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Tag-shedding rates for tropical tuna species in the Atlantic Ocean estimated from double-tagging data

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Summary

An objective of the Atlantic Ocean Tropical tuna Tagging Programme (AOTTP) was to estimate Type-I (immediate) and Type-II (long-term) tag-shedding rates for tropical Atlantic tunas from double-tagging experiments. Historical information on tuna tag-tagging studies conducted in different parts of the world was incorporated as prior distributions using a Bayesian approach to estimate the new tag-shedding parameters. Type-I and Type-II tag-shedding rates were respectively estimated at 0.007 and 0.084/yr for bigeye tuna, 0.021 and 0.051/yr for skipjack and 0.021 and 0.088/yr for yellowfin tuna. Using realizations derived from the MCMC posterior distributions, the shedding rate was estimated to reach 50% of the tags after seven and a half years at sea for yellowfin and after eight years at sea for bigeye tuna. The loss rate of conventional tags is lower for skipjack. Our results suggested that continuous Type-II shedding rate is size-dependant for yellowfin and bigeye (i.e., showing a three-fold increase between individuals less than 45 cm fork length (FL) at release and fishes larger than 65 cm FL). This study reinforces the need to account for tag-shedding along with other sources of uncertainty, such as reporting rate, in order to accurately estimate the exploitation and mortality rates derived from tagging data.

Keywords

Tropical tunas, Atlantic Ocean, tag-shedding estimates, Bayesian analysis

Highlights

- Immediate and long-term tag-shedding rates were estimated with a Bayesian model for tropical tuna in the Atlantic Ocean.
- Beta prior distributions of tag-shedding parameters were elicited from historical studies found in the literature.
- The proportion of tag loss reached 50% for yellowfin and bigeye after 7.5 and 8 years at liberty, respectively.
- The long-term tag-shedding rate increased with size at release.

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1. Introduction

The 5-year Atlantic Ocean tropical Tuna Tagging Programme (AOTTP) was designed to improve estimates of key parameters commonly used as inputs in the stock assessments of the three main species of tropical tunas: bigeye (*Thunnus obesus*), skipjack (*Katsuwonus pelamis*) and yellowfin (*T. albacares*). To date, 119 427 tropical tunas have been marked and released in different places in the Eastern Atlantic (Azores, Madeira, Canary Islands, Senegal, Gulf of Guinea, St Helena, South Africa) and in the Western Atlantic (Brazil, Caribbean, U.S.A.) with approximately 15.6% of the released fish recovered¹¹.

Tag-return data are commonly used for estimating mortality rates, either in stand-alone models (e.g., Brownie et al., 1985; Kleiber et al., 1987; Hoenig et al., 1998; Polacheck et al., 2010) or by incorporating the tagging data into an integrated stock assessment package (e.g., Hampton and Fournier, 2001). The results of tagging studies can, however, be compromised if tags or data are lost (i.e., through tag-shedding and non-reporting). Both occurrences can lead to underestimations in tag-return rates, which create a negative bias in fishing mortality estimates, rates of fishery interactions, and tuna movements (Gaertner and Hallier, 2015). Ultimately, this leads to biased estimates of stock status. The objective of this paper is to use AOTTP double-tagging experiments to estimate the tag-shedding rates for the three species of tropical tunas in the Eastern Atlantic Ocean.

There are two types of tag losses (Wetherall, 1982; Hampton and Kirkwood, 1990): Type-I losses, which reduce the number of tags initially put out (immediate tag-shedding), and Type-II losses which occur steadily over time (long-term tag-shedding). In this paper, we estimate the Type I and II tag-shedding components of total tag losses for Atlantic Ocean tropical tunas, combining prior knowledge on these parameters from other regions with AOTTP release-recapture data from double-tagging experiments within a Bayesian framework.

2. Material and Methods

2.1. Data

Double-tagging experiments, “i.e., experiments in which a fish is tagged with two conventional “spaghetti” tags simultaneously, were conducted in the Atlantic Ocean from 2016 to 2020. The dataset was analysed by AOTTP staff and after the quality control process a total of 20 009 double-tagged release records remained from which 3 095 were recovered (15.5%), which includes 256 fishes (0.13%) that have lost one of their tags (**Table 1**).

2.2. Methods

Calculations to estimate tag-shedding rates from double-tagging experiments rely on the assumption that the first and second tags are shed at the same rate, independently of one another (e.g., Kirkwood, 1981; Wetherall, 1982; Kirkwood and Walker, 1984).

The most appropriate approach to model the tag-shedding process is to use individual exact times-at-liberty that account for differences in the reporting rates of double and single tags (including differences in detection rates). This approach also accounts for differences in tag loss driven by the choice of insertion point (i.e., left side or right side) of each double tag (e.g., Barrowman and Myers, 1996; Xiao, 1996; Lenarz and Shaw, 1997; Cadigan and Bratney, 2006; Smith et al., 2009). Based on previous tag-shedding studies (Gaertner and Hallier, 2015), exact time-at-liberty tag-shedding models are formulated by constant-rate model as follows. The probability $Q_A(t)$ of a tag-type A being retained at time t after release can be expressed as:

$$Q_A(t) = \alpha_A e^{-(\lambda_A t)} \text{ (Bayliff and Mobrand, 1972),}$$

where α_A is the retention probability of the immediate Type-I shedding rate and λ_A is the continuous Type-II shedding rate of this tag-type A .

