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ARTICLE

Southern bluefin tuna (*Thunnus maccoyii*) shed tags at a higher rate in tuna farms than in the open ocean — two-stage tag retention models

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Abstract: Tag shedding rates are estimated for southern bluefin tuna (SBT, *Thunnus maccoyii*) from double-tagging data arising from two tagging studies run in the 1990s and 2000s. Since the early 1990s, a high proportion of SBT tag recoveries has been sourced from juveniles captured by purse seine vessels in the Great Australian Bight and transferred to tuna farms off Port Lincoln in the state of South Australia. When tags have been shed by wild-caught SBT fattened in tuna farms, it is generally not known if the tags were shed in the open ocean before purse seine capture or after purse seine capture while the fish were on farm. Using a Bayesian approach, we fit separate tag retention curves for time in the ocean and time on farms as Weibull distribution reliability functions. The study suggests SBT shed tags at a much higher rate in on-farm enclosures than in the open ocean. Biofouling on tags in tuna farms may contribute to higher tag shedding rates.

Résumé : Les taux de perte d'étiquettes sont estimés pour le thon rouge du Sud (TRS, *Thunnus maccoyii*) à partir de données de marquage double tirées de deux études de marquage menées dans les années 1990 et 2000. Depuis le début des années 1990, une forte proportion d'étiquettes de TRS récupérées proviennent de juvéniles capturés par des navires à senne coulissante dans la Grande Baie australienne, puis transférés dans des élevages de thons au large de Port Lincoln, dans l'État d'Australie-Méridionale. Quand les étiquettes perdues proviennent de TRS capturés dans la nature et engraissés dans des élevages, on ne sait généralement pas si elles ont été perdues en pleine mer avant la capture par senne coulissante ou après cette capture, alors que les poissons étaient en élevage. En utilisant une approche bayésienne, nous avons calé différentes courbes de rétention d'étiquettes pour le temps passé en pleine mer et le temps passé en élevage en tant que fonctions de fiabilité de la distribution de Weibull. L'étude donne à penser que les TRS se départet de leurs étiquettes à un taux beaucoup plus élevé dans les bassins d'élevage qu'en pleine mer. L'encrassement biologique des étiquettes dans les élevages pourrait en partie expliquer les taux plus élevés de perte d'étiquettes. [Traduit par la Rédaction]

Introduction

Tag recovery data from fish tagging studies are used to estimate a range of quantities important for the management of harvested fish stocks. Some information, such as growth rates and stock delineation can be inferred by considering the particular characteristics of many individual tag recoveries. However, statistical inference for the three basic tagging study designs useful for analysis of commercial fisheries (Polacheck et al. 2010), the Petersen, the tag attrition, and the Brownie designs, all rely upon either the proportion of tags recovered or the rate at which tags are recovered.

In their most basic form, tagging experimental designs assume there is no tag loss due to shedding of tags and no increased mortality of tagged fish compared with untagged fish (Polacheck et al. 2010). However, in many situations the assumption of no tag loss is unreasonable (Xiao et al. 1999). In these cases, reliable inference from tag recovery data requires accounting for the effects of tag shedding.

Beverton and Holt (1957) describe how, given certain assumptions, if two tags instead of one are attached to some or all tagged fish, tag shedding rates can be estimated from the relative numbers of initially double-tagged fish recovered that retain one and two tags. They propose tag losses might occur by two modes: type 1 losses that occur essentially immediately after tagging, such as when tags are poorly inserted, and type 2 losses that occur at random at any time after at some steady rate. Improvements on the original theory are summarized in Wetherall (1982). More recent developments are described in Kirkwood and Walker (1984), Xiao (1996) and Cadigan and Brattey (2003).

Tagging programs for southern bluefin tuna (SBT, *Thunnus maccoyii*) have been run intermittently since the late 1950s. Double-tagging of all fish has been routinely practiced and tagging procedures have been refined over time. Recoveries from these programs have been considered a number of times for the purpose of estimating rates of tag shedding in SBT (Kirkwood 1981; Hearn 1986; Hampton and Kirkwood 1990; Hearn et al. 1991). Historically, the majority of tag recoveries were sourced from the Australian surface fishery that harvested juveniles using pole and line and purse seine, with smaller numbers recovered from Japanese longline fleets (Caton 1991, their table 23).

In 1992 the first commercial SBT farms began fattening wild-caught SBT in large mesh enclosures moored offshore near Port Lincoln in South Australia (see for e.g., Carter et al. 2010). Since the commencement of tuna farming, a large proportion of SBT tag recoveries has been sourced from the tuna farms. Most tags recovered from farms are not detected until the tunas are harvested, meaning the recovered tags were necessarily retained for a certain

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Fig. 1. Dissection of double-tagged southern bluefin tuna (SBT) showing properly inserted tags (source: CSIRO).

period in the open ocean as well as an additional period on the tuna farm. More importantly, when tags are observed to have been shed, it is not known if they were shed before purse seine capture in the open ocean or after purse seine capture in the on-farm enclosures. Tag recovery data from the 1990s SBT tagging study have been modelled previously (Polacheck et al. 2006*a*, 2006*b*) to estimate rates of juvenile natural mortality as well as the population size and exploitation rates of tagged cohorts. These data are also an important input in the integrated stock assessment model used to estimate the global population of SBT (Anonymous 2011). These previous analyses do not consider the possibility that SBT might shed tags at different rates in tuna farms as compared with the open ocean. If tag shedding rates in farms are different to the open ocean, reliable estimation of the proportion of tags lost due to tag shedding will require accounting for this difference.

