

ESTIMATE OF NATURAL MORTALITY OF BIGEYE TUNA (*THUNNUS OBESUS*) IN THE EASTERN ATLANTIC FROM A TAG ATTRITION MODEL

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ABSTRACT

Conventional “spaghetti” tags and tags originally designed for “sport fishing” (referred to as Betyt tags), were used during a tuna tagging program conducted on board Dakar baitboats in 1999. A tag-attrition model has been used to estimate type-1 and type-2 tag losses and the rate of instantaneous natural mortality of bigeye tuna (*Thunnus obesus*). The immediate mortality on bigeye due to the Betyt tags has been estimated at about 31.1 % and the extra continuous mortality rate at 0.30 year⁻¹. The instantaneous rate of natural mortality for juveniles of bigeye (average FL = 56.6 cm) provided by this model (0.615 year⁻¹ for the mean and 0.675 year⁻¹ for the median) is consistent with previous estimates. In a Bayesian approach, we used the Sampling-Importance Resampling algorithm for updating Hampton’s estimate of M in light of information provided by the data analyzed in the present study. Based on the simulated posterior distribution, it appears likely that for juveniles of bigeye, M is close to 0.62-0.67 year⁻¹, with confidence bounds at 0.25-0.86 year⁻¹. In addition, potential causes affecting differences in return rates between both types of tags are analyzed.

RÉSUMÉ

Des marques classiques “spaghetti” et des marques créées à l’origine pour la pêche sportive, et appelées marques Betyt, ont été utilisées au cours d’un programme de marquage réalisé à bord des canneurs basés à Dakar en 1999. Un modèle dit de “tag-attrition” a été utilisé pour estimer les pertes de marques de type 1 et 2 ainsi que le taux instantané de mortalité naturelle du thon obèse (*Thunnus obesus*). La mortalité additionnelle du thon obèse due aux marques Betyt a été estimée à 31,1 % immédiatement après le marquage et à 0.30 an⁻¹ sur le long terme. Le taux instantané de mortalité naturelle pour les jeunes thons obèses (LF moyenne = 56.6 cm) estimée par ce modèle (0.615 an⁻¹ pour la moyenne et 0.675 an⁻¹ pour la médiane) est en accord avec les estimations antérieures à cette étude. Dans un contexte Bayésien, nous avons employé l’algorithme du “Sampling-Importance Resampling” afin d’actualiser les estimations de M fournies par Hampton à l’aide des informations contenues dans notre jeu de données. En nous basant sur une simulation de la distribution à posteriori, il apparaît vraisemblable que pour les juvéniles de thon obèse M soit proche de 0.62-0.67 an⁻¹, avec un intervalle de confiance aux environs de 0.25-0.86 an⁻¹. Enfin, les facteurs susceptibles de causer une différence dans les taux de recapture des deux types de marques sont analysés.

RESUMEN

Se han utilizado las clásicas marcas “espagueti” y las marcas creadas originariamente para la pesca deportiva y denominadas marcas betyp durante un programa de marcado realizado a bordo de barcos de cebo vivo en 1999. Se utilizó un modelo de tasa de pérdida de marcas para estimar las pérdidas de marcas de tipo-1 y tipo-2 y la tasa instantánea de mortalidad natural del patudo (*Thunnus obesus*). Se estimó la mortalidad adicional del patudo debida a las marcas betyp en aproximadamente un 31,1% inmediatamente después del marcado, y en 0,30 año⁻¹ a largo plazo. La tasa instantánea de mortalidad natural para los juveniles de patudo (FL media = 56,6 cm) proporcionada por este modelo (0,615 año⁻¹ para la media y 0,675 año⁻¹ para la mediana) coincide con las estimaciones anteriores a este estudio. En un contexto bayesiano, hemos empleado el algoritmo “Sampling-Importance-Resampling” con el fin de actualizar las estimaciones de M proporcionadas por Hampton a la luz de la información contenida en los datos analizados en este estudio. Basándonos en una simulación de la distribución a posteriori,

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parece posible que para los juveniles de patudo M se sitúe en un valor cercano a $0,62-0,67 \text{ año}^{-1}$, con un intervalo de confianza de entorno a $0,25-0,86 \text{ año}^{-1}$. Finalmente, se analizan factores susceptibles de crear diferencias en las tasas de recuperación de los dos tipos de marcas analizados

KEYWORDS

Bait fishing, Tropical tunas, Tagging mortality, Natural mortality, Numerical analysis, Bayesian analysis

MOTS-CLEFS

Canneurs, Thons tropicaux, Mortalité due au marquage, Mortalité naturelle, Analyse des données, Analyse Bayésienne