¹¹ <https://www.iccat.int/AOTTP/en/aottp-tagging.html>

Given this assumption, the probability $P_A^A(t)$ of observing a fish released with a single A-tag at time t after release is a combination of the reporting rate γ_A , and the probability $Q_A(t)$ of tag A being retained, which can be expressed as:

$$P_A^A(t) = \gamma_A Q_A(t)$$

A similar expression can be used to determine differences in the proportion of tags returned over time for fish that were tagged with a different type of tag or at a different insertion position. For non-permanent double-tagging experiments, the reporting rate did not factor into the above equation because the only recapture information available to estimate shedding rates is whether a fish has retained one or both its tags. If we assume that when a fish is recovered with two tags, both tags are always reported, i.e., there is no loss of one of the tags due to non-reporting, which would then be incorrectly attributed to shedding, the possible tag combinations at recapture are two tags (RL), right-tag only (R), and left-tag only (L), which can be expressed as the following outcomes:

$$(1) \quad P_{RL}^{RL}(t) = Q_R(t) Q_L(t)$$

$$(2) \quad P_R^{RL}(t) = Q_R(t)[1 - Q_L(t)]$$

$$(3) \quad P_L^{RL}(t) = Q_L(t)[1 - Q_R(t)], \text{ respectively}$$

The probability of observing the outcome i (i.e., one of the recovered tag combination with n_i occurrences), for a fish captured at time t , for each of these three possible outcomes is given by:

$$P_i^{RL}(t) / \sum_{i=1}^3 P_i^{RL}(t)$$

Estimates of the model parameters are obtained by minimizing the negative log-likelihood of the data conditional on recapture times (Barrowman and Myers, 1996):

$$LL = - \sum_{i=1}^3 \sum_{j=1}^{n_i} \text{Ln} \left[P_i^{RL}(t_{ij}) / \sum_{i=1}^3 P_i^{RL}(t_{ij}) \right]$$

The Bayesian information criterion (BIC) was used to objectively select a model from the set of candidate models considered (Schwarz, 1978).

$$BIC = -2 \text{Ln} L(\hat{\beta}, \hat{\gamma} / \text{data}) + K \text{Ln}(n)$$

where n is the number of observations, K is the number of model parameters, and $L(\hat{\beta}, \hat{\gamma} / \text{data})$ is the value of the maximized log-likelihood over the unknown parameters, conditional on the data. The lowest BIC value identifies *a posteriori* which is the most probable model.

However, it is problematic to choose the most probable model among R candidate models when the BIC values are nearly equal. To account for any uncertainty associated with model selection, a Bayesian posterior model probability (Pr_i) was calculated for each candidate model i as:

$$Pr_i = \exp\left(\frac{-\Delta BIC_i}{2}\right) / \sum_i \left[\exp\left(\frac{-\Delta BIC_i}{2}\right) \right]$$

where, $\Delta BIC_i = BIC_i - \min BIC$, (Burnham and Anderson, 2002).

It is noteworthy that the inferential model weights from the BIC selection have the same formula as the Akaike weights (Akaike, 1978), but may be interpreted as probabilities of the model, given the data, model set, and prior model probabilities of each model (Raftery, 1995; Burnham and Anderson, 2004). The above posterior

model probabilities are based on assuming that prior model probabilities are all $1/R$. Therefore, the model with the largest Pr_i is the one with the highest probability of being the best model for the data set.

Notice that in the absence of any effect of the insertion point on the tag loss, i.e., $P_L^{RL} = P_R^{RL}$, the negative log-likelihood of the data can be simplified as follows:

$$LL = - \sum Ln [P_2^{RL}(t)/(1 - P_0^{RL}(t))] - \sum Ln [P_1^{RL}(t)/(1 - P_0^{RL}(t))]$$

with the probabilities of 2, 1 and no tags being retained at time t after release, respectively as:

$$P_2^{RL}(t) = P_{RL}^{RL}(t) = Q^2(t); P_1^{RL}(t) = P_R^{RL}(t) + P_L^{RL}(t) = 2 Q(t) [1 - Q(t)]; P_0^{RL}(t) = [1 - Q(t)]^2$$

where $Q_R(t) = Q_L(t) = Q(t)$

Numerous tropical tuna tagging programs have been carried out for several decades in different oceans, and thus results of previous analyses with a similar setting are available in the literature. Such historical data may provide information that is relevant to the research questions of the current Atlantic tagging program. For instance, including this historical information in the analysis of the shedding rate could improve the precision of the current estimates. However, historical studies should only be considered relevant if there are no reasons to believe that the shedding rate parameters in the historical and actual double tagging experiments differ systematically. This means that the same shedding rate model must have been used in the historical studies and that there are no deviations due to time or local phenomena, even if this does not imply identical parameter values. Unlike tag-reporting rates which commonly depict large variability between fishing gears, landing ports and over time, it can be assumed that tuna species tagged and released in similar conditions have comparable shedding rates. This assumption is supported by the very close estimates of type-I and type-II shedding rates from previous double tagging experiments on tunas conducted in different oceans (**Table 2**). Based on these estimates, we can reasonably express our prior knowledge on tag loss by eliciting a prior distribution for each parameter of tag-shedding before analyzing the AOTTP data.

To derive a prior from historical information we assumed that the Beta distribution was a suitable model for describing the distributions of the immediate and long-term shedding rates obtained in the literature (**Fig. 1**). Note that because Lambda is measured in yr^{-1} and has no upper limit, a gamma distribution would be a logical choice. However considering that the observed values for Lambda are lower than 1, for the sake of simplicity we also used a Beta distribution as the prior distribution for this parameter. Instead of using the method of moments, with the sample mean and sample variance, to estimate the hyperparameters of the Beta distribution, it is easier to evaluate them indirectly through statements about the two distinct quantiles of the distribution (Van Dorp and Mazzuchi, 2000; Albert, 2009). To find the shape parameters that matches best-guess estimates of two quantiles of each of the shedding rate distributions, we used the `beta.select()` function found in the R library(LearnBayes)^{12,13}.

