, single R_{max}). Two periods were examined for these potential extra levels of mortality, the full period of the fishery, and just from 1991 on. The latter test was done to represent any possible change in levels of reporting that might have occurred at the onset of the IDCP, when individual vessel accountability was increased.

The final series of runs done with the generalized logistic model projected population growth for 200 yrs beyond the present, using parameters estimated from past data. This was done with fishery mortality set to zero, as a contrast with the hypothetical case of continued mortality at the 2000 level, which was very low. Runs were made for both the single R_{max} and two R_{max} cases. For all runs, the years were recorded when projected abundance reached OSP range (i.e. achieved or exceeded maximum net productivity level, with MNPL estimated by the model). Lower and upper 95th percentiles of the growth trajectory were tracked as well to indicate upper and lower bounds of time to OSP level.

Age structured model

The methods were nearly identical to those in Wade (1994) and the methods used in the preliminary assessment. The details of the model are briefly summarized here.

The model used was an age-structured density-dependent model in the form of a Leslie matrix (Breiwick et al. 1984). Parameters of the model were juvenile survival (s_j), adult survival (s_a), maximum fecundity rate (f_{max}), age of sexual maturity (asm), age of transition to adult survival (ia), maximum age (iw), and carrying capacity or equilibrium population size (K). In this model, density-dependence acts on fecundity, and the amount of non-linearity in the density dependent response is in the form of the generalized logistic, with a shape parameter (z) which determines the maximum net productivity level. The maximum population growth rate (R_{max}) was calculated as λ_{max}-1, where λ_{max} was the λ associated with the Leslie matrix with fecundity equal to f_{max}. The estimate of R_{max} essentially comes from the realized growth rate estimated from the 1975-2000 abundance data, in concert with the estimate of where the population was relative to R_{max}. The population size was assumed to be equal to K in 1958, and to be in the stable age distribution associated with the equilibrium Leslie matrix (where the fecundity rate was equal to f_0, the fecundity rate at equilibrium or zero population growth). In each year, (1) the population was projected using the model, (2) the fisheries mortality was, and (3) the model population size was compared to the abundance data (if available in that year). Age-specific selectivities were calculated using an iterative convergence routine, such that the age structure of the fisheries mortality in 1984 was equal to the observed age distribution of the kill from 1974-1992 (Chivers, unpublished data), calculated from fisheries kill data.

A variation of this model was also used where survival was modeled as a function of a covariate, the number of sets on dolphins divided by the estimated size of the dolphin population. This comparison investigates whether the population dynamics can be better explained by changes in the number of dolphin sets per dolphin in the population (dolphin sets per capita), which is a proxy for the potential affect the fishery may be having on either population above and beyond the observed direct kill.

The mortality rate in each year (M_y) was modeled as:

$$M_y = M_0 \exp(h * E_y),$$

where M_0 is the natural mortality rate in the absence of the covariate, E_y is the number of dolphin sets per capita in each year, calculated as the number of sets divided by the model population size, and h scales the effect of the covariate. Survival in each year (S_y) is then calculated as:

$$S_y = \exp(-M_y)$$

Estimation

The model parameters were estimated using Bayesian statistical methods. The Bayesian joint posterior distribution was approximated using the SIR routine (Smith and Gelfand 1992). Log-normal likelihoods were used for the abundance estimates. In the exponential model, uniform prior distributions were specified for N_{init} and $_r$. Similarly, uniform prior distributions were specified for all 3 parameters of the generalized logistic model. In the age-structure model, prior distributions were specified for the 7 parameters K, s_a, s_j, f_{max}, z, asm, and a. The parameters ia and iw were set to fixed values. Marginal probability distributions were calculated for all the parameters of interest.

For the analyses using TVOD data, the estimates were scaled as in Wade (1994), and a linear bias term was also used as suggested by McAllister (2002). The linear bias function was specified as:

$$B_y = a_{bias} * (y - y_0),$$

where y is the year, y_0 is the first year of the projection, and a_{bias} is the parameter that scales the bias. Then the TVOD estimate was scaled in each year as:

$$TVOD_{SC} = q * B_y * TVOD.$$

Model comparison

The Bayes factor is a summary of the evidence provided by the data in favor of one model as opposed to a second model (Kass and Raftery 1994). The Bayes factor is defined to be the ratio of the probability of the data given by one hypothesis to the probability of the data given by a second hypothesis. Here we can consider two models to be two hypotheses, and the Bayes factor will thus give the ratio of the probability of the data under one model to the probability of the data under the second model.

We assume equal prior probability for each model; we have no reason to favor one model versus another before we examine the data. In this case, the Bayes factor is identical to the posterior odds ratio. In other words, it is the probability of one model divided by the probability of a second model. Notationally, B_{12} is the probability of model 1 divided by the probability of model 2. If B_{12}=2.0, this means that the data indicate model 1 is twice as probable as model 2. If B_{12}=10.0, this means that model 1 is ten times more probable than model 2. Thus, the Bayes factor provides a measure of the relative probability of two competing models.

For interpretation, it is standard practice to give verbal descriptions to different ranges of values of the Bayes factor. A Bayes factor of from 1 to 3 is considered weak evidence, 3-12 is positive evidence, 12-150 is strong evidence, and >150 is considered decisive evidence for one model versus another (Kass and Raftery 1994).

As is the case with other model comparison statistics (e.g., AIC), it is not possible to compare analyses using different data sets. The Bayes factor comparison is conditioned on the relative probability of a common data set under each model. Therefore, the Bayes factor cannot be used to compare analyses using the TVOD estimates to analyses not using them.

RESULTS

Eastern spinner

Exponential model

The estimate of the productivity of the population was 0.010 (-0.013, 0.035) (Table 1). This can be interpreted as what the population growth rate would have been in the absence of the estimated observed fisheries kill. The majority of the posterior distribution was below 0.02 (Figure 1B), meaning there was relatively little probability the population could have grown at a rate higher than that. Given this estimated productivity, the population was not estimated to be at a substantially higher population size currently than it was in the late 1970s.

A look at the fit of the population model to the abundance estimates (Fig. 1A) shows a bit of a pattern in the residuals, as the first three estimates are all below the estimated model trajectory. This indicates there is somewhat of a lack of fit of the model to the data, suggesting an alternative model might be appropriate.

2-slope exponential model

This model gave fairly different results from the 1-slope model. This model breaks the time period into two sections, with a high probability that the population was increasing during the first period ($r1$ = 0.040, 95% probability interval from -0.015 to 0.078), and a high probability the population was declining or stable during the second period ($r2$ = -0.021, 95% probability interval from -0.077 to 0.041) (Table 2). The change in slope or population growth rate was estimated to have occurred around 1990. The difference in slopes was estimated at 0.066 (-0.047, 0.137), a fairly large change, but the distribution overlaps with 0.0. This indicates the data are not sufficient to decisively conclude that the population growth rate actually did change, but the data suggest the growth rate may have declined substantially.

The population trajectory for this model is in the shape of a flat arc, with the population gradually increasing until 1990, followed by a declining trend to the current time (Fig. 2A). The fit of the model to the data is better for this model than the 1-slope model, in the sense that there is no longer a slight pattern to the residuals; the model goes approximately through the middle of the first 3 abundance estimates. Two of these estimates were still well below the model. The 2-slope model would have fit these estimates even better if it had been allowed to, but the prior distribution did not allow the population to grow at greater than 0.08, which is considered an extreme upper limit to the potential growth rate of a dolphin with its life history (Reilly and Barlow 1986).

The model comparison using the Bayes factor favored the 2-slope model by a 2 to 1 ratio, indicating the evidence led to the 2-slope model being twice as probable as the 1-slope model. This is considered a weak level of evidence, and does not provide justification for concluding the 2-slope model was the correct model. The weak result could be due to the relative paucity of data, particularly the absence of data throughout most of the 1990s, or it could be because the population growth rate did not change, and the data only suggest that by random chance.

Exponential model additionally fit to the TVOD data

The exponential model fit to the TVOD data provided nearly identical results to the fit to the research vessel estimates alone, with the point estimate of r the same, but with slightly narrower probability interval (Table 3). The additional variance parameter was estimated to be 0.330, just above the lower bound of the prior distribution for this parameter. This value ensures the TVOD estimates have the same weight in the result as do the research vessel estimates.

Although it may not be surprising that the two analyses gave consistent results, it was expected that the TVOD data might lead to a more precise estimate, and thus a narrower posterior distribution for r (Fig. 3B). However, although this was the case, the difference was not large. It appears that the flexibility given the fitting process counter-balances the additional data, and does not lead to a more precise answer. The ability to "tilt" the TVOD trend-series in either direction (using the linear-bias function), the ability to scale the trend-series up or down, and correctly reflecting the observed variance in the estimates from the model, removes much of its information on the trend in the population. In this formulation, it appears that the scaled TVOD data are essentially fit to the research vessel data, and therefore by design can be expected to provide similar results, unless the fine-scale variability of the TVOD can provide a better fit to the model than is the case for the research vessel estimates.

The same lack of model fit is seen with negative residuals in the early years, with the TVOD estimates from 1978-1982 all well below the estimated population model (Figure 3A).

2-slope exponential model additionally fit to the TVOD data

In this case, the TVOD data do lead to more precise results, and lead to more conclusive results that the population was increasing in the early period and declining in the later period. This appears to be because the scaled TVOD data from 1978 to 1988 can match the increasing trend of the population, and from 1995 to 2000 can match the declining trend in the population.

The 2-slope model again can be seen to provide a better fit to the data in terms of the residuals, as now the population model goes right through the middle of the estimates from 1978-82 (Fig. 4).

The model comparison gives a more conclusive result that did the model comparison using only research vessel estimates. Although the gain in precision of the parameter estimates from using the TVOD data does not seem substantial, the gain in the Bayes factor comparison is substantial, as it moves the result from a weak result to a positive result with a Bayes factor of 5.11. Thus, the 2-slope model is estimated to be 5 times more probable than the one slope model. Therefore, conditioned on accepting the use of the TVOD data, the analysis now leads to a conclusion that the data suggest the growth rate of the population did change in the last 1980s or early 1990s, but this result is not strong. The decline in the population growth rate ($r1$-$r2$) is estimated to have been between -.02 and 0.20, with a point estimate of 0.08 (Table 4), meaning there is a high probability (i.e., 0.975) that the decline in the population growth rate was by at least 0.02.

Generalized logistic model

The fit of the generalized logistic model to the eastern spinner data results in a relatively low estimate of R_{max} of 0.014 (Table 5). This repeats the result seen in the exponential model fit, but now puts it in perspective regarding what the expected maximum population growth rate would be given the observed rate of change and the estimated depletion level of the population. The prior distribution constrained R_{max} in this analysis to be greater than 0.00, but it can be seen that part of the posterior distribution would have been below 0.00 if it was allowed (Figure 5C). In other words, the lower tail of the posterior distribution did not approach zero probalility density at a value of R_{max} of 0.00.

The population trajectory shows the same pattern in the residuals seen in the exponential fit, as the first three estimates are all below the estimated model trajectory (Fig. 5B). This lack of fit suggests this model does not capture all the dynamics of the population.

2-K Generalized logistic model

The generalized logistic model with 2 Ks or carrying capacities does not lead to substantially different results from the single K model. The posterior distribution for the second carrying capacity (K2) shows that this parameter is not well estimated. There is a small spike at the current population level (~500 thousand), indicating weak support for a lack of growth in the population caused by a shift in carrying capacity around 1990, but there is not enough information to estimate an upper bound for K2, so otherwise the posterior distribution simply reflects the prior distribution (Fig. 6D).

The model comparison indicates that both models are approximately equally probable (as the Bayes factor is close to 1), and thus there is no evidence from the abundance data for a shift in carrying capacity.

2 R_{max} Generalized logistic model

The generalized logistic model with 2 R_{max}'s gives analogous results to the 2-slope exponential model. The population growth rate was estimated to be higher prior to about 1990, and then declined (Table 7). The posterior distribution for R_{max1} is now centered at about 0.04, which is often used as an expected maximum growth rate for dolphins (Fig. 7C). However, it can be seen that the estimate of R_{max1} is not very precise (much less than the estimate of the single R_{max} in the simple generalized logistic), and spans the range of the prior distribution. This is due to splitting the time series in two, which makes the estimate of the growth rate in each time period less precise than the overall population growth rate.

The model comparison indicates that this model has the highest probability relative to the other generalized logistic models, but the difference is not large. Bayes factors of 1.38 and 1.25 are too small to be considered a positive result in favor of this model. Therefore, all three generalized logistic models are approximately equally probable (as the Bayes factors are all close to 1), and thus there is not strong enough evidence from the abundance data to be able to conclude that R_{max} has changed for this population.

Additional Fishery Mortality with generalized logistic model

Because the generalized logistic growth model allows fishery mortality estimates as one of its inputs, we can explore the response of the stock's growth rates to hypothetical increases fishery mortality. If reported fishery mortality is increased by 50% the maximum growth rate estimate actually increases by a small amount, to 0.016 (up from 0.014) (Table 8). If mortality is increased by 100%, the estimated maximum growth rate increases to 0.02 (Table 9). However, the comparison of these models' results to the model we ran with the actual reported fishery mortality resulted in low Bayes factor, indicating that the base run of the generalized logistic model described above was favored over these models.

To further explore the stock's potential response to increased mortality, another model run was conducted with increased mortality only after 1991, to investigate whether mortality reporting might have changed with the inception of the International Dolphin Conservation Program[1] (IDCP). The resulting maximum population growth estimate from this model run was 0.014, the same result obtained from the base run of this generalized logistic model (Table 10). When we compared these two models, the Bayes factor of 1.13 indicated that either model was about equally probable.   In summary, none of the model runs in which fishery mortality was hypothetically increased as a simple multiple of reported mortality performed better than the base model that included actual reported fishery mortality.

Future projections with generalized logistic model

With the generalized logistic model we can use the maximum growth rate that resulted from the base model run to determine when the stock size will be within its OSP range. For the eastern spinner dolphin, the median trajectories of the model indicated that this stock reaches OSP range in about 65 years (Table 11, Fig. 8A). Probability intervals for this time estimate were computed by tracking the lower and upper 95% limits of this growth trajectory. The minimum time for the stock to reach OSP was estimated to be 10 years. An maximum time could not be estimated because the stock size did not reach OSP range within the 200-year period projected by the model. No change in these long term stock size projections arose when we reduced the mortality to zero in the model from its most recently published level from the year 2000 (275 animals, IATTC 2002) (Table 12). In other words, no detectable difference in the model results regarding when the stock would reach OSP existed between the scenario where annual mortality was set at zero for each year in the projection and the scenario where mortality was set at 275 animals for each year in the projection.

The results are very different when we do the same projection with the generalized logistic model that allows for two different maximum growth rates over the time period. The median trajectories of the model show that the stock does not reach OSP range within 200 years (Fig. 8B). The minimum time for the stock to reach OSP was estimated to be 10 years. An maximum time could not be estimated because the stock size did not reach OSP range within the 200-year period projected by the model. As with the projection above with a single maximum growth rate, no detectable difference in the model results regarding when the stock would reach OSP existed between the scenario where annual mortality was set at zero for each year in the projection and the scenario where mortality was set at 275 animals for each year in the projection (Tables 13, 14).

Age-structured model

The age-structured model contains a similar density-dependent function as the generalized logistic model, and so results can often be similar to that model. The advantage of the age-structured model is the ability to bring in life history data (estimates of pregnancy rates and age of sexual maturity), the observed age distribution of the kill, and to correctly model any time lags that might occur in population response due to shifts in the age distribution of the population through time.

In this case, the results of the age-structured model, in terms of estimates of R_{max} (1-λ) and K, are essentially identical to the generalized logistic model (Fig. 9). The population is currently estimated to be at about 0.34 of K (Table 15).