1 INTRODUCTION

In the 1980s, the bait boats operating from Dakar (Senegal) have developed an efficient fishing technique, which consists of keeping a permanent association between the fishing boat and the fished tuna school (Fonteneau and Diouf; 1994; Hallier and Delgado, 2000). From 1996 to 2000 a research program, called MAC for “Mattes de thons Associées aux Canneurs”, was implemented on this fishing technique and its consequences (Hallier *et al.*, 2001). One of the main working tools used by this program was ordinary tuna tagging (Kearney, 1982). In 1999, two different types of tags were used: the conventional “spaghetti” tags commonly used by all large tuna tagging programs and a new tag designed for opportunistic tagging of tunas and billfishes by the sport fishermen. The technical aspects related to their implementation and their respective effect on recapture, growth and survival rates of tropical tunas were analyzed and discussed by Hallier and Gaertner (2002). These authors concluded to the lower efficiency of the new tag type, specifically for the recapture rate of bigeye tuna (*Thunnus obesus*).

Because natural mortality (M) is a major source of uncertainty in stock assessment models, the main objective of this paper is to differentiate between initial mortality/tag loss and long term mortality/tag loss for both type of tags and consequently correctly estimate the natural mortality of juveniles of bigeye tuna. To deal with this objective we fitted a tag attrition model to a time series of tag-recapture data (Kleiber *et al.*, 1987; Hampton, 1997; Hampton, 2000). Then, in light of the information resulting from the present study, we used a Bayesian method in order to update previous estimates on M provided by Hampton (2000). Depending on different choices for the prior distribution, we calculated the central values and the range of uncertainty of M from a simulated posterior distribution.

2 MATERIALS AND METHODS

2.1 Tagging data

Conventional and new designed tags were provided by the International Commission for the Conservation of the Atlantic Tuna (ICCAT). The second being adopted by the Bigeye Tuna Year Program (BETYP) is termed Betytag hereafter in opposition to the conventional tag. Both tags are manufactured in the USA by Floy Tag and Manufacturing inc. Conventional and Betytag tags with their barbed heads (**Figure 1**) were placed at the base of the second dorsal fin in order to get the barbs tangled into the bones that join this fin to the central backbone of the fish (Kearney, 1982). The target is to firmly attach the barbs of the tag’s head into these bones (**Figure 2**). Betytag tags have a bigger head with one hook on each side; the head is joined to the corpse of the tag by two thin and strong nylon threads (**Figure 1**). This bigger head with two barbs gives a firmer hold of the tag into the fish.

This design is well suited for tagging fish, just pulled alongside the boat, directly into the hump behind the head or near the base of the first dorsal (Miyake, 1990), i.e. mostly into muscle. Conventional tags have a smaller head with only one barb on one side therefore to ensure a better grip into the fish it is necessary to set them into the bones of the second dorsal. The spaghetti tag is commonly chosen for tagging large numbers of small to medium size tunas (Fork Length < 100 cm) that are pulled out of the sea onto a tagging cradle and then returned to the sea with their tag on. In contrast, sport designed tags were originally geared to tag small numbers of large size billfishes and tunas (FL > 80 cm) directly at sea (Bayliff and Holland, 1986).

The tagging database (a total of 2463 tunas were tagged with conventional tags and 902 with Betyt tags) was obtained from three tagging trips done in 1999. Tagging took place off the Mauritanian coast in a square from 16°N to 21°N and 16°30W to 19°30W (**Figure 3**) and from August to December 1999. Although tagged tunas were skipjack (*Katsuwonus pelamis*), juvenile yellowfin (*Thunnus albacares*) and juvenile bigeye (*Thunnus obesus*), only tag releases and recaptures of bigeye were analysed in this paper (i.e., a total of 1095 conventional tags and 581 Betyt tags released). Because both types of tags were randomly released during each tagging operation, we assumed that every tag has approximately the same chance of being recaptured.

2.2 Data analysis

Recoveries per unit of time are commonly used to estimate population parameters, such as movement patterns, growth, mortality and population size of exploited stocks (Jones, 1976; Kleiber *et al.*, 1987; Hilborn, 1990; Hampton, 1997; Hampton and Fournier, 2001). With the aim of quantifying a possible difference in mortality rate between the conventional and the Betyt tags, we perform the return rate as a function of time from release. The model, referred to as the tag-attribution model (Kleiber *et al.*, 1987, Hampton, 1997), can be expressed as:

$$\hat{r}_{ij} = (1 - \alpha_i) T_i \frac{F_j}{Z_{ij}} [1 - \exp(-Z_{ij} \Delta t)] \exp\left(-\sum_{k=1}^{j-1} Z_{ik} \Delta t\right)$$

where \hat{r}_{ij} is the predicted recoveries for tag type i at time j , α_i represents all type-1 tag losses (from tag shedding and non-reporting) for tag type i , T_i is the number of tag released for tag type i , $Z_{ij} = M + F_j + \lambda_i$ is the instantaneous rate of total mortality, with M = instantaneous rate of natural mortality (assumed constant), F_j = instantaneous rate of fishing mortality at time j and λ_i = continuous type-2 tag losses (from tag shedding) for tag type i , and Δt represents the time step relative to the units of the instantaneous rates (Hampton, 2000).