Assuming both independence in tag-shedding (as showed in the Result section) and that double-tag recoveries and single-tag recoveries are reported with the same probability, we followed the approach described by Chambers et al., 2014, 2015) in which the observed double-tag recoveries were modelled as realizations of a Bernoulli random variable (1 for both tags recovered, 0 for a single tag recovery) with a success probability $\pi(t)$ as follows:

$$\pi(t) = \{Q(t)\}^2 / [\{Q(t)\}^2 + 2 Q(t)[1 - Q(t)]] = Q(t) / [2 - Q(t)]$$

The Bayesian analysis was conducted in R using the R2jags¹⁴ package, with informative Beta priors elicited from previous tag-shedding studies as mentioned previously. However, to test the sensitivity of the posterior distributions to their priors, we generated Markov chain Monte Carlo (MCMC) samples with alternative non-informative Beta(1,1) priors. Final inference was based on posterior distributions obtained by generating 50000 MCMC samples and discarding the first 1000 as burn-in. The convergence of MCMC chains was evaluated

¹² <https://cran.r-project.org/web/packages/LearnBayes/index.html>

¹³ <https://www.r-bloggers.com/2013/09/the-beta-prior-likelihood-and-posterior/>

¹⁴ <https://cran.r-project.org/web/packages/R2jags/index.html>

visually by plotting the generated values of the parameter against the iteration number after running 3 chains that have different starting values and by checking convergence diagnostics: e.g., the potential scale factor (Rhat), known as the Gelman-Rubin convergence statistic, and a measure of effective sample size (n.eff) which is an estimate of the number of independent draws from the posterior distribution of the estimate of interest (Gelman and Rubin, 1992).

To assess potential differences in terms of types I and II tag-shedding according to the size (FL) at release, the tag-shedding Bayesian model was applied to three size-at-release categories for bigeye and yellowfin (i) ≤ 45 cm FL, (ii) between 45 and 65 cm FL and (iii) > 65 cm FL, and only two categories for skipjack: ≤ 45 cm, > 45 cm.

3. Results

To investigate the effect of tag position on the tag-shedding rate for tropical tuna, we assumed that the potential effect of the insertion position on the tag loss was related to the skill of the tagger, the at-sea conditions during the tagging experiment, the tagging place onboard the tagging vessel, etc. These effects were not explicitly modelled for two reasons: 1) a large number of different vessels and taggers were used with little overlap of taggers across vessel types, making it difficult, if not impossible, to tease out effects; and 2) tagging events lacked detailed information on the tagging conditions onboard. To test this effect, we assessed four different models in which tag-retention parameters were varied according to the position of the tag.

- Model 1 (A1) assumed that tag position had no effect on tag loss;
- Model 2 (A2; three model parameters) allowed both λ_R and λ_L to vary as a descriptor of position effect on the instantaneous rate of long-term tag loss (α is assumed unique);
- Model 3 (A3; three model parameters) assumed a position effect in the probability that a fish retained its tag immediately after tagging (α_R and α_L can differ, but λ is assumed to be independent of the insertion point(s));
- Model 4 (A4) assumed a specific position estimate for all four parameters ($\alpha_R, \alpha_L, \lambda_R$, and λ_L).

To reflect the uncertainty associated with ranking and selecting the most plausible model to depict the probability of observing the various combinations of right- and left-tagged releases possible, we used both the Akaike information criterion corrected for small sample sizes (AICc) and BIC.

Although AIC and BIC are both penalized-likelihood criteria, they reflect subtle theoretical differences: AIC focuses on the best variance-bias trade-off in a set of candidate models (i.e., the parsimonious model in terms of a frequentist approach), while BIC identifies the “quasi-true” model. Consequently, the type of criteria used can drive some differences in which model is selected. In this analysis, the BIC-selected model (A1) suggests that tag position did not affect tag-shedding. For the AICc, except for the full model, which has the less evidence, neither model dominated the others (**Table 3**). It should be noted that the study conducted in the Indian Ocean showed that the tag position did affect Type-1 shedding for bigeye and yellowfin (Gaertner and Hallier, 2015). Accounting for this aspect can be relevant in single-tagging experiments, and considering that about 90% of the human population are right hand dominant¹⁵, tags are likely most-commonly inserted into the right side of the fish. However, this effect was not confirmed with AOTTP data and the simplest model (A1) assuming no tag location effect was retained in this study.

The recovery over time of double-tagged individuals with two tags or one tag remaining is presented in **Figure 2**. The estimates of the shedding parameters according to different approaches or assumptions are presented in **Table 4**. The trace plot and the density plot for each parameter are provided by species in the supplementary material for the Bayesian model using an informative Beta (**Figures S1 to S3**). On average, from the frequentist model to the Bayesian model using informative Beta priors, there is an increase of the immediate tag-shedding estimates (i.e., $1-\alpha$) and a decrease in the long-term tag-shedding. Retaining the Bayesian model with informative Beta prior, Type-I and Type-II tag-shedding rates were estimated at 0.007, 0.084/yr for bigeye tuna, 0.021, 0.051/yr for skipjack and 0.021, 0.088/yr for yellowfin tuna, and are close to the values obtained in previous tagging studies. Based on these results and using draws from the MCMC posterior distributions, we estimated that the shedding rate reaches 50% of the tags after seven and a half years at sea for yellowfin and after eight years at sea for bigeye tuna. Surprisingly, the loss rate for skipjack was lower than for the two other

15 <https://en.wikipedia.org/wiki/Handedness>

tropical tuna species (**Table 5 and Fig. 3**), despite the fact that skipjack are reported to be extremely hardy during the tagging operation (Hallier, 2004).