Age-structured model with survival covariate

This model changes the estimate of R_{max}, because survival is estimated to be a function of the per capita number of sets on dolphins in each year. Per capita number of sets on dolphins in each year gradually increased over time, with a sharp rise in the mid 1980s, and then a small decline after 1990 (Fig. 10). Therefore, survival modeled as a covariate of this declined from 1958 to 1970, was constant until the mid 1980s, then it sharply declined to its lowest point in the late 1980s, then rose slightly in the 1990s. This decline in survival since 1958 leads to an estimate of R_{max} that is greater than the previous age-structured analysis, 0.033 (0.004, 0.069), but this is an estimate of R_{max} in 1958 (when there were no sets on dolphins), and the effective R_{max} was lower during the latter half of the population trajectory (Table 16).

Using per capita sets per dolphin leads to different fine-scale dynamics of the model population. In particular, it leads to a greater decline in the population in the early 1980s, which itself leads to an even greater lack of fit to the first 3 abundance estimates (Fig. 10B). This lack of fit leads to the covariate model not being favored by the Bayes factor analysis. The standard age-structured model is estimated to be 3 times more probable than the covariate model, which is just in the range of positive evidence against the covariate model. In other words, the fine-scale dynamics provided by the covariate do not match the available data better than the age-structured model that has survival constant across the time period.

On the other hand, contradictory evidence arose from finding a positive relationship between mortality and set frequency (the 95% probability interval did not include zero). That is, while the models with the mortality covariate did not fit the data as closely as models without the covariate, there still was estimated to be a pattern of lower mortality rates in years with fewer sets per individual. This is consistent with the idea that the growth rate of the population declined through time (*i.e.*, on average more sets through time leads to lower survival and thus a lower growth rate). It is unclear whether this contradictory set of results would have been resolved by inclusion of the TVOD abundance indices in these analyses.

Northeastern offshore spotted

Exponential model

The estimate of the productivity of the population was 0.017 (-0.001, 0.036) (Table 18). This can be interpreted as what the population growth rate would have been in the absence of the estimated observed fisheries kill. Essentially all of the posterior distribution was above 0.00, meaning there was high probability the population had a positive productivity over the 1979-2000 time period. The underlying population growth rate of 0.017 was well below the 0.04 assumed to be a maximum rate for odontocetes, and in fact there was essentially zero probability that a growth rate as high as 0.04 was occurring.

A look at the fit of the population model to the abundance estimates does show a pattern in the residuals, as the first two estimates are high and the next 4 are all below the estimated model trajectory, followed by 3 estimates that are above the model trajectory (Fig. 11A). This indicates there is somewhat of a lack of fit of the model to the data, suggesting an alternative model might be appropriate.

2-slope exponential model

This model gave similar results as the 1-slope model, but with a slight decline in the population growth rate in the 1990s. This model breaks the time period into two sections, with a growth rate during the first period of 0.026 (-0.066, 0.071), which was slightly higher than the 1-slope rate. During the second period, the growth rate was estimated to be lower at 0.002 (-0.090, 0.074) (Table 19). However, this is really a function of the imprecision of the estimate of *r2*, as the posterior distribution has a mode or peak at about 0.02, which is similar to the distribution for *r1*. The data are not sufficient to bound the lower limit of *r2*, so the median and lower probability interval are partly a function of the prior distribution, which was bounded at -0.10. The change in slope was estimated to have occurred in the early 1990s. The difference in slopes (*r1-r2*) was estimated at 0.030 (-0.091, 0.135), a moderate change, but the distribution broadly overlaps with 0.0. Given these results, the interpretation is that the data are not sufficient to decisively conclude whether the population growth rate actually did change in the 1990s or not.

The population trajectory for this model is fairly similar to the 1-slope model, but shows a flat trend in the 1990s rather than the slightly increasing trend of the 1-slope model (Fig. 12). This allows the model trajectory to hit the last 3 abundance estimates better. However, this is the only improvement in fit of the model to the data, as there is no improvement in the pattern of residuals seen in the 1-slope model in the earlier years.

The model comparison using the Bayes factor favors neither model. This is not surprising given that the estimates of *r1* and *r2* had peaks around a similar value. Therefore, the research vessel estimates do not provide evidence of a shift in the population growth rate.

Exponential model additionally fit to the TVOD data

The exponential model fit to the TVOD data provided nearly identical results to the fit to the research vessel estimates alone, with the point estimate of *r* similar at 0.013, but with a slightly narrower probability interval from -0.005 to 0.030 (Table 20). The linear bias parameter a_{bias} was estimated to be about 0.003, indicating there was no substantial bias correction applied to the TVOD data. The TVOD scalar parameter q was estimated to be 0.700 (0.499, 0.983), indicating the TVOD data were too high and needed to be scaled down to the research vessel estimates. The additional variance parameter was estimated to be 0.320, just above the lower bound of the prior distribution for this parameter. This value ensures the TVOD estimates have similar weight in the result as do the research vessel estimates.

As in the eastern spinner analysis, the TVOD data improve the precision of the estimate, but not dramatically. Again, the flexibility in the scaling of the TVOD apparently down-weights the influence of the TVOD when the finer scale dynamics of the model cannot match the finer scale dynamics of the TVOD. This is the case here, as the model is going slightly up while the TVOD index declines, and is going down when the TVOD index is increasing (Fig. 13).

The same lack of model fit is seen with negative residuals in the early years. Here, this includes the TVOD estimates, as well, which show a similar pattern in residuals as do the research vessel estimates. Estimates from 1981-1983 are all well below the estimated population model, then estimates from 1985-1997 are above the model, and then the estimates from 1998-2000 are well below the model. All in all, the 1-slope exponential model does not fit the TVOD data very well.

2-slope exponential model additionally fit to the TVOD data

In this case, the TVOD data do lead to more precise results, and lead to more conclusive results that the population was increasing in the early period and declining in the later period. The population growth rate in the early period was estimated at 0.046, with a probability interval from 0.011 to 0.077 (Table 21). The estimated growth rate matches more closely what is assumed to be a maximum growth rate of a spotted dolphin. The rate of change in the latter period (*r2*) has a high probability of being negative, indicating the population was declining. The difference in slopes (*r1-r2*) does not overlap with 0.0. Therefore, conditioned on accepting this as an adequate model, the data would lead to the conclusion that the population growth rate changed in the early 1990s.

The TVOD scalar parameter q was estimated to be 0.649 (0.471, 0.928), indicating the TVOD data were too high and needed to be scaled down to the research vessel estimates. The linear bias parameter a_{bias} was estimated to be 0.015 (-0.012, 0.046), indicating there was some change in the data over time. Positive values of this parameter increase the TVOD data in later years relative to earlier years, indicating the TVOD data, after scaling, were too high in the early years.

The reason the TVOD data lead to more precise results for this model appears to be because the model can match well the relatively stable trend of the scaled TVOD data from 1985 to 1996, and can match the declining trend of the scaled TVOD from 1997 to 2000 (Fig. 14). The model does not match the earlier data as well; it captures the overall increasing trend from 1977 to 1992, but cannot match the dip in the early 1980s.

The 2-slope model can be seen to provide a better fit to the TVOD data in terms of the residuals, as now the population model goes right through the middle of the estimates from 1985-2000. However, a careful look indicates the 2-slope model provides a slightly poorer fit to the research vessel estimates, as the model can no longer come close to any of the first 4 research vessel estimates (1979-83) and is farther away from the low estimates in 1986-87 (which is penalized more with the assumed log-normal error structure).

The improved fit the 2-slope model provides to the TVOD data makes this model have a higher probability. The Bayes factor of 5.92 means the 2-slope model has a probability 6 times higher than the 1-slope model. This is considered positive evidence for the 2-slope model over the 1-slope model. This model also provides a substantially better fit to the data than the 1-slope model, with only the early years now showing a slight pattern in the residuals. Conditioned upon acceptance of the use of the TVOD data, this leads to the conclusion that these data indicate the population growth rate changed substantially in the early 1990s, declining from what appears to be an expected maximum rate for a spotted dolphin (0.046) to a declining rate (-0.042).

Generalized logistic model

The fit of the generalized logistic model to the northeastern spotted dolphin data results in a relatively low estimate of R_{max} of 0.017 (0.002, 0.036) (Table 22). This repeats the result seen in the exponential model fit, but now puts it in perspective regarding what the expected maximum population growth rate would be given the observed rate of change and the estimated depletion level of the population. The prior distribution constrained R_{max} in this analysis to be greater than 0.00, but it can be seen that only a small part of the posterior distribution would have been below 0.00 if it was allowed.

The population trajectory shows the same pattern in the residuals seen in the exponential fit, as the four estimates from 1982-1987 are all below the estimated model trajectory. This lack of fit suggests this model does not capture all the dynamics of the population (Figure 15).

2-K Generalized logistic model

The generalized logistic model with 2 Ks or carrying capacities does not lead to substantially different results from the single K model, and is similar to the eastern spinner results (Table 23). The posterior distribution for the second carrying capacity (K2) shows that this parameter is not well estimated, There is a small spike at the current population level (~650 thousand), indicating weak support for a lack of growth in the population caused by a shift in carrying capacity around 1990, but there is not enough information to estimate an upper bound for K2, so otherwise the posterior distribution simply reflects the prior distribution. The year of the shift is also poorly estimated (Fig. 16).

The model comparison indicates that both models are approximately equally probable (as the Bayes factor is close to 1), and thus there is no evidence from the abundance data for a shift in carrying capacity.

2 R_{max} Generalized logistic model

The generalized logistic model with 2 R_{max}'s gives analogous results to the 2-slope exponential model (Table 24). The population growth rate was estimated to be higher prior to about 1990, and then declined. The posterior distribution for R_{max1} is now centered at a higher value of 0.026, which is a more expected rate for a maximum growth rate for dolphins. The estimate of R_{max1} is not as precise as the estimate of the single R_{max} in the simple generalized logistic. R_{max2} is estimated less precisely than R_{max1}, but has a similar mode centered at about 0.02. The shift in R_{max} was estimated to have occurred in the early 1990s (Fig. 17).

The model comparison indicates that this model has the highest probability relative to the other generalized logistic models, but the difference is not large. Bayes factors of 1.38 and 1.25 are too small to be considered a positive result in favor of this model. Therefore, all three generalized logistic models are approximately equally probable (as the Bayes factors are all close to 1), and thus there is not strong enough evidence from the research vessel abundance data to be able to conclude that R_{max} has changed for this population.

Additional Fishery Mortality with generalized logistic model

Because the generalized logistic growth model allows fishery mortality estimates as one of its inputs, we can explore the response of the stock's growth rates to hypothetical increases fishery mortality. If reported fishery mortality is increased by 50% the estimate of R_{max} actually increases by a substantial amount to 0.025 (up from 0.017) (Table 25). If mortality is increased by 100%, the estimate of R_{max} increases to 0.035 (Table 26). However, the comparison of these models' results to the model we ran with the actual reported fishery mortality resulted in low Bayes factor, indicating that the base run of the generalized logistic model described above was strongly favored over these models (Bayes factor is 2.43 for the 50% increase in fishery mortality scenario and 7.43 for the 100% increase scenario).

To further explore the stock's potential response to increased mortality, another model run was conducted with increased mortality only after 1991, to investigate whether mortality reporting might have changed with the inception of the IDCP. The resulting maximum population growth estimate from this model run was 0.018, nearly the same result obtained from the base run of this generalized logistic model (Table 27). When we compared these two models, the Bayes factor of 1.05 indicated that either model was about equally probable. In summary, none of the model runs in which fishery mortality was hypothetically increased as a simple multiple of reported mortality performed better than the base model which included actual reported fishery mortality.

Future projections with generalized logistic model

With the generalized logistic model we can use the maximum growth rate that resulted from the base model run to determine when the stock size will be within its OSP range. For the northeastern offshore spotted dolphin, the median trajectories of the model indicated that this stock will reach OSP range in about 78 years (Table 29, Fig. 18A). Confidence limits for this time estimate were computed by tracking the lower and upper 95% limits of this growth trajectory. The minimum time for the stock to reach OSP was estimated to be 28 years. A maximum time could not be estimated because the stock size did not reach OSP range within the 200-year period projected by the model. No change in these long term stock size projections arose when we reduced the mortality to zero in the model from its most recently published level from the year 2000 (295 animals, IATTC 2002) (Table 28). In other words, no detectable difference in the model results regarding when the stock would reach OSP existed between the scenario where annual mortality was set at zero for each year in the projection and the scenario where mortality was set at 295 animals for each year in the projection.

The results are very different when we do the same projection with the generalized logistic model that allows for two different maximum growth rates over the time period. The median trajectories of the model show that the stock does not reach OSP range within 200 years (Fig. 18B). The minimum time for the stock to reach OSP was estimated to be 19 years. A maximum time could not be estimated because the stock size did not reach OSP range within the 200-year period projected by the model. As with the projection above with a single maximum growth rate, no detectable difference in the model results regarding when the stock would reach OSP existed between the scenario where annual mortality was set at zero for each year in the projection and the scenario where mortality was set at 295 animals for each year in the projection (Tables 30, 31).

Age-structured model

The results of the age-structured model, in terms of estimates of R_{max} (which is actually λ_{max}-1.0) and K, are essentially identical to the generalized logistic model. R_{max} is estimated to be 0.017 (0.002, 0.035), which is very similar to the estimate from the logistic model (Table 32). The population is currently estimated to be at about 0.214 of

K, with a probability interval from 0.124 to 0.378. The population is thus estimated to be well below Maximum Net Productivity Level (MNPL).

The fit of the population trajectory is essentially identical to that of the logistic model, which was expected given the similar estimates of R_{max} and K (Fig. 19). Given the similar results to the logistic model, it can be concluded that the limited age-specific information in the analysis to not contradict the results seen for the non-age-structured model.

Age-structured model with survival covariate

This model changes the estimate of R_{max}, because survival is estimated to be a function of the per capita number of sets on dolphins in each year. The model assumes that the population growth rate was higher initially prior to the start of sets on dolphins, but has declined due to the influence of the per capita number of sets on dolphins in each year. The results are similar to the eastern spinner dolphin analyses. This decline in survival since 1958 leads to an estimate of R_{max} that is greater than the previous age-structured analysis, 0.027 (0.006, 0.053), but this is an estimate of R_{max} for when there are no sets on dolphins, as in 1958 (Table 33).

During the last 20 years, the effect on the finer scale dynamics of the population is that this model estimates the population to be increasing slightly more than the standard model in the early 1980s, and to be declining slightly more during the latter 1980s (Fig. 20). However, this does not provide a substantially better fit to the data.

This lack of fit leads to the covariate model not being favored by the Bayes factor analysis. The standard age-structured model is estimated to be 4.6 times more probable than the covariate model, which is well within the range of positive evidence against the covariate model. In other words, the fine-scale dynamics provided by the covariate of per capita sets on dolphins does not match the available data better than the age-structured model that has survival constant across the time period.

DISCUSSION AND SUMMARY

The main focus of these analyses has been to estimate growth rates for these two populations of tropical dolphins. There are few estimates of dolphin or even odontocete population growth rates in the literature (Wade 1998). A dolphin with a life history where sexual maturity does not occur until 10 or more years, and where females gives birth approximately every 3 years, cannot be expected to sustain very high population growth rates. Reilly and Barlow (1986) estimate that dolphins with these life history characteristics might be able to grow at a rate of 0.04 at a sensible maximum, and values as high 0.08 are possible but unlikely. However, these are theoretical calculations for which little observed data are available. Some of the best observed rates of increase for a dolphin are the published estimates for killer whales, which are in the range of 0.025-0.028 (Olesiuk et al. 1990, Brault and Caswell 1994). Given the lack of observed rates of increase available for most species, NMFS uses a default value for odontocetes of 0.04 in PBR calculations if no species-specific estimate is available (Wade and Angliss 1997).

Eastern spinner

For the eastern spinner dolphin population, the overall population growth rate was estimated to be fairly low, around 0.01, but the estimate was not precise enough to exclude lower values such as 0.0, or higher values such as 0.035. However, it was clear that the overall rate was not as high as the assumed expected value of 0.04 for odontocetes. Note that the exponential models included the estimated fisheries kill, so the estimates of r are strictly estimates of productivity, and not the actual observed trend in the population. These estimates represent what the population growth rate would have been in the absence of the estimated fisheries kill.

