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Tag shedding by tropical tunas in the Indian Ocean and other factors affecting the shedding rate

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A key objective of the Regional Tuna Tagging Project—Indian Ocean was to estimate tag-shedding rates, Type-I (immediate tag shedding) and Type-II (long-term tag shedding). To assess this, a series of double-tagging experiments (26,899 double tags released with 4555 recoveries) were conducted as part of the broader tagging program. After omitting data from tags placed by less experienced taggers, the results of our analyses did not show any evidence that individual differences between taggers (i.e., a tagger effect) impacted estimates of tag-shedding rates. However, it was shown that the probability of retaining the second tag (inserted in the left side of the fish) was larger than retaining the first tag (inserted in the right side, i.e., the side typically tagged in single-tagging experiments). We used a Bayesian model averaging approach to account for model uncertainty in the estimates of the parameters α and L used to calculate the probability of tag retention $Q(t) = \alpha\, e^{-(L\,t)}$ for the right tag. The parameter estimates were $\alpha = 0.993$ and L (per year) $= 0.030$ (skipjack); $\alpha = 0.972$ and L (per year) $= 0.040$ (yellowfin); and $\alpha = 0.990$ and L (per year) $= 0.021$ (bigeye). These results agree with estimates obtained by other large-scale tropical tuna tagging projects. We showed that tag loss has a moderate impact on the underestimation of the exploitation rate (bias $= 2$–6% depending on the tuna species). However, non-reporting leads to a bias of around 7% when using the high reporting rate estimate of purse seiners. Finally, tag shedding (specifically Type-II shedding) modified the individual weights of the samples of recaptures. Consequently, the total instantaneous mortality estimates (Z; calculated from mean times-at-large) were reduced by a range of 1–3%.

1. Introduction

Mark-recapture techniques can facilitate the collection of useful information for stock assessments, such as stock structure, growth and mortality rates, gear selectivity, and migration patterns. Consequently, tagging studies have become one the key tools used by tuna Regional Fisheries Management Organisations (RFMOs) to improve understanding of how populations are spatially structured and the effects of fishing on these populations. Integral to the use of tagging data are standardization models, such as tag-attrition models for single release events (Kleiber et al., 1987; Hampton, 1997) or Brownie models (derived from bird-banding studies) for multiyear studies (Brownie et al., 1985; Hoenig et al., 1998; Polacheck et al., 2010). 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. Ultimately, this leads to biased estimates of stock status. Thus, the objective of this paper is to update preliminary estimates of tag-shedding rates by tropical tuna in the Indian Ocean (Gaertner and Hallier, 2008, 2009).

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, immediate tagging mortality, and non-reporting), and Type-II losses which occur steadily over time (natural mortality, fishing mortality, permanent emigration, and long-term tag shedding). The current paper is only estimating the Type I and II tag shedding components of total losses. Immediate tag shedding and immediate tagging-induced mortality rates can be estimated by observing tagged fish under controlled laboratory conditions or in field cages (Pollock and Pine, 2007). However, post-release mortality estimates derived under these circumstances may be biased: in general, unlike wild fish, captive

Table 1
Number of double-tagged tuna (released in good condition, see Section 2.1) and the percentages of recaptures made (by species) between 2006 and 2012 with two tags (Both) and one tag (Right or Left) for bigeye (BET), skipjack (SKJ), and yellowfin (YFT).

BET				SKJ				YFT			
7310				Released 9309 Recaptured (%)				10,280			
Total	Both	Right	Left	Total	Both	Right	Left	Total	Both	Right	Left
15.84	15.14	0.25	0.45	15.65	14.94	0.32	0.39	18.87	16.81	0.90	1.16

fish are not affected by post-release predation. On the other hand, the act of restraining fish in confined conditions can have lethal or sublethal effects. An alternative approach to estimating mortality that is commonly used is double-tagging experiments in which a fish is tagged with two tags simultaneously. Double tagging can also be used to estimate tag-shedding rates by identifying fish that have lost a tag.

In general, shedding rates cannot be estimated from tag-return data directly. Consequently, different methods have been proposed to estimate shedding rates from double-tagging experiments. To maximize the accuracy of these estimates, it is crucial to have a firm understanding of the functioning of the range of other variables known to impact tag shedding. The Regional Tuna Tagging Project—Indian Ocean (RTTP—IO), which focuses on tropical tuna in the Indian Ocean, has already examined some of these variables. For example, there is no evidence, or it remains unclear, whether factors such as tag length (11 cm and 14 cm length tags) or tag position (right side versus left side of the fish) influence the rate of tag returns in RTTP-IO double-tagging experiments (Gaertner and Hallier, 2008). However, multiple taggers have been used over the duration of the program, and tag-return rates are known to vary substantially between taggers. Therefore, in this context, it is desirable to estimate how shedding rates vary among taggers.

