

EXAMINATION OF ALTERNATIVE STOCK DISTRIBUTION MODELS FOR THE INTERPRETATION OF BLUEFIN TUNA (*THUNNUS THYNNUS*) TAG-RECOVERY DATA

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SUMMARY

Tag-recovery data for bluefin tuna in the north Atlantic are analyzed using two alternative conceptual models of fish distribution and movement. In the first model, the feeding areas of different stocks are assumed not to overlap, but individuals can transfer between stocks according to a diffusion process. In the second model, the feeding areas of different stocks can overlap, but there is no transfer of individuals between stocks.

RESUMÉ

Les données de récupération de marques de thon rouge dans l'Atlantique Nord sont analysées au moyen de deux modèles conceptuels de la distribution et du déplacement du poisson. Le premier modèle suppose que les zones trophiques des différents stocks ne se chevauchent pas, mais que des poissons peuvent se déplacer d'un stock à l'autre selon un processus de diffusion. Le deuxième modèle postule qu'il peut y avoir un chevauchement des zones trophiques des différents stocks, mais qu'il n'y a pas d'échange de poissons entre les stocks.

RESUMEN

Se analizan datos de recuperación de marcas en el Atlántico norte, empleando dos modelos conceptuales alternativos de distribución y movimiento de peces. En el primer modelo, se asume que las zonas tróficas de los diferentes stock no están solapadas, pero que los individuos pueden cambiar de un stock a otro de acuerdo con un proceso de difusión. En el segundo modelo, las zonas tróficas de los diferentes stocks pueden estar solapadas, pero no hay intercambio de individuos entre los stocks.

INTRODUCTION

The recent SCRS assessments of bluefin tuna included VPA's in which the migration between the eastern and western stocks was set to various specific values (ICCAT, 1995: p.58). The values had been estimated from tag-recapture data, analysed either in isolation (e.g. NRC, 1994), or within a VPA framework (Punt and Butterworth, 1995). As noted in subsequent SCRS discussions, the analyses had been based on a particular model of the migration process, and exploration of alternative models was recommended (ICCAT, 1995: p.108-10). Two alternative models, one of them corresponding to the model previously used, are described in this paper, and some exploratory analysis of the data with respect to the two models is conducted.

ALTERNATIVE MODELS

Diffusion model

The diffusion model corresponds to that assumed in the analyses by NRC (1994) and Punt and Butterworth (1994). There are two stocks, one associated with the ICCAT West Atlantic management area, and one associated with the ICCAT Eastern Atlantic & Mediterranean management area. When a fish transfers from one area to the other, it becomes a "member" of the other stock. Each fish in the eastern stock/area has a fixed annual probability of switching to the western stock/area, while each fish in the western stock/area has a fixed annual probability of switching to the eastern stock/area. The two transfer rates are allowed to take different values.

Under the model, all fish within an area at a given time are equivalent: their future behaviour is independent of their migration history.

If d_{ew} and d_{we} are the instantaneous diffusion rates from east to west and west to east respectively, then the probability $P_{ij}(t)$ that a fish currently in area i will be in area j after a time t , given that it is still alive, is given by $P(t) = \exp(tD)$, where P is the matrix of the P_{ij} and D is the matrix:

$$\begin{pmatrix} -d_{ew} & d_{ew} \\ d_{we} & -d_{we} \end{pmatrix}$$

Provided the diffusion rates are reasonably small the probability of a transfer from one area to the other increases steadily with the time elapsed.

Overlap model

Under the overlap model, there is no interchange between stocks, but the feeding ranges of different stocks overlap. Let a_{ki} be the probability that a given individual, l , belonging to stock k , will be in area i at a random time. We further suppose that the probabilities at two times at least one year apart are independent. The probability that a random fish currently in area i will be found in area j in a subsequent year is given by:

$$P_{ij} = \frac{\sum_k \sum_l a_{ki} a_{jl}}{\sum_k \sum_l a_{ki}}$$

A key difference between the overlap model and the diffusion model is that under the overlap model the transfer probability, P_{ij} , is not a function of the elapsed time, provided that at least one year has elapsed.