To assess potential differences in tag-shedding with size (FL) at release, the AOTTP double-tagging dataset was divided into 3 size categories for bigeye and yellowfin and only two categories for skipjack. Estimates of tag-shedding were obtained using the Bayesian model with informative Beta prior. Due to the low number of recaptures with one tag lost for some combinations of species - size category results must be interpreted with caution. Although there is not a clear change in Type-I shedding by size category (**Table 6, Fig. 4**), the results suggest that the continuous Type-II shedding rate increases for larger bigeye and larger yellowfin at-release; e.g., between $FL \leq 45\text{cm}$ and $FL > 65\text{cm}$: from 0.040 to 0.128 per year and from 0.051 to 0.163 per year, respectively (**Table 6, Fig. 5**). This corresponds to a three-fold increase.

4. Discussion

In double-tagging studies, where two temporary tags are lost, it is assumed that both tags were shed independently of one another (and thus an adjustment is made to the remaining number of fish assumed to be alive). In situations where individuals are prone to losing (or retaining) both their tags in the same event, the assumption of tag independence may lead to underestimation in tag losses, which has broader implications for the estimation of vital life-history traits. Given the lack of evidence suggesting otherwise, we followed the assumption that losing the first tag did not affect the probability of losing the second tag (i.e., independent tag shedding) but assessed the assumption that both tags have an equal probability of retention. Our results did not show evidence of an effect of the insertion of the tag on the right, or left side of the body on the loss rate. The same conclusion was drawn by Vincent et al. (2019) in the Western Pacific. Differences in shedding rate due to the location of the tag has also been reported for some species of marine mammals (Diefenbach and Alt, 1998; Bradshaw et al., 2000; McMahon and White, 2009; Oosthuizen et al., 2010; Schwarz et al., 2012) and marine turtles (Rivalan et al., 2005). This aspect is linked to the behaviour of the tagged individuals but as far we know that was not observed for tunas.

Another important point discussed in many double tagging studies is the presence of a tagger effect. The underlying idea is that less-experienced taggers may increase Type-I and Type-II shedding rates, as noted by Hearn et al. (1991), and Chambers et al. (2015) in tagging programs targeting southern Bluefin tuna. However, after comparing the parameter estimates with and without less-experienced taggers, Gaertner and Hallier (2015) concluded that shedding-rate models applied to tropical tunas in the Indian Ocean did not require adding estimates of individual shedding rates associated with each tagger. This is further supported by the findings of Hampton (1997) who reported that, despite identifying an apparent tagger effect, the subsequent consideration of this effect in the shedding-rate model did not significantly improve model performance. Although estimating a tagger effect on a variable of interest (e.g., shedding rate, tagging induced mortality) makes sense from a theoretical point of view, uncertainty in the way the tag release data were recorded and the lack of contrast and balance in the data (i.e., some taggers operating only in a few strata), is likely to be problematic. In addition, as mentioned by Hoyle et al. (2015), the efficiency of the tagging assistants who supply fish to the taggers as well the decision of whether or not to release a fish given its condition, may be additional sources of variation among taggers, which make it difficult to isolate the effect of skill when manipulating fish during tagging operations.

This study reinforces the needs to account for tag shedding rate with other sources of uncertainty, such as the reporting rate, in order to estimate exploitation and mortality rates derived from tagging data. For instance, large variations in return rates by unloading locations, flags and years have been highlighted (Hampton, 1997, Akia et al. (a) submitted in this issue). Carruthers et al. (2015) showed that although reporting rates in the Indian Ocean can be high for the European purse seiners (94%), they were estimated at 26% for baitboats and only between 2 and 16% for different fleets of longliners.

In this paper we focused only on estimating the Type I and II tag-shedding components of total loss. The tagging-induced mortality is not estimable by double tagging experiments as the entire statistical procedure is based on selecting individuals that have survived the tagging operation. In analyzing the recapture rates of large-scale tuna tagging programs in the Western Pacific and Indian Oceans, Hoyle et al. (2015) proposed to account for “tagging failure” by estimating the difference in return rates between the “base levels” of mortality and tag shedding (i.e., fish tagged and release in good condition by an expert tagger) and all other situations in which additional effects were due to factors being less than ideal (i.e. suboptimal release condition, lower levels of tagging experience). Based on low shedding rate estimates, they assumed that the majority of the high tagging failure estimates (20.5% in the Indian Ocean, and up to 28.4% (skipjack) and 44.9% (bigeye and yellowfin) in

the western Central Pacific) may be due to post-release mortality. It should be noted that based on this study, stock assessments conducted in the Indian Ocean used larger initial tag loss (i.e., “For the bigeye tuna, the recent assessments applied an initial tag loss of 30.5%, based on the initial tag mortality estimate of 20.5% (Hoyle et al. 2015), with a further 10% increase to account for an assumed level of tag mortality associated with the best (base) tagger” (IOTC, 2020)).