The 2-slope exponential model appears to fit the data better, and suggests the population was increasing at a rate similar to the expected 0.04 rate from 1979 to about 1990, but then stopped increasing. However, the improvement of this model was not large enough to lead to any conclusion that this model is a more accurate portrayal of the true population. In other words, these results may be from chance alone, and so cannot lead to any firm conclusion regarding these two models.

When the model is additionally fit to the TVOD estimates, the results do lead to the conclusion that the 2-slope model is better. Additionally, this model improves the patterns of residuals, meaning this model fits the data better than the 1-slope exponential. In other words, conditioned on the acceptance of the use of the TVOD data, the conclusion is that there is positive evidence the growth rate of the eastern spinner population changed in the early to mid 1990s. The population growth rate prior to that time was at a rate close to the expected rate for a dolphin (~0.04). However, the population was estimated to have declined over the 1990s.

The fits of the generalized logistic models to the eastern spinner data gave similar results. The maximum population growth rate (R_{max}) was estimated to be fairly low (0.014). The data did not provide any evidence that carrying capacity had changed, as the 2-K generalized logistic model did not have a higher probability. As seen with the exponential models, the data did slightly suggest that R_{max} had changed, and might have been at an expected rate for a dolphin prior to the early 1990s, then declined, but the result was not strong enough to be able to draw any conclusion from. Runs with fishery mortality increased by 50% and 100% produced fits to the abundance estimates that generally were worse than when the reported levels of mortality were included. That is, the modeling conducted here does not provide support for the possibility that unobserved or unreported mortality is occurring at those levels.

The age-structured model analysis led to very similar results to the generalized logistic model. This is not a surprising result, given that the most important data (the abundance estimates) are not age-structured. The main reason for looking at an age-structured model was the ability to incorporate the age-structure of the kill, and some additional life history data on pregnancy rates and age of sexual maturity. Incorporating this kind of age-specific information could potentially lead to differences in the population dynamics, from the effects of a selective age-structure of the kill, or from lags in response of the population caused by delayed sexual maturity. That the results were so similar to the logistic model indicates none of these incorporated factors had a strong influence on the results.

The age-structured model incorporating per capita sets on dolphins as a covariate for survival could have potentially picked up whether any of the finer-scale dynamics of the abundance data could be better explained by changes in survival as a function of changes in the number of sets on dolphins. However, the standard age-structured model with constant survival provided a better fit to the data. The standard model was estimated to have a probability 5 times greater than the covariate model, which is strong enough to be considered a positive result in favor of the standard model.

Northeastern offshore spotted

The results for the northeastern offshore spotted dolphin population were fairly similar to those for the eastern spinner. The overall population growth rate was estimated to be somewhat low, around 0.017, but the estimate was precise enough to be able to conclude that the population growth rate was positive. The overall rate was not as high as the assumed expected value of 0.04 for odontocetes, but was not quite as low as the eastern spinner estimate.

The 2-slope exponential model appears to fit the data better, and suggests the population was increasing at a rate more like 0.026 from 1979 to about 1992, but then stopped increasing. However, the improvement of this model was not large enough to lead to any conclusion that this model is a more accurate portrayal of the true population. In other words, these results may be from chance alone, and so cannot lead to any firm conclusion regarding these two models.

When the exponential models were additionally fit to the TVOD estimates, the results did lead to the conclusion that the population growth rate had changed. Additionally, the 2-slope model improved the patterns of the residuals, meaning this model fits the data better than the 1-slope exponential. In other words, conditioned on the acceptance of the use of the TVOD data, the conclusion is that there is positive evidence the growth rate of the northeastern offshore spotted dolphin population changed in the early to mid 1990s. The population growth rate prior to that time was at a rate close to the expected rate for a dolphin (0.046). After 1992, the population was estimated to have declined, with a point estimate of -0.04.

The fits of the generalized logistic models to the northeastern offshore spotted data led to an estimate of the maximum population growth rate (R_{max}) of 0.017. This was the same as the estimated growth rate from the exponential model, which happened because this population was also estimated to be at such a low level relative to carrying capacity that it would be expected to be increasing at essentially its maximum rate. The data did not provide any evidence that carrying capacity had changed, as the 2-K generalized logistic model did not have a higher probability. However, the data are likely insufficient to be able to resolve a change in carrying capacity. As seen with the exponential models, the data did slightly suggest that R_{max} had changed, and might have been at a rate (0.026) closer to the expected rate for a dolphin prior to the early 1990s, then declined, but the result was not strong enough to be able to draw any conclusion from. Runs with fishery mortality increased by 50% and 100% produced fits to the abundance estimates that generally were worse than when the reported levels of mortality were included. That is, the modeling conducted here does not provide support for the possibility that unobserved or unreported mortality is occurring at those levels.

As with the spinner dolphin analysis, the age-structured model analysis led to very similar results to the generalized logistic model. That the results were so similar to the logistic model indicates none of the incorporated age-specific factors had a strong influence on the results.

The standard age-structured model with constant survival provided a better fit to the data than did the age-structured model incorporating per capita sets on dolphins as a covariate for survival. The standard model was estimated to have a probability nearly 5 times greater than the covariate model, which is strong enough to be considered a positive result in favor of the standard model.

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Table 1. Eastern spinner, exponential model.

	Median	L 0.95	U 0.95
N_{init}	480	341	671
r	0.010	-0.013	0.035
N_{2002}	492	364	660

Table 2. Eastern spinner, 2-slope exponential model.

	Median	L 0.95	U 0.95
N_{init}	400	281	624
$r1$	0.040	-0.015	0.078
$r2$	-0.021	-0.077	0.041
y_{change}	1990	1981	1998
N_{2002}	427	303	617
$r1-r2$	0.066	-0.047	0.137
$(r1-r2)*N_{2002}$	27	-26	53

Table 3. Eastern spinner, exponential model, TVOD fit.

	Median	L 0.95	U 0.95
N_{init}	475	334	670
r	0.010	-0.011	0.032
y_{change}	6975	6975	6975
q	1.391	0.896	1.895
a_{bias}	-0.005	-0.019	0.032
$TVOD\ CV_{add}$	0.330	0.301	0.439
N_{2002}	495	376	658

Table 4. Eastern spinner, 2-slope exponential model, TVOD fit.

	Median	L 0.95	U 0.95
N_{init}	355	246	581
$r1$	0.047	-0.007	0.078
$r2$	-0.033	-0.142	0.020
y_{change}	1991	1980	1996
q	1.355	0.854	1.885
a_{bias}	0.001	-0.018	0.043
$TVOD\ CV_{add}$	0.327	0.301	0.433
N_{2002}	401	264	582
$r1-r2$	0.084	-0.021	0.197
$(r1-r2)*\ N_{2002}$	34	-11	63

Table 5. Eastern spinner, generalized logistic model.

	Median	L 0.95	U 0.95
K	1566	835	2757
R_{max}	0.014	0.001	0.052
MNPL	0.630	0.505	0.791
N_{2002}	508	404	668

Table 6. Eastern spinner, 2-K generalized logistic model.

	Median	L 0.95	U 0.95
K	1566	898	2878
R_{max}	0.016	0.001	0.070
K_2	2028	325	4858
y_{change}	1987	1974	1999
N_{2002}	497	383	650

Table 7. Eastern spinner, 2-R_{max} generalized logistic model.

	Median	L 0.95	U 0.95
K	1370	717	2528
R_{max1}	0.039	0.003	0.078
R_{max2}	-0.016	-0.076	0.045
y_{change}	1991	1975	1999
N_{2002}	442	312	625

Table 8. Eastern spinner, generalized logistic model with additional 50% fishery mortality for 1958-2001.

	Median	L 0.95	U 0.95
K	2293	1919	2604
R_{max}	0.016	0.001	0.043
N_{2002}	504	393	675
N/K	0.219	0.158	0.337
N/MNPL	0.347	0.225	0.564

Table 9. Eastern spinner, generalized logistic model with additional 100% fishery mortality for 1958-2001.

	Median	L 0.95	U 0.95
K	2883	2432	3298
R_{max}	0.02	0.002	0.047
N_{2002}	509	394	684
N/K	0.176	0.125	0.271
N/MNPL	0.281	0.178	0.449

Table 10. Eastern spinner, generalized logistic model with additional 100% fishery mortality for 1992-2001.

	Median	L 0.95	U 0.95
K	1670	1364	1913
R_{max}	0.014	0.001	0.042
N_{2002}	501	396	657
N/K	0.299	0.22	0.463
$N/MNPL$	0.478	0.312	0.778

Table 11. Eastern spinner, generalized logistic model with future projections, no mortality added to future years.

	Median	L 0.95	U 0.95
K	1677	1384	1908
R_{max}	0.014	0.001	0.040
N_{2002}	506	403	663
N/K	0.300	0.225	0.459
$N/MNPL$	0.479	0.318	0.777
N_{Pro}	1541	524	1727
N/K_{Pro}	0.995	0.279	1.000
$N/MNPL_{Pro}$	1.430	0.438	1.938
Y_{MNPL}	65	10	DNR

Table 12. Eastern spinner, generalized logistic model with future projections, 2002 mortality added to future years.

	Median	L 0.95	U 0.95
K	1679	1385	1909
R_{max}	0.014	0.001	0.040
N_{2002}	506	402	668
N/K	0.299	0.224	0.462
$N/MNPL$	0.480	0.317	0.778
N_{Pro}	1544	518	1724
N/K_{Pro}	0.994	0.274	1.000
$N/MNPL_{Pro}$	1.430	0.416	1.943
Y_{MNPL}	64	10	DNR

Table 13. Eastern spinner, 2-R_{max} generalized logistic model with future projections, no mortality added to future years.

	Median	L 0.95	U 0.95
K	1450	1095	1865
R_{max1}	0.038	0.003	0.077
R_{max2}	-0.015	-0.076	0.044
y_{change}	1991	1975	1999
N_{2002}	439	310	629
N_{Pro}	21	0	1751
N/K_{Pro}	0.014	0.000	1.000
$N/MNPL_{Pro}$	0.022	0.000	1.887
Y_{MNPL}	DNR	12	DNR

Table 14. Eastern spinner, 2-R_{max} generalized logistic model with future projections, 2002 mortality added to future years.

	Median	L 0.95	U 0.95
K	1451	1093	1868
R_{max1}	0.037	0.003	0.077
R_{max2}	-0.016	-0.076	0.044
y_{change}	1991	1975	1999
N_{2002}	439	312	628
N/K	0.302	0.196	0.468
$N/MNPL$	0.486	0.292	0.764
N_{Pro}	19	0	1755
N/K_{Pro}	0.013	0.000	1.000
$N/MNPL_{Pro}$	0.021	0.000	1.874
Y_{MNPL}	DNR	12	DNR

Table 15. Eastern spinner, age-structured model.

	Median	L 0.95	U 0.95
K	1500	716	2451
s_a	0.975	0.943	0.996
s_j	0.880	0.821	0.953
f_{max}	0.253	0.172	0.326
asm	11	10	13
R_{max}	0.014	0.001	0.051
$MNPL$	0.719	0.518	0.798
N_{2002}	521	409	682
N/K	0.342	0.197	0.897
$N/MNPL$	0.498	0.272	1.266

Table 16. Eastern spinner, age-structured model with survival covariate.

	Median	L 0.95	U 0.95
K	1411	787	2384
s_a	0.978	0.949	0.996
s_j	0.918	0.838	0.973
f_{max}	0.253	0.172	0.326
asm	11	10	13
R_{max}	0.033	0.004	0.069
$MNPL$	0.723	0.521	0.798
N_{2002}	497	353	676
N/K	0.349	0.181	0.755
$N/MNPL$	0.502	0.257	1.106
h	0.019	0.001	0.070

Table 17. Bayes factors for eastern spinner dolphin model comparisons. The Bayes factor represents the ratio of the probability of one model to the probability of a second model. The Bayes factor is reported on the line of the model with the higher probability in the pair.

	Bayes factor
Exponential	
2-slope Exponential	2.12
Exponential additionally fit to TVOD	
2-slope Exponential additionally fit to TVOD	5.11
Generalized logistic	
2-K Generalized logistic	1.11
Generalized logistic	
2-R_{max} Generalized logistic	1.38
2-K Generalized logistic	
2-R_{max} Generalized logistic	1.25
Generalized logistic	1.43
150% fishery mortality	
Generalized logistic	2.12
200% fishery mortality	
Generalized logistic	
200% fishery mortality, 1991 forward	1.13
Age-structured	3.12
Age-structured with survival covariate	

Table 18. Northeastern offshore spotted, exponential model.

	Median	L 0.95	U 0.95
N_{init}	683	535	877
r	0.017	-0.001	0.036
N_{2002}	695	559	867

Table 19. Northeastern offshore spotted, 2-slope exponential model.

	Median	L 0.95	U 0.95
N_{init}	648	463	977
$r1$	0.026	-0.066	0.071
$r2$	0.002	-0.090	0.059
y_{change}	1992	1981	1998
N_{2002}	646	449	874
$r1-r2$	0.030	-0.091	0.135
$(r1-r2)*N_{2002}$	19	-68	68

Table 20. Northeastern offshore spotted, exponential model, TVOD fit.

	Median	L 0.95	U 0.95
N_{init}	708	547	921
r	0.013	-0.005	0.030
y_{change}	6975	6975	6975
q	0.700	0.499	0.983
a_{bias}	0.003	-0.017	0.034
$TVOD\ CV_{add}$	0.321	0.301	0.411
N_{2002}	678	549	835

Table 21. Northeastern offshore spotted, 2-slope exponential model, TVOD fit.

	Median	L 0.95	U 0.95
N_{init}	536	396	772
$r1$	0.046	0.011	0.077
$r2$	-0.042	-0.138	0.014
y_{change}	1992	1986	1996
q	0.649	0.471	0.928
a_{bias}	0.015	-0.012	0.046
$TVOD\ CV_{add}$	0.315	0.301	0.388
N_{2002}	538	368	736
$r1-r2$	0.092	0.009	0.193
$(r1-r2)*N_{2002}$	50	6	81

Table 22. Northeastern offshore spotted, generalized logistic model.

	Median	L 0.95	U 0.95
K	3479	2831	4281
R_{max}	0.017	0.002	0.036
$MNPL$	0.635	0.506	0.791
N_{2002}	691	568	855

Table 23. Northeastern offshore spotted, 2-K generalized logistic model.

	Median	L 0.95	U 0.95
K	3434	2703	4259
R_{max}	0.018	0.002	0.052
K_2	2664	508	5349
y_{change}	1990	1981	1999
N_{2002}	684	553	849

Table 24. Northeastern offshore spotted, 2-R_{max} generalized logistic model.

	Median	L 0.95	U 0.95
K	3146	2116	5005
R_{max1}	0.026	0.002	0.068
R_{max2}	0.001	-0.074	0.062
y_{change}	1993	1982	1999
N_{2002}	646	474	866

Table 25. Northeastern offshore spotted, generalized logistic model with additional 50% fishery mortality added for 1958-2001.

	Median	L 0.95	U 0.95
K	4783	4187	5386
R_{max}	0.025	0.007	0.045
N_{2002}	710	576	890
N/K	0.149	0.11	0.205
$N/MNPL$	0.235	0.159	0.341

Table 26. Northeastern offshore spotted, generalized logistic model with additional 100% fishery mortality added for 1958-2001.

	Median	L 0.95	U 0.95
K	5941	5207	6449
R_{max}	0.035	0.019	0.055
N_{2002}	744	607	917
N/K	0.126	0.097	0.17
$N/MNPL$	0.199	0.136	0.28

Table 27. Northeastern offshore spotted, generalized logistic model with additional 100% fishery mortality added for 1992-2001.

	Median	L 0.95	U 0.95
K	3457	3072	3908
R_{max}	0.018	0.003	0.036
N_{2002}	690	564	844
N/K	0.2	0.149	0.265
$N/MNPL$	0.317	0.215	0.463

Table 28. Northeastern offshore spotted, generalized logistic model with future projections, no mortality added to future years.