Type-1 tag losses include immediate mortality and tag shedding, as well as recovered tags non reported. Type-2 tag losses include continuous tag shedding, continuous mortality due to the tag and emigration. In general, tag losses estimates cannot be calculated directly from tagging data but are based on information obtained from double-tagging and tag-seeding experiments or from observations of fish held in captivity (Hampton, 1997). However, using both types of tags in the same time allow us to estimate the difference in tag losses. Assuming that the number of observed recoveries r_{ij} by tag

type i and by time j are expected to be Poisson distributed with expected values \hat{r}_{ij} , the joint Poisson

probability mass function of r_{ij} is :

$$\prod_i \prod_j \frac{e^{-\hat{r}_{ij}} \hat{r}_{ij}^{r_{ij}}}{r_{ij}!}$$

Consequently, the parameters of the tag-attribution model were estimated by minimizing the negative of the log likelihood : $\sum_i \sum_j r_{ij} \log(\hat{r}_{ij}) - \sum_i \sum_j \hat{r}_{ij}$ (Agresti, 1990). Approximate 95% confidence intervals for the parameters of interest (α_i, M, λ_i) were obtained using the percentiles method applied to distributions of the parameters generated from 500 bootstrap replicates.

In the Bayesian approach, the current state of knowledge about the parameter under study can be reflected by a prior distribution. This prior is then combined with the information contained in the data (e.g., in our case after using the tag attrition model), resulting in the posterior distribution, as follows:

$$\Pr(\theta/data) = \frac{\Pr(data/\theta)\Pr(\theta)}{\int \Pr(data/\theta)\Pr(\theta)}$$

where $\Pr(\theta / data)$ is the posterior distribution of θ given the data,

$\Pr(data / \theta)$ is the likelihood of the data given parameter θ ,

$\Pr(\theta)$ is the prior probability of the parameter θ .

As a consequence, this posterior distribution can be viewed as a revised version of the prior distribution updated in light of information contained in the data. Based on biological knowledge or information from other studies (e.g., a range of values from 0.15 to 0.90 year⁻¹ has been found by Hampton, 2000), Bayesian procedure enables to construct the prior distribution of the instantaneous rate of natural mortality. Because the posterior distribution can be sensitive to the choice of the prior, we conducted a sensibility analysis regarding posterior inferences according to the nature of the prior, as suggested by Punt and Hilborn (1997). First we considered an uniform prior which is generally represented by a rectangular distribution. This terminology appears more suitable than "non informative" because it implies, at least, that we believe that the probability of M falling in an interval of a given length is the same, independently where the interval is located between the lower and the upper confidence bounds (0.15-0.90). In contrast, using a more informative prior allows the incorporation of some available prior knowledge based on previous study. For instance, if we consider likely that the distribution of M approximates a normal distribution, we can use a normal prior with a mean at about 0.525 and a standard deviation at 0.191.

When using the Bayes' theorem, it is convenient mathematically to select a prior [$\Pr(\theta)$] which is a conjugate distribution of the probability of the observed data [$\Pr(data / \theta)$]. In contrast, deriving the posterior distribution in the case of non-conjugate problems can be very difficult. Alternative Bayesian Monte Carlo approaches for numerical integration, such as Sampling-Importance-Resampling (SIR), Adaptive Importance Sampling (AIS), Markov Chain Monte Carlo (MCMC) have been used in stock assessment studies to illustrate the usefulness of the Bayesian approach even when the posterior distribution can be characterized only numerically (Kinas, 1996; Punt and Hilborn, 1997; McAllister and Kirkwood, 1998).