Consequently, this study focused on (1) an analysis of the tagger effect and other explanatory variables that were hypothesized *a priori* to influence tag loss, (2) comparing the constant-rate and time-varying approaches to modeling tag-shedding rates, (3) an analysis of how the insertion position of the tag affects shedding rates, and (4) an investigation into the consequences of ignoring tag shedding and non-reporting on the estimates of exploitation rate and total instantaneous mortality.

2. Material and methods

2.1. Data

Over the duration of the RTTP-IO, a number of different tag types (e.g., conventional, archival) and tag colors have been used. Tag colors are used to indicate the presence of other tag types. Conventional tags are traditionally yellow, but a white version is used if oxytetracycline is also injected into the fish, and a red version is used when an additional archival tag is inserted. In the RTTP-IO, the single- and double-tagging experiments have been alternately performed and always used the conventional yellow 'spaghetti' tags. Our analysis focused on data collected from double-tagging experiments. We used only updated tagging data, which is comprised of tag recaptures reported from January 15, 2006 up until June 2012 for double-tagging experiments conducted onboard RTTP-IO bait boats. These experiments focused on the three main species of tropical tuna, yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*), and skipjack (*Katsuwonus pelamis*). Data for fish that were in a suboptimal condition, including those that showed signs of bleeding, had tail or mouth damage, were dropped on the deck, hit the side of the boat, or had shark bite injuries, were omitted from this analysis. This ensured that our analysis only considered fish that were

in good condition at release. In addition, we further restricted the data to only include records where the species were clearly identified at both release and recovery (for more information on how tag data are collected at release and recovery, see Hallier (2004) and Athayde et al. (2006)). Once these data were omitted, the data set analyzed in this paper included a total of 26,899 double-tagged release records and 4555 recoveries (thus far), which includes 329 records of fish that have lost one of their tags (Table 1).

To analyze the potential tagger effect on the shedding rate, double- and single-tag recoveries were pooled by tagging cruise and by tagger (hereafter referred to as a 'batch'). The proportion of single- and double-tagged fish can vary between batches and it is important to note these differences as they can potentially lead to biases in tag-shedding estimates (Hearn et al., 1991). Further, to avoid the high variability in shedding rates caused by low sample sizes, batches with <10 recoveries were omitted.

Recapture dates are needed to calculate the number of days at sea. When the exact date was lacking from the tagging data set, the date of recapture was estimated. This was done by averaging the dates of the sets in which the recaptured tag was most plausibly caught by purse seiners.

2.2. Methods

2.2.1. Estimate of a potential tagger effect on the shedding rate

Although a more sophisticated approach to evaluate differences between individual taggers has been proposed (Xiao, 1996), in this study, we assumed that the proportion of double-tagged fish recovered with only one tag is a linear combination of three categorical variables and one continuous variable. The categorical variables are the species S (yellowfin, bigeye, or skipjack), the tagger identification T, and the cruise identification C. The continuous variable is the tagger experience E, which is gained by each tagger over the length of the tagging program. Tagger experience was expressed as the cumulative number of fish tagged (single and double tags; all species) that were previously released by a tagger t, at the beginning of a cruise c. Consequently, to determine if shedding rates differed between taggers, we fit several candidate models, using different combinations of explanatory variables (assumed *a priori* to influence tag shedding, e.g., a cruise effect or the effect of a tagger's experience).

Owing to the clustered structure of the tagging data, it is logical to assume that the shedding rate y has extra-binomial variation. One way to account for this overdispersion is to use a probability model that applies a more general distribution, i.e., a beta-binomial model. The beta regression model is based on an alternative parameterization of the conventional beta density, and includes the variate mean μ, and a precision parameter ϕ. The beta density can thus be expressed as:

$$f(y; \mu, \phi) = \frac{\Gamma(\phi)}{\Gamma(\mu\phi)\Gamma((1-\mu)\phi)} y^{\mu\phi-1}(1-y)^{(1-\mu)\phi-1},$$

where $0 < y < 1$, $0 < \mu < 1$ and $\phi > 0$ (Ferrari and Cribari-Neto, 2004).

A beta-distributed variable y has the mean $E(y) = \mu$, and the variance $VAR(y) = \mu (1 - \mu)/(1 + \emptyset)$.

