VIRTUAL POPULATION ANALYSES OF ATLANTIC BLUEFIN TUNA WITH ALTERNATIVE MODELS OF TRANSATLANTIC MIGRATION: 1970-1997

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SUMMARY

This paper presents a VPA implementation of a model for two-stocks with overlapping ranges. The model is applied to catch, abundance, and tag-recapture data for Atlantic bluefin tuna (Thunnus thynnus). The resulting estimates of abundance, mortality, and mixing are compared with the corresponding estimates from the diffusion VPA model used previously by the SCRS and NRC. The overlap model provides the best fit to the index data and the diffusion model provides the best fit to the tagging data. The estimated values for the mixing coefficients are significantly different from zero with both the overlap and diffusion models, but the corresponding abundance trends are similar to those of the VPA without mixing. The use of tagging data has a greater impact on the assessment than the choice of abundance models.

RÉSUMÉ

Le présent document fait état de l’application par VPA d’un modèle pour deux stocks dont les zones se chevauchent. Le modèle est appliqué aux données de capture, d’abondance et de marquage-recapture du thon rouge de l’Atlantique (Thunnus thynnus). Les estimations qui en découlent sur l’abondance, la mortalité et le mélange sont comparées aux estimations correspondantes du modèle VPA de diffusion utilisé antérieurement par le SCRS et par la NRC. Le modèle de chevauchement donne le meilleur ajustement aux données de l’indice et le modèle de diffusion est celui qui s’ajuste le mieux aux données de marquage. Les valeurs estimées pour les coefficients de mélange différent de façon significative de zéro dans le modèle de chevauchement comme dans le modèle de diffusion, mais les tendances correspondantes de l’abondance sont semblables à celle de la VPA sans mélange. L’utilisation des données de marquage a une plus forte incidence sur l’évaluation que le choix des modèles d’abondance.

RESUMEN

Este documento presenta una implementación del VPA de un modelo para dos stocks con franjas solapadas. El modelo se aplica a la captura, la abundancia, y los datos de marcado-recaptura para el atún rojo (Thunnus thynnus) del Atlántico. Las estimaciones resultantes de abundancia, mortalidad y mezcla se comparan con las estimaciones correspondientes del modelo de difusión VPA utilizado previamente por el SCRS y el NRC. El modelo de solapamiento proporciona el mejor ajuste a los datos del índice y el modelo de difusión proporciona el mejor ajuste a los datos de marcado. Los valores estimados para los coeficientes de mezcla son significativamente diferentes de cero tanto con el modelo de solapamiento como con el de difusión, pero las tendencias de abundancia correspondientes son similares a las del VPA sin mezcla. La utilización de los datos de marcado tiene mayor impacto sobre la evaluación que la elección de los modelos de abundancia.

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1. INTRODUCTION

The International Commission for the Conservation of Atlantic Tunas (ICCAT) has managed the bluefin tuna populations in the eastern and western Atlantic Ocean as distinct stocks since 1982 (Brown and Parrack, 1985). During this time the ICCAT Standing Committee on Research and Statistics (SCRS) has considered the possible implications of limited east/west intermixing indirectly through various means. In 1993 the SCRS began examining the implications of a particular mixing hypothesis directly by use of a two-area virtual population analysis model (Butterworth and Punt, 1994; ICCAT, 1994). The SCRS found that the predictions from this two-area model were very sensitive to the level of intermixing assumed and strongly recommended further investigations. Subsequently, researchers with the National Research Council (NRC) attempted to estimate the rate of intermixing and showed that the SCRS two-area model predicted slightly higher abundances of older bluefin tuna when their estimates of mixing were used compared to when no mixing was assumed (NRC, 1994). They then recommended that future assessments of bluefin tuna be based on models that account explicitly for mixing. Shortly thereafter, the ICCAT Commission resolved that the SCRS should develop recovery options for bluefin tuna that take into account the possible effects of mixing.

The two-area mixing model used by the SCRS and NRC (hereafter referred to as the diffusion model) assumes that fish movement depends on location—fish located in the East Atlantic transfer west with probability $T_{ew}$ and fish located in the West Atlantic transfer east with probability $T_{we}$. It implies that fish moving from one side of the ocean to the other ‘forget’ where they came from. The SCRS has expressed concern that such a model is an unlikely characterization of bluefin tuna migration and that it may be more likely that bluefin tuna return to the area where they were born (ICCAT, 1995, p. 108-110). Cooke and Lankester (1996) suggested an alternative model where the ranges of the eastern and western populations are assumed merely to overlap, which would imply that fish ‘remember’ which side of the ocean they came from and how to return. Using a form of survival analysis, they found that this “overlap” model was at least as consistent with the tagging data as the diffusion model.

This paper presents an implementation of the overlap model in the context of virtual population analysis (VPA) and applies it to the catch, abundance and tag-recapture data used by the 1998 SCRS bluefin tuna working group (SCRS, 1999). The diffusion VPA was also applied to these data for comparison.

2. THE OVERLAP AND DIFFUSION VPA MODELS

The overlap model implemented here assumes there are two stocks living in a region that can be divided into two distinct fishing zones. The fish in each stock $j$ are assumed to move at the beginning of the year such that a fraction $T_{j1}$ resides in one fishing zone and a fraction $T_{j2}$ ( = 1-$T_{j1}$) in the other.

The corresponding population equations are:

1. $N_{j,a+1,y+1} = N_{j,y} \sum_{k=1}^{2} T_{jkay} e^{-Z_{kay}}$ (for $a < A - 1$)
2. $N_{j,A,y+1} = N_{j,y} \sum_{k=1}^{2} T_{jkay} e^{-Z_{kay}} + N_{j,Ay} \sum_{k=1}^{2} T_{jkAy} e^{-Z_{kAy}}$ (for $a = A - 1$)
3. $\tilde{N}_{kay} = \sum_{j=1}^{2} T_{jkay} N_{j,y}$
4. $C_{kay} = \tilde{N}_{kay} \frac{F_{kay}(1 - e^{-Z_{kay}})}{Z_{kay}}$

where $j,k,a,y$ subscripts denoting stock, fishing zone, age and year
The equations for the diffusion model are similar except that the accounting is done in terms of the abundance in each zone \( \bar{N}_k \) rather than the abundance of each stock. The fish in zone \( j \) are assumed to move at the beginning of the year such that a fraction \( T_{j1} \) (transfer to and migrate like) one fishing zone and a fraction \( T_{j2} \) (among each other) fishing zones:

\[
\bar{N}_{j, a+1, y+1} = \sum_{k=1}^{2} \bar{N}_{kay} T_{kjay} e^{-Z_{joy}}
\]

for \( a < A - 1 \)

\[
\bar{N}_{j, A, y+1} = \sum_{k=1}^{2} \bar{N}_{kay} T_{kjay} e^{-Z_{joy}} + \sum_{k=1}^{2} \bar{N}_{kAy} T_{kjAy} e^{-Z_{jay}}
\]

for \( a = A - 1 \)