For summarizing the posterior distribution of M , we used the Sampling-Importance-Resampling (SIR) algorithm (Rubin, 1988; Gelfand and Smith, 1992). Suppose that we are interested in simulating a sample from a probability distribution $g(\theta)$, but that it is difficult to simulate from $g(\theta)$ directly. The SIR algorithm requires a second distribution $h(\theta)$ as close as possible to $g(\theta)$ and which is easy to simulate. A simple approximation method of sampling from $g(\theta)$ proceeds as follows :

- generate a sample $\theta_1, \dots, \theta_m$ from $h(\theta)$
- compute the importance sampling weights $w(\theta_i) = g(\theta_i) / h(\theta_i), i = 1, \dots, m$

- take a new sample $\theta^*_1, \dots, \theta^*_m$ with replacements from $\{\theta_1, \dots, \theta_m\}$ with probabilities proportional to $\{w(\theta_1), \dots, w(\theta_m)\}$

The sample $\{\theta^*_i\}$ is approximately distributed from the density of interest $g(\theta)$. Given the sample, we can roughly recreate the density and summary statistics (Kinas, 1996).

The simplest choice for $h(\theta)$ is the prior distribution $\Pr(\theta)$, although this choice may not be efficient if the likelihood supports only a small part of $\Pr(\theta)$ (Punt and Hilborn, 1997). The weight function is given by $w(\theta) = \Pr(\theta/data)/\Pr(\theta) = \Pr(data/\theta)$. As a consequence, an approximate sample from the posterior distribution is obtained by drawing a sample $\theta^*_1, \dots, \theta^*_n$ with replacements from $\{\theta_1, \dots, \theta_m\}$ with unequal probabilities weights $\{\Pr(data/\theta_1), \dots, \Pr(data/\theta_m)\}$. Consequently this procedure can be viewed as a weighted bootstrap. Notice that for estimating more complex posterior distributions (e.g. multimodal), alternative importance sampling procedures, such as AIS, are more efficient than the SIR algorithm (Kinas, 1996; McAllister and Ianelli, 1997). In the present study, the unequal probabilities weights were calculated from the bootstrapped estimates of M resulting from the tag-attribution model.

3 RESULTS

The percentage of tags returned were 62.7 % and 43,0 % for conventional and Bety tags respectively. The plot of observed and predicted tags returns by time at liberty and by tag type for bigeye indicates that the tag-attribution model provides a good fit of the data (**Figure 4**). **Table 1** shows the estimates of the natural mortality rate (M), the type-1 (α) and type-2 tag losses (λ) from the tag-attribution model and their respective confidence intervals. It appears that the population of tagged fish is reduced (i.e., type-1 tag losses) by 33.7 % and 2.6 % for Bety tags and for conventional tags, respectively. There are also large differences for type-2 tag losses: 0.538 year⁻¹ for Bety tags vs 0.238 year⁻¹ for conventional tags. The instantaneous rate of natural mortality has been evaluated at 0.615 year⁻¹ for the mean (and 0.675 year⁻¹ for the median, which is a preferable estimate of location for a skewed distribution). There are large 95% confidence intervals on M , but 50% of the bootstrapped estimates (i.e., 1st and 3rd quantile) are within the range (0.512 – 0.760).

The initial uncertainty about M is depicted by the range of values (95% C.I. = 0.15-0.90) provided by Hampton (2000). A comparison of the SIR posterior distributions shows that the range of the most likely value of M depends weakly on the choice of the prior. The mode of M is about 0.70 year⁻¹ in the case of the informative (i.e. normal) prior, and about 0.74 year⁻¹ in the case of the uniform (i.e., rectangular) prior (**Figures 5 and 6**, respectively). Concerning the parameters of interest (e.g., the mean, the median), there are no significant differences (**Table 2**). One of the advantage of the Bayesian procedure is that our current uncertainty expressed in terms of 95 % confidence intervals has been reduced approximately to 0.25-0.86 year⁻¹ (**Table 2**). In light of the information provided by the present analysis, and based on prior knowledge (i.e., the Hampton's study), we conclude that the instantaneous rate of natural mortality for juveniles of bigeye tunas (FL < 103 cm, average FL = 56.6 cm, $\sigma = 137.6$) can be estimated at about 0.62-0.67 year⁻¹.

4 DISCUSSION

First, it should be noted that tag losses estimates for conventional tag type obtained from this study (0.0263 for type-1 and 0.2385 year⁻¹ for type-2) are consistent with the proportion of tags lost immediately following release (0.0289) and with the continuous tag losses (0.216 year⁻¹) reported by Adam and Sibert (2002) in the Skipjack Maldivian pole and line fishery. In contrast, Kleiber *et al.*, (1987) and Hampton, (1997) reported smaller type-2 values (0.0876 year⁻¹ and 0.0276 year⁻¹, respectively). Because these two last tagging programs were conducted in a very broad area, comparatively to the small fishing grounds of the Senegalese (**Figure 3**) and Maldivian bait boat

fisheries, this discrepancy may be due to a difference in emigration rate of tagged tuna away from the area of the fishery.