Let $y_1, \ldots, y_n$ be a random sample such that $y_i \sim B(\mu_i, \phi)$, where $i = 1, \ldots, n$. The beta regression model is defined as:

$$g(\mu_i) = \beta_1 x_{i1} + \cdots + \beta_j x_{ij},$$

where β is a vector of unknown coefficient and x is the vector of the j explanatory variables (e.g., tagger, cruise, etc.). A link function, $g(.)$, such that logit $g(\mu)$, probit $g(\mu)$, log–log $g(\mu)$, etc., allows for the mean μ to be linearly related to a set of regressors. This approach naturally incorporates the heteroskedasticity or skewness commonly observed in rate or proportion data. In addition, if the precision parameter is assumed not to be constant for all observations (i.e., $y_i \sim B(\mu_i, \phi_i)$), it can be modeled in a similar fashion to the mean parameter, i.e.,

$$g(\phi_i) = \gamma_1 z_{i1} + \cdots + \gamma_j z_{ij}$$

The analysis was conducted in R with the package betareg (Cribari-Neto and Zeileis, 2010;http://CRAN.R-project.org/package=betareg). The Bayesian information criterion (BIC) was used to objectively select a model from the set of candidate models considered. Each model had different explanatory variables; some, but not all, assumed a constant precision parameter.

$$\text{BIC} = -2 \log \left[L\left(\hat{\beta}, \hat{\gamma}/data\right) \right] + K \log(n)$$

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

However, it is problematic to choose the most probable model 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:

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

where

$\Delta BIC_i = BIC_i - \text{minBIC}$ (Burnham and Anderson, 2002).

It is noteworthy that the inferential model weights from the BIC selection have the same formula as the Akaike weights, but may be interpreted as probabilities of the model (given the data, model set, and prior model probabilities of each model). Therefore, the model with the largest Pr_i is the one with the highest probability of being the best model for the data set.

2.2.2. Modeling the shedding rate over time

Calculations to estimate tag-shedding rates from double-tagging experiments make 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). To determine the proportion of tags lost over time, recaptures are pooled by time intervals as follows (Chapman et al., 1965):

$$P.Obs.(t) = \frac{n^{ds}(t)}{\left(n^{ds}(t) + 2n^{dd}(t)\right)}$$

where n^{ds} is the number of fish recovered with one tag (ds), n^{dd} is the number of fish recovered with two tags (dd) and t is the mid-point of the time since release. Plotting the proportion of tags lost over time informs our understanding of the relationship between the shedding rate and the time-at-liberty. However, due to the low sample sizes for some of the time-at-liberty classes, there may
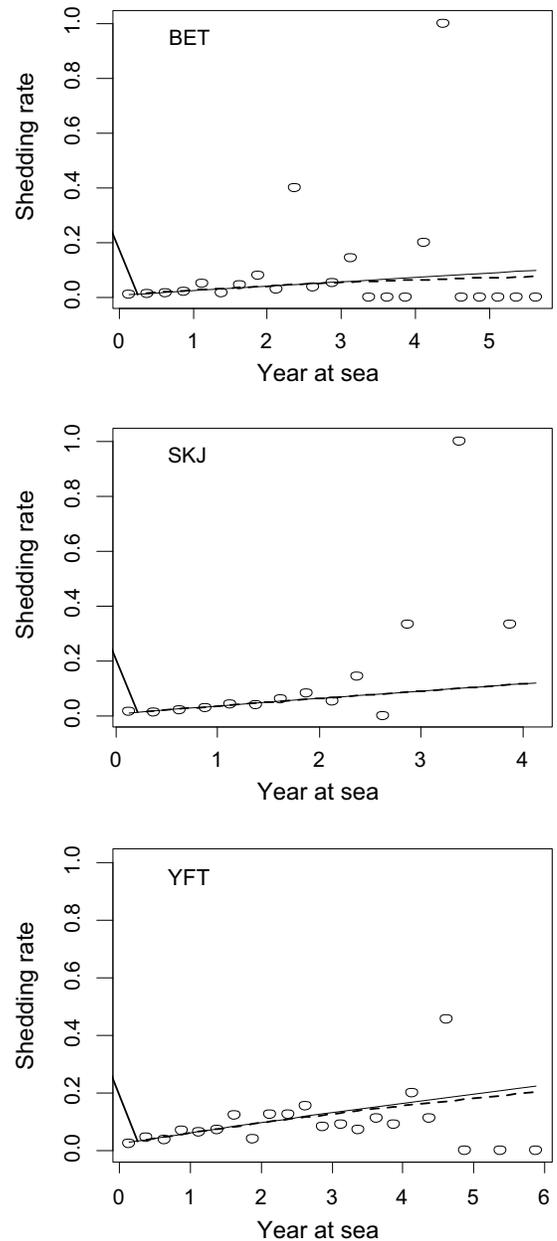
Fig. 1. Proportion of tags lost at sea per year in double-tagged fish by species: bigeye (upper panel), skipjack (middle panel), and yellowfin (lower panel). Hollow circles represent the observed tag-shedding rates by 90-day time periods, the solid line is the tag-shedding rate as estimated by the constant-rate model, and the dotted line is the tag-shedding rate as estimated by the time-varying model. Note that the apparent lack of fit is due to the models being fitted with exact time-at-liberty values, while the observed shedding rates represent observations pooled at a 90-day time period.