Note that the overlap and diffusion equations both reduce to the canonical forms for two independent stocks when \( T \) or \( \bar{T} \) are set to zero. Otherwise the magnitudes of \( T \) and \( \bar{T} \) are not directly comparable because the diffusion model allows fish born in one area to accumulate in the other while the overlap model does not. Suppose, for example, the westward and eastward values are both 10%. With the diffusion model the odds that a fish born in the West will be living in the East is 10% after one year, 18% after two years and 24.4% after three years. With the overlap model the odds are always 10% because the same fraction of the stock occupies the East every year. In this paper we will sometimes refer to \( T \) and \( \bar{T} \) collectively as the transfer coefficients \( T \), but the reader should keep the distinction in mind.

Equations 1-6 contain numerous variables representing the transfer coefficients, natural mortality rates, fishing mortality rates, catches and population abundances. Of these, it is often only the catches that are actually observed. The VPA approach to this problem is to develop a backwards recursion that determines the historical abundance and fishing mortality rate of each cohort from the observed catches (given values for \( M, T, F_{ay}, \) and \( F_{A_y} \)). We derive the recursion for the overlap model in Appendix 1.

The challenge that remains is to choose appropriate values for \( M, T, F_{ay}, \) and \( F_{A_y} \). The value of \( M \) is usually fixed to some assumed value. In the present case, for example, we use the age-specific vector adopted by the SCRS, which itself was borrowed from estimates for southern bluefin tuna because the biology of the two species is similar. There is, however, no reason to expect Atlantic and southern bluefin tuna to have similar values of \( T \) and \( F \) inasmuch as they inhabit different oceans with very different fisheries. One alternative is to fix those parameters to several values that seem plausible and compare the resulting solutions. Another is to estimate them by use of auxiliary information such as indices of abundance or tag-recapture data. We accomplish the latter by use of maximum likelihood techniques outlined in Appendix 2.
3. APPLICATION TO WESTERN ATLANTIC BLUEFIN TUNA

We endeavored to emulate the 1998 SCRS assessments of East and West Atlantic bluefin tuna as closely as possible. Apart from accounting for mixing and tag recoveries, the same data and procedures were employed. A brief account is given below, but the reader is referred to SCRS (1997, 1999) for more thorough discussions of the data and modeling rationale.

Catch at age data were available from 1970 to 1997 along with 17 indices of abundance. The indices were assumed to represent the abundance of all bluefin tuna within the specified age range in a given fishing zone. The annual values of each index were assumed to be lognormally distributed with coefficients of variation as prescribed by the SCRS. Bluefin older than age 9 were lumped together as a 'plus-group'. The natural mortality rate was fixed at 0.49, 0.24, 0.24, 0.24, 0.2, 0.175, 0.14, 0.125, and 0.1 yr\(^{-1}\) for ages 1 to 10+, respectively.

The fishing mortality rates in the West during the last year, \(F_{w,a,Y}\), were estimated by four parameters—one for ages 2 and 3, one for ages 4 and 5, one for ages 6 and 7, and one for ages 8 and 9. The fishing mortality rate on age 1 in the last year was set to a fraction 0.318 of the rate on ages 2 and 3 (\(F_{1,Y}=0.318 F_{2,3,Y}\)). The ratios \(\phi_{w,Y} = F_{w,10,Y}/F_{w,9,Y}\) (see Appendix 1) for the years prior to 1974 were fixed to 1.0, whereas the ratios for subsequent years were estimated by two parameters representing the years 1974-1981 and 1982-1997. A penalty term, \(0.5(\log_{10}\phi/1.14)/0.25)^2\), was added to the overall likelihood expression to constrain the F-ratio representing 1982-1997 (\(\phi\)) to a value near 1.14 as done by the SCRS.

The fishing mortality rates in the East during the last year, \(F_{e,a,Y}\), were estimated by three parameters—one for ages 2 and 3, one for ages 4 to 7, and one for ages 8 and 9. The fishing mortality rate on age 1 in the last year was set to a fraction 0.6 of the rate on ages 2 and 3. The ratios \(\phi_{e,Y} = F_{e,10,Y}/F_{e,9,Y}\) were fixed to 1.0 for all years.

3.1 Set 1 analyses

The diffusion and overlap mixing models were first applied to the catch and abundance index data alone (hereafter referred to as Set 1). When the movement coefficients were fixed to zero the results were nearly identical to the corresponding SCRS assessments. Minor differences occurred because the solution was not penalized for departures from a Beverton-Holt stock recruitment relationship (as the SCRS did in its assessment of the West) and no post-facto adjustments were made. When these factors were accounted for, the results were exactly as reported by the SCRS.

As discussed earlier, trans-Atlantic movements (across fishing zones) were assumed to occur at the beginning of each calendar year. Previous analyses (Punt and Butterworth, 1995; Porch et al., 1995) have demonstrated that the movement coefficients are poorly estimated from abundance index data alone, therefore no attempt was made to estimate age-specific coefficients and ages 2 through 10 were represented by a single parameter for each zone. The movement coefficients for age 1 were set to 0 as trans-Atlantic movements of this age group appear to be exceedingly rare.

3.2 Set 2 analyses

The Set 1 analyses were repeated using the tagging data in addition to the catch at age and the suite of abundance indices. The tagging data were obtained for all nations reporting tagging results to ICCAT. The U.S. tagging was conducted by scientists and by volunteer anglers while the tagging data reported by other nations was exclusively or nearly exclusively conducted by scientists. The U.S. data were examined to determine whether tagger type (scientist and volunteers) influenced recapture rate; therefore data for all nations except the U.S. was extracted from the ICCAT data base and for the U.S. from the
Cooperative Tagging Center (CTC) database because the ICCAT database did not have information on tagger identity or tagger type. The latter database includes information on bluefin tuna from multiple tagging programs but primarily the NMFS SEFSC and the Billfish Foundation. The influence of tagger type on recapture rate was examined for (1) scientists, (2) anglers (or groups of anglers such as family units) which had released at least 50 fish in their life times and (3) anglers (or groups of anglers) which had released less than 50 fish. A general linear model using a binomial error assumption revealed significantly (p < 0.05) higher recapture rates for scientists particularly in the early 1970's. Therefore VPA's which included the tagging data were conducted using either the entire data set or only tags released by scientists which substantially reduced the years and ages covered by the U.S. data.