Secondly, the difference in type-1 tag losses between both type of tags is estimated at about 30 %. There are also large differences for long-term losses: 0.538 year⁻¹ for Betyt tags versus 0.238 year⁻¹ for conventional tags. Bearing in mind that the M range values is in agreement with previous estimate (Hampton, 2000), a difference in returns rate between both types of tags may be due to differences in (1) tag shedding (immediate and/or continuous), (2) non report of recovered tags, and (3) mortality directly attributable to the tag (immediate and/or continuous). By contrast, there are no reason to account for a different emigration rate of tagged fish away the fishery and for non-reporting of recovered tags.

Non-reporting of tags and tag shedding will be counted as an increase of the mortality rate. Tag reporting and tag shedding problems were addressed by Hallier and Gaertner (2002) and they concluded that there is no difference in tag reporting between both tags and most certainly it should be the same for tag shedding. However, if tag shedding would not be the same for both tags, it should be to the detriment of conventional tags. As mentioned in the data section of this article, Betyt tag should hold better into the fish than conventional tag because of its technical characteristics. Therefore, tag shedding could be lower for Betyt tags than for conventional tags and consequently should lower the mortality rate. The fact that mortality rate is higher for Betyt tags than for conventional tags is somehow an indirect proof that tag shedding is not higher for conventional tags than for Betyt tags. For all these reasons, we conclude that using Betyt tag reduces the effective number of tagged fish by 31.1 % (i.e., mortality immediately following tagging) and produces an extra mortality due to carrying this type of tag close to 0.30 year⁻¹.

The fact Betyt tags are responsible for a higher mortality for bigeye and not for skipjack can be due to several causes (we do not address this question for yellowfin as there is at first a problem of small sample size). First of all, tagged bigeye are all juvenile fish (FL < 103 cm, average FL = 56.6 cm, $\sigma = 137.6$) while most skipjack are adult fish (FL > 45 cm, average FL = 49.7 cm, $\sigma = 23.7$). It is generally considered that juveniles are weaker than adults therefore bigeye might suffer more than skipjack from the bigger injury inflicted by the Betyt tag. Secondly, as recapture rate of skipjack is much lower than for bigeye, 22.5 % and 55.9 % respectively for all tag combined, statistical tests to demonstrate a possible mortality rate induced by tagging will be less sensitive for skipjack than for bigeye. Thirdly, natural mortality rate (M) is higher for skipjack than for bigeye. Hampton (2000) found for skipjack, between 41 and 70, cm values of M between 1.2 and 2.0 year⁻¹ (average 1.9) instead of 0.15 to 0.9 year⁻¹ for bigeye between 41 and 100 cm. The 0.30 year⁻¹ additional continuous mortality due to Betyt tags will represent an increased mortality around 20 % for skipjack against 50 % or more for bigeye. Therefore it will be more difficult to demonstrate this increased mortality for skipjack than for bigeye.

In this study, Betyt tags have been set in the same way as conventional tags, i.e. at the base of the second dorsal fin. However as Betyt tag head is bigger than conventional tag head, it may not be advisable to set Betyt tags at this place onto the fish but directly into the hump behind the head. It is possible that Betyt tags, when implanted directly into the muscle flesh, do not cause additional mortality.

As demonstrated by Hampton (2000), natural mortality in tuna populations is dependent on size. Although the details may vary among species, it is commonly admitted that the instantaneous rate of natural mortality exhibits an “U-shaped” function (i.e., M is likely to be high during early juvenile stages, decreasing to relatively low level during the adult stage, then increasing with senescence). Based on the evidence that for tropical tunas M follows this general pattern, a value of 0.65 year⁻¹ can reasonably be used such as a minimum level for bigeye tunas smaller than 50 cm. For the same reason, bigeye larger than 100 cm also should exhibit greater M than estimated for the size classes analyzed in the present study. Because we performed a separate F for each time period, one can argue that this model is over parameterized. In addition, the number of tags remaining at sea in the last time period

can be larger than the observed number of recoveries in this period. As a consequence there is a possibility that several trajectories of F would predict the recoveries (M. Maunder, IATTC, comm. pers.). Therefore further studies are necessary to confirm this result. However, the histogram of the bootstrapped M values showed evidence that the most likely values are centered around 0.6 – 0.8.