The date of purse seine capture is known to within a few days for most recoveries sourced from the tuna farms. Given this information, we use a Bayesian graphical model approach to model tag retention of SBT recovered from tuna farms as a two-stage process: the first stage while the tags were in the open ocean and the second stage while they were on farms. For each stage we assume the probability of tag retention follows a Weibull distribution reliability function expressed in terms of exact time at liberty.

Materials and methods

Tagging SBT

Tagging studies of juvenile SBT have been run off the southern and eastern coasts of Australia since the late 1950s. Juvenile SBT are caught with barbless hooks using pole and line. Once onboard the tagging vessel, the tuna is placed in a specially designed vinyl cradle where a tagging technician inserts a tag into the musculature on either side of the fish between 1 and 5 cm below the posterior insertion of the second dorsal fin (Hampton and Kirkwood 1990). Ideally, the tags are inserted such that the barbs are anchored behind the ray extensions of the second dorsal fin (Fig. 1). Refer to Bradford et al. (2009) for more information on tagging procedures used in SBT tagging studies.

Ranching of SBT

In 1992, the first commercial SBT farms began fattening wild-caught SBT in large meshed enclosures inside static ranching pontoons moored offshore. The commercial enterprises followed promising early results from an experimental trial started in 1991 (Bergin and Haward 1994).

Commercial spotter planes are used to locate suitable surface schools of juvenile SBT, most between 2 and 5 years of age, in the Great Australian Bight. Purse seine vessels are used to capture the schools of tuna. Once a school has been captured, transfer gates are used to create a connection between the purse seine net and a specially designed tow pontoon. The purse seine net is then hauled onboard the vessel to reduce the water volume in the capture net, directing the juvenile tuna through the transfer gates and into the tow pontoon enclosure. Once the catch from between three and seven purse seine shots has been transferred to the tow pontoon, it is towed slowly to tuna farms in the Spencer Gulf near Port Lincoln, South Australia. Upon arrival, the tuna from the tow pontoon are transferred to static ranching pontoons. Up to five static ranching pontoons can be stocked from a single tow pontoon (Jeffriess 1999).

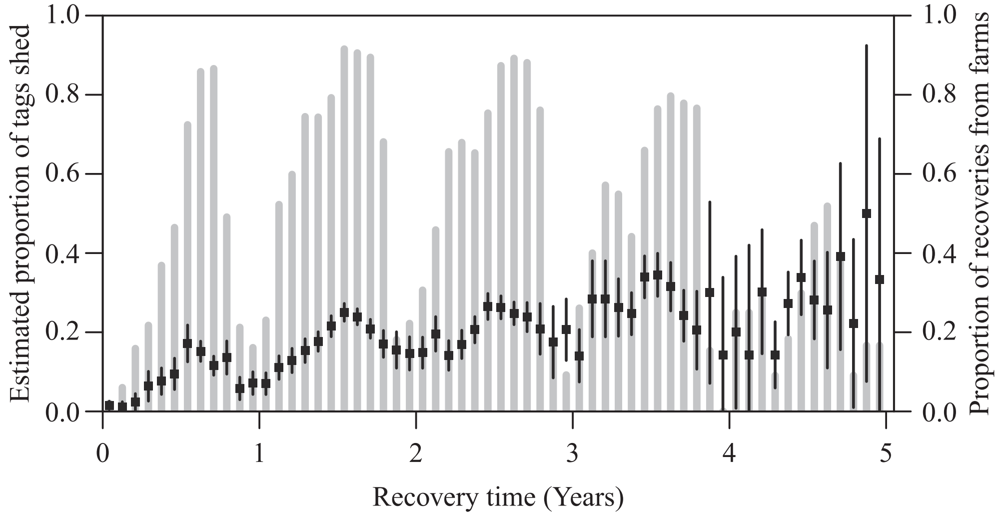
The economic benefits derived from farming SBT stimulated rapid investment in the industry, and by 1999 the entire catch of the Australian surface fishery was transferred to tuna farms for fattening prior to harvest and export (D. Ellis, Australian Southern Bluefin Tuna Industry Association, Port Lincoln, South Australia, personal communication, 2013).

Recent tagging studies

Around 150 000 juvenile SBT were double-tagged off the southern coast of Australia during the austral summers between 1990–1991 and 2006–2007 in two separate studies. The first study was run between 1990–1991 and 1996–1997 and is described in detail by Polacheck et al. (2006*a*). The second study was run between 2000–2001 and 2006–2007 with a similar design, but recoveries from the 2000s study have not yet been comprehensively analysed.