The structure of the overlap and diffusion models in Set 2 was identical to that of Set 1 in order to isolate on the effect of the tagging data. However, the use of tagging data requires the specification of several additional parameters: the immediate loss of tags (owing to tag-induced mortality or misapplication of the tag), chronic loss of tags (e.g., tag shedding) and non-reporting rate. The immediate tag loss rate was fixed at 20% (Mather et al., 1974) and the chronic tag loss/shedding rate was set to 0.26 yr⁻¹ (consistent with the results of double tagging analyses by Baglin et al., 1980 and NRC, 1994). The reporting rate in each fishing zone was assumed to be relatively constant through time and estimated (but see Set 3 below).

An issue of some concern is the degree to which the tagged population has intermixed with the untagged population in the fishing zone where they were released. Inasmuch as most of the fish were tagged on the fishing grounds, incomplete mixing could result in spuriously high recapture rates during the first few weeks after release and bias the estimates of fishing mortality. The distribution of recaptures with time at large (Figure 1) gives little indication of excessive recapture rates during the first year, but the distribution of recovered tags among different fisheries is in some years statistically different from the distribution of the total catch (Powers et al., 1983; Turner, 1986). Therefore, adjustment factors were included to allow the effective fishing mortality rate on each tag cohort to differ from that of the untagged population during the first calendar year after release (see Appendix 2). Too few fish were tagged to allow unique adjustment factors to be estimated for every cohort, therefore a single parameter was used to represent all of the tags released in each fishing zone (but see Set 3 below).

3.3 Set 3 analyses

These analyses use the same data as Set 2, but incorporate more parameters to allow for possible ontogenic movement patterns and temporal changes in the tagging program. With respect to the former, Mather et al., (1995) used tagging data and other evidence collected prior to the late 1970's to show that the migratory patterns of small, medium and large bluefin tuna are different. Data collected since then has largely confirmed this observation within fishing zones (ICCAT, 1995, p. 108-110, Porch et al., 1998), but little light has been shed on the ontogenic nature of trans-Atlantic movements. In the Set 3 analyses, it is supposed that bluefin tuna in the West Atlantic do not cross over to the East during their first two years of life. After that they are permitted to cross at different rates according to whether they are young juveniles (age 2-3), intermediate juveniles (age 4-7) or spawning adults (age 8+). The complement of this hypothesis was examined for fish in the East Atlantic except that only two mixing coefficients were estimated, one representing ages 2-3 and the other representing ages 4 and older. This was done because bluefin tuna older than age 2 were rarely tagged in the East and recoveries of age 8+ fish were extremely rare.

Additionally, there have been important changes in the tagging program over time. Between 1970 and 1980, some age 8+ fish were tagged by fishers working with the Cooperative Tagging Center (CTC) of the National Marine Fisheries Service, but most of the tagging in the West was on young fish caught in purse seines under scientific supervision. The number of fish tagged was greatly reduced after 1980,
being limited mostly to volunteers fishing in the mid-Atlantic Bight. In 1990, however, the CTC entered into an agreement with the Billfish Foundation (Ortiz et al., 1999) and the number of bluefin tagged by volunteers greatly increased (mostly small and medium fish off the mid-Atlantic Bight). Beginning in 1995, a large number of larger fish were also tagged in the vicinity of Cape Hatteras, North Carolina. We hypothesize that there may have been a change in the western reporting rate coincident with the increased volunteer tagging effort in the 1990's and therefore have estimated separate reporting rate parameters for the periods before and after 1990. We also allow this flexibility for the East, although in that case the tagging data come almost entirely from scientific expeditions and the difference between the two time periods lies mainly in a shift in tagging effort from the Bay of Biscay to the Mediterranean Sea.

The Set 3 analyses also allow for greater flexibility with regards to the first-year post-release adjustment factors (γ) to accommodate possible variations in the initial distribution of the tagged population with respect to the untagged population. Unique factors were estimated for cohorts similar in age, year and method or place of release-- the number of cohorts under the mantle of any one parameter depending in part on the combined number of fish released. In the East, where all the fish released were small, we estimated separate parameters for release dates prior to 1981, 1981-83, 1984-85, 1986-87, 1988-89, and 1990-97. The parameters for the West and the reasoning behind their selection are summarized in Table 1.

Finally, an attempt was made to estimate the natural mortality rate on each age. In theory this becomes possible when tagging and catch information are modeled simultaneously because the catch information primarily reflects fishing mortality whereas the tagging data reflect natural and fishing mortality together.

3.4 Set 4 analyses

The fourth set of analyses duplicates the third except that only the scientific tagging data were used. This was done because it was found that the recovery rates of scientific and nonscientific releases were different. Unfortunately, this eliminated most of the releases of medium and large fish and essentially all of the data for the West after 1980. For this reason the only first-year post-release adjustment parameters retained from Table 1 were S1-S5, M1 and L3.

4. RESULTS

Likelihood ratio tests and Akaike’s (1972) information criterion (AIC) were used to determine the most parsimonious of the various model formulations discussed above. The AIC is especially useful in this regard because it allows comparisons of fundamentally different models, whereas comparisons with likelihood ratio tests are made with the understanding that one model is a reduced version of the other. The parameter estimates and ‘parsimony’ criteria are summarized for Sets 1-3 in Table 2 and discussed below.

4.1 Set 1

This set of analyses attempted to estimate the two (age-independent) trans-Atlantic movement coefficients by use of the index data alone. The overlap model fit the indices of abundance (logL = -37.9) better than the diffusion model (-38.7), which in turn fit slightly better than the model without mixing (-38.8). However, using likelihood ratio criteria, a model with two added parameters fits significantly better (at the 10 percent level) than a given null hypothesis when the difference in their corresponding logL values exceeds 2.30. Thus, neither model was statistically better than the model without mixing and one would therefore conclude that the no-mixing model provided the most parsimonious explanation of
the data by virtue of having fewer parameters. The AIC statistic also argues in favor of the no-mixing model as the most parsimonious.