5 CONCLUSIONS

This study reinforces the statistical analysis of Hallier and Gaertner (2002), which indicate a negative effect of Betyt tags on recapture rate and on time at liberty for bigeye. For yellowfin, values show similar trends but the small sample sizes do not permit to be affirmative on the negative effect of Betyt tags. In contrast, these authors found that there were no negative effects of Betyt tags on recapture rate, growth rate and time at liberty for skipjack. If we assume a similar behaviour of tagged tunas whatever the type of tag used, only a difference in mortality rate can account for these results. If Betyt tags induce a higher mortality rate, Betyt tagged tunas would show a lower recapture rate and a lower time at liberty. Lower growth rate can reveal that the wound resulting from the tagging can get cure less easily with this tag than with conventional tags and therefore this can stunt the growth of the fish (but this has not been validated) and more dramatically lead the fish to its death. Assessing the effect of tag type on mortality rate is therefore a good way to determine its possible negative effects. The tag-attribution model developed in the present study confirms that Betyt tags induced an additional instantaneous (type-1) and continuous (type-2) mortality.

The increased mortality for bigeye tagged with Betyt tags will need to be taken into account when analysing tag-recapture data from BETYP program. In-tank experiments will be necessary in order to confirm these results and to conduct other trials on the best place where to set these Betyt tags. Even if Betyt tags set directly into muscle flesh do not add extra mortality, their technical characteristics prevent their efficient use for large-scale tropical tuna tagging program.

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Table 1. Bootstrapped estimates (n=500) of α_c , α_b , M, λ_c , and λ_b for the two types of tags (c = conventional “spaghetti” tags; b = Bety tags) for bigeye tuna .

Parameter	Mean	Median	Confidence intervals (95%)
α_c	0.02632	0.00870	(5.89 e-06__ 0.13390)
α_b	0.33737	0.33898	(0.11041__ 0.61495)
M	0.61500	0.67134	(0.02696__ 0.93792)
λ_c	0.23849	0.20736	(0.00005__ 0.77352)
λ_b	0.53777	0.53584	(0.00080__ 1.19240)

Table 2. Sensitivity analysis on Sampling-Importance Resampling posterior distribution in instantaneous rate of natural mortality for bigeye tuna, depending on the choice of the prior

Prior	Normal	Rectangular
Mean	0.604	0.632
Median	0.620	0.667
Lower C. I.	0.269	0.236
Upper C. I.	0.844	0.881

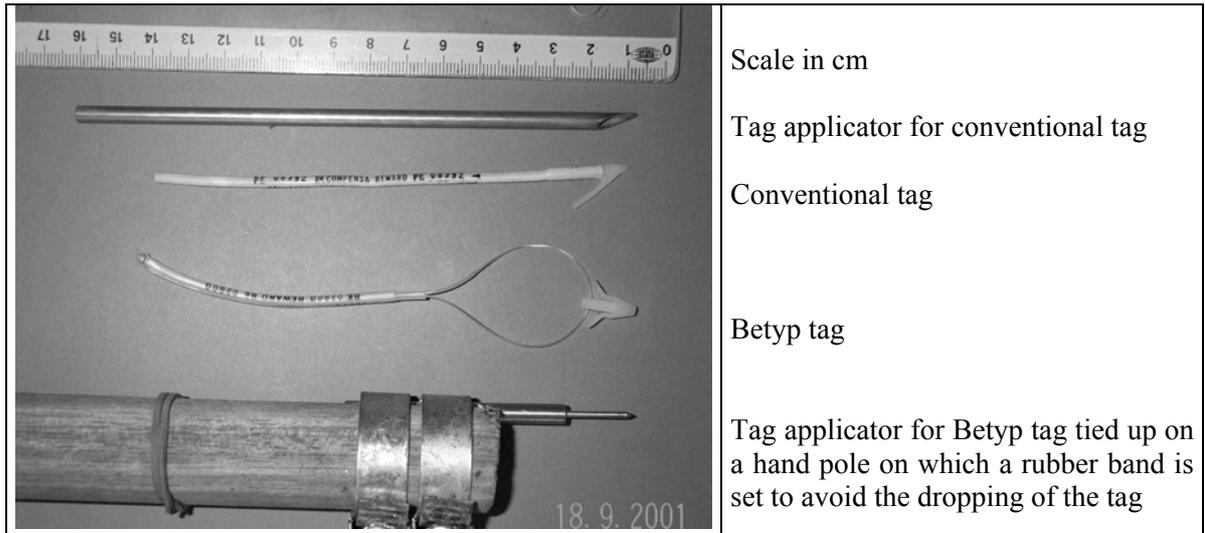


Figure 1: Conventional and Bety tags and their applicators.