be some bias in the corresponding proportions (Fig. 1). Thus, it is more appropriate to model the tag-shedding process using 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 Brattey, 2006; Smith et al., 2009). Exact time-at-liberty tag-shedding models are formulated as follows. Assume that the probability $Q_A(t)$ of a tag-type A (as mentioned in Section 2.1, types of tags can differ in their form, color,

and size) being retained at time t after release can be expressed with the different models as:

model A: $Q_A(t) = \alpha_A e^{-(L_A t)}$ (Hampton, 1997; Adam and Kirkwood, 2001), or

model B: $Q_A(t) = \alpha_A \left[\beta_A / \left(\beta_A + \lambda_A t \right) \right]^{\beta_A}$ (Kirkwood, 1981; Hampton and Kirkwood, 1990) where α is the retention probability of the immediate Type-I shedding rate, L is the continuous Type-II shedding rate, and λ and β are the gamma parameters of L, allowing for the time-varying shedding rate to be a gamma-distributed random variable. Given this assumption, the probability of observing a tagged fish at time t after release is a combination of the reporting rate γ, and the probability of tag $Q(t)$ 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 have been tagged with a different type of tag or at a different insertion position. For non-permanent double-tagging experiments, the only recapture information available is whether a fish has retained one or both its tags. If reporting rates for double- and single-tagged fish are assumed to be equal 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

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

The probability of observing the outcome i, for a fish captured at time t, for each of these three possible outcomes is given by:

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

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

$$L_L = -\sum_{i=1}^{3} \sum_{j=1}^{n_i} Ln \left(\frac{P_i^{RL}\left(t_{ij}\right)}{\sum_{i=1}^{3} P_i^{RL}\left(t_{ij}\right)} \right)$$

2.2.3. Impact of tag shedding and tag reporting on population parameter estimates

Tag shedding and the non-reporting of recovered tags can potentially bias estimates of population parameters. Here, we explored this issue by examining (1) the exploitation rate and (2) the total instantaneous mortality rate, from 2006 to 2012. The corrected exploitation rate was estimated as the fraction of returned tags corrected for tag loss and assuming 100% retention and reporting of recaptured tagged fish. As suggested by Miranda et al. (2002), each return i was corrected for tag loss by dividing by the tag retention rate that corresponded to the amount of time that had elapsed between tagging and recapture (Q_{ti}). The corrected returns for this period were then summed (N_c) and corrected for the reporting rate (RR). This was then divided by the number of fish released (N_r):

$$E.R. = \frac{\sum_{i=1}^{N_c} \left[Q^{-1}(t_i) \right] RR^{-1}}{N_r}$$

Because the tag-shedding and reporting rates are never known with certainty, corrected fishery indicators include an error that propagates with each correction applied. To account for this uncertainty, and in particular, the correlation among the retention parameters, we performed a Monte Carlo simulation of 1000 pairs of joint values of α and L. These were generated previously for the

calculation of the bootstrapped confidence intervals of the simplest constant-rate tag-shedding model (A1). We assumed that the reporting rate was beta distributed, with parameters β_1 and β_2 calculated by the method of moments from mean μ and standard-deviation σ as follows:

$$\beta_1 = \mu \left(\frac{\mu(1-\mu)}{\sigma^2} - 1 \right)$$

$$\beta_2 = (1 - \mu) \left(\frac{\mu(1-\mu)}{\sigma^2} - 1 \right),$$

with $\mu = 0.9364$ and $\sigma = 0.0058$, estimated for purse seiners by Carruthers et al. (2013).

Consequently, 1000 reporting proportions were randomly drawn from this beta distribution during the Monte Carlo simulation.

For the mortality rate derived from single-tag recoveries, we used an estimator of total instantaneous mortality rate (Z) that only uses the mean of times-at-large from tag recoveries ($\bar{t}$). The Chapman estimator (finite-sample corrected) is assumed to be unbiased in comparison with Gulland's original formulation (McGarvey et al., 2009);

$$Z_{chap} = \left(\frac{N_c - 1}{N_c} \right) \frac{1}{\bar{t}}$$

The adjusted number of recaptures (N_{ccor}) was corrected in the same manner as the numerator of the corrected exploitation rate, while the mean time-at-large was calculated as a weighted mean in which individual times-at-large t_i were corrected for tag shedding and non-reporting:

$$\bar{t} = \frac{\sum_{i=1}^{N_r} W_i t_i}{N_{ccor}}$$

where

$$W_i = Q^{-1}(t_i) RR^{-1}$$

Essentially, this correction procedure will have the greatest impact on those recaptures with the longest times-at-large.