The likelihood ratio test criteria discussed in the preceding paragraph can be used to construct approximate 90% confidence regions for the mixing coefficient estimates by noting that they are statistically indistinguishable from any other pair of movement coefficients with log$L$ values greater than -40.2 for the overlap model or -41 for the diffusion model. A contour plot of the log$L$ values associated with a wide range of movement pairs reveals that this 90% confidence region is rather broad for both model types and therefore that the movement coefficients are probably poorly estimated (Figure 2).

The estimates of the fishing mortality rate parameters for the East were similar for the three models. The estimates for the West, especially the F-ratios ($\phi$), were somewhat different (see Table 2).

4.2 Set 2

These analyses employed the same model configurations as Set 1 except that the tagging data were used in addition to the catch-at-age and indices of abundance. The estimates of the movement coefficients were substantially higher than was the case for Set 1, and significantly different from zero (Figure 3). The overlap model again provided the best fit to the indices of abundance, but the diffusion model provided the best fit to the tagging data. Inasmuch as the tagging data are somewhat more voluminous than the indices of abundance, the AIC statistic identified the diffusion model as the most parsimonious overall explanation of the data. However, when the weight given to the tagging data was reduced by a factor of 10, that conclusion was reversed.

The use of the tagging data had little effect on the mortality rate estimates for the East, but substantially reduced the estimated F-ratios ($\phi$) and fishing mortality rates on ages 6 and older in the West (Table 2).

4.3 Set 3

The models in this set of analyses were the same as in Set 3 except that 21 parameters were added for more flexibility. Both the likelihood ratio test and AIC statistic indicate that the addition of these parameters provides a much more parsimonious explanation of the data. The fishing mortality estimates from Sets 2 and 3 are similar except that the fishing mortality rates on age 6 in the West are notably higher with Set 3 (see Table 2). The reporting rates were estimated to be about 20 percent in the East and 60 percent in the West with some indication of a slight decline in the 1990's. The first-year post-release adjustments ($\gamma$) were highly variable and often less than 1.0.

An attempt was also made to estimate the natural mortality rate. Preliminary runs showed the age-specific values to be somewhat erratic, therefore the parameters were linked as a random walk with a CV of 0.1 (see Porch, 1998). This allows the estimates to vary from one age to the next by about 10%. The results were very similar for all three models— the estimates of $M$ increasing monotonically from a low of 0.06 at age 1 to a high of about 0.15 at age 10. The likelihood ratio test and AIC statistic both indicate that estimating $M$ significantly improves the fit of each model.

4.4 Set 4

These analyses duplicated Set 3 except that only tags released during scientific expeditions were used. For the most part the estimates were nearly identical to those from the corresponding models in Set 3. The only substantial difference was in the estimates for the fishing mortality rate on age 8 in the west, which were much higher when using only the scientific tagging data and more like the values obtained
without the tagging data in Set 1 (see Table 2). Presumably this is because most of the large fish have been tagged by non-scientists, therefore the scientific tagging data has relatively less influence on the estimates for large fish in the VPA.

5. DISCUSSION

The model fits to the indices of abundance hint of low westward (east to west) transfer coefficients and somewhat higher eastward coefficients (Figure 2). However, the case of no transfer lies within the 90% confidence region and is, by Akaike’s information criterion, the most parsimonious explanation of the index data. This is consistent with other investigations that used somewhat different abundance indices and model formulations (Butterworth and Punt, 1994, Punt and Butterworth, 1995; and Porch et al. 1995, Porch and Turner, 1998). The situation is a bit more interesting when the tagging data are used inasmuch as the 90% confidence regions for the transfer coefficients are smaller and no longer include zero (Figure 3). The diffusion model suggests westward transfers of about 1% and somewhat higher eastward transfers of between 2 and 3%. The overlap model, on the other hand, suggests the opposite—westward coefficients on the order of 2% and eastward coefficients of about 1%.

The earliest attempts to estimate the level of trans-Atlantic mixing for bluefin tuna from tagging data centered on various manipulations of the diffusion model. The NRC (1994) applied an ad hoc approach to the tagging data to produce diffusion rates on the order of 2% east to west and 1% east to west. Turner and Powers (1995), however, pointed out that the NRC’s methodology is inconsistent—some computations allow the estimates of fishing mortality and transfer coefficients to be linked while others do not. They avoided this inconsistency by use of an alternative approach to solving the same equations and obtained estimates of 3-5% west to east and 1% east to west.

Punt and Butterworth (1995) incorporated tagging data into the diffusion VPA itself by adding likelihood components composed of various constructs of the total number of tag recaptures in each fishing zone. They found that the indices favored low westward transfers of 1% or less and higher eastward transfers on the order of 6%, but that the tagging data favored just the opposite. Subsequently however, Porch (1995) and Porch and Turner (1998) found that recapture statistics aggregated across years were not especially useful for estimating mixing rates because of large inter-annual changes in tag releases and fishing mortality. Summing over years simply masked the signal.

Cooke and Lankester (1996) estimated transfer coefficients of 7.3% westward and 9.8% eastward by use of a form of survival analysis. Their results indicated that these values did not change much with time, which they interpreted as implying that the overlap model was as or more consistent with data than with the diffusion model. Similarly, Porch and Turner (1998) integrated the overlap model into a VPA and found that it provided a better fit to the tagging data than diffusion VPA, but cited the aforementioned problems with using aggregated tagging statistics as an important weakness in the analysis. The present study overcomes that problem and indicates that the overlap model provides the best fit to the index data whereas the diffusion model provides the best fit to the tagging data. The model providing the best overall fit therefore depends on the relative weight given to the index and tagging data.

The effect of using the tagging data and the choice of models on the perceived status of the resource is examined in Figure 5. The absolute values of the estimated abundances of the West Atlantic bluefin stock were greater with the tagging data than without it, particularly for age 8 and older where the difference was several fold (although the relative trends were similar). The choice of models was much less important. Generally the overlap model predicted slightly lower 8+ abundances than the no-mixing model and the diffusion model slightly higher, but the diffusion model was also more likely to predict severe recruitment failures in the West. (It should be remembered that the abundance estimates for the diffusion model in Figure 5 represent the abundance of fish in the western zone, which, if one assumes
that spawning behavior is dictated by location as well, is equivalent to the abundance of the western stock.)