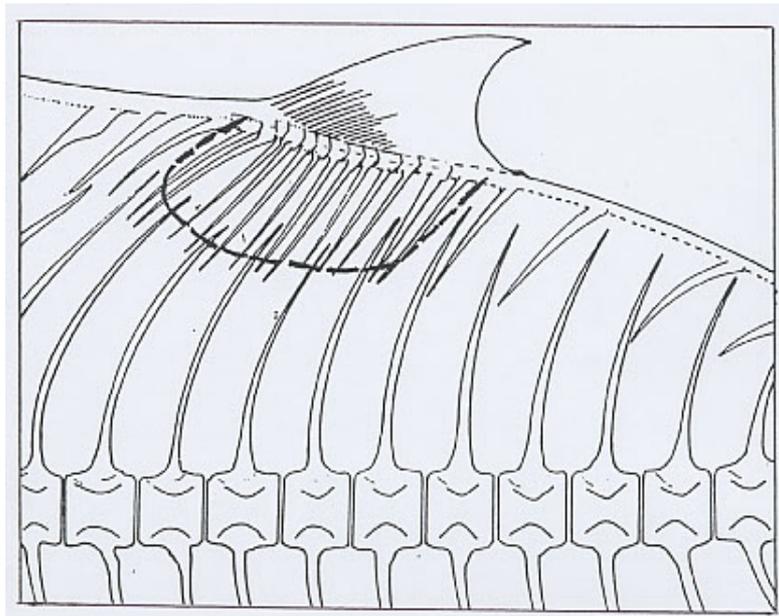


Figure 2: Location on the back of the tuna where conventional and Bety tags were set during MAC tagging operations

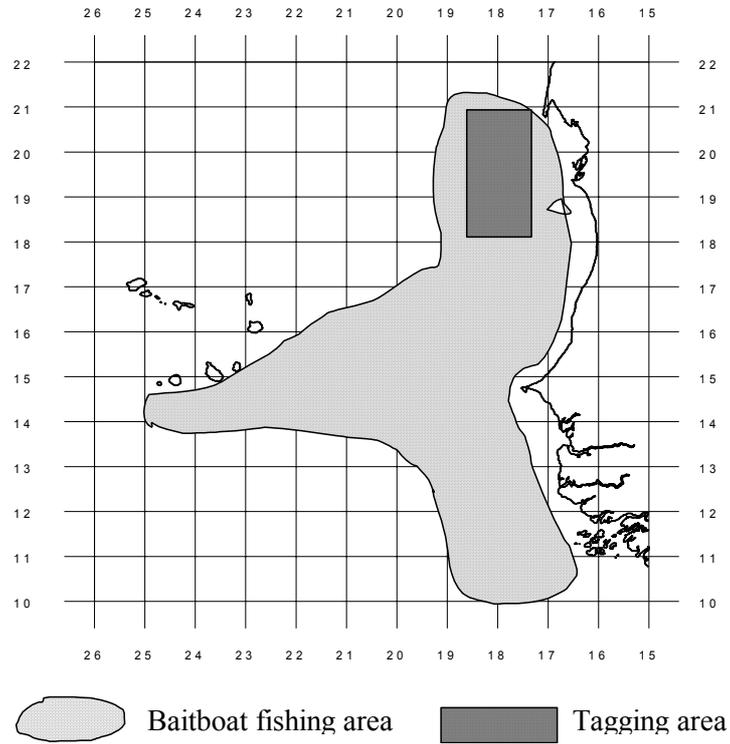


Figure 3. Location of the tagging area corresponding to the 3 tagging cruises analysed in this study and baitboat fishing grounds.