It is unclear however if these estimates reflect only tag-induced mortality, as previous studies suggested that the combination of type 1 tagging mortality and tag shedding should be low (Kleiber et al., 1987). They based their conclusion on the high return rate (> 50%) observed in the eastern Pacific and on the absence of difference in mortality on about 16 tagged and 14 untagged control skipjacks maintained in captivity for 7 weeks at Kewalo Basin, Honolulu. In the absence of further quantitative information, they assumed a figure of 10% for the total Type-1 losses. However, correcting the tagging database to account for these different uncertainties before introducing the tagging information in stock assessments models is fundamental and correcting procedures have been proposed (Berger et al., 2014).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRedit authorship contribution statement

Daniel Gaertner: Conceptualization, Formal analyze, Writing. **Lorelei Guery:** Conceptualization, Reviewing. **Nicolas Goñi:** Resources. **Justin Amandé;** Resources. **Pedro Pascual Alayon:** Resources. **Fambaye N’Gom:** Resources. **Joao Pereira:** Resources. **Ebenezer A. Addi:** Resources. **Lisa Ailloud:** Data curation, Reviewing; **Doug Beare:** Project administration.

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Table 1. Number of tropical tunas double-tagged by the AOTTP and percentage of recaptures made with two tags (Both) and one tag (Tag 1, assumed to be Left or Tag 2 assumed to be Right).

Species	Releases	Recovered	%Both	%Right	%Left
BET	4872	1172	93.69	3.92	2.39
SKJ	8786	486	90.74	4.94	4.32
YFT	6351	1437	90.47	4.66	4.87
Total	20009	3095			

Table 2. Parameter estimates for the constant-rate shedding model for different tuna species; bigeye (BET), skipjack (SKJ), yellowfin (YFT), albacore (ALB), bluefin (BFT), southern bluefin (SBY) from previous double-tagging studies in the world's oceans.

Species	α	95% C.I.	λ (per year)	95% C.I.	Study
BET	0.993	(0.985 - 1.000)	0.017	(0.008 - 0.025)	Gaertner and Hallier 2015 Hampton 1997
	0.953		<0.001		
SKJ	0.993	(0.987 - 1.000)	0.028	(0.018 - 0.040)	Gaertner and Hallier 2015 Adam and Kirkwood 2001 Hampton 1997 Kleiber et al. 1987
	0.970	(0.940 - 1.000)	0.220	(0.090 - 0.350)	
	0.965		0.086		
	?		0.088		
YFT	0.977	(0.968 - 0.986)	0.038	(0.027 - 0.050)	Gaertner and Hallier 2015 Hampton 1997 Bayliff and Mobrand 1972
	0.934		0.018		
	0.913	(0.852 - 0.974)	0.278	(0.271 - 0.285)	
ALB	0.880		0.092	(0.086 - 0.098)	Laurs et al. 1976
BFT	0.973		0.310		Lenarz et al. 1973
BFT	0.960		0.205		Baglin et al. 1980
SBT	0.979	(0.960 - 0.998)	0.066	(0.060 - 0.072)	Hearn et al. 2002
SBT	0.960	(0.900 - 0.976)	0.170	(0.049 - 0.290)	Hampton and Kirkwood 1989

Table 3. The different parameterizations of the constant-rate shedding model (A1, A2, A3, and A4) considered to determine how tag position (subscripts L and R , insertion in the left or right side of the fish, respectively) differentially affects shedding rates. K is the number of model parameters, nll is the negative log-likelihood, BIC is the Bayesian information criterion, Pr_i is the Bayesian posterior model probability, AICc is the small-sample-size corrected version of the Akaike information criterion, and W_i is the AICc weight.

Model	α	α_R	α_L	λ	λ_R	λ_L	K	nll	BIC	Pr_i	AICc	W_j
A1	0.992	NA	NA	0.102	NA	NA	2	424.923	864.549	0.950	853.854	0.529
A2	0.992	NA	NA	NA	0.098	0.106	3	424.880	871.800	0.025	855.755	0.202
A3	NA	0.992	0.992	0.102	NA	NA	3	424.923	871.886	0.024	855.861	0.194
A4	NA	0.992	0.993	NA	0.098	0.107	4	424.872	879.136	0.001	857.769	0.075

Table 4. Parameter estimates with 95% C.I. (bootstrapped confidence intervals for the frequentist model and MCMC credible intervals for the Bayesian model) for the constant shedding rate model for the 3 main tropical tuna species in the Atlantic Ocean. N.2 and N.1 represent the number of recaptures with 2 or 1 tag(s), respectively. Note that Type-I shedding is $1 - \alpha$

Species	α	95% C.I.	λ (per year)	95% C.I.	N. 2	N. 1	Model
BET	0.999	(0.995 - 1.000)	0.096	(0.080 - 0.108)	568	35	Frequentist approach
BET	0.997	(0.991 - 1.000)	0.095	(0.063 - 0.134)	568	35	Bayesian prior non informative
BET	0.993	(0.986 - 0.998)	0.087	(0.056 - 0.122)	568	35	Bayesian prior calculated
SKJ	0.988	(0.972 - 1.000)	0.062	(0.000 - 0.120)	228	13	Frequentist approach
SKJ	0.985	(0.965 - 0.998)	0.068	(0.010 - 0.143)	228	13	Bayesian prior non informative
SKJ	0.980	(0.964 - 0.992)	0.059	(0.016 - 0.116)	228	13	Bayesian prior calculated
YFT	0.985	(0.972 - 0.996)	0.108	(0.048 - 0.166)	706	56	Frequentist approach
YFT	0.984	(0.970 - 0.994)	0.110	(0.052 - 0.176)	706	56	Bayesian prior non informative
YFT	0.980	(0.968 - 0.990)	0.094	(0.047 - 0.146)	706	56	Bayesian prior calculated

Table 5. MCMC simulated yearly breakdown of proportions of tags lost, beginning immediately post-tagging and up to ten years post-release, estimated using the Bayesian constant-rate shedding model incorporating informative Beta priors.