For both population parameters, we calculated the percentage bias against the non-corrected parameter. For example, for the mortality rate derived from single-tag recoveries $Zchap$, the bias was calculated as:

$$\bar{Z}_{bias} = \frac{\sum_{b=1}^{1000} \left(Z_{corb} - Z_{chap} \right) / Z_{chap}}{1000}$$

3. Results

Although the beta-binomial model already naturally incorporates a certain pattern in the variances of the response, it can be necessary to also explore a variable dispersion model by incorporating an additional set of regressors in the precision sub-model. It then becomes possible to check whether the precision parameter $\emptyset$ is constant for all observations. With this in mind, the set of candidate models in this study were ranked on the basis of their BIC values, with the lowest value indicating the best approximating model (Table 2). Posterior model probabilities confirmed that the model with the highest posterior probability was the most plausible, given the data and the set of candidate models. The best model ($Pr_i = 0.992$) only considers the species effect S in the parameterization of the beta density (in terms of the variate mean). Accordingly, our results suggest that there is no evidence that individual taggers affect tag-shedding rates differently.

However, after further screening, the data indicated that the single-tag shedding rates showed greater variability in less
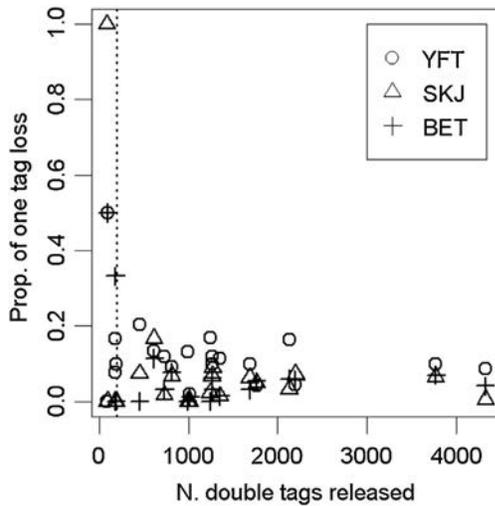
Fig. 2. Proportion of the total number of double-tagged fish that retained only one tag, by the total number of fish tagged by each tagger. The vertical dotted line represents the threshold of 200 fish per tagger, which we used to differentiate between more- and less-experienced taggers. Data values to the left of this line were omitted from our analyses.

experienced taggers (<200 double-tag releases) than experienced taggers (Fig. 2). Consequently, a 200 tag-release threshold was implemented to remove unusually large proportions of single-tag losses. This was done even in cases where a less-experienced tagger showed similar shedding rates to more experienced taggers. We used this restricted data set to make a comparison between

Table 2
The set of candidate models (and corresponding values calculated to select the best model) to determine tag-shedding rates from data collected in double-tagging experiments. K is the number of model parameters; BIC is the Bayesian Information Criterion; and Pr_i is the Bayesian posterior model probability. Models have been ranked from best to worst according to the Pr_i. Explanatory variables, used to build the mean and the precision submodels of the candidate beta-binomial models, were species (S), tagger (T), cruise (C), and experience gained by the tagger over the period considered (E).

Mean	Beta-binomial precision	K	BIC_i	Pr_i
S		4	−565.31	0.992
S	S	6	−555.54	0.001
S	C	17	−522.06	0.000
$S+T$		22	−496.55	0.000
S	T	22	−494.93	0.000
$S+T+E$		23	−491.56	0.000
$S+T$	S	24	−488.80	0.000
$S+T$	C	35	−481.95	0.000
$S+T$	T	40	−480.77	0.000
T		20	−474.97	0.000
$S+T$	$T+C$	53	−466.29	0.000
$S+T+C$		35	−447.61	0.000
S	$C+T$	35	−445.85	0.000
$S+T+C+E$		36	−443.05	0.000

the constant-rate (A) and the time-varying (B) tag-shedding models. Both models use exact times-at-liberty values gathered in double-tagging experiments. In this study, as compared with the preliminary analysis undertaken by Gaertner and Hallier (2008), updated tagging data were used that integrated longer recovery periods. This enabled us to make an assessment as to whether a time-varying shedding rate may be used as an acceptable alternative to the constant-rate shedding rate. However, the updated analysis indicated that substituting L (the constant, long-term Type-II shedding) with two gamma parameters (i.e., to allow a time shedding rate) does not improve the model fit (Table 3). Therefore, we support the continued use of a constant-rate model for characterizing tag-shedding rates of tropical tunas (Fig. 1).