Unlike previous tagging studies of SBT, a large proportion of recoveries from the two most recent studies were sourced from the farm sector. This has important implications for the interpretation of these tagging data, since the process used to capture and transfer the wild-caught juvenile SBT to the on-farm ranching pontoons, as described earlier, provides very limited opportunity to inspect the captured SBT for tags while they are transferred. Consequently, for most recoveries sourced from tuna farms, the time interval from tagging to tag inspection comprises two distinct stages: time in ocean (t_O) and time on farm (t_F). We shall refer to the time interval between tagging and tag inspection as the

Fig. 2. Maximum likelihood estimates (black squares) of proportion of tags shed with asymptotic 95% confidence intervals (black vertical lines) for recoveries from the 1990s and 2000s tagging studies with recovery times up to 5 years. Also shown are the proportions of recoveries sourced from farms by recovery time (thick gray bars). Recovery time is discretized to one-twelfth of a year intervals.



"recovery time". That is, recovery time is the sum of t_O and t_F. We use the term recovery to refer to the reported recapture or return of the tag or tags that were retained by an individual fish at the time it was inspected for tags. We classify the recovery of one of two tags from a fish as a single-tag recovery and the recovery of both tags from a fish as a double-tag recovery.

As with most other high-value commercial fish species, SBT are rarely re-released at the time of first recapture. This means very few multiple recaptures of tagged SBT are observed. A small number of tagged juveniles are recaptured during tagging operations and inspected for tags before being re-released. Also, some tags captured by Australian purse seine vessels are detected during routine monitoring of the catch before being transferred to the on-farm enclosures. For the purposes of this analysis, where multiple recaptures of the same fish are reported, we consider only the first recapture.

The process of transferring wild-caught SBT to tuna farms is closely monitored so that when tags are detected in tuna farms, the date of purse seine capture can usually be inferred to within a few days. This allows both t_O and t_F to be calculated with known uncertainty for the majority of recoveries. For these "two-stage" recoveries, an "inferred recapture" is recorded in the Commission for the Conservation of Southern Bluefin Tuna (CCSBT) database, with the inferred recapture date given as the date of purse seine capture. Although the transfer of wild-caught SBT to tuna farms is closely monitored, tags are only incidentally observed at this time, and in general individual tag numbers will not be observed or reported. Since tags are not actually observed at the time of an inferred recapture, the presence of tags at the time of purse seine capture is inferred from the observed presence of tags at the time of recovery, which occurs later. For individuals observed to have shed a tag at the time of recovery, it cannot be known whether tags were shed in the ocean before purse seine capture or on farm after purse seine capture. Sometimes wild-caught juveniles from more than one tow cage are transferred to the same on-farm ranching pontoon. The date of purse seine capture for tags recovered from these pontoons will be subject to greater uncertainty. However, the earliest and latest possible dates of purse seine capture are known and the corresponding uncertainty indicated by an associated date quality code for each recapture record in the CCSBT database including inferred recaptures. For this analysis, we have selected only recoveries for fish where all recaptures have date quality codes indicating precisely known recapture dates.

Table 1. Observed recoveries of southern bluefin tuna tagged since 1990 with recovery times of up to 2000 days and accurate recapture dates.

1990s study		2000s study	
Single-tag	Double-tag	Single-tag	Double-tag
Recoveries from ocean ($t_O > 0$, $t_F = 0$)			
731	2909	300	791
Recoveries from farms ($t_O > 0$, $t_F > 0$)			
687	1620	3137	4617

Note: All recoveries considered were originally double-tagged.

Some tags are detected without entering tuna farms (i.e., $t_F = 0$). The largest group of recoveries, however, come from purse seine recaptures of tagged SBT where the presence of tags was not discovered until some time after the tagged fish was transferred to a tuna farm (i.e., $t_O > 0$, $t_F > 0$). The number of tags recovered for each recovery category with total recovery times up to 2000 days for the two most recent SBT tagging studies is given in Table 1.

The recovery data arise from reported recaptures of SBT that were all originally double-tagged. Each tag has its own unique identifying number, and rewards are issued for the return of all recaptured tags.

Exploratory data analysis

As an exploratory measure, Wetherall (1982, p. 700) suggests grouping recoveries by discretized recovery time and calculating estimates of the proportion of tags shed at the midpoint of each interval from the number of single-tag and double-tag recoveries observed in each interval of recovery time. If the tag shedding rate is constant with respect to time at liberty, a plot of the estimated proportion of tags shed versus time at liberty will resemble a von Bertalanffy growth curve.

Since the SBT recovery data are quite plentiful, we partition recovery time between 0 and 5 years into 60 discrete bins, each spanning one-twelfth of a year. After excluding recoveries where the recapture date is not accurately known, there remain 14 792 recoveries with recovery times of up to 2000 days. We use expressions given in Wetherall (1982, p. 692) to calculate maximum likelihood estimates and asymptotic 95% confidence intervals for the proportions of tags shed with times at liberty at the midpoints of each of the 60 bins. These estimates are plotted in Fig. 2. The proportions of tag recoveries sourced from farms for the same intervals are plotted on the same axes.