	Median	L 0.95	U 0.95
K	3488	3036	3911
R_{max}	0.017	0.002	0.036
N_{2002}	692	567	859
N/K	0.198	0.150	0.275
$N/MNPL$	0.314	0.212	0.460
N_{Pro}	3312	904	3558
N/K_{Pro}	0.997	0.231	1.000
$N/MNPL_{Pro}$	1.443	0.360	1.929
Y_{MNPL}	78	28	DNR

Table 29. Northeastern offshore spotted, generalized logistic model with future projections, 2002 mortality added to future years.

	Median	L 0.95	U 0.95
K	3492	3046	3917
R_{max}	0.017	0.002	0.037
N_{2002}	693	569	854
N/K	0.198	0.150	0.272
$N/MNPL$	0.314	0.213	0.461
N_{Pro}	3311	875	3558
N/K_{Pro}	0.997	0.224	1.000
$N/MNPL_{Pro}$	1.449	0.345	1.928
Y_{MNPL}	78	28	DNR

Table 30. Northeastern offshore spotted, 2-R_{max} generalized logistic model with future projections, no mortality added to future years.

	Median	L 0.95	U 0.95
K	3288	2583	3861
R_{max1}	0.027	0.002	0.070
R_{max2}	0.001	-0.072	0.063
y_{change}	1993	1982	1999
N_{2002}	645	473	866
N/K	0.198	0.139	0.277
$N/MNPL$	0.314	0.206	0.464
r_{MNPL}	0.001	-0.055	0.046
N_{Pro}	807	0	3798
N/K_{Pro}	0.246	0.000	1.000
$N/MNPL_{Pro}$	0.385	0.000	1.904
Y_{MNPL}	DNR	19	DNR

Table 31. Northeastern offshore spotted, 2-R_{max} generalized logistic model with future projections, 2002 mortality added to future years.

	Median	L 0.95	U 0.95
K	3303	2592	3857
R_{max1}	0.026	0.002	0.069
R_{max2}	0.001	-0.073	0.061
y_{change}	1993	1981	1999
N_{2002}	645	466	865
N/K	0.196	0.138	0.278
$N/MNPL$	0.312	0.204	0.465
r_{MNPL}	0.001	-0.056	0.045
N_{Pro}	826	0	3798
N/K_{Pro}	0.253	0.000	1.000
$N/MNPL_{Pro}$	0.402	0.000	1.911
Y_{MNPL}	DNR	19	DNR

Table 32. Northeastern offshore spotted, age-structured model.

	Median	L 0.95	U 0.95
K	3220	2023	5214
s_a	0.982	0.949	0.997
s_j	0.874	0.818	0.937
f_{max}	0.248	0.171	0.325
asm	12	10	13
R_{max}	0.016	0.002	0.035
$MNPL$	0.720	0.518	0.797
N_{2002}	691	568	859
N/K	0.214	0.124	0.378
$N/MNPL$	0.308	0.171	0.568

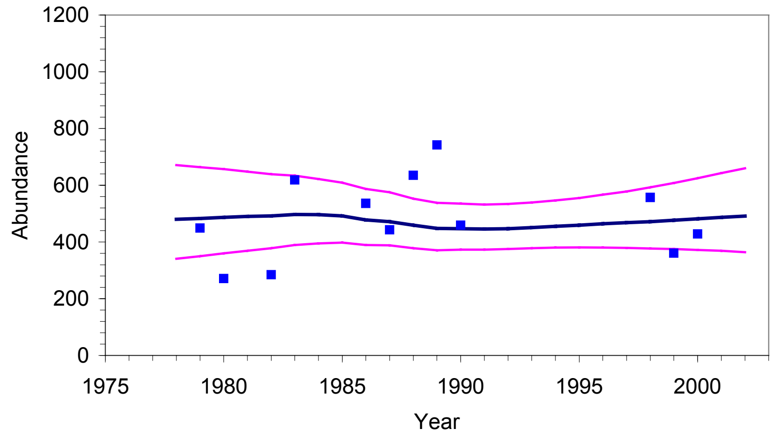
Table 33. Northeastern offshore spotted, age-structured model with survival covariate.

	Median	L 0.95	U 0.95
K	3504	2164	5517
s_a	0.984	0.955	0.997
s_j	0.901	0.834	0.962
f_{max}	0.237	0.170	0.325
asm	12	10	13
R_{max}	0.027	0.006	0.053
MNPL	0.717	0.519	0.798
N_{2002}	691	552	858
N/K	0.196	0.114	0.352
N/MNPL	0.286	0.158	0.523
h	0.013	0.001	0.059

Table 34. Bayes factors for northeastern offshore spotted dolphin model comparisons. The Bayes factor represents the ratio of the probability of one model to the probability of a second model. The Bayes factor is reported on the line of the model with the higher probability in the pair.

	Bayes factor
Exponential	1.02
2-slope Exponential	
Exponential additionally fit to TVOD	
2-slope Exponential additionally fit to TVOD	5.92
Generalized logistic	
2-K Generalized logistic	1.03
Generalized logistic	1.34
2-R_{max} Generalized logistic	
2-K Generalized logistic	1.38
2-R_{max} Generalized logistic	
Generalized logistic	2.44
150% fishery mortality	
Generalized logistic	7.43
200% fishery mortality	
Generalized logistic	
200% fishery mortality, 1991 forward	1.05
Age-structured	4.59
Age-structured with survival covariate	

A.



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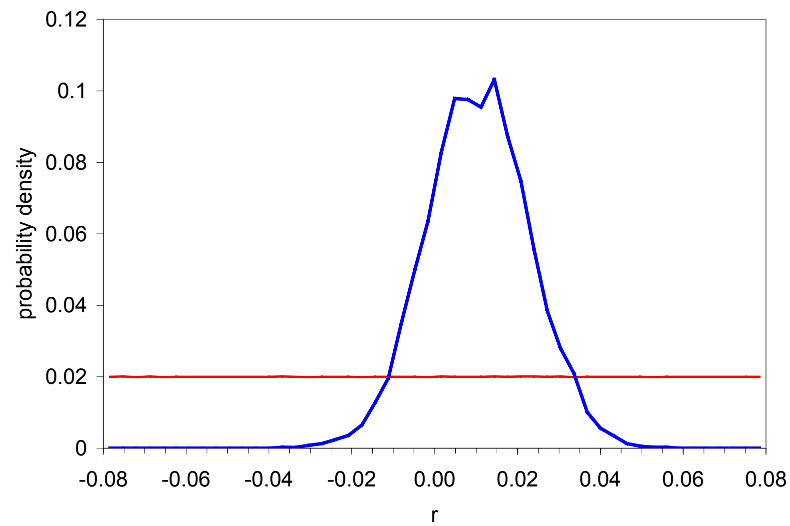


Figure 1. Eastern spinner, exponential model. (A) Estimated population trend (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Posterior probability distribution (blue line) for r, the population growth rate. The prior distribution (red straight line) is also shown.

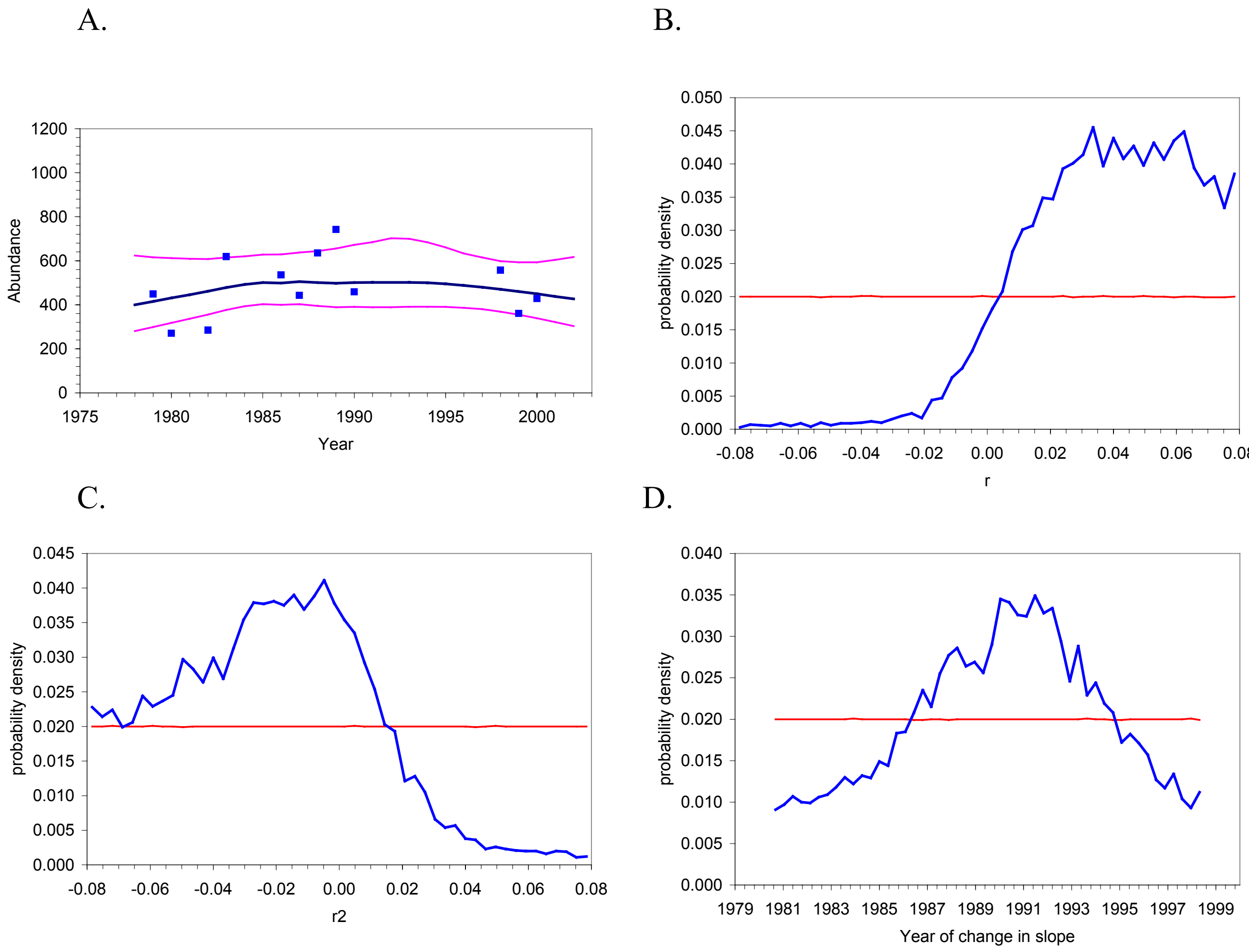
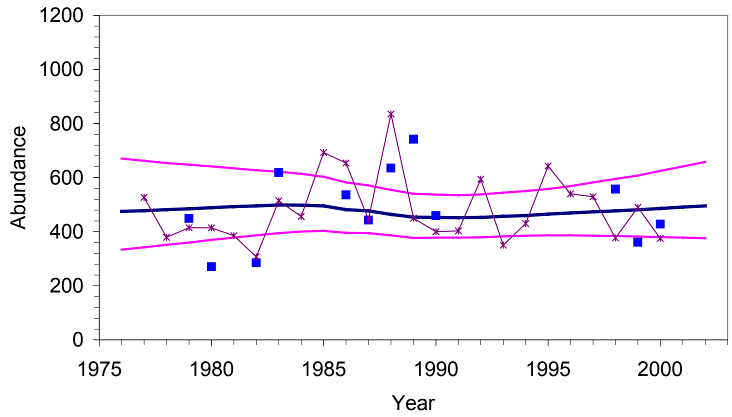


Figure 2. Eastern spinner, 2-slope exponential model. (A) Estimated population trend (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Posterior probability distribution (blue line) for *r1*, the first population growth rate. The prior distribution (red straight line) is also shown. (C) Posterior probability distribution (blue line) for *r2*, the second population growth rate. The prior distribution (red straight line) is also shown. (D) Posterior probability distribution (blue line) for y_{change}, the year in which the population growth rate changes. The prior distribution (red straight line) is also shown.

A.



B.

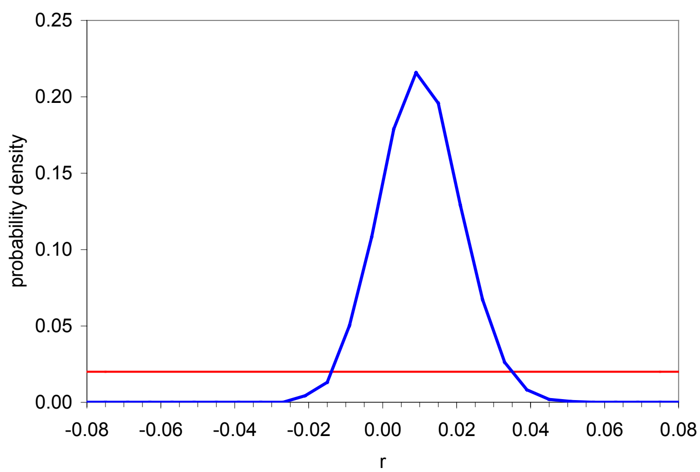


Figure 3. Eastern spinner, exponential fit to TVOD estimates. (A) Estimated population trend (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Posterior probability distribution (blue line) for r, the population growth rate.

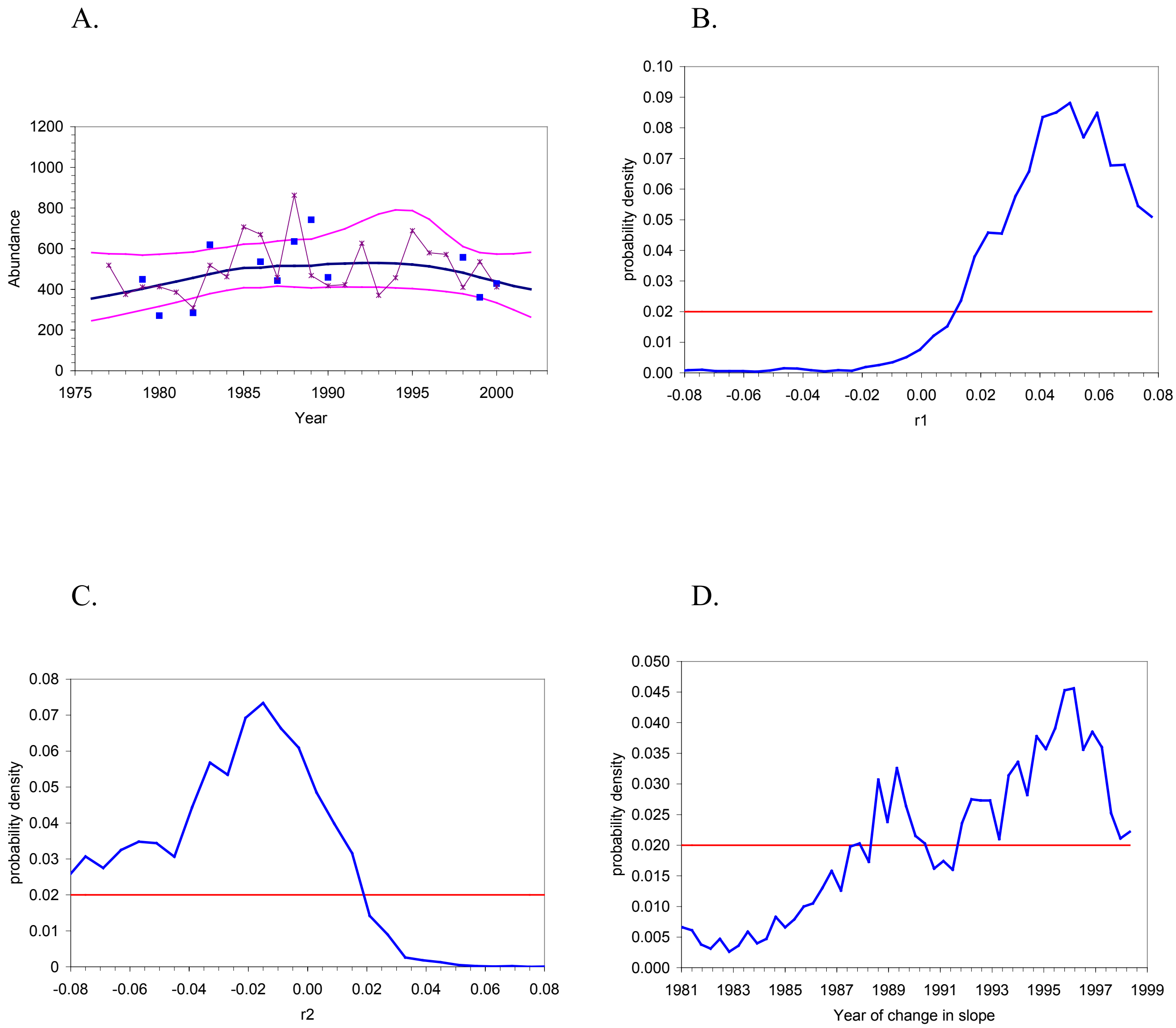


Figure 4. Eastern spinner, 2-slope exponential fit to TVOD estimates. (A) Estimated population trend (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Posterior probability distribution (blue line) for *r1*, the first population growth rate. The prior distribution (red straight line) is also shown. (C) Posterior probability distribution (blue line) for *r2*, the second population growth rate. The prior distribution (red straight line) is also shown. (D) Posterior probability distribution (blue line) for y_{change}, the year in which the population growth rate changes. The prior distribution (red straight line) is also shown.