To investigate the effects of tag position on the tag-shedding rate, 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 L_R and L_L to vary as a descriptor of position effect in 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 L is assumed to be independent of the insertion point(s)); and Model 4 (A4) assumed a specific position estimate for all four parameters (α_R, α_L, L_R, and L_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. Recapture percentages for the second tag (located on the left side of the fish; Table 1) are presented in terms of the different retention parameter values (Table 4). In this study, our analysis did not suggest that there was a single best model for all three tuna species. Although the AIC and BIC are both penalized-likelihood criteria, they reflect subtle theoretical differences: AIC focuses on the best variance-bias tradeoff in a set of candidate models (i.e., the parsimonious model in terms of a frequentist approach), while the BIC identifies the "quasi-true" model. Consequently, the type of criteria used can drive some differences in which model is selected. In this analysis, for skipjack, the BIC-selected model (A2) suggests that tag position affects Type-II shedding, while the parsimonious model selected with AICc (A1) assumes tag position has no effect. For bigeye and yellowfin, the AICc and BIC selected the same model, A3, which assumes tag position affects Type-I shedding (A3; Table 4). Neither model dominates the others and there is no clear biological reason for why tag position on the side of the body affects tag-shedding rates differently between the three species. Given these uncertainties, and considering that the main objective of this study is to correct the bias in population parameters estimated from single-tagging experiments, we used a Bayesian model averaging approach (Hoeting et al., 1999) to calculate a weighted average of the retention parameters for both right- and left-sided tags. It should be noted that Type-I $(1-\alpha)$ and Type-II (L) shedding rates are higher for tags inserted on the right side of the fish rather than the left (Table 5). In

Table 3
A comparison between parameter estimates for the constant-rate (A) and time-varying (B) models used to estimate tag shedding rates, where Ndd is the number of double-tagged fish caught with two tags; Nds is the number of double-tagged fish caught with only one tag; BIC is the Bayesian information criterion; and Pr_i is the Bayesian posterior model probability. Both models were ranked from best to worst (according to the Pr_i) by species: bigeye (BET), skipjack (SKJ), and yellowfin (YFT).

Species	Model	α	L (per year)	β	Ndd	Nds	BIC_i	Pr_i
BET	A	0.993	0.017		1079	48	396.37	0.958
	B	0.995	0.023	0.081			402.61	0.042
SKJ	A	0.993	0.029		1374	65	520.44	0.974
	B	0.993	0.029	90315.9			527.72	0.026
YFT	A	0.977	0.038		1717	204	1264.65	0.977
	B	0.978	0.042	0.454			1272.11	0.023

Sp.	Model	α	α_R	α_L	L	L_R	L_L	K	BIC	Pr_j	AICc	W_j
BET	A1	0.993	NA	NA	0.017	NA	NA	2	441.78	0.026	432.39	0.048
	A2	0.993	NA	NA	NA	0.025	0.008	3	436.83	0.306	428.75	0.297
	A3	NA	0.988	1	0.017	NA	NA	3	436.64	0.336	428.56	0.327
	A4	NA	0.990	0.999	NA	0.022	0.014	4	436.66	0.333	428.56	0.328
SKJ	A1	0.993	NA	NA	0.028	NA	NA	2	590.00	0.252	580.61	0.393
	A2	0.993	NA	NA	NA	0.033	0.023	3	589.67	0.297	581.59	0.240
	A3	NA	0.991	0.995	0.027	NA	NA	3	590.13	0.236	582.05	0.191
	A4	NA	0.993	0.993	NA	0.033	0.023	4	590.32	0.215	582.21	0.176
YFT	A1	0.977	NA	NA	0.038	NA	NA	2	1527.95	0.074	1518.57	0.133
	A2	0.977	NA	NA	NA	0.047	0.031	3	1526.00	0.204	1517.85	0.191
	A3	NA	0.970	0.984	0.038	NA	NA	3	1524.49	0.420	1516.41	0.392
	A4	NA	0.970	0.983	NA	0.039	0.037	4	1525.16	0.301	1517.05	0.284

Sp.	Right side		Left side	
	α	L	α	L
BET	0.990	0.021	0.997	0.013
SKJ	0.993	0.030	0.993	0.025
YFT	0.972	0.040	0.982	0.036

Sp.	Non corrected	Corrected shedding	Bias (%)	Shedding + reporting	Bias (%)
BET	16.19	16.52 (16.49–16.54)	2.01 (1.88–2.13)	17.64 (17.44–17.88)	8.98 (7.69–10.44)
SKJ	16.53	16.92 (16.91–16.94)	2.37 (2.28–2.47)	18.07 (17.87–18.30)	9.31 (8.08–10.69)
YFT	18.61	19.72 (19.68–19.76)	5.98 (5.80–6.18)	21.06 (20.81–21.34)	13.17 (11.86–14.69)

single-tagging experiments, tags are most-commonly inserted into the right side of the fish.