Porch (1995) and Porch and Turner (1998) demonstrated that the ad hoc VPA methods previously employed by the SCRS were insufficient to distinguish between transfer hypotheses with widely different implications. This does not appear true of the present method, which uses a more powerful statistical technique that does not smear the signal across years and can estimate quantities reflecting reporting rate and incomplete mixing. Figure 6 shows that, for a given model, the estimates of the abundance of the West Atlantic stock are similar for combinations of mixing rates lying within the 90% confidence region (shown in Figure 3). Thus, while it may be that the assessment results for the West Atlantic population are sensitive to the transfer rate in general, they are quite insensitive over the range of values that are statistically indistinguishable from the maximum likelihood estimates. This was even more true of the East Atlantic population which, owing to its greater overall abundance, is little affected by immigration from the West.

The estimates of the natural mortality rate from all three models (no-mixing, overlap, diffusion) indicated an increase with age from about 0.06 yr\(^{-1}\) on age 1 to about 0.15 yr\(^{-1}\) on age 10. In contrast, the values used as an alternative base case by the SCRS (the estimates for southern bluefin tuna) are much larger and have a decreasing trend with age. Both the likelihood ratio and AIC criteria suggest that these estimates significantly improved the fits of all three models. The specific values of the estimates may be questionable owing to insufficiencies of the tagging data (see below), however they do lend support for the use of \( M = 0.14 \text{ yr}^{-1}\) over the southern bluefin tuna estimates.

Given the sensitivity of the model predictions to the use of tagging data, a question of considerable importance is the reliability of the tagging data for tuning the VPA. There are indications that the first-year adjustment factors (level of intermixing with the untagged population) may vary by an order of magnitude over time even with scientific tagging in the same areas at about the same time of year (see Table 2). Similarly, the average reporting rate of recovered tags is estimated to be low (about 20% in the East and 60% in the West) and declining through time. It is likely that these estimated changes in the adjustment factors and reporting rates reflect the combined effects of smaller-scale variations in each fleet. Ideally it would be desirable to partition the returned tags according to the fleet that returned them (using the partial catches to help determine the fishing mortality rates pertaining to those fleets) and estimate fleet-specific reporting and cohort-specific mixing coefficients. It might also allow the fraction of tagged bluefin that die or shed their tags shortly after release to be estimated, which of course is likely to vary with the tagging procedure and age of the fish being tagged. Such an approach, however, may require several times as many tag releases than we have now. It would also be helpful to initiate further double tagging experiments to examine possible changes in tag shedding over time and with age.

The overlap and diffusion models discussed in this paper represent opposite extremes in terms of homing behavior, however both are rather simple abstractions of the undoubtedly more complex movement patterns. Mather et al. (1995)suggested that trans-Atlantic migrations of bluefin tuna may be episodic, perhaps in response to some unusual stimuli. There is also some indication that the probability that a fish will travel across the Atlantic depends on where it was originally released. For example, the proportion of large fish recovered in the East was much greater for fish tagged off the Bahamas than for fish tagged off New England (Mather et al., 1995). At present the data are still insufficient to elucidate this hypothesis, let alone attempt to estimate the parameters for a more complicated movement pattern.

The picture that has emerged from limited recoveries of archival and pop-off satellite tags suggest that a substantial proportion (9-30%) of large bluefin tuna tagged in the NW Atlantic move east of 45° longitude (the delineation between the eastern and western management units) during the late winter and return west in the late summer and fall (Lutcavage et al., 1999; Block et al., 2000). This would seem to
favor the overlap model as the best characterization of gross bluefin tuna movements. As yet, however, the data are limited to rather few large fish that were tagged mostly in two locations in the Northwest Atlantic. Therefore it is premature to reject the diffusion model as a viable candidate.

The archival and pop-off tagging data pose an additional problem in that most of the fish that crossed the 45° line did not go far enough to encounter the intense fishing pressure exerted in the vicinity of the Mediterranean Sea. It might be very useful, therefore, to extend the overlap and diffusion models to three zones (e.g., West, East and Mediterranean). It is possible to do this within the context of a VPA, but the stability of the backwards recursion may be questionable and should be examined carefully. A forward recursion may perform better. If the number of tags were increased sufficiently, it might also be possible to apply a more detailed advection-diffusion type model (see Sibert and Fournier, 1994).

The possibility that the movement patterns of Atlantic bluefin tuna may be complex is cause for concern in regards to the ability of simpler models to capture enough of the essential dynamics to produce useful estimates. Porch et al. (1998) examined the original SCRS diffusion VPA in this context by applying it to artificial data generated by an advection-diffusion model that was parameterized to simulate several perceptions of the possible movement patterns of bluefin tuna. They found that the diffusion and no-mixing VPA’s gave similar predictions under a wide variety of circumstances, but that the diffusion VPA sometimes predicted erroneous recruitment failures and was more likely to give misleading results because of unresolved problems in the tagging data. They concluded that, unless the diffusion model is correct, it is unlikely to improve the performance of a management procedure in terms of resource conservation. On the other hand, Punt and Restrepo (1995) found that, when the diffusion model is in fact correctly specified, the performance of the management procedure may or may not be improved, depending on factors such as the initial state of the system and ability of management to enforce regulations. It is unclear how the conclusions from these two studies might be affected by use of the overlap model or the method of incorporating the tagging data espoused in this paper.

Another concern is whether the structure of the model adequately reflects the goals of management. Powers and Cramer (1996), for example, demonstrate that the reproductive behavior of the stock is crucial if there is concern to maintain a viable western spawning population. The diffusion VPA, as it is currently formulated, produces estimates for the total abundance of spawners and recruits in each fishing zone (regardless of their origin), therefore any spawner-recruit relationship derived from that output essentially implies that each fish spawns wherever it happens to be located during the spawning season rather than exhibit fidelity to a particular spawning location. In principle the diffusion VPA may be restructured to compute the abundance by origin as well so that the possibility of spawning site fidelity may be accommodated. However, this is only possible only for the cohorts with recruitment estimates, which reduces the number of points for constructing the spawner recruit relationship by one less than the number of age classes. More importantly, it seems inconsistent to assume that a fish which moves into the opposite zone will adopt the movement habits of the fish born there but won’t spawn with them. The overlap model implicitly keeps track of the abundance both by area and by stock, so it is easy to accommodate spawning site fidelity without loss of data points. In this case the notion of spawning site fidelity is quite compatible with the underlying mixing model which assumes some form of homing. On the other hand, it does not seem completely implausible that a population capable of homing may still spawn with a similar population outside of its home spawning ground, which would be modeled as before by computing spawning biomass according to fishing zone irrespective of origin. One could also assume that all of the spawning-age fish located in the home area spawn there and that some fraction of those abroad return to the spawning grounds each year, but essentially this would have no effect on the spawner-recruit relationship since this ‘fraction’ would only be a constant that scales the spawning biomass (unless of course the fraction that does not return spawns abroad).