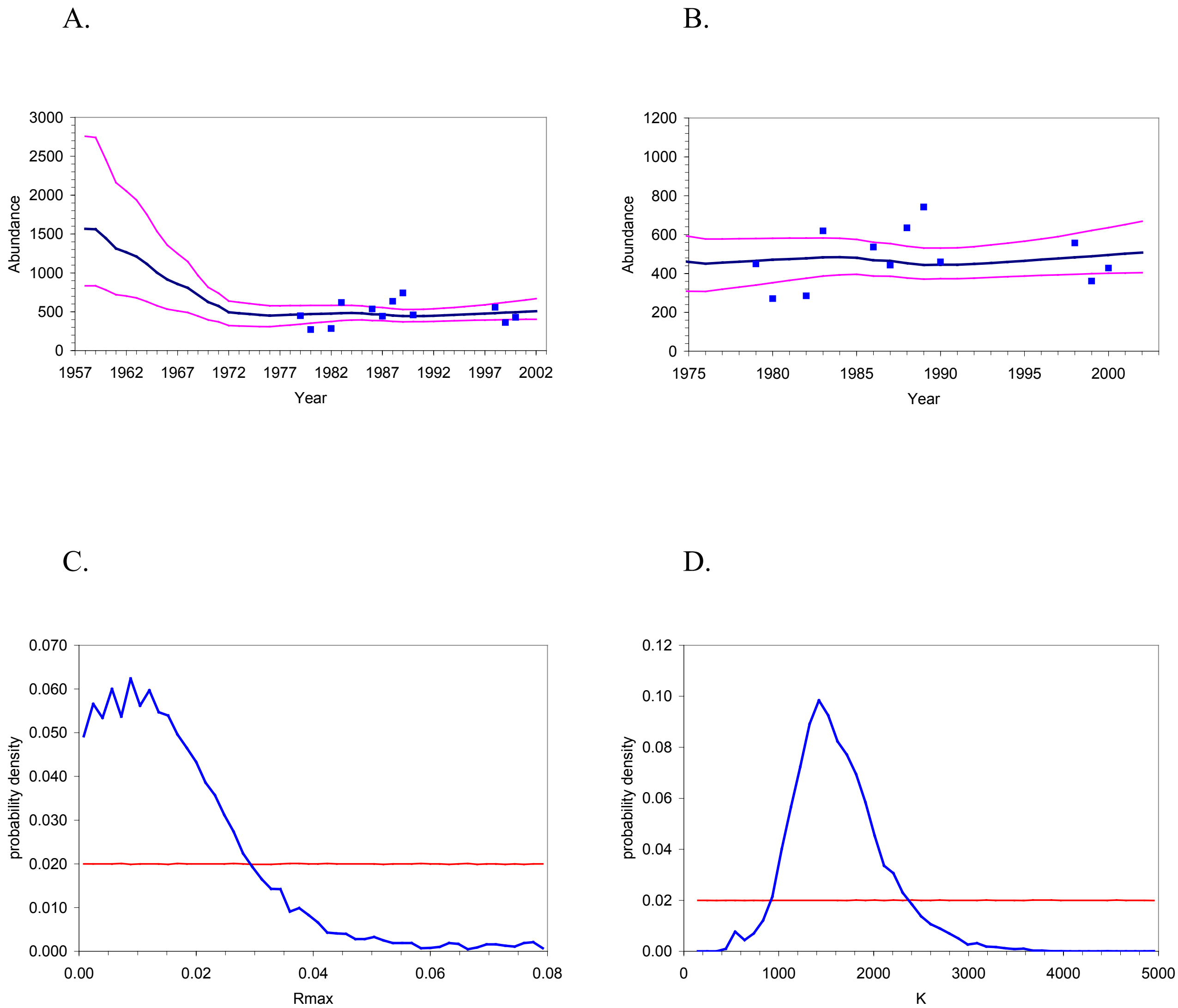


Figure 5. Eastern spinner, generalized logistic model. (A) Estimated population trend for the entire time series (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Estimated population trend for the period of 1975-2002 (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (C) Posterior probability distribution (blue line) for R_{max}, the maximum population growth rate. The prior distribution (red straight line) is also shown. (D) Posterior probability distribution (blue line) for K, the carrying capacity. The prior distribution (red straight line) is also shown.

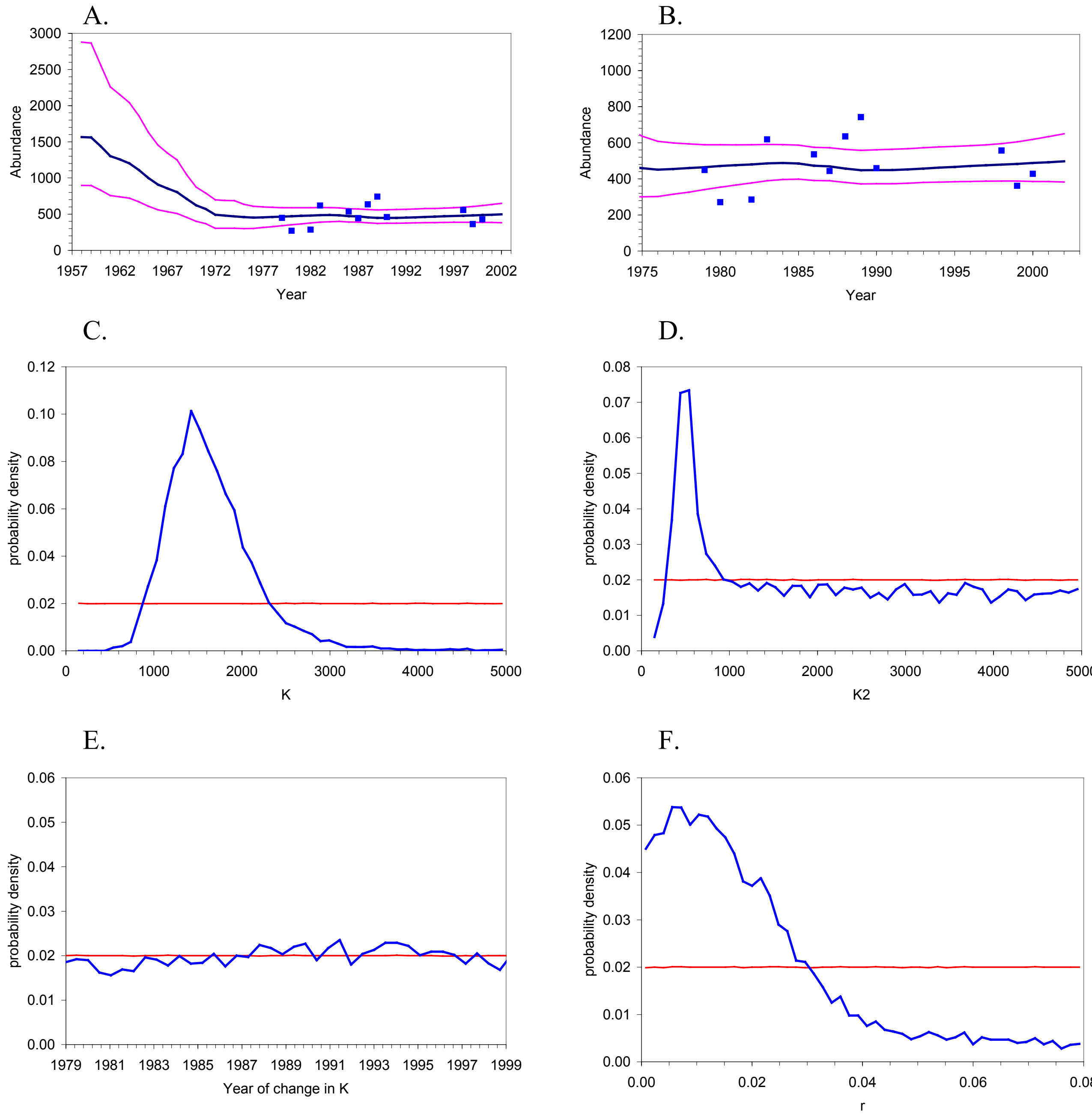


Figure 6. Eastern spinner, 2-K generalized logistic model. (A) Estimated population trend for the entire time series (lines), and (B) for the period of 1975-2002 (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (C) Posterior probability distribution (blue line) for K, the initial carrying capacity, (D) K2, the second carrying capacity, (E) $y_{\text{change},}$ the year in which the population growth rate changes, and (F) R_{max}, the maximum growth rate of the population. The prior distribution (red straight line) is also shown.

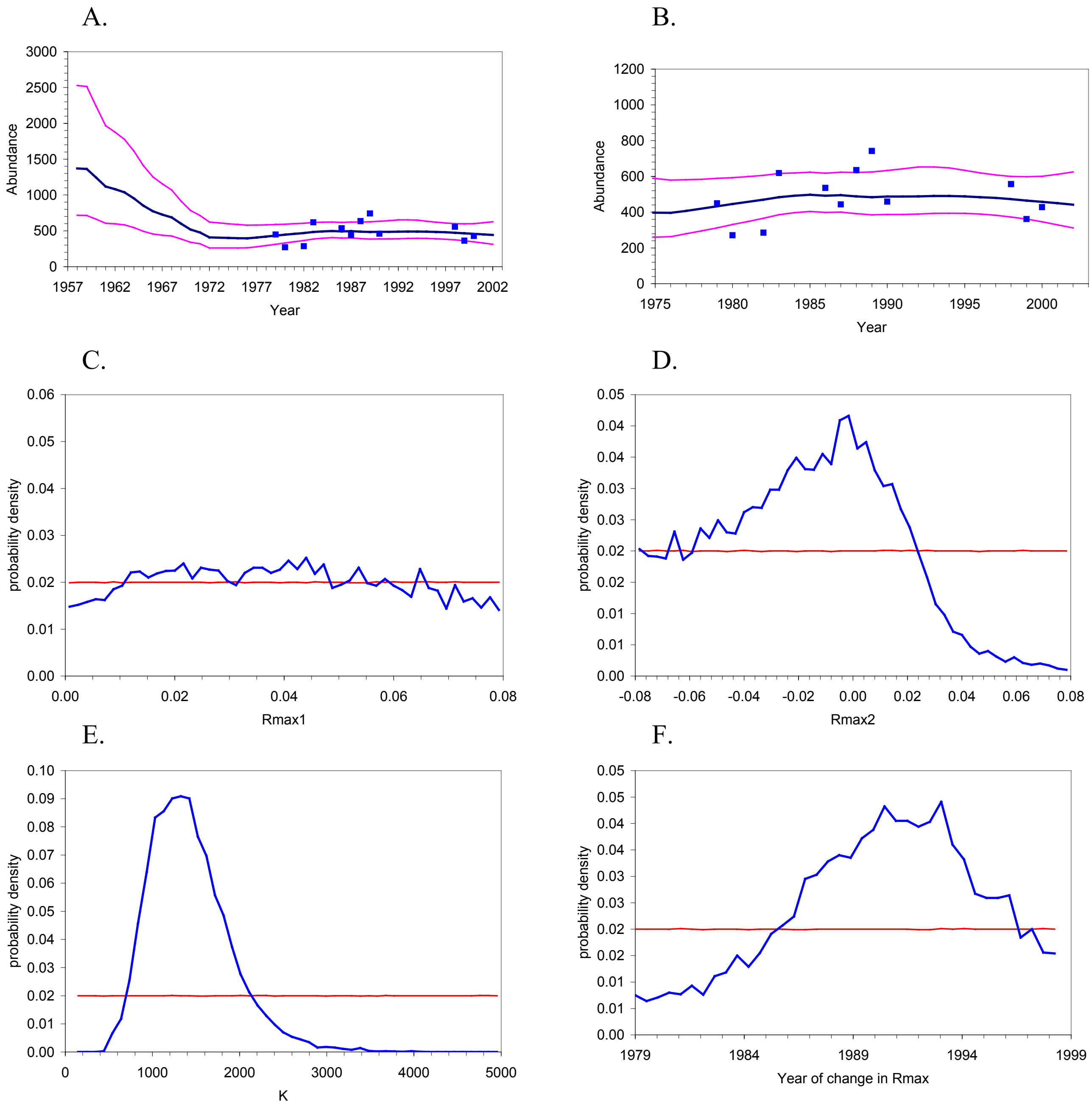
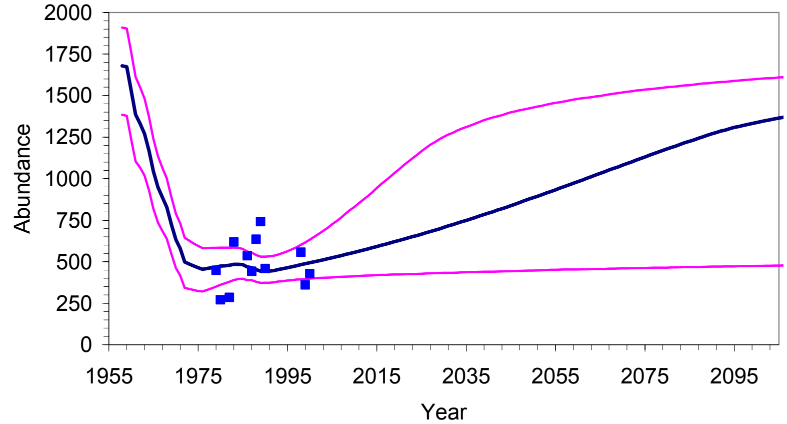


Figure 7. Eastern spinner, 2-R_{max} generalized logistic model. (A) Estimated population trend for the entire time series (lines), and (B) for the period of 1975-2002 (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (C) Posterior probability distribution (blue line) for R_{max1}, the first maximum growth rate of the population, (D) R_{max2}, the second maximum growth rate of the population, (E) K, the carrying capacity, and (F) $y_{change,}$ the year in which the population growth rate changes. The prior distribution (red straight line) is also shown.

A.



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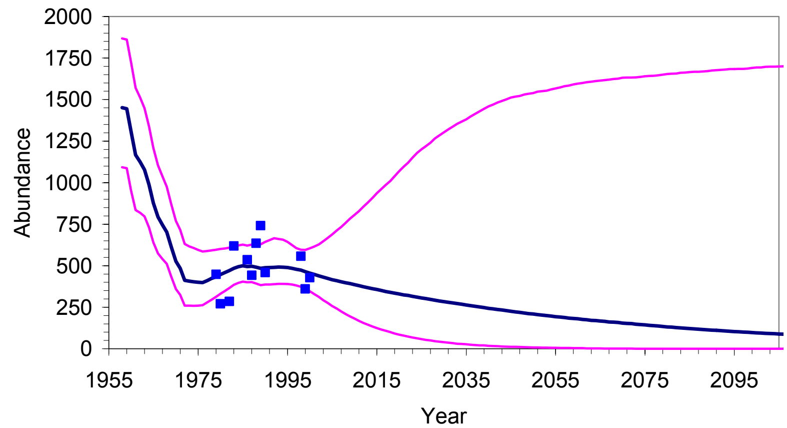


Figure 8. Eastern spinner. Future projection using two variants of the generalized logistic model. (A) Standard generalized logistic model with the median population size in each year from the posterior distribution (blue line), and the 0.95 probability interval for the population size in each year (purple line), with abundance estimates (squares) that the model was fit to. (B) 2-R_{max} generalized logistic model with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates that the model was fit to.