Not accounting for tag-shedding losses or the non-reporting of tag recaptures can potentially bias stock assessment studies and we simulated these events to examine these biases further (Tables 6 and 7, respectively). As expected, correcting for tag losses and non-reporting increases the number of potential recoveries. Consequently, the exploitation rate estimate increases and the corresponding confidence intervals widen. Depending on the species, not accounting for tag shedding creates a bias of between 2% and 6% in the exploitation rate estimate (Table 6). This is comparatively low as compared with the bias caused by the combined effect of non-reporting and tag shedding (9–13%). The total instantaneous mortality (estimated using mean times-at-large) is not impacted by non-reporting and Type-I shedding (α), as they are not time-dependent (as every tagged fish has the same probability of being present or not present in the sample of recoveries). However, the Type-II shedding (L) rate is time-dependent and may bias estimates of Z because fish that spend the longest time at sea will have the largest probability of shedding a tag. This means that the proportion of the fish with high times-at-sea values will be underrepresented in the recapture samples. Ours results show that Type-II shedding causes a moderate bias, i.e., 3% for yellowfin (the longest living of the three tuna species; Table 7).

4. Discussion

A number of factors are known to affect tag-shedding rates. For example, it has been established that shedding rates may be impacted by the type of external tag used, with several studies having shown differences in the retention rates of dart and T-bar tags (Boucek and Adams, 2011). For tropical tunas, a comparison

Sp.	Non corrected	Corrected shedding	Bias (%)	Shedding + reporting	Bias (%)
BET	1.28	1.27 (1.26–1.28)	−1.19 (−1.73 to −0.55)	1.27 (1.26–1.27)	−1.19 (−1.73 to −0.55)
SKJ	1.73	1.71 (1.70–1.72)	−0.99 (−1.37 to −0.62)	1.71 (1.70–1.72)	−0.99 (−1.37 to −0.62)
YFT	1.13	1.09 (1.08–1.10)	−3.06 (−3.89 to −2.14)	1.09 (1.08–1.10)	−3.06 (−3.89 to −2.14)

Table 8

Parameter estimates with bootstrapped 95% confidence intervals (95% B.C.I.) for the constant-rate shedding model (with a retention probability $Q(t) = \alpha \exp^{(-Lt)}$; Model A1) by species; bigeye (BET), skipjack (SKJ), and yellowfin (YFT). For comparison, estimates developed using a Bayesian averaging model (BMA) approach for the right tag and those calculated in previous studies are presented (noting that Chapman et al., 1965 did not consider Type-I shedding in their calculations).

Species	α	95% B.C.I.	L (per year)	95% B.C.I.	
BET	0.993	(0.985–1.00)	0.017	(0.008–0.025)	Present study (A1)
	0.990		0.021		Present study (right tag)
	0.953		<0.001		Hampton (1997)
SKJ	0.993	(0.987–1.00)	0.028	(0.018–0.040)	Present study (A1)
	0.993		0.030		Present study (right tag)
	0.97	(0.94–1.00)	0.22	(0.09–0.35)	Adam and Kirkwood (2001)
	0.965		0.086		Hampton (1997)
YFT	0.977	(0.968–0.986)	0.038	(0.027–0.050)	Present study (A1)
	0.972		0.040		Present study (right tag)
	0.934		0.018		Hampton (1997)
	0.913		0.278		Bayliff and Mobrand (1972)
	NA		0.814		Chapman et al. (1965)

has been made between the conventional yellow 'spaghetti' tag and another tag commonly used by sport fishermen to opportunistically tag tunas and billfishes, the Betyp tag. Results from a tag-attrition model and Bayesian analysis showed that immediate post-release mortality in bigeye tuna tagged in the Atlantic Ocean was around 23% higher when Betyp tags were used, as compared to conventional tags (Gaertner et al., 2004; Gaertner and Hallier, 2004). Another factor that is thought to influence tag-shedding rates is the experience of the tagger. If this factor is not accounted for, it is suggested that estimates of tag-shedding rates will be biased (Hearn et al., 1991).