Punt and Butterworth (1995) give a formulation for incorporating the diffusion model into a VPA framework. A similar formulation is available for the overlap model. The parameters of relevance are Q_{ij} , the proportion of stock i found in area j in any one year. With two stocks and two areas, this leaves only two free parameters, because the proportions must sum to one. The parameters are estimated in a VPA framework by matching the observed and predicted proportions of recaptures in each area that come from the two areas. In the VPA, the abundance indices for each area are related to the predicted abundance in each area:

$$A_{jt} = \sum_i Q_{ij} s_{it}$$

where A_{jt} is the predicted abundance in area j in year t , and s_{it} is the abundance of the relevant ages classes of stock i in year t .

DATA

A version of the ICCAT tag-recapture data file for bluefin tuna was kindly supplied by NMFS. It contains records of tags and recaptures, mainly from US, Canadian and Spanish tagging programmes.

Only records containing the data and location of tagging, and, where applicable, recapture, were used. The locations were used to assign tags and recapture locations to the ICCAT western and eastern Atlantic management areas (W and E), excluding the Mediterranean.

A preliminary analysis of the data revealed that the size at tagging was the principal factor influencing the probability of recovery. Hence the data were stratified by size class at tagging.

The following size classes were chosen, based on a feeling that sample sizes were insufficient to support more than 4-5 strata, and with a view to achieving roughly equal numbers in each stratum:

- (1) 40-60 cm
- (2) 60.1-80 cm
- (3) 80.1-100 cm
- (4) > 100 cm

Tags placed in fish smaller than 40 cm or with no recorded size were discarded. Size at recapture was available only for a minority of recoveries, and was not used.

To provide for adequate mixing, it was considered desirable only to use recoveries of tags which had been at sea for at least 12 months, the presumed length of the migratory cycle. Since the model used was formulated in discrete time by calendar year, the only way to ensure that the 12-month limit was respected was to consider only recoveries from year $n+2$ onwards for tags placed in year n .

Tags placed in all years were used, but recoveries only from 1970 onwards. The data file contained recoveries up to and including 1994.

Since the number of tags attached (usually 1 or 2) to a fish will *a priori* affect the chance of recapture in the presence of tag shedding, it was included as a factor in the analysis. The very few records with more than two tags attached were discarded.

ANALYSIS

Statistical model

The probability of recovering in area j in year t a tag numbered l that was placed in year $t-T$ in area i , is given by:

$$y_{jt}(l) = F_{jt} \exp(\sum_j x_{ij} \beta_j + T_i \sum_k z_{ik} \gamma_k)$$

where F_{jt} is an array of composite parameters representing the fishing rate, the recovery efficiency, and the reporting rate in area j in year t . The β_j are coefficients for simple covariates x_{ij} , while the γ_j are coefficients for covariates z_{ik} which interact with the time elapsed since tagging, T_i .

Since the recovery probabilities in each year are considerably less than one, it is acceptable to approximate the numbers of observed recoveries in each cell as being Poisson distributed random variables sampled with replacement.

The F_{jt} are nuisance parameters of no direct interest here. They can be eliminated by conditioning on the reported number of recoveries in each area in each year: it is then only the composition of those recoveries, not their number, which is used for inference about inter-area movement and other factors. Conditioning on the numbers of recoveries by area and year is equivalent to working with the marginal likelihood maximised over the F_{jt} .

Results and discussion

The parameters fitted and their estimates and standard errors are listed in Table 1.

From the coefficients for length class and their interaction with elapsed time, we see that the smaller fish have a much higher initial rate of recovery, but this declines steeply with time. The length-time interaction can be regarded as the apparent instantaneous mortality rate by length class, although it is affected not only by mortality *per se*, but possibly also by declining selectivity by size as the fish grow.

The point estimate of the double tagging coefficient indicates a 20% higher recovery rate for double-tagged animals, but it is not significant. The interaction of double tagging with elapsed time is slightly negative, but not significantly so. A positive value for this coefficient would reflect a continued tag shedding over time: the result suggests that after 1-2 years there is little further shedding. More precise (lower variance) estimates of the shedding rate would be obtainable by analysing the proportion of double tags recovered as singles, although there are several reasons why the two approaches will not necessarily yield consistent results.

There is no significant area-specific difference in the apparent mortality rate (the estimated difference is 0.05 higher in the east, but the s.e. of this difference is 0.10).