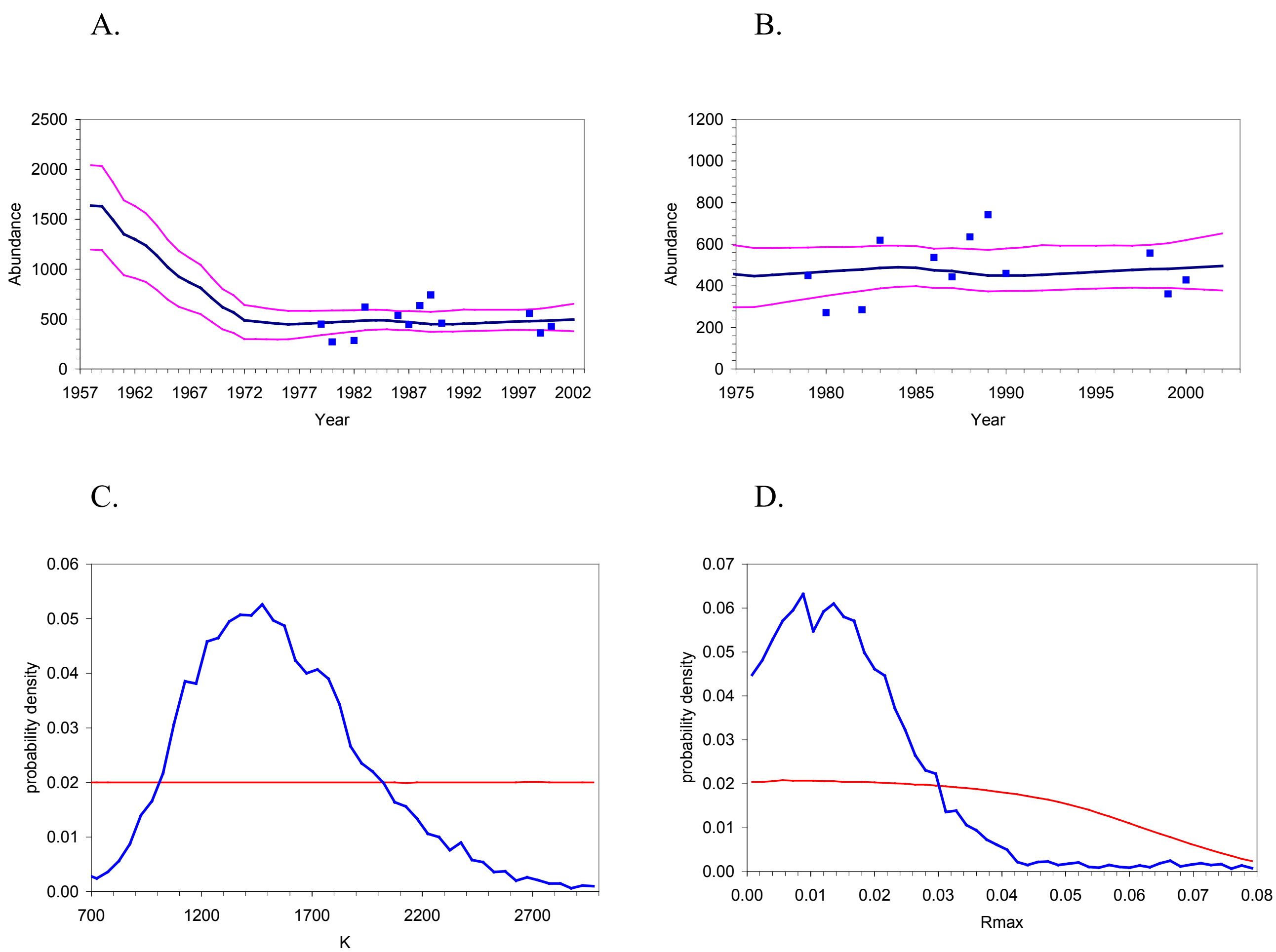


Figure 9. Eastern spinner, age-structured model.

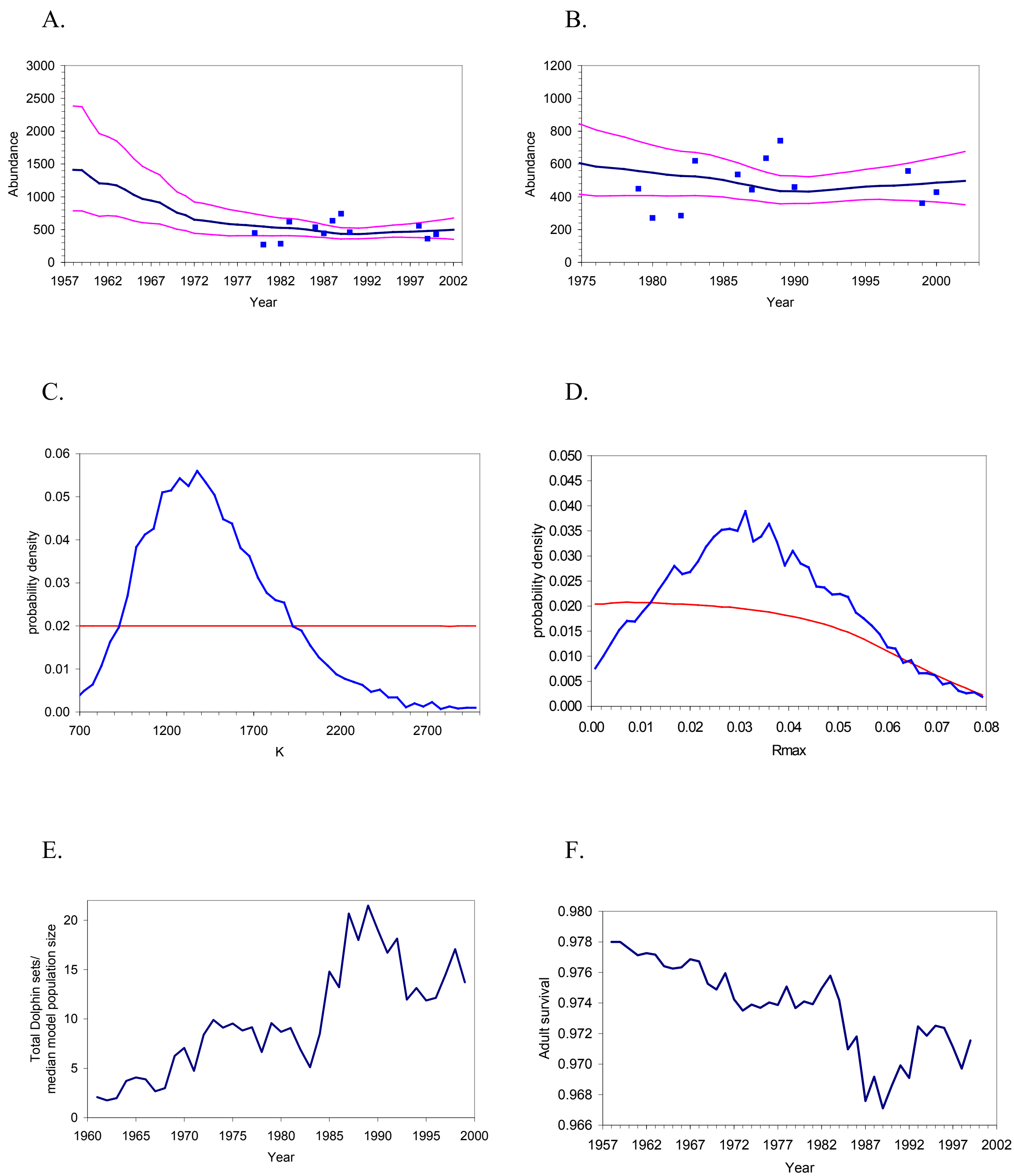
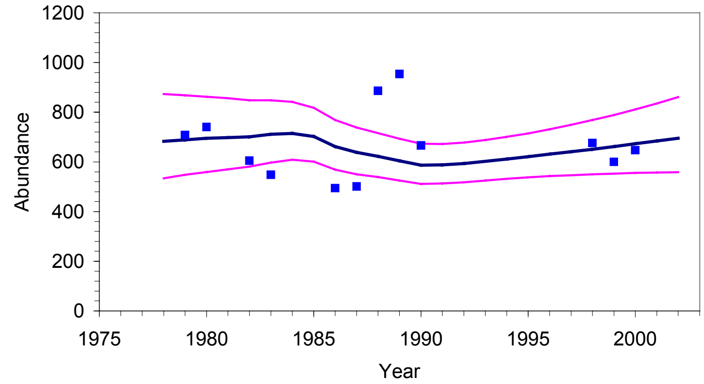


Figure 10. Eastern spinner, age-structured model with survival covariate.

A.



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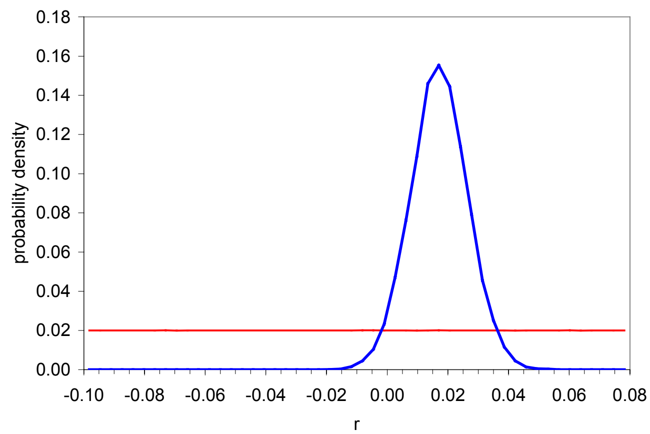


Figure 11. Northeastern offshore spotted. Exponential model. (A) Estimated population trend (lines), with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates (squares) that the model was fit to. (B) Posterior probability distribution (blue line) for r, the population growth rate. The prior distribution (red straight line) is also shown.

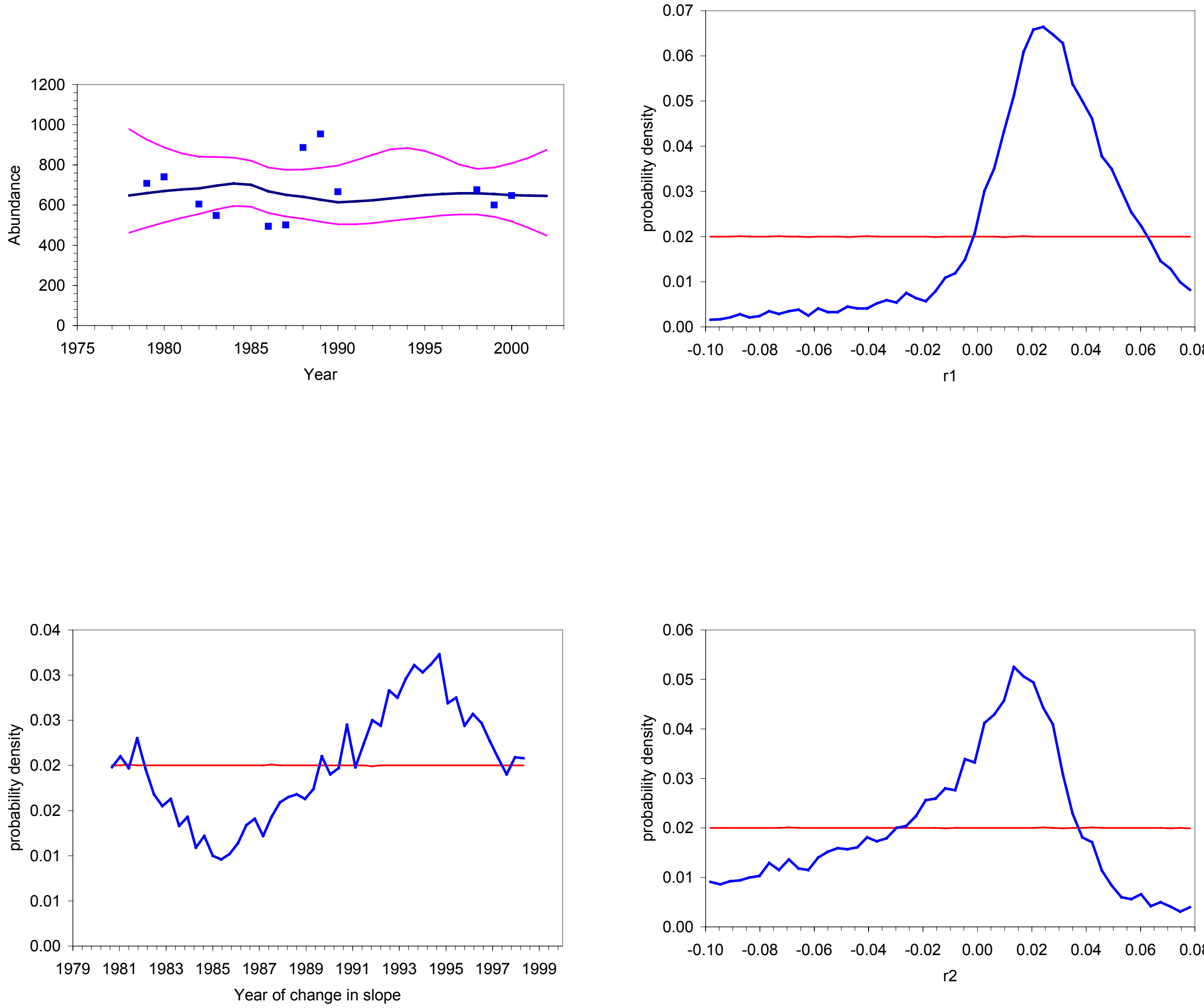
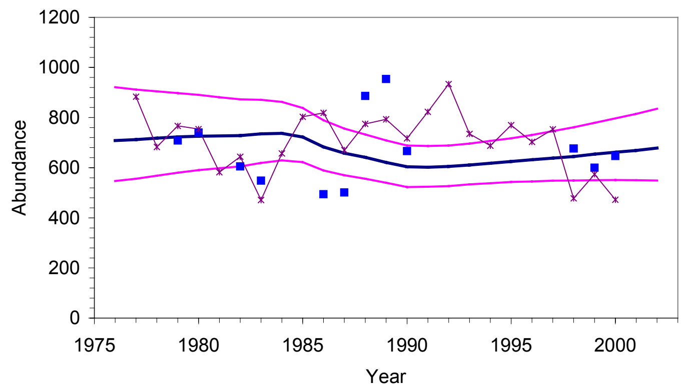


Figure 12. Northeastern offshore spotted. 2-slope exponential model.



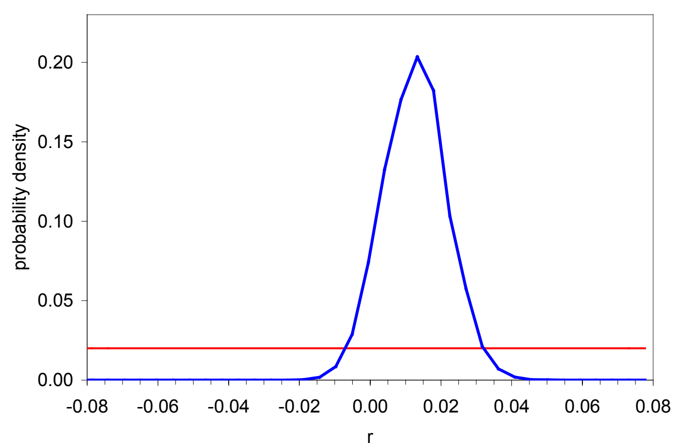


Figure 13. Northeastern offshore spotted. Exponential model fit to TVOD estimates.