To assess whether the individual experience of a tagger had an effect, we fit a set of beta-binomial models to updated tagging data. These models related tag loss to four different explanatory variables, one of which was tagger effect. From our results, it can be concluded that (after omitting data from less-experienced taggers) there was no evidence that a tagger's level of experience affected tag-shedding rates. To reinforce this point, the constant-rate model parameters were recalculated after reintroducing the data from the less-experienced taggers. From this, tag-shedding estimates (with their associated 95% confidence intervals) were α (0.993; 0.985–1.000) and L (0.017; 0.008–0.025) for bigeye, α (0.993; 0.986–1.000) and L (0.028; 0.016–0.040) for skipjack, and α (0.974; 0.964–0.983) and L (0.037; 0.025–0.049) for yellowfin. None of these estimates showed evidence of bias, and all are very close to the estimates calculated from the reduced data set (Table 8). This result suggests that shedding-rate models do not require parameters that describe a tagger effect. 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.

The second objective of this study was to compare two approaches to modeling tag-shedding rates: the constant-rate model and the time-varying model. Our analysis indicated that adding a time variable did not improve model fit, which leads us to support the ongoing use of the constant-rate model. Using this model, we generated low tag-shedding parameters (the Type-I retention probability α, and Type-II shedding rate L), which are similar to values previously reported in the literature (Table 8; Hampton, 1997; Adam and Kirkwood, 2001). An exception to this is the relatively high L value (0.22) reported by Adam and Kirkwood (2001) for skipjack in Maldivian waters. Emigration from the fishing ground may, in part, explain why this value is higher.

During tagging operations, there are marked differences in the behavior of the three species, with bigeye and yellowfin remain relatively calm, while skipjack become frenetic. This frenetic behavior might be expected to increase immediate tag losses and/or immediate tagging-related mortality. However, this assumption is not

supported by our findings, which showed that the Type-I shedding rates are very similar between the three species.

Given the effort required to accurately assess Type-I and Type-II tag losses, we also set out to investigate the consequences of not accounting for either tag-shedding or tag-shedding and non-reporting rates when estimating key population parameters. For exploitation rate estimates, our simulations indicated that not accounting for these tag losses would cause substantial bias. In this study we used tag-reporting values estimated for European Union purse seiners by Carruthers et al. (2013). This estimate was high (93.6%) in comparison with estimates derived for handline fisheries (18.8%), gillnet fisheries (12%), and different longline fisheries (3.5% to 16.4%). As such, it might be inferred that the effects of tag shedding on the accuracy of exploitation rate estimates was smaller than the effects of non-reporting.

With regard to time-at-large Z estimates, we showed that biases have a moderate range because only continuous type-II shedding rate (L) may affect this index and that no bias is introduced by non-reporting, as previously reported by McGarvey et al. (2009). However, as suggested by simulations study under particular mortality combinations, immediate shedding and handling mortality can have significant effects on estimates of M (Brenden et al., 2010). It is of particular importance to know the influence of these factors when estimating mortality rates. Furthermore, before tagging data is used in sophisticated integrated stock assessment models, it should be analyzed separately to evaluate the potential biases generated by the violation of these assumptions.

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) their tags, this assumption may not be valid, which has broader implications for the estimation of vital life-history traits. Further, for species for which it is possible to combine permanent and temporary tags, the assumption of tag independence may lead to underestimations in tag losses, e.g., for marine mammals, specifically in relation to the behavior of the tagged individuals (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). In this study, we followed the assumption of independent tag shedding but assessed the assumption that both tags have an equal probability of retention. The benefits of coupling temporary double tags with a permanent tag in double-tagging experiments have been suggested by simulation studies (Venerus et al., 2013). Using this approach would enable scientists to distinguish individuals who have lost both tags from individuals who were never tagged. With this additional information, the need to make a generalized assumption of independence in tag shedding events is removed, and the tag-shedding rate could

Table 9
Yearly estimated breakdown of proportions of species in tags lost, beginning immediately post-tagging until five years-at-liberty, by the constant-rate shedding model.

	Years					
Species	0	1	2	3	4	5
BET	0.004	0.020	0.035	0.051	0.066	0.081
SKJ	0.007	0.035	0.063	0.090	0.116	0.141
YFT	0.018	0.053	0.086	0.119	0.150	0.180

be determined for each tag separately. However, to the best of our knowledge, this approach has not been implemented in tuna tagging programs.

Finally, a key conclusion of this analysis is that the updated estimates of yearly tag loss proportions (by species) appear moderate, but the cumulative proportion of tags (lost over the five-year post-release period) are significant. For instance, for yellowfin, which experienced the largest shedding rate, 18% of tags were lost after five years at liberty (Table 9).

Author contributions

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