Year(s) post-release	0	1	2	3	4	5	6	7	8	9	10
BET	0.007	0.089	0.164	0.233	0.296	0.354	0.406	0.455	0.499	0.539	0.576
SKJ	0.020	0.075	0.127	0.175	0.221	0.263	0.302	0.339	0.374	0.407	0.437
YFT	0.020	0.107	0.185	0.256	0.321	0.379	0.432	0.481	0.525	0.564	0.601

Table 6. MCMC parameter estimates (with informative Beta priors) and credible intervals (95% C.I.) for the constant shedding rate model by size category for the 3 main tuna species in the Atlantic Ocean. N.2 and N.1 represent the number of recaptures with 2 or 1 tag(s), respectively. Note that Type-I shedding is $(1 - \alpha)$.

Species/size	α	95% C.I.	λ (per year)	95% C.I.	N. 2	N. 1
BET <= 45 cm	0.984	(0.964 - 0.996)	0.039	(0.007 - 0.101)	72	0
BET 45 - 65 cm	0.989	(0.978 - 0.996)	0.071	(0.037 - 0.113)	336	20
BET > 65 cm	0.987	(0.971 - 0.997)	0.128	(0.066 - 0.202)	158	15
SKJ <= 45 cm	0.979	(0.958 - 0.993)	0.064	(0.014 - 0.139)	99	4
SKJ > 45 cm	0.976	(0.954 - 0.991)	0.057	(0.014 - 0.122)	129	8
YFT <= 45 cm	0.974	(0.949 - 0.992)	0.052	(0.010 - 0.124)	65	3
YFT 45 - 65 cm	0.976	(0.962 - 0.989)	0.065	(0.020 - 0.126)	377	27
YFT > 65 cm	0.981	(0.962 - 0.994)	0.163	(0.077 - 0.255)	262	26

Table 7. MCMC simulated yearly estimated breakdown of proportions of Atlantic yellowfin tags lost for 3 size categories at release, beginning immediately post-tagging until ten years-at-liberty, by the Bayesian constant-rate shedding model incorporating informative Beta priors.

Year after release	0	1	2	3	4	5	6	7	8	9	10
BET <= 45 cm	0.016	0.054	0.090	0.125	0.157	0.188	0.217	0.245	0.272	0.297	0.321
BET 45 - 65 cm	0.011	0.079	0.142	0.200	0.254	0.304	0.350	0.393	0.433	0.470	0.505
BET > 65 cm	0.013	0.131	0.235	0.325	0.403	0.472	0.533	0.586	0.633	0.674	0.710
SKJ <= 45 cm	0.020	0.081	0.137	0.189	0.236	0.281	0.322	0.360	0.395	0.428	0.459
SKJ > 45 cm	0.024	0.078	0.129	0.175	0.219	0.260	0.298	0.334	0.367	0.399	0.428
YFT <= 45 cm	0.026	0.074	0.120	0.162	0.202	0.239	0.274	0.307	0.338	0.367	0.394
YFT 45 - 65 cm	0.024	0.085	0.142	0.195	0.244	0.289	0.332	0.371	0.408	0.442	0.474
YFT > 65 cm	0.020	0.166	0.289	0.392	0.479	0.553	0.615	0.668	0.714	0.752	0.785

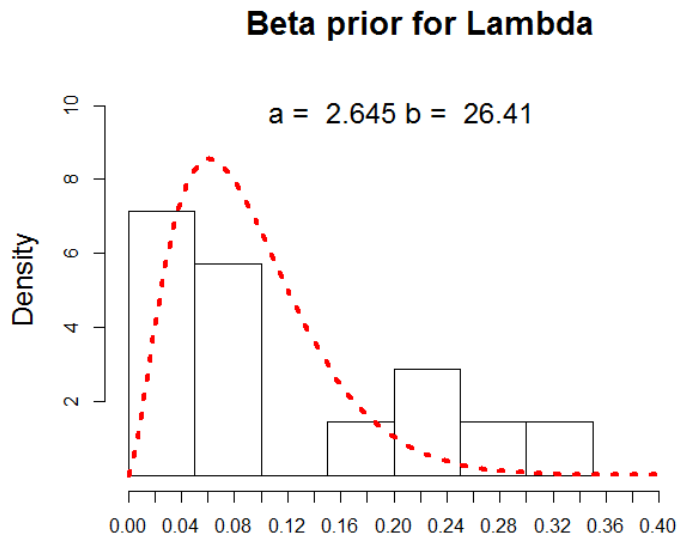
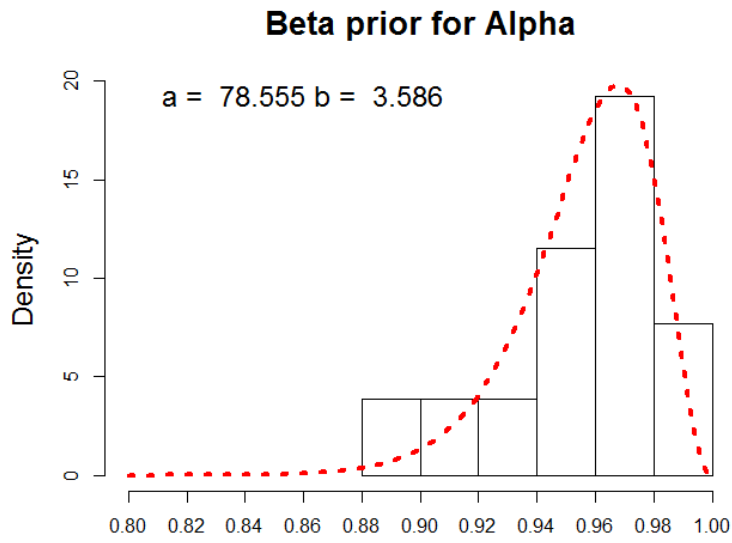