The series of proportions of tags recovered from farms represented by the thick gray bars in Fig. 2 is distinctly periodic. The periodicity occurs because of the seasonal nature of the Australian surface fishery. Tagging of SBT is mostly carried out in January and February when surface schools of juveniles are present in the Great Australian Bight. The Australian commercial purse seine fleet that captures juvenile SBT operates in the Great Australian Bight at about the same time of year. The SBT captured by the purse seine vessels can include individuals that were tagged just prior to purse seine capture as well as others that were tagged 12 months earlier or 24 months earlier and so on. These juveniles, however, spend a further 4–8 months in the farms before they are harvested, when most tags are recovered, usually around August. The result is the pattern exhibited in Fig. 2, with peaks in the proportion of recoveries from farms occurring near the midpoints of integer years of recovery time.

Approximately coinciding with the peaks in the proportion of recoveries from farms are peaks in the estimated proportion of tags shed, as represented by the black squares in Fig. 2. The 95% confidence intervals for the estimated proportions of tags shed, represented by the vertical black lines in Fig. 2, are quite precise for bins with recovery times of up to 4 years. The series of estimated proportions of tags shed departs considerably from what would be observed if tags recovered in each interval were subject to the same average instantaneous shedding rates. Indeed the periods for which the estimated proportion of tags shed decreases as recovery time increases are suggestive of negative shedding rates, which of course is impossible. We assert that tags in SBT have some nonzero probability of being shed at any instant they are in the open ocean or in on-farm enclosures. This probability can be thought of as an instantaneous tag shedding hazard rate, which needs not be constant with time and, as we show later, tends to be considerably higher in tuna farms than in the open ocean. If the instantaneous tag shedding hazard rate is higher in tuna farms than in the open ocean, then for a given recovery time, the cumulative hazard of tags sourced from farms will be higher than tags from other sources. As a consequence, when recoveries sourced from tuna farms are pooled with recoveries from other sources, apparent negative tag shedding rates can be suggested over intervals of recovery time where the proportion of recoveries sourced from farms is decreasing. This scenario occurs periodically for SBT as shown in Fig. 2. Hearn et al. (1991) point out that intervals of apparent negative shedding rates are theoretically possible when tag recoveries from groups with large differences in shedding rates are pooled to estimate a single common shedding rate.

Two-stage SBT tag shedding model

We apply a Bayesian graphical modelling approach to the problem of estimating tag retention rates. Each observed single-tag and double-tag recovery is modelled as the realisation of a Bernoulli random variable. The probability that a particular recovery will be a double-tag recovery given its exact recovery time is assumed to be a function of a tag retention process model. For SBT recovered from farms, we allow total recovery time to comprise two distinct stages where tags are shed at potentially different rates in each stage.

Consider tags inserted into SBT released off the coast of southern Australia since 1990. Let the proportion of tags not lost through tag shedding after t_O be given by $R_O(t_O)$. If $R_O(t_O)$ is assumed to be the reliability function of some Weibull distribution, then adopting a parameterisation used to fit Weibull models in a Bayesian context

$$R_O(t_O) = \exp(-\beta_O t_O^{\lambda_O}) \tag{1}$$

where both the scale parameter β_O and the shape parameter λ_O are strictly positive. We note at this point that tags may be lost through mortality and nonreporting as well as tag shedding, but as pointed out by Xiao (1996), these losses do not affect estimates of tag shedding rates if models are fitted to exact recovery times and single-tag recoveries are reported with the same probability as double-tag recoveries. To improve readability, hereafter we use "retained" tags to mean tags that were not lost through tag shedding without considering the effects of mortality and nonreporting.

Next consider tags captured from the ocean by purse seine vessels and transferred to tuna farms. Let the proportion of these tags retained after t_F be given by $R_F(t_F)$. If $R_F(t_F)$ is assumed to be given by the reliability function of a second Weibull distribution, then

$$R_F(t_F) = \exp(-\beta_F t_F^{\lambda_F}) \tag{2}$$

where, as before, β_F and λ_F are strictly positive.

We have assumed in eq. 2 that $R_F(t_F)$ is not affected by the length of time that the tag spends in the open ocean before purse seine capture. It follows that the proportion of tags retained after time t_O in the ocean and t_F on farm is given by the product of $R_O(t_O)$ and $R_F(t_F)$. Let this product be $R(t_O, t_F)$, so that the overall tag retention process model is given by

$$R(t_O, t_F) = R_O(t_O)R_F(t_F) = \exp(-\beta_O t_O^{\lambda_O} - \beta_F t_F^{\lambda_F}) \tag{3}$$

Let observed recoveries be indexed by i and let the total time between tagging and inspection for tags for recovery i be specified by a time in ocean, t_{O_i}, and a time on farm, t_{F_i}. Finally let D_i be an indicator variable for double-tag recoveries such that if recovery i corresponds to a double-tag recovery, then $D_i = 1$, else if recovery i corresponds to a single-tag recovery, then $D_i = 0$.