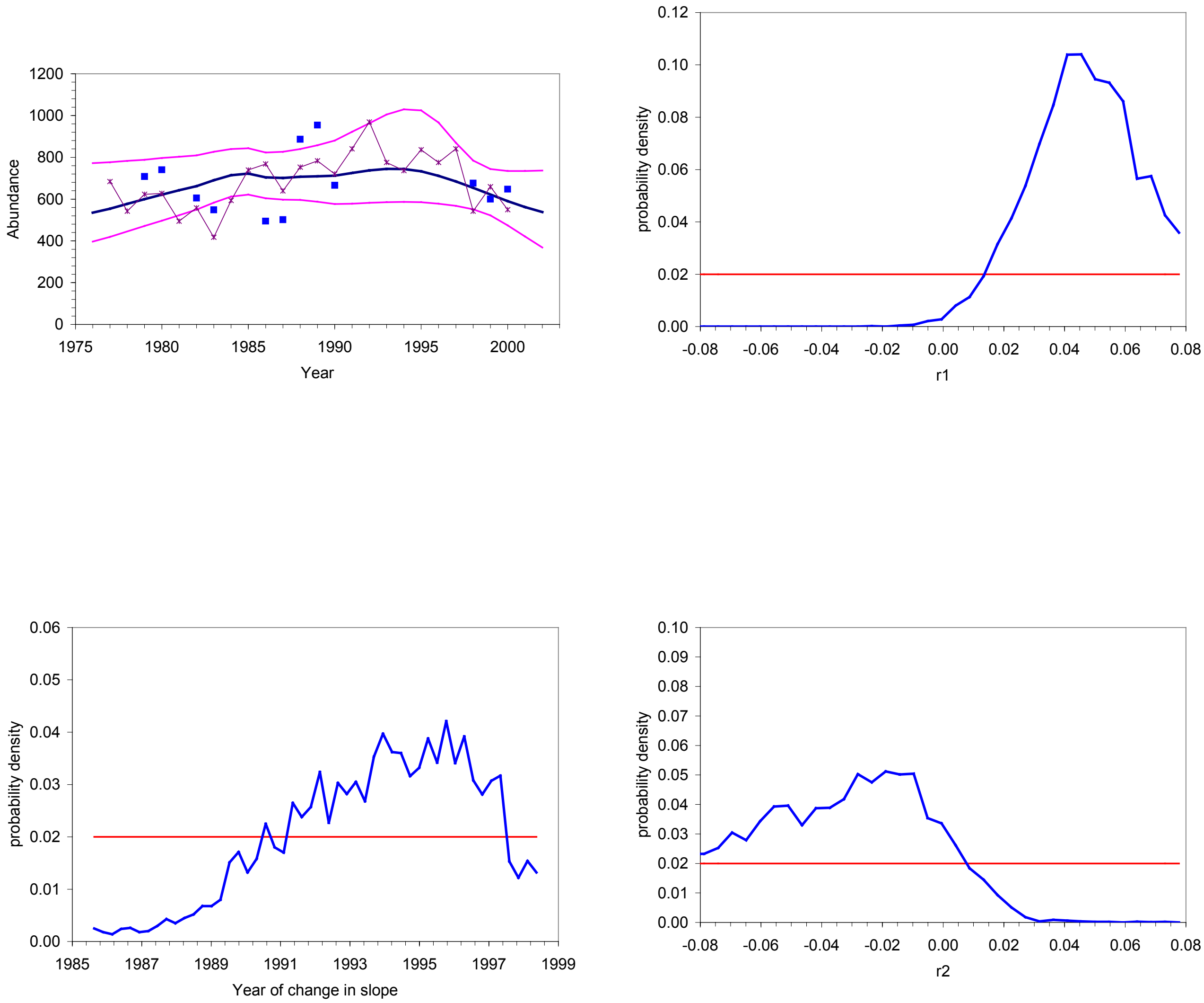


Figure 14. Northeastern offshore spotted. 2-slope exponential model fit to TVOD estimates.

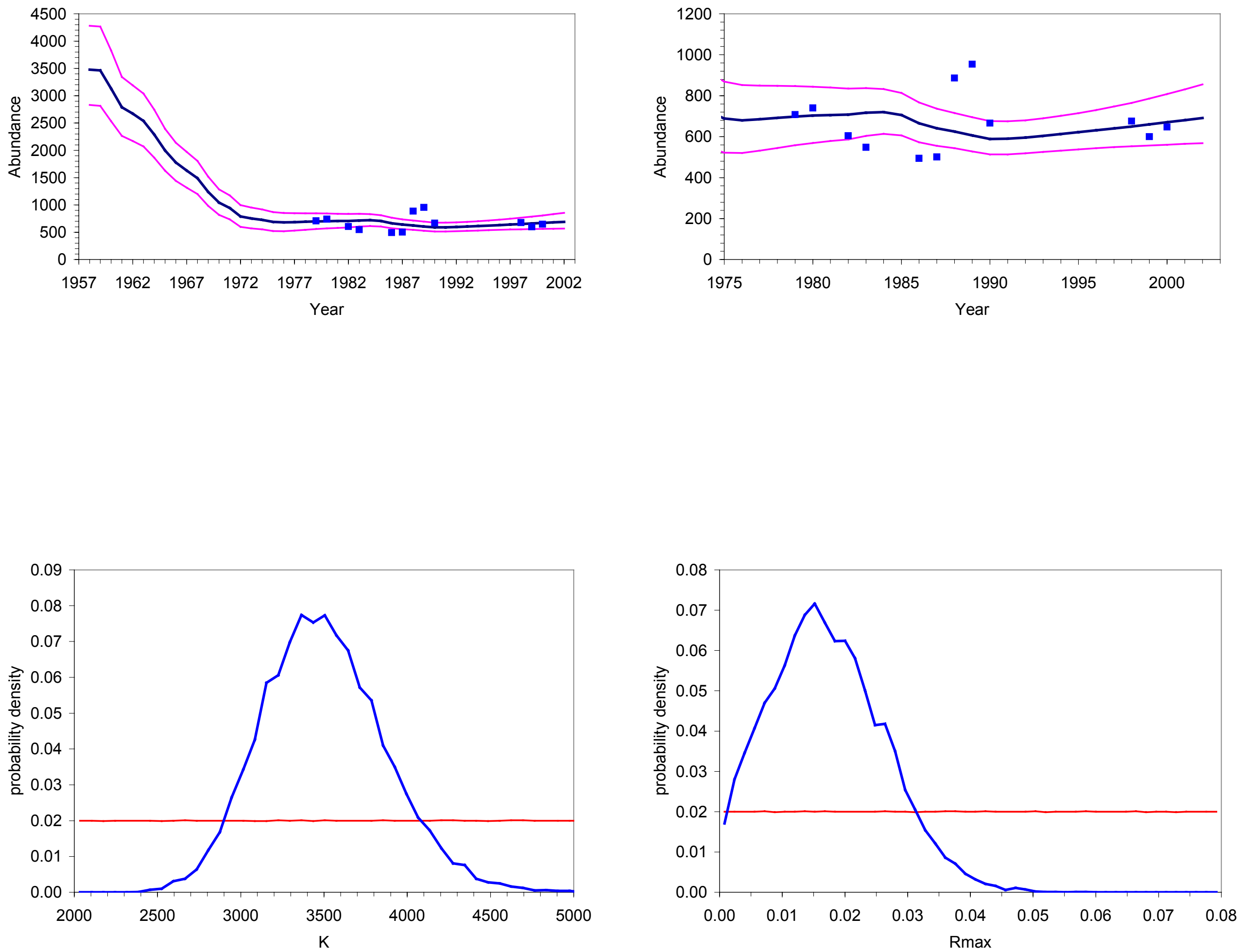


Figure 15. Northeastern offshore spotted. Generalized logistic model.

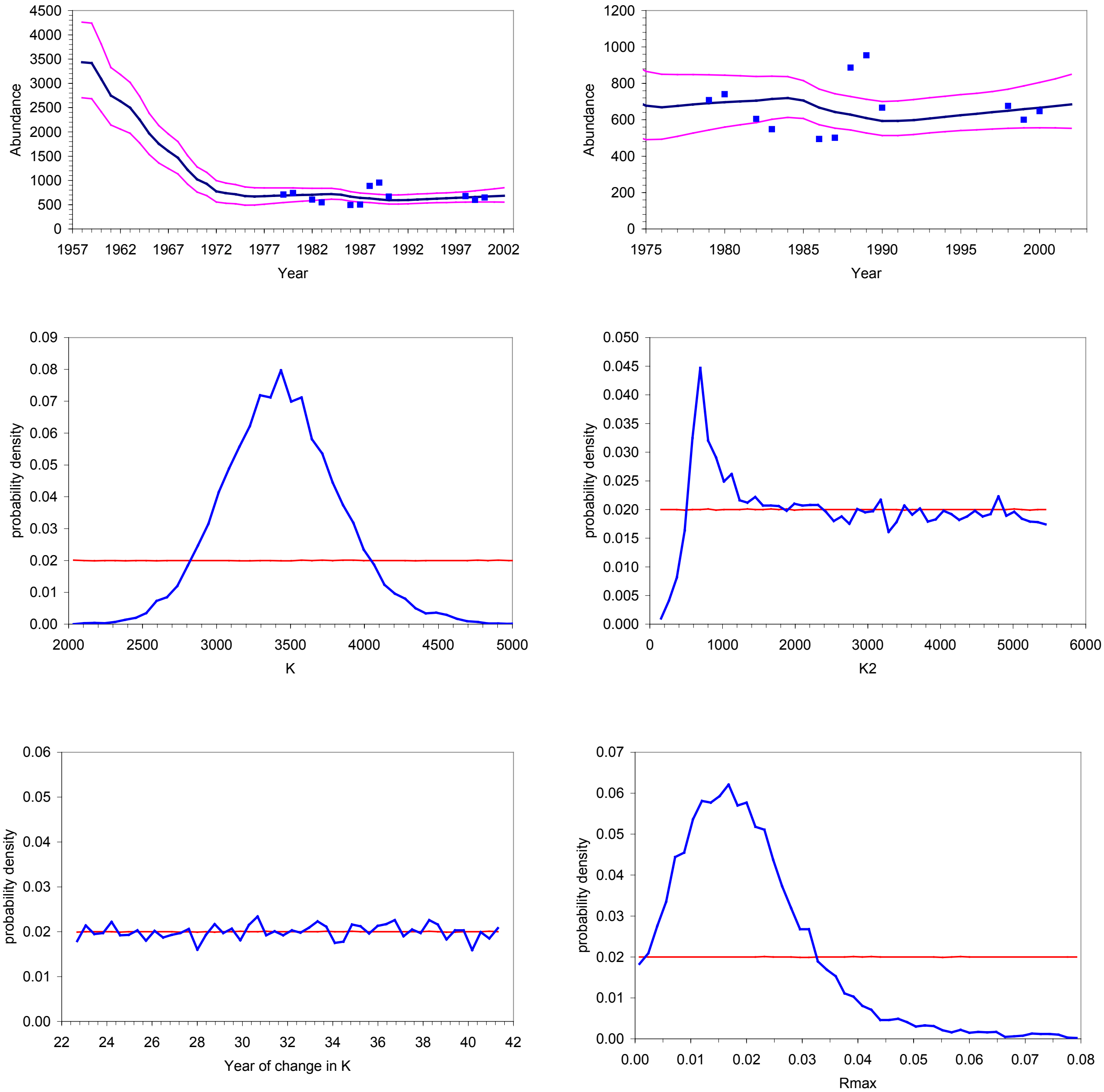


Figure 16. Northeastern offshore spotted. 2-K Generalized logistic model.

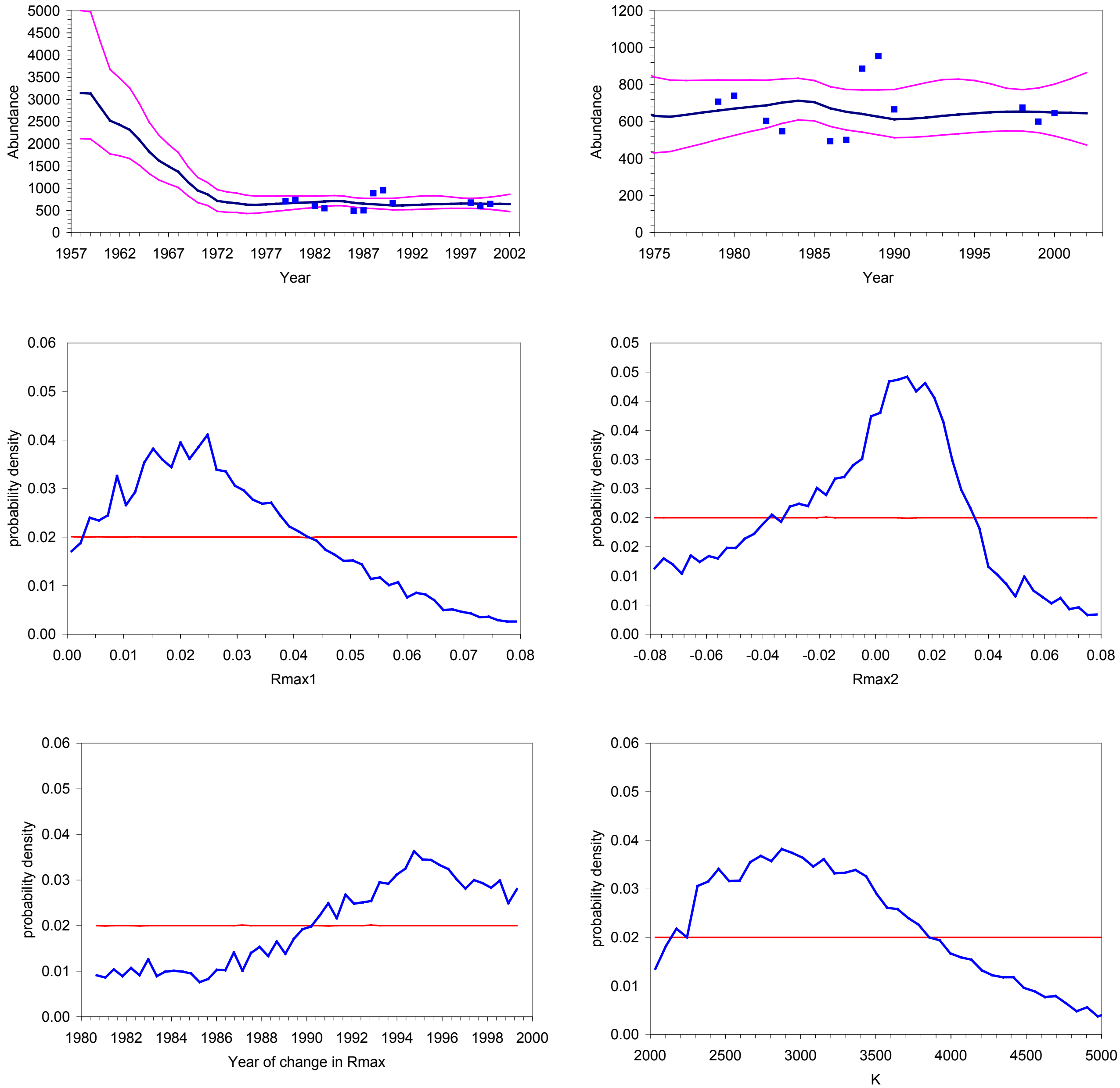
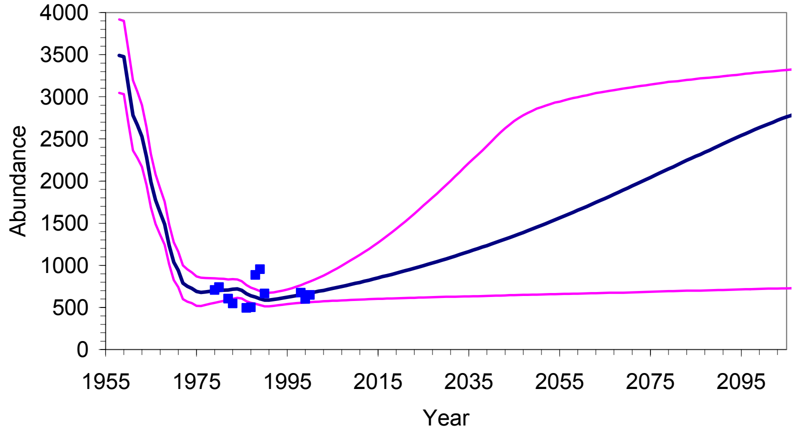


Figure 17. Northeastern offshore spotted. 2-R_{max} Generalized logistic model.