It has also been suggested that, if there is little fidelity to breeding locations, it may be profitable to consider a single-stock VPA of the combined eastern and western catches. While this approach may be
useful as a reference of total population size, it is risky as a basis for setting management policies as severe overfishing of the less abundant stock may go undetected (Brown and Parrack, 1985). Moreover, Fahrig (1993) has shown that managing two stocks separately is generally more effective than managing them as a single combined stock unless the level of intermixing is large.

We recommend the SCRS continue to provide advice to the commission that includes separate assessments of the eastern and western bluefin tuna stocks assuming negligible intermixing in addition to assessments that incorporate the latest thinking on mixing models. Nevertheless, it should not be assumed that any accounting of mixing is necessarily better than none and considerable effort should be devoted to understanding the true dynamics of bluefin tuna movement.

REFERENCES


APPENDIX 1: THE OVERLAP VPA RECURRENCE

Equation 1 can be substituted into the formula for catch (equation 4) to yield:

\[
C_{\text{way}} = F_{\text{way}} \left(1 - e^{-Z_{\text{way}}}\right) \left(\frac{T_{\text{wwya}} N_{w, y+1, a+1}}{T_{\text{weya}} e^{-Z_{\text{way}}} + T_{\text{wwya}} e^{-Z_{\text{way}}}} + \frac{T_{\text{ewya}} N_{e, y+1, a+1}}{T_{\text{ewya}} e^{-Z_{\text{way}}} + T_{\text{ewya}} e^{-Z_{\text{way}}}}\right)
\]

\[
C_{\text{eay}} = F_{\text{eay}} \left(1 - e^{-Z_{\text{eay}}}\right) \left(\frac{T_{\text{eeya}} N_{e, y+1, a+1}}{T_{\text{weya}} e^{-Z_{\text{eay}}} + T_{\text{wwya}} e^{-Z_{\text{way}}}} + \frac{T_{\text{ewya}} N_{w, y+1, a+1}}{T_{\text{ewya}} e^{-Z_{\text{eay}}} + T_{\text{wwya}} e^{-Z_{\text{way}}}}\right)
\]

These two equations can be solved for \(F_{w,a,y}\) and \(F_{e,a,y}\) given \(N_{w,a+1,y+1}\) and \(N_{e,a+1,y+1}\) (and \(T\) and \(M\)) using Newton’s method or some other numerical technique. \(N_{w,y,a}\) and \(N_{e,y,a}\) can then be computed from the estimates of \(F_{w,y,a}\) and \(F_{e,y,a}\) by use of equation (1), thus constituting the backward recursion required by the VPA.

In case of a plus-group, the four catch equations corresponding to ages \(A\) and \(A-1\) in the east and west can be solved for \(N_{w,A-1,y}, N_{e,A-1,y}, N_{w,A,y}, N_{e,A,y}\) in terms of \(C, F, M\) and \(T\) by linear decomposition. These results in turn are substituted into equation (2), yielding 2 equations in four unknowns \((F_{w,A-1,y}, F_{e,A-1,y}, F_{w,A,y}, F_{e,A,y})\). We adopt the common convention of expressing the fishing mortality rate on the plus group as a fraction \(\phi\) of the fishing mortality rate on the next younger group,

\[
F_{k,y,A} = \phi_{k,y} F_{k,y,A-1} \quad \text{for} \quad k=1,2
\]

This reduces the number of unknowns to 2 and allows the system to be solved for \(F_{w,y,A-1}\) and \(F_{e,y,A-1}\) using Newton’s method for 2 equations or some other iterative technique (the \(\phi\) values either being imposed or estimated).
APPENDIX 2: PARAMETER ESTIMATION

The unknown parameters are the movement coefficients $T$, the ratios of the fishing mortality rate on the last two ages, $\phi_y$ and $\phi_w$, and the fishing mortality rates on each age in the last year, $F_{aY}$. The maximum likelihood method for estimating these parameters by use of abundance indices and tag-recapture data are outlined below.

Indices of abundance

The SCRS (1999) treated some of these parameters as constants and estimated the others by maximum likelihood using several indices of abundance. Assuming the indices of abundance are lognormally distributed, this involves finding the parameter values that minimize the negative log-likelihood expression

$$\text{(A.1) } -\log L(\mathbf{I}|\Theta) = \sum_k \sum_i \sum_y \frac{(\log \hat{I}_{kiy} - \log \hat{\mathbf{I}}_{kiy})^2}{V_{kiy}},$$

$$\hat{I}_{kiy} = q_{kiy} \sum_a s_{kiay} w_{kiay} \hat{N}_{kay},$$

where
- $I_{kiy}$ the observed value of index type $i$ in year $y$ and fishing region $k$,
- $V_{kiy}$ the variance of $\log \mathbf{I}$,
- $\hat{I}_{kiy}$ the predicted value of the index from the VPA,
- $q_{kiy}$ scale of index relative to the absolute abundance of the resource,
- $s$ the relative availability of different age groups to the index,
- $w$ an adjustment factor to account for time of year and whether the units were measured in terms of numbers or biomass.

Notice that there are now several additional variables that need to be accounted for-- $V$, $q$, and $s$. The SCRS fixed the index variances to the values reported with the various standardized index observations. The proportionality coefficients $q$ were assumed to be constant through the years and estimated along with the $\phi$’s and $F_{aY}$’s. The relative availability coefficients $s$ were set to fixed values in a few cases, but otherwise assumed to be constant from year to year and determined from the observed catches by use of the formula

$$\text{(A.2) } \hat{s}_{kiay} = \frac{\sum_y C_{kiay} \hat{F}_{kay}/C_{kay}}{\text{MAX}_a \left\{ \sum_y C_{kiay} \hat{F}_{kay}/C_{kay} \right\}},$$

which is discussed in Butterworth and Geromont (1999). Here $C_{kiay}$ is the observed catch attributed to index $i$ and $\hat{F}_{kay}$ is the fishing mortality rate estimated from the backwards recursion.
Tag-recapture data