The crossover coefficient (tagged in different area than recovered) is large and significant. The estimate of -2.6 on a log scale means that if equal numbers of fish were tagged and recovered in each area, only about 7% would be expected to be recovered on the opposite side to where they were placed. The coefficient for the difference in crossover rates in each direction is positive (0.29) for fish crossing from west to east, but is not significantly different from zero (s.e. 0.59). This implies point estimates of the crossover rates of 7.3% east-to-west and 9.8% west-to-east, but no significant difference between the two.

Of particular interest is the interaction of the crossover rate with elapsed time. If the diffusion model pertained, this coefficient would be expected to be positive, since the probability of crossover increases with time under that model. The estimate of the coefficient is negative, but not significantly different from zero. The results is therefore as or more consistent with the overlap model than with the diffusion model, but given the poor precision of the coefficient estimate the diffusion model can probably not be rejected.

GENERAL DISCUSSION

The assumptions behind the diffusion model have been questioned (ICCAT, 1995: p.108-10). One of the problems with the model is the difficulty of conceiving of a biological mechanisms which would enable the fish to behave in the way required by the model. For example, a migrant from the east is assumed to adopt the habits of the western population and become indistinguishable from western "natives". There would need to be some mechanism, such as some kind of social cohesion, that would result in the immigrant adopting the pattern of spawning migration of the other fish in the area.

In the cases investigated, the mechanism behind spawning migrations is usually found to be imprinting of features of the environment on the fish early in its life, so that as an adult it seeks

out the area or set of environmental conditions to spawn where it hatched itself (e.g. Cury, 1994). Since the homing mechanism is not 100% foolproof, new spawning habitat can be colonized, even though the majority return to their home area to spawn. Even if the rate of strays is small enough to be negligible in population dynamics terms, it can still allow colonisation of new habitat on time scales much shorter than evolutionary. In the absence of environmental factors providing strong selection pressure for genetic divergence, a low stray rate may also be enough to prevent genetic divergence of different spawning stocks.

Under the overlap model, the fish retain their pattern of spawning migration regardless of which areas they visit to feed, so it is consistent with the notion of spawning site fidelity.

The issues discussed in this paper have arisen in the work of the IWC Scientific Committee with respect to inter-area movements of minke whales in the Antarctic. The IWC Scientific Committee (IWC, 1991) developed a range of models to account for the observed movements: these included the "leakage" model, which corresponds to the diffusion model described above, and the "overlap" model. Various versions of a "shift" model were defined in which the feeding range of a stock fluctuates from year to year: for our purposes these can be regarded as variants of the overlap model. Buckland and Duff (1989), in an analysis of tag-recapture data, found that the proportion of "out-of-area" tags (tags recovered in subsequent seasons in areas other than where they were placed) seemed to be independent of the number of years elapsed between tag and recapture. This was interpreted as evidence in favour of movement models of the overlap type rather than models of the diffusion type for that species.

Although the analysis of this paper is not decisive, it would seem prudent to give at least equal consideration to the overlap model as to the diffusion model in future bluefin assessments.

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Table 1.

Generalized Linear Model analysis of bluefin tuna tag-recovery data

Parameter	estimate	s.e.
Length class 1 (40-60cm)	2.022	0.3568
Length class 2 (60-80cm)	1.424	0.3521
Length class 3 (80cm-1m)	1.282	0.3650
Length class 4 (> 1m)	0.000	aliased
Length class 1 x Time	-1.000	0.09065
Length class 2 x Time	-0.5478	0.05268
Length class 3 x Time	-0.6246	0.08066
Length class 4 x Time	-0.2651	0.07224
Double tagged	0.1961	0.1463
Double tagged x time	-0.03096	0.06562
Recovered in E x Time	0.05514	0.1029
Recovered in W x Time	0.000	aliased
Crossover	-2.612	0.3702
Crossover x Recovered in E	0.2935	0.5910
Crossover x Recovered in W	0.000	aliased
Crossover x Time	-0.03455	0.1586
Degrees of freedom:		
Listed parameters	13	
Nuisance parameters	40	(Recovery year x Recovery area)
Residual	7012	

Scale parameter taken as 1.000

Notes:

Time = calendar year of recovery - calendar year of tagging - 2

Crossover = tagged in E, recovered in W or tagged in W, recovered in E