In this case we can model D_i as a Bernoulli random variable with

$$P(D_i = 1 \mid t_O = t_{O_i}, t_F = t_{F_i}) = \pi(t_{O_i}, t_{F_i}) \tag{4}$$

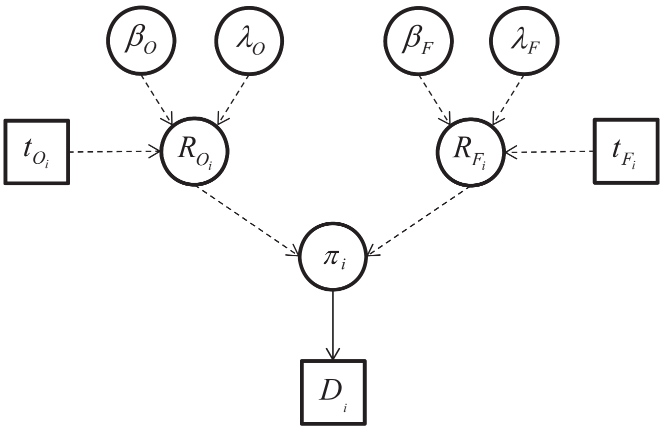
where $\pi(t_{O_i}, t_{F_i})$ is the probability an observed recovery inspected for tags after time t_{O_i} in the ocean and time t_{F_i} on farm will be a double-tag recovery. Note that recaptures of originally double-tagged SBT that shed both tags prior to inspection are unobservable.

Assuming both independence in tag shedding and that double-tag recoveries and single-tag recoveries are reported with the same probability, we can relate the observation model (eq. 4) to the process model (eq. 3). In this case the probability that any given tagged SBT (observed or unobserved) would retain both tags after a time t_{O_i} in the ocean and t_{F_i} on farm is $[R(t_{O_i}, t_{F_i})]^2$, while the probability it would have retained exactly one of two tags is $2R(t_{O_i}, t_{F_i})[1 - R(t_{O_i}, t_{F_i})]$. For an observable recovery, either one tag or both tags need to be retained at the time the fish is inspected for tags. It follows that the probability a tagged SBT inspected for tags after time in ocean t_{O_i} and time on farm t_{F_i} is a double-tag recovery, given that it is an observable recovery, is

$$\pi(t_{O_i}, t_{F_i}) = \frac{[R(t_{O_i}, t_{F_i})]^2}{[R(t_{O_i}, t_{F_i})]^2 + 2R(t_{O_i}, t_{F_i})[1 - R(t_{O_i}, t_{F_i})]} = \frac{R(t_{O_i}, t_{F_i})}{2 - R(t_{O_i}, t_{F_i})} \tag{5}$$

The basic structure of the overall probability model can be represented using a directed acyclic graph (Fig. 3).

Fig. 3. Directed acyclic graph representation of two-stage SBT tag shedding model. A stochastic relationship is represented by the solid line, deterministic relationships are represented by dashed lines. Recovery-specific parameters are denoted by *i* subscript. Squares represent observed data (evidence nodes). Nodes representing constant prior parameters have been excluded for clarity.



The model was fitted using OpenBUGS (Thomas et al. 2006), which was called from within R (R Development Core Team 2012) using the BRugs package. The parameters of the Weibull distribution are strictly positive. Aside from being positive, we assumed no prior knowledge of the values of these parameters in this application. Reflecting this prior ignorance, we specified noninformative Gamma($1,10^{-4}$) prior distributions for all parameters. The Gamma($1,10^{-4}$) probability density function is slowly decreasing in the positive real numbers. To test the sensitivity of the posterior distributions to their priors, we generated Markov chain Monte Carlo (MCMC) samples with alternative Uniform(0,5) priors. We found that the differences in posterior estimates produced with the alternative priors were negligible in this case.

The model was fitted to recoveries from the 1990s study and the 2000s study separately, but in each case recoveries from the ocean and recoveries from farms (see Table 1) were modelled together. Final inference was based on posterior distributions obtained by generating 510 000 MCMC samples and discarding the first 10 000 as burn-in. Thereafter, every 50th sample was kept giving 10 000 samples from the posterior with minimal autocorrelation (see Figs. S1 and S2 in the supplementary materials[1]). The CODA package in R was used to check whether the MCMC algorithm had converged to the posterior distribution of the parameters. Additional posterior summaries (Figs. S1 and S2[1]) are included in supplementary materials. Figures S1 and S2[1] were produced using the summMCMC R function (Marley and Wand 2010).

Results

Summary statistics for the estimated parameters of the fitted model for the 1990s study and 2000s study are given in Table 2. In each study, the parameters defining the ocean tag retention curve, β_O and λ_O, are resolved more precisely than the corresponding parameters for the farm tag retention curve, as evidenced by lower relative standard errors.

In each study, the estimated shape parameter for the ocean tag retention curve, λ_O, is wholly less than unity, suggesting that in the open ocean the rate that SBT shed tags decreases with time in the ocean. Conversely, the posterior means of the shape parameter for the tag retention curves in tuna farms, λ_F, are greater than unity in each study, suggesting that in tuna farms, the rate that SBT shed tags most likely increases with time on farm.

Table 2. Parameter posterior means of two-stage Weibull model fitted to 1990s and 2000s double-tagging studies of southern bluefin tuna.