The overlap equations for tagged populations are

\[
\begin{align*}
\text{(A.3)} \quad n_{j\tau, y+1} &= \begin{cases} 
    r_{j\tau} e^{-t} e^{-(Z_{kay} + \lambda_{\tau})(1-t_{\tau})} & (y = \psi) \\
    n_j \sum_{k=1}^{2} T_{jkay} e^{-(Z_{kay} + \lambda_{\tau})} & (y > \psi)
\end{cases}
\end{align*}
\]

\[
\text{(A.4)} \quad \tilde{n}_{k\tau y} = \begin{cases} 
    0 & (y = \psi, \ k \neq \kappa) \\
    (1-d_{\tau}) r_{\tau} & (y = \psi, \ k = \kappa) \\
    \sum_{j=1}^{2} T_{jkay} n_{j\tau y} & (y > \psi)
\end{cases}
\]

\[
\text{(A.5)} \quad c_{k\tau y} = \begin{cases} 
    \rho_{kay} \tilde{n}_{k\tau y} F_{kay} \left(1 - e^{-(Z_{kay} + \lambda_{\tau})(1-t_{\tau})}\right) / (Z_{kay} + \lambda_{\tau}) & (y = \psi) \\
    \rho_{kay} \tilde{n}_{k\tau y} F_{kay} \left(1 - e^{-(Z_{kay} + \lambda_{\tau})}\right) / (Z_{kay} + \lambda_{\tau}) & (y > \psi)
\end{cases}
\]

where

- \(\tau\) denotes a unique group (cohort) of tagged fish distinguished by the age (\(\alpha\)), year (\(\psi\)) and fishing zone (\(\kappa\)) of release.
- \(a\) denotes the current age of fish (\(a = \alpha + y - \psi\)).
- \(r_{\tau}\) number of fish released from tag cohort \(\tau\) (and stock \(j\) when subscript \(j\) is added).
- \(n_{j\tau y}\) number of survivors from tag cohort \(\tau\) and stock \(j\) at beginning of the year.
- \(\tilde{n}_{k\tau y}\) number of survivors from tag cohort \(\tau\) in zone \(k\) at beginning of the year.
- \(c_{k\tau y}\) catch from tag cohort \(\tau\) in zone \(k\).
- \(d_{\tau}\) fraction of cohort \(\tau\) that died shortly after the tagging procedure.
- \(\lambda_{\tau}\) rate of tag loss owing to shedding and chronic mortality.
- \(\rho_{kay}\) fraction of tags reported in fishing zone \(k\).

The equations for the diffusion model are similar.

\[
\text{(A.6)} \quad \tilde{n}_{k\tau, y+1} = \begin{cases} 
    r_{k\tau} e^{-t} e^{-(Z_{kay} + \lambda_{\tau})(1-t_{\tau})} & (y = \psi) \\
    e^{-t} e^{-(Z_{kay} + \lambda_{\tau})} \sum_{j=1}^{2} T_{jkay} \tilde{n}_{j\tau y} & (y > \psi)
\end{cases}
\]

Allowance is made for the possibility that the effective fishing mortality on the tagged population may not be the same initially as that on the untagged population by use of an inflation factor \(\gamma_{\tau}\) that is applied only during the calendar year of the release (\(\psi\)).

\[
\text{(A.7)} \quad \mathcal{F}_{kay} = \gamma F_{kay}.
\]

This could happen if the catchability of the tagged population was temporarily reduced (e.g., they are less likely to take a hook) or if the tagged population does not rapidly intermix with the untagged.
population and the fishing pressure where the tagging occurred is different from the average over the distribution of the population.

It is not currently possible to distinguish members of the eastern and western stocks during the tagging process. In the case of the diffusion model this is unimportant because the two stocks are defined by fishing zone (rather than by origin)-- therefore fish born in the East and tagged in the West were considered to be members of the West stock (and vice versa). In the case of the overlap model, where the two stocks are defined by origin, eastern and western fish were assumed to be tagged in proportion to their relative abundance in each fishing zone, i.e.,

\[
\gamma_{j \tau} = \frac{T_{j \tau} \hat{N}_{j \tau}}{2 \sum_{j=1}^{2} T_{j \tau} \hat{N}_{j \tau}}
\]

where the \( \hat{N}_{j \tau} \) are estimates from the VPA. This assumption would be violated if, for example, the tagging events were concentrated in locations where fish are more or less prone to trans-Atlantic movements than the population as a whole.

The number of recoveries expected from each cohort \( \tau \) in each fishing zone and year can be modeled as multinomial distributions (Schwarz et al., 1993; Anganuzzi et al., 1994):

\[
L(c_{\tau} | \Theta) = \frac{r_{\tau}!}{(r_{\tau} - c_{\tau})!} \prod_{k, y} p_{k \tau y}^{c_{k \tau y}} q_{\tau}^{r_{\tau} - c_{\tau}}
\]

\[
c_{\tau} = \sum_{k, y} c_{k \tau y}
\]

\[
q_{\tau} = 1 - \sum_{k, y} p_{k \tau y}
\]

\[
p_{k \tau y} = \hat{c}_{k \tau y} / r_{\tau}
\]

where \( \hat{c}_{k \tau y} \) is the catch of tagged fish according to the model (equation A.5 in the case of the overlap model) and \( \Theta \) is a given set of values for the parameters (which now may include \( \lambda \), \( d \), and \( \rho \)). The corresponding negative log-likelihood expression representing all of the cohorts, with the constant terms omitted, is

\[
-\log L(c_{\tau} | \Theta) = -\chi \sum_{\tau} \left( r_{\tau} \log q_{\tau} - \sum_{k, y} c_{k \tau y} \log p_{k \tau y} \right)
\]

where the variable \( \chi \) is added to allow the investigator to modify the emphasis given to the tagging data relative to the indices of abundance represented by equation (A.1). The parameters are thus estimated by minimizing the sum of equations (A.10) and (A.1).
Table 1. Summary of nonmixing adjustment factors used to represent the various age groups released in the West each year and the reasoning behind them. The letters under each size group heading indicate the size group most represented (released). The parameter S1, for example, is used to represent medium fish prior to 1978 because very few medium fish were tagged during that period.