A.



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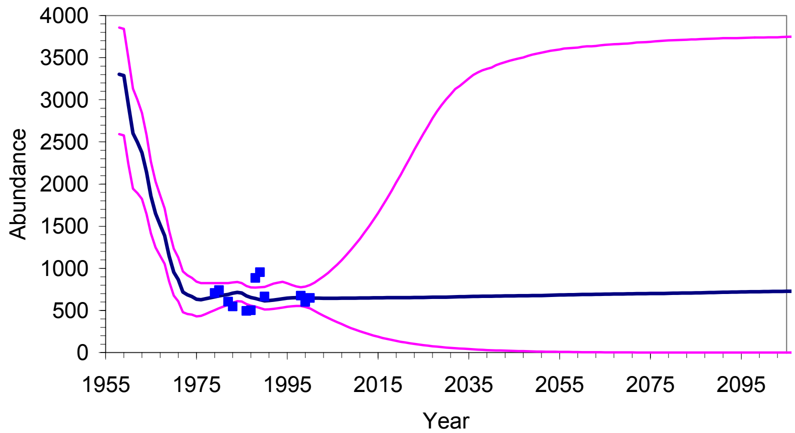

Figure 18. Northeastern offshore spotted. Future projection using two variants of the generalized logistic model. (A) Standard generalized logistic model with the median population size in each year from the posterior distribution (blue line), and the 0.95 probability interval for the population size in each year (purple line), with abundance estimates (squares) that the model was fit to. (B) 2-R_{max} generalized logistic model with the median population size in each year from the posterior distribution, and the 0.95 probability interval for the population size in each year, with abundance estimates that the model was fit to.

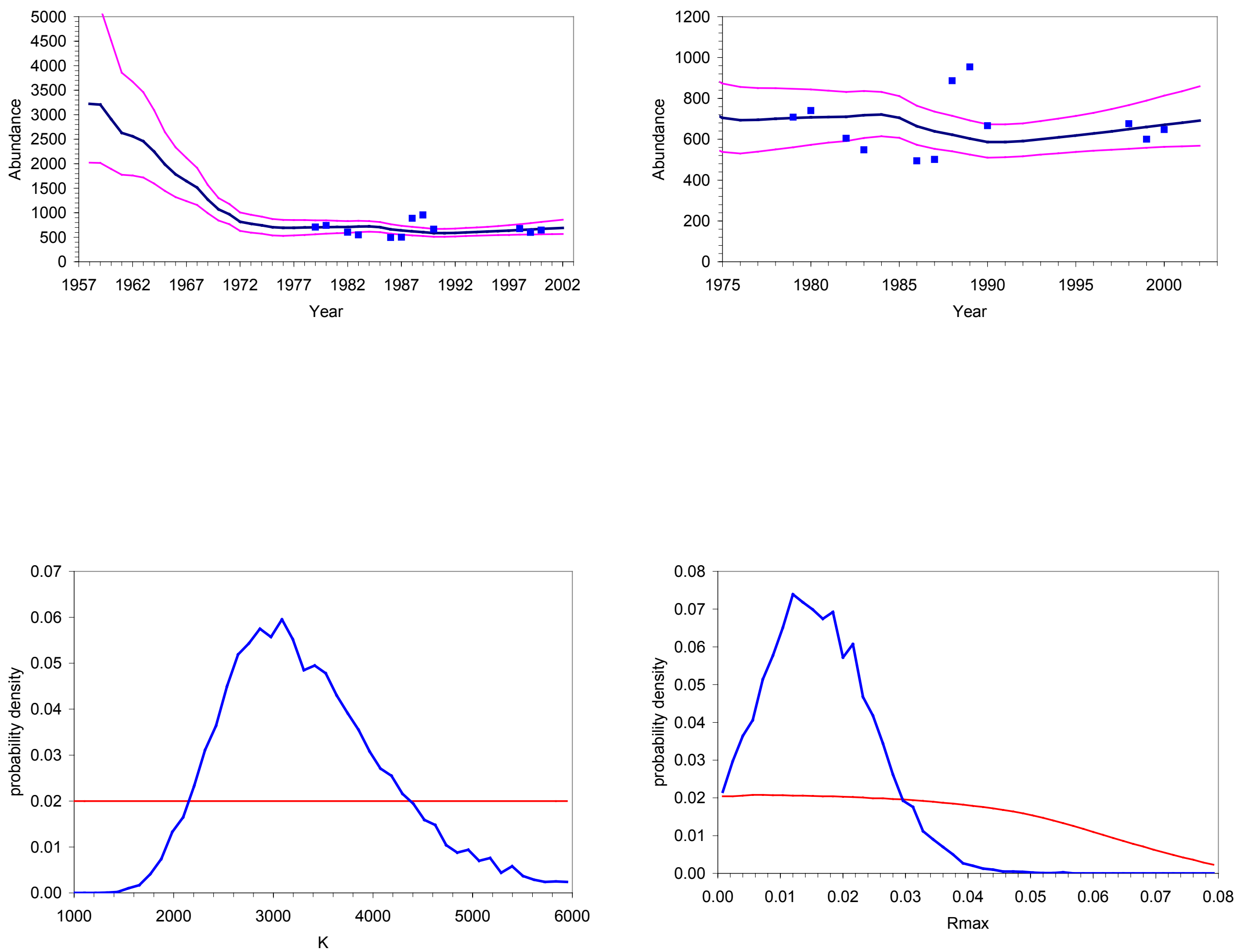

Figure 19. Northeastern offshore spotted. Age-structured model.

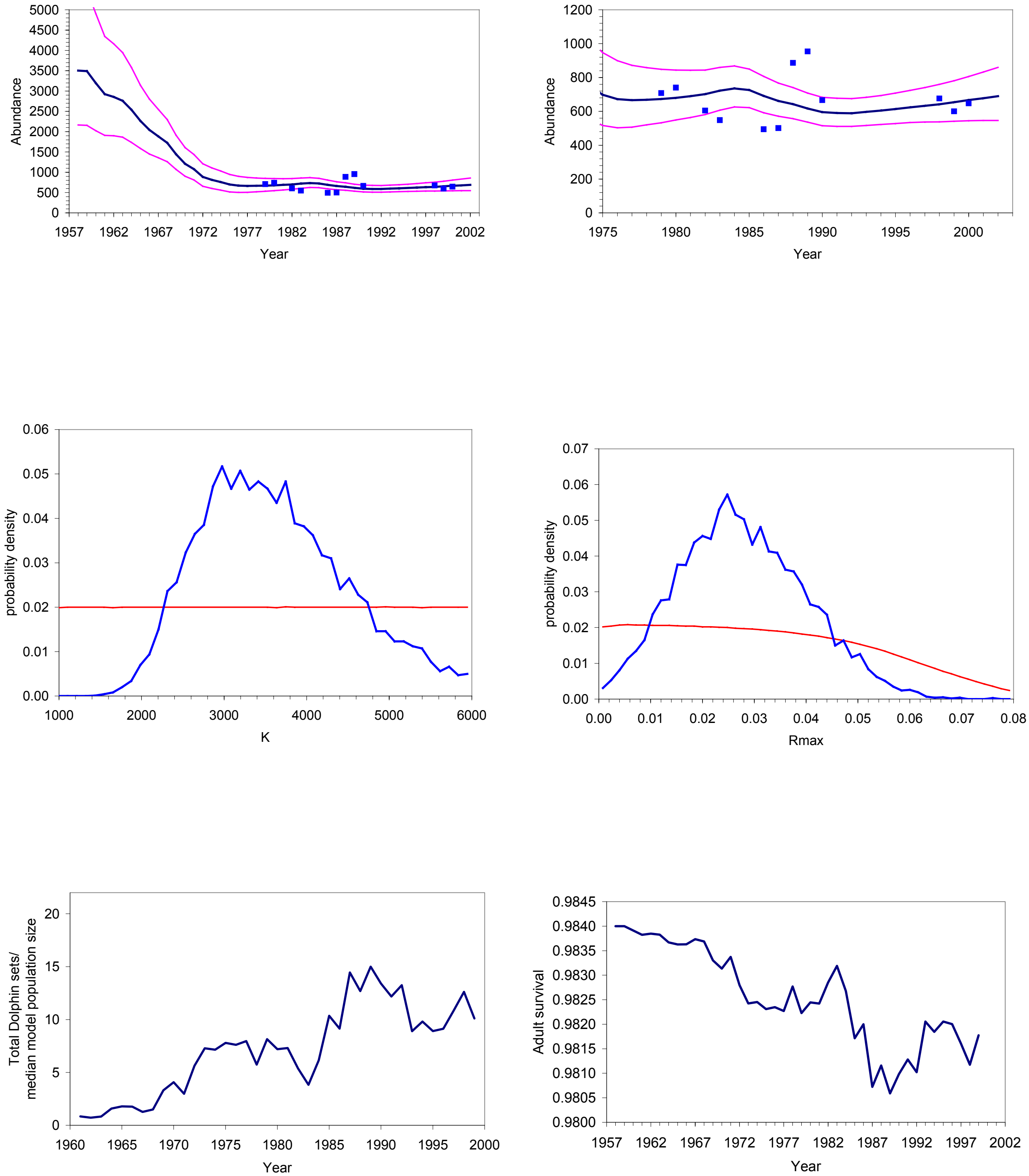

Figure 20. Northeastern offshore spotted. Age-structured model with survival covariate.

Appendix A. Responses to comments by reviewers from the Center for Independent Experts. References to page numbers refer to the documents produced by each reviewer.

Comments from reviewer, Dr. Malcolm Haddon

Conclusions and recommendations (from p. 21):

1. The limited number of data points available to which to fit the models. This will limit the number of parameters that can be estimated with confidence.

   Response: We agree that the main data for fitting a population model, twelve abundance estimates over twenty-two years, are limited. For this reason, we performed the majority of the analyses using simple models that require less parameters. A more complicated age-structured model was used to investigate possible effects of age-structured information, such as the age-structure of the kill.

2. The inability of the data to provide information concerning any expected density dependent effects. This makes the density dependent terms effectively redundant at current population sizes.

   Response: We agree there is little contrast in the abundance data, meaning we do not have the population growth rate measured at two fairly different population levels. That would be the kind of data that would provide information about density dependent responses. Lacking this knowledge, we chose to integrate over a fairly broad prior distribution for the shape of the density dependent function.

3. That the dynamics of the different models be considered as they are expressed at current population densities, and whether each type is telling the same things for each species being considered.

   Response: We do compare two different density dependent models (aggregate and age-structured) in order to see if they lead to different dynamics. For each species, the different models did not lead to appreciably different results. The age-structured effects are not large enough to make the age-structured model depart substantially from the aggregate model's dynamics.

4. That the uncertainty around the estimates of unfinished equilibrium dolphin population abundance and the related estimates of current depletion rates is poorly determined when only one model is included in the analysis. The different density dependent models need to be compared or both included in a single Bayesian analysis so as to include model uncertainty into the estimates.

   Response: We present results for equilibrium population size and depletion level for the two different models, and they give fairly similar results. We do include an analysis using the TVOD index estimates, but we agree with the reviewer that we are concerned about the basic validity of the index, based on concerns of Lennert-Cody (2001), Perkins (2000), and work of Ward and Goodman (in progress, under contract from NMFS).

5. That calf mortality has not been taken into account in the modelling nor in the estimates of total mortality. Both of these things (combined with the actual number of sets on dolphins) will have a marked effect on the modeling outcomes.

Response: Unobserved calf mortality has been taken into account by including the mean per capita set rate as a covariate acting on the survival of the juvenile age class. This is an approximation of a mortality effect only on dolphins of age 1, but should be sufficeint if the effect is strong. A related effect was tested for by scaling up recorded mortality by 50% and 100% in a subset of model runs.

6. That the TVOD data be reconsidered to determine whether there are any sub-sets that could be taken from it and included in the model. These would need to be more homogenous in how the estimates were made than in the complete data set.

   Response: If such an investigation could show there was a homogeneous data set, it could be used, but no convincing argument has yet been made regarding what constitutes a homogeneously estimated series within the TVOD index series.

7. That the comparisons between the 1-slope and 2-slope models be treated with great caution because of the lack of data and lack of a mechanism for the regime shift (other than a correlation with oceanography).

Response: There are other mechanisms that could be responsible for a change in population dynamics as implied by a 2-slope model. In particular, in the early 1990s a new management structure for dealing with the dolphin bycatch was put into place.

Comments from reviewer, Dr. Murdoch McAllister

Recommendations for immediate implementation (from p. 2):

1. That within the stock assessment model, the annual rate of change of bias in the fd indices of abundance be estimated using a linear model for trend-bias while assuming no trend-bias in fi indices. However, this should be done applying the constraint that the fd indices are given no more weight in the estimation than the fi indices.

   Response: This has been done.

2. That an additional age-structured model be developed that models incidental mortality rates on one-year-old calves as a function of the annual per capita index of exposure to dolphin purse-seine sets, the latter measured by the number of dolphin sets on the species x the annual average number of animals caught or chased per set divided by the population abundance.

   Response: This has been done, modeling mortality rates as a function of the annual per capita index of exposure to dolphin sets, calculated as number of sets on dolphins divided by population size.

3. When different population dynamics model structures were compared, the criterion for choice was AIC. Although AIC is widely accepted and considered a rigorous and objective criterion, it is difficult to interpret and leads to only one model being selected. It is recommended that Bayes' marginal posterior probabilities be computed instead for each alternative model considered.

   Response: This has been done.

4. That a scenario-based approach be applied to evaluate the plausibility of various factors that might have been impeding population recovery over the last few decades since the reported kills in

dolphin sets were substantially decreased. Bayes' marginal posterior probabilities should be computed and presented with each alternative population dynamics model to indicate the relative credibility/plausibility of each given both the fi and fd data.

Response: We have explored several scenarios, including change in the environment (2-K models) as well as 50% and 100% greater mortality than reported.

5. That particular attention be given to evaluating the plausibility of the fishery-induced calf-mortality model (Recommendation 2) against that of other models that do not implicate the tuna-purse seine fishery as the chief cause for impeding ETPD recovery.

Response: This was done, using the Bayes factor for comparison of different models.

Recommendations to be considered in the near future:

1. That the estimation performance of alternative estimators be evaluated by repeatedly simulating data with known model structures and values for model parameters, applying each estimator to estimate the parameters and then computing the bias and precision in each alternative estimator. This should be applied to evaluate the relative improvement in estimation performance of estimators that use both the fi and fd indices of abundance versus only the fi indices of abundance.

2. That the fishery independent indices of abundance be treated as relative instead of absolute indices of abundance and that an informative prior probability distribution be constructed for the constant of proportionality that relates the true abundance to the relative abundance indices.

3. That the "mu-model" which is a perfectly sensible and useful model to apply, be renamed and not discarded but still applied as an explanatory and predictive model for ETPD population dynamics, along with the various other models recommended and already applies.

4. That a formal Chi-square statistical measure of model deviance be computed for each estimation as a diagnostic of the goodness of fit of the model to the data.

5. That both the spotted and spinner stocks be modeled simultaneously as separate stocks in the same population dynamics model to estimate parameters that could be considered to be similar or the same between the two populations.

Response to all five recommendations for future work: We agree that all these ideas are worthy of consideration, and plan to pursue them as soon as possible. This may not be in time for inclusion in our final science report from the IDCPA research program, but we will view these directions as potential improvements to our longer-term efforts regarding the tuna-dolphin problem. Thank you both for your very helpful and constructive reviews.