Fig. 1. Hyper-parameters of the Beta prior distribution (dashed line in red) for type I and II tag-shedding rates obtained from previous double-tagging experiments (histogram) conducted on different species of tunas in different parts of the world (see table 2).

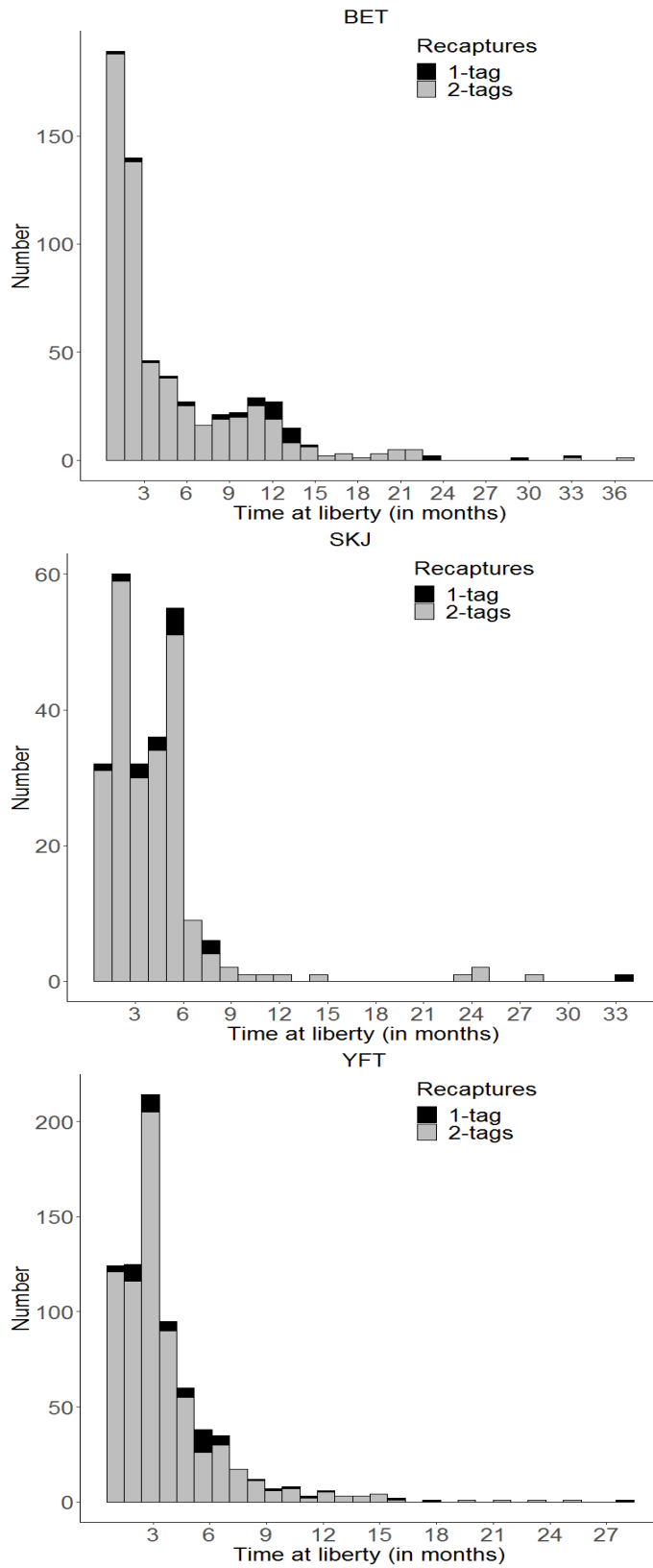


Fig. 2. Recaptures by time at liberty of tunas with 1 or 2 tags. From top to bottom: Bigeye (BET), Skipjack (SKJ), Yellowfin (YFT). Each bin represents one month at sea.