	β_O	β_F	λ_O	λ_F
1990s study	0.0837 (0.056)	0.283 (0.30)	0.732 (0.076)	1.70 (0.26)
2000s study	0.106 (0.091)	0.699 (0.17)	0.858 (0.097)	1.95 (0.13)

Note: Values in parentheses are estimated relative standard errors.

Tag retention curves for time in ocean and time on farm over the first 2 years fitted separately to recoveries from each study are compared in Fig. 4. Higher estimated tag retention rates for time in ocean are readily apparent. The tag retention function for time on farm is not extrapolated beyond 250 days because farmed SBT are usually harvested before this time.

The degree of uncertainty in the fitted tag retention curves suggested by their pointwise credible intervals (as shown in Fig. 5) are conditional on the assumed Weibull process models and also on the assumption of independence in tag shedding. It is likely, therefore, that the overall uncertainty in the proportions of tags retained with time in ocean and time on farm is underestimated somewhat.

The ocean retention rates are comparable with Hampton and Kirkwood (1990), who estimated that after 4 years SBT tagged in the 1980s shed about 20% of tags, whereas SBT tagged in the 1960s and 1970s shed between 50% and 70% of tags after 4 years. The two-stage model (as depicted in Fig. 3) fitted separately to the 1990s and 2000s data studies suggests that just over 20% of tags would have been shed from SBT that remained in the open ocean for 4 years during the 1990s (Fig. 5*a*) and just under 30% for SBT tagged in the 2000s (Fig. 5*c*).

Most wild-caught SBT that are transferred to tuna farms are fattened in the on-farm enclosures for around 150 days. Despite quite high rates of tag shedding in farms, approximately 90% of tags retained at the time of purse seine capture would be expected to be retained after 150 days on farm (Figs. 5*b* and 5*d*).

The hazard rate functions for tag shedding in the open ocean (Figs. 6*a* and 6*c*) are broadly consistent with the modes of tag shedding described by Beverton and Holt (1957). Initially, shedding rates are estimated to be relatively high, consistent with a brief period of type 1 shedding, immediately after tagging, before quickly settling down to an approximately constant shedding rate, consistent with what Beverton and Holt (1957) referred to as type 2 tag shedding. In contrast, the estimated hazard rate function for time on farm (Figs. 6*b* and 6*d*) suggests the rate at which farmed SBT shed tags increases with time on farm.

Assessment of model fit

Bayesian analysis conditions on the whole structure of a probability model, including the defined prior distributions. As a consequence, Bayesian inference can be misleading when the fitted model does not reasonably approximate the process that generated the observed data (Gelman and Meng 1996). The graphical model fitted to the SBT double-tagging data are moderately complex, so it is particularly important to check model fit.

We examine model fit by plotting simulated versus realised discrepancy statistics (Gelman et al. 1996) for each set of posterior parameter values (Figs. S3 and S4[1]). Following Brooks et al. (2000), we use the Freeman–Tukey statistic (Freeman and Tukey 1950) to measure the realised discrepancy between the model and the observed data. Posterior predictive *p* values are calculated as the proportion of plotted points above the 45 degree line. Bayesian *p* values close to 0.5 are realised when the fitted probability model is consistent with the observed data. Considering the two SBT tag

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0325.

Fig. 4. Comparison of fitted curves for retention of tags released during (*a*) the 1990s and (*b*) the 2000s in the open ocean (solid line) and in tuna farms (dashed line) up to 2 years. The curves for tag retention on farms are truncated at 250 days. Shaded areas are 95% credible intervals for the Weibull fits.

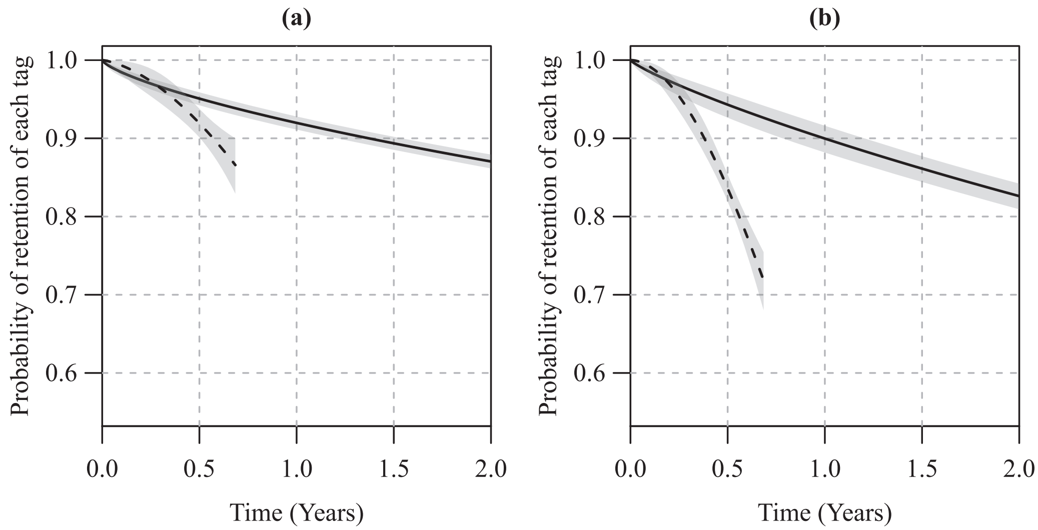


Fig. 5. Fitted curves showing probability of retention of tags released during the 1990s (*a*) in the open ocean and (*b*) in tuna farms and tags released during the 2000s (*c*) in the open ocean and (*d*) in tuna farms. Shaded areas are pointwise 95% credible intervals for the Weibull fits. Note the difference in the scales of the horizontal axes.