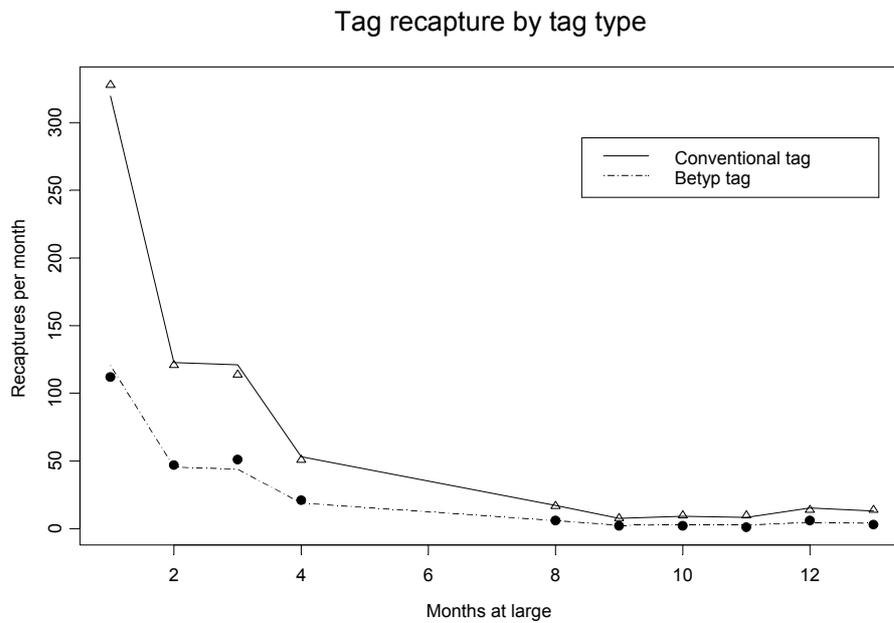


Figure 4: Observed and predicted tag recaptures over time for the tag attrition model by tag type for bigeye

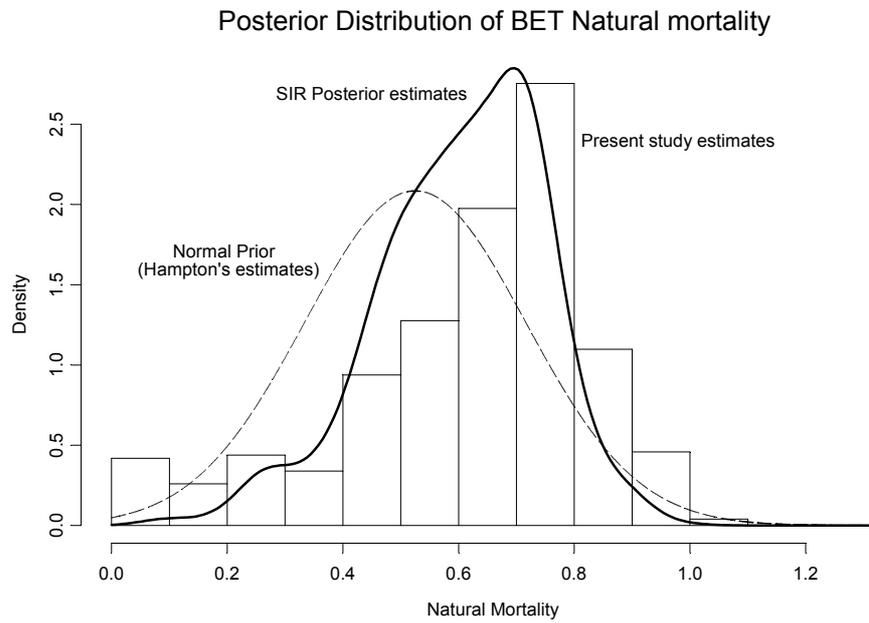


Figure 5. SIR posterior distribution of BET rate of natural mortality, assuming a normal prior

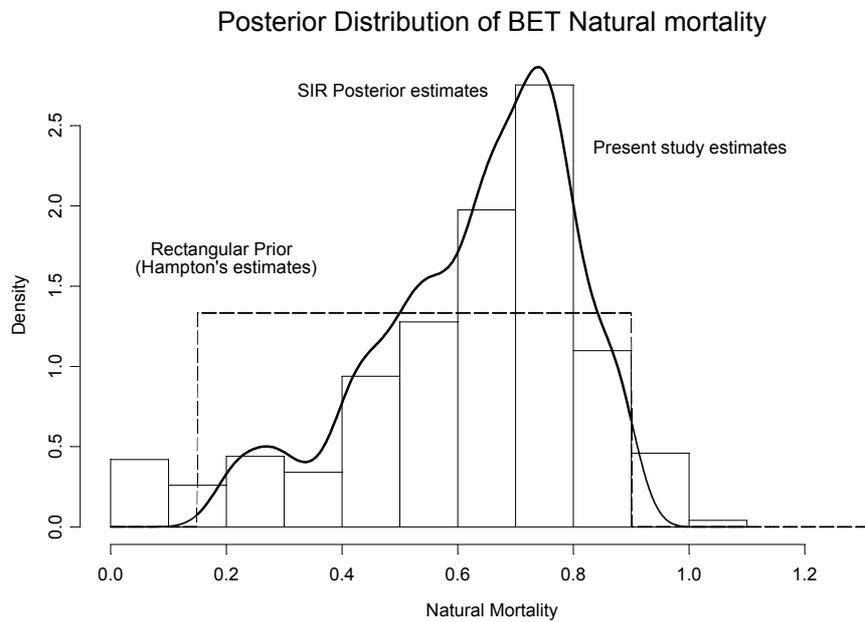


Figure 6. SIR posterior distribution of BET rate of natural mortality, assuming a rectangular prior