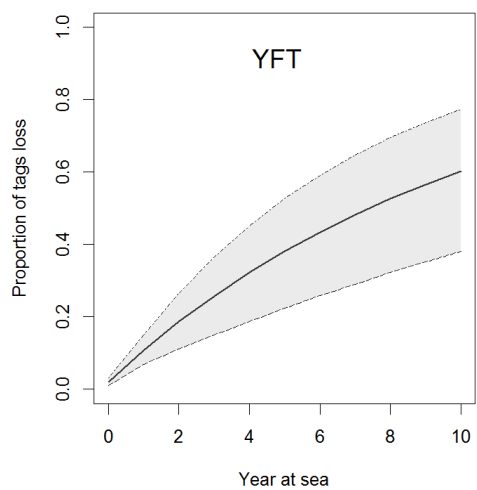
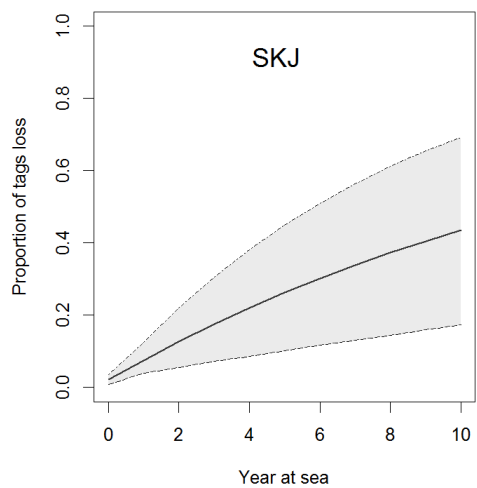
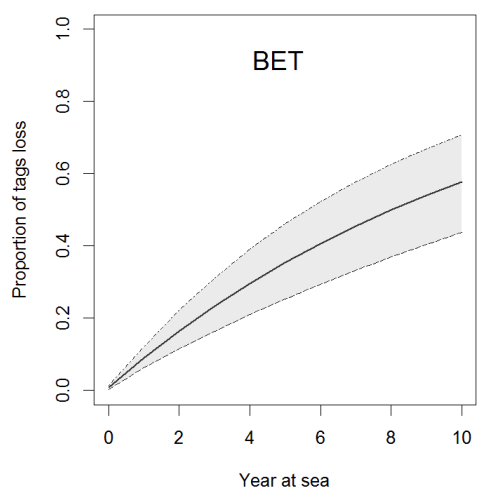


Fig. 3. Simulated proportion of tags lost ($1 - Q(t)$) from date at release for the Bayesian tag-shedding model with Beta priors estimated from previous double tags experiments conducted in different parts of the world. From top to bottom: Bigeye (BET), Skipjack (SKJ), Yellowfin (YFT).

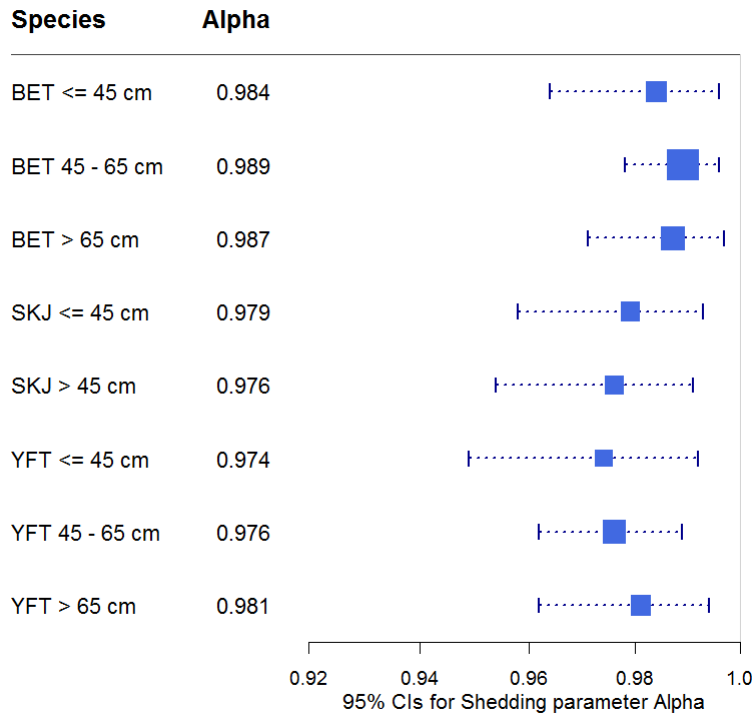


Fig. 4. MCMC posterior mean and 95% credible interval estimates of the Type-I shedding parameter α using the Bayesian model with informative Beta prior for the constant shedding rate model by tuna species and size category at release.

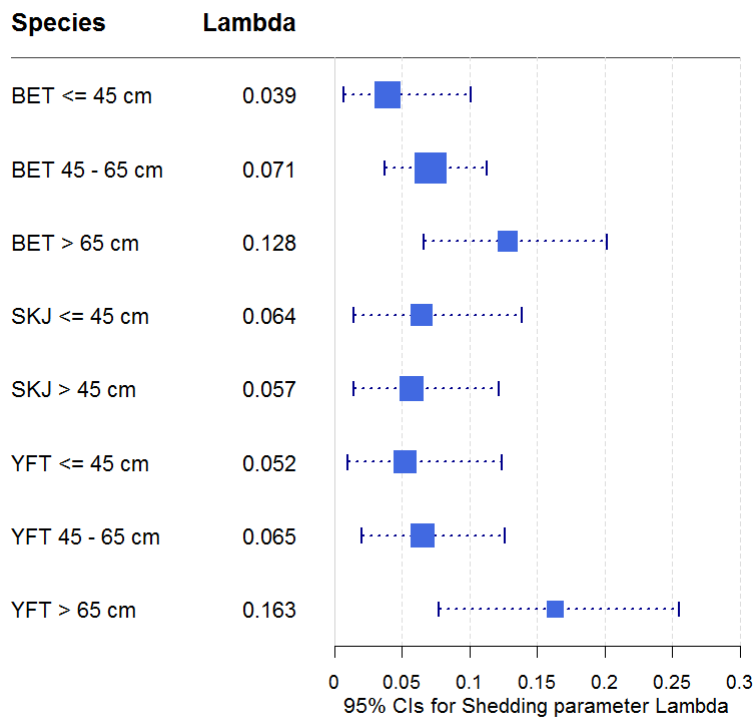


Fig. 5. MCMC posterior mean and 95% credible interval estimates of the Type-II shedding parameter λ using the Bayesian model with informative Beta prior for the constant shedding rate model by tuna species and size category at release.