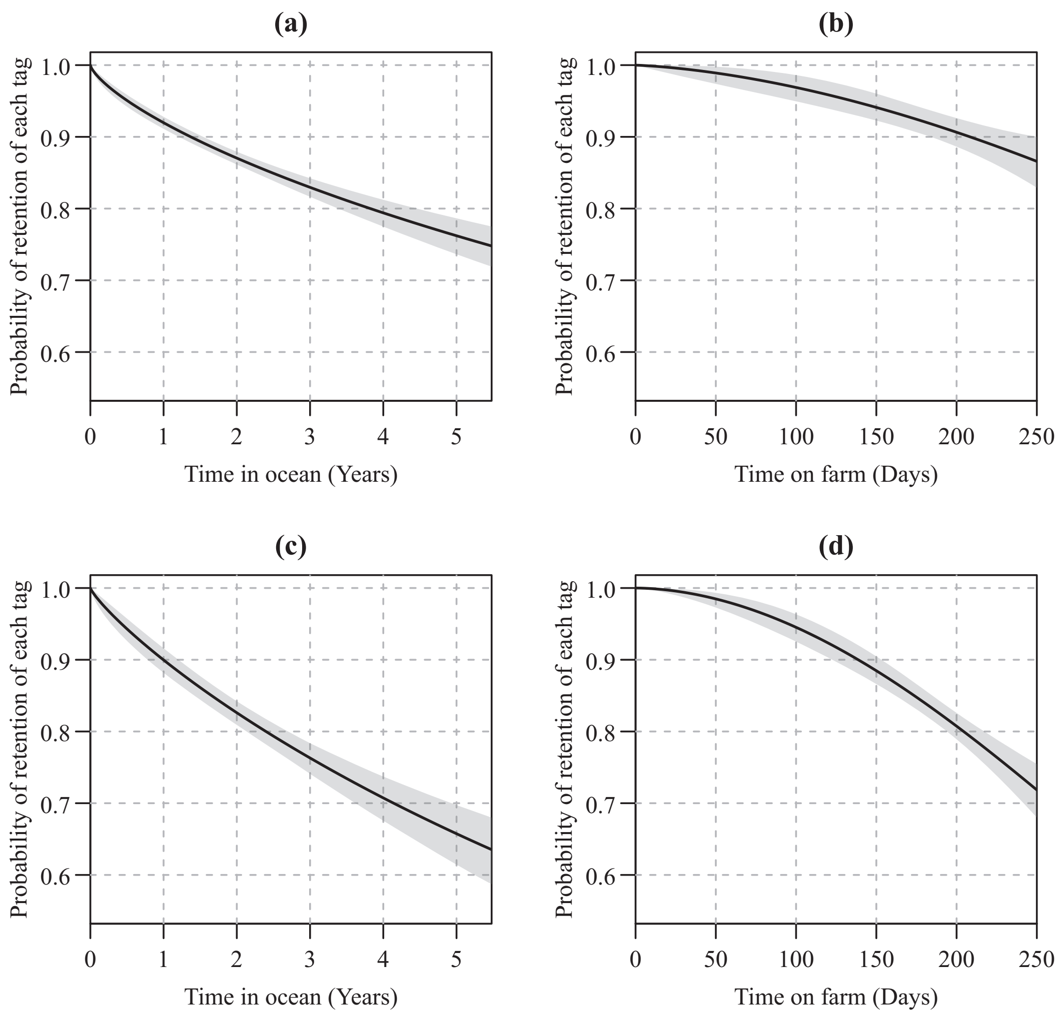
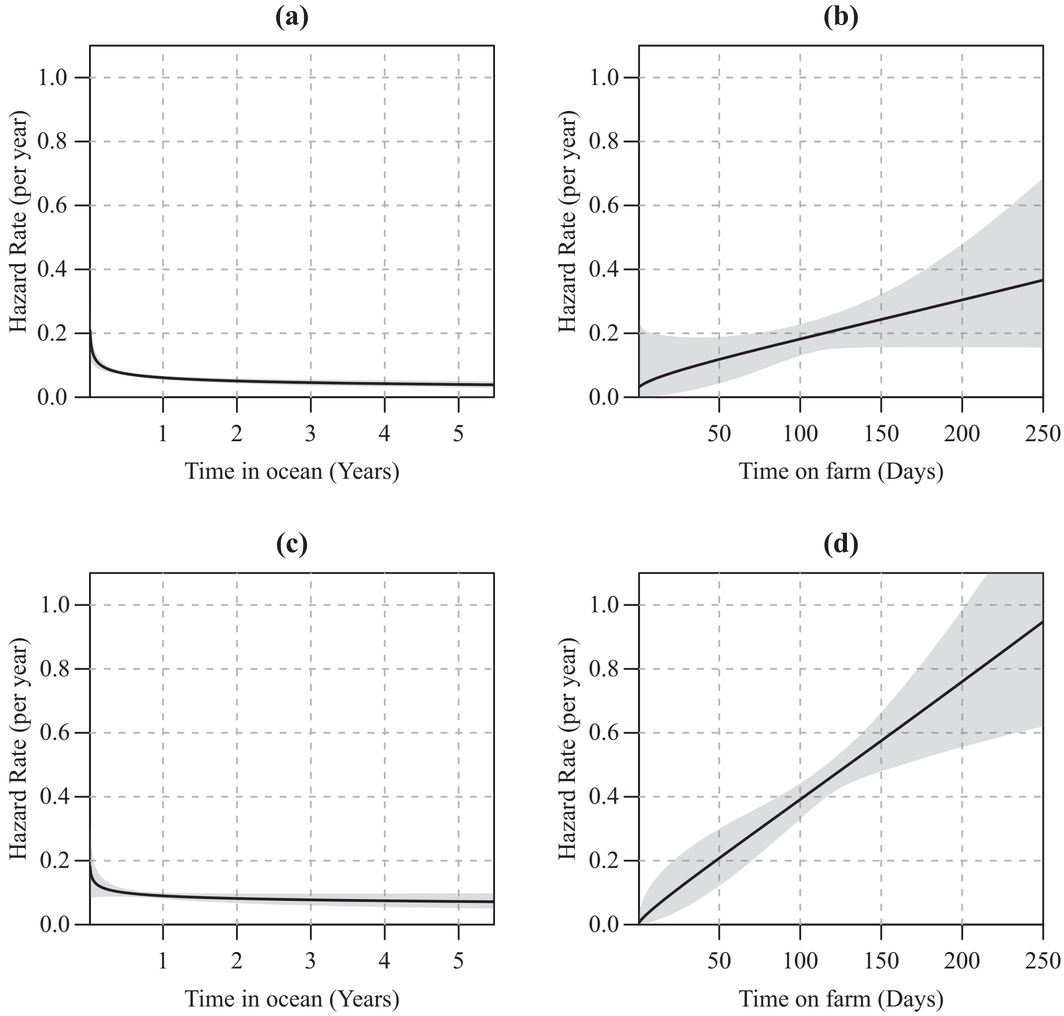