<table>
<thead>
<tr>
<th>Year</th>
<th>comment</th>
<th>size (age) group</th>
</tr>
</thead>
<tbody>
<tr>
<td>70-75</td>
<td>mostly sparse scientific tagging of small fish (but heavy in 1974) off mid-Atlantic Bight (MAB) and moderate tagging of large fish in various places</td>
<td>S1</td>
</tr>
<tr>
<td>76</td>
<td>heavy scientific tagging of small fish off MAB and moderate tagging of large fish in various places</td>
<td>S2</td>
</tr>
<tr>
<td>77</td>
<td>heavy scientific tagging of small fish off MAB and increased tagging of large fish in various places</td>
<td>S3</td>
</tr>
<tr>
<td>78</td>
<td>heavy scientific tagging of small fish off MAB, some scientific tagging of medium fish and increased tagging of large fish in various places, some scientific tagging of medium fish</td>
<td>S4</td>
</tr>
<tr>
<td>79</td>
<td>sparse scientific tagging of small fish off MAB, some scientific tagging of medium fish and heavy scientific tagging of large fish</td>
<td>S4</td>
</tr>
<tr>
<td>80</td>
<td>heavy scientific tagging of small fish off MAB, other age groups sparse</td>
<td>S5</td>
</tr>
<tr>
<td>81-89</td>
<td>sparse to moderate tagging of small and mediums by fishers in MAB</td>
<td>S6</td>
</tr>
<tr>
<td>90-94</td>
<td>increased tagging of all sizes by fishers in MAB</td>
<td>S7</td>
</tr>
<tr>
<td>95-97</td>
<td>heavy tagging of large sizes off Cape Hatteras</td>
<td>S7</td>
</tr>
</tbody>
</table>
Table 2. Selection criteria and parameter estimates for each model. Values in bold indicate constants, blanks indicate the parameter was not used and asterisks indicate the parameter was set equal to the estimate listed above it. AIC stands for Akaike’s information criterion and \( \text{L}_{\text{ind}} \) is the likelihood term for the abundance indices. The mixing coefficients \((T)\) are percentages.

<table>
<thead>
<tr>
<th>SET 1 (no tagging data)</th>
<th>SET 2 (with tagging data)</th>
<th>SET 3 (full model)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-log ( \text{L} )</td>
<td>no mix overlap diffusion</td>
<td>no mix overlap diffusion no mix overlap diffusion</td>
</tr>
<tr>
<td>38.8</td>
<td>37.9</td>
<td>38.7</td>
</tr>
<tr>
<td>-log ( \text{L}_{\text{ind}} )</td>
<td>38.5</td>
<td>36.3</td>
</tr>
<tr>
<td>AIC</td>
<td>312</td>
<td>315</td>
</tr>
<tr>
<td>( \text{F}_{e2Y} )</td>
<td>0.7</td>
<td>0.69</td>
</tr>
<tr>
<td>( \text{F}_{e4Y} )</td>
<td>0.23</td>
<td>0.22</td>
</tr>
<tr>
<td>( \text{F}_{e8Y} )</td>
<td>0.67</td>
<td>0.69</td>
</tr>
<tr>
<td>( T_{ew,2-3} )</td>
<td>0</td>
<td>2.1</td>
</tr>
<tr>
<td>( T_{ew,4-10} )</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td>( \rho_{e,70-89} )</td>
<td>0.2</td>
<td>0.19</td>
</tr>
<tr>
<td>( \rho_{e,90-97} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{e,70-80} )</td>
<td>1.1</td>
<td>1.1</td>
</tr>
<tr>
<td>( \gamma_{e,81-83} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{e,84-85} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{e,86-87} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{e,88-89} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{e,90-97} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \text{F}_{w2Y} )</td>
<td>0.023</td>
<td>0.023</td>
</tr>
<tr>
<td>( \text{F}_{w4Y} )</td>
<td>0.027</td>
<td>0.028</td>
</tr>
<tr>
<td>( \text{F}_{w6Y} )</td>
<td>0.12</td>
<td>0.17</td>
</tr>
<tr>
<td>( \text{F}_{w8Y} )</td>
<td>0.48</td>
<td>0.55</td>
</tr>
<tr>
<td>( \phi_{w,74-81} )</td>
<td>2.2</td>
<td>1.5</td>
</tr>
<tr>
<td>( \phi_{w,82-97} )</td>
<td>0.94</td>
<td>0.73</td>
</tr>
<tr>
<td>( T_{we,2-3} )</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>( T_{we,4-7} )</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td>( T_{we,8-10} )</td>
<td>0</td>
<td>*</td>
</tr>
<tr>
<td>( \rho_{w,70-89} )</td>
<td>0.61</td>
<td>0.66</td>
</tr>
<tr>
<td>( \rho_{w,90-97} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S1)} )</td>
<td>0.66</td>
<td>0.6</td>
</tr>
<tr>
<td>( \gamma_{w(S2)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S3)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S4)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S5)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S6)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(S7)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(M1)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(L1)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(L2)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(L3)} )</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>( \gamma_{w(L4)} )</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>
Figure 1. Distribution of tag recoveries with time after release by fishing zone.
Figure 2. Likelihood contours for the movement coefficients $T_{we}$ (west to east) and $T_{ew}$ (east to west) of the overlap and diffusion models without the tag-recapture data (Set 1). The triangles and shaded areas represent the point estimates and their corresponding 90% confidence regions.
Figure 3. Likelihood contours for the movement coefficients $T_{we}$ (west to east) and $T_{ew}$ (east to west) of the overlap and diffusion models with the tag-recapture data (Set 2). The triangles represent the point estimates ($[T_{we}, T_{ew}] = [0.5, 1.8]$ for the overlap model and $[2.5, 1.1]$ for the diffusion model) The shaded regions are the corresponding 90% confidence regions.
**Figure 4.** Estimated abundance of East Atlantic bluefin tuna (age 8 and older). The lines, solid symbols, and hollow symbols represent the no-mixing, overlap, and diffusion models, respectively. The triangles, squares and circles represent sets 1, 2, and 3.
Figure 5. Estimated abundance of West Atlantic bluefin tuna stock (age 1 and age 8 and older). The lines, solid symbols, and hollow symbols represent the no-mixing, overlap, and diffusion models, respectively. The triangles, squares and circles represent sets 1, 2, and 3. The estimates for the diffusion model reflect the abundance in the western fishing zone and the estimates for the overlap model reflect the abundance of the stock (both zones combined). In the case of age 1 fish, which do not mix, these are conceptually identical. The estimates of 8+ abundance from the diffusion model, however, are equivalent to stock abundance only if one assumes that spawning, like movement, is dictated by location.
Figure 6. Abundance of the West Atlantic bluefin tuna stock (age 8 and older) estimated by the overlap and diffusion models with mixing rate coefficients equal to the values at the extremes of the 90% confidence region in Figure 3. The line represents the estimates without mixing. As for Figure 5, the abundances are strictly comparable only if one assumes for the diffusion model that spawning, like movement, is dictated by location.