Fig. 6. Hazard rates as functions of time of tags released during the 1990s while (*a*) in the open ocean and (*b*) on farms and tags released during the 2000s while (*c*) in the open ocean and (*d*) on farms. Note the difference in the scales of the horizontal axes.



recovery types separately, we observe p values of 0.52 and 0.46 for two-stage recoveries in the 1990s and 2000s, respectively, and p values of 0.55 and 0.57 for respective ocean recoveries in the 1990s and 2000s. The posterior p values calculated are quite close to 0.5, suggesting minimal lack of fit.

Discussion

This analysis represents the first attempt to separately model SBT tag shedding rates in the open ocean and in on-farm enclosures. It provides an improved understanding of the tag recovery data arising from the two most recent SBT tagging studies. The finding that SBT shed tags at a higher rate in the on-farm enclosures than in the open ocean is particularly important. We have also described a new approach to modelling double-tag recoveries and used this approach to fit separate tag retention curves for the time tagged SBT spend in the open ocean and in tuna farms. An interesting additional finding is that tag shedding rates in tuna farms appear to increase with time on farm as evidenced by increasing hazard rate functions estimated for both the 1990s and 2000s studies (Figs. 6*b* and 6*d*).

Since all of the SBT tagged in the two most recent studies were double-tagged, the tag shedding estimates that are of greatest importance are the proportions of double-tagged fish estimated to have shed both tags. To estimate these proportions, it is necessary to apply the two-stage tag retention model to a joint distribution of times in the ocean and times on farm. A reasonable approach might be to scale up each observed recovery by the probability that a double-tagged tuna that was in the ocean and on farm for the same time as the observed recovery would have shed both tags.

As mentioned earlier, farmed SBT are kept in the on-farm enclosures for about 150 days on average. Despite relatively high shedding rates on farms, this analysis suggests, assuming independence in tag shedding, only about 0.4% of double-tagged fish would have shed both tags in 150 days on a tuna farm during the 1990s study and about 1.3% during the 2000s study. After 3 years in the ocean and a further 150 days on farm, approximately 4.8% are estimated to have shed both tags during the 1990s study and around 8.2% during the 2000s study. In reality then, the effects of high shedding rates on tuna farms in terms of estimates of the number of tags unobserved due to tag shedding may be fairly modest.

The finding that tag shedding rates on farms increase with time on farm possibly lends support to the theory that increased fouling of tags in tuna farms may contribute to higher rates of tag shedding (D. Ellis, Australian Southern Bluefin Tuna Industry Association, Port Lincoln, South Australia, personal communication, 2013). It might be expected that as biofouling on tags accumulates while the tags are in the farms, associated increases in hydrodynamic drag forces acting on the tags would lead to increasing tag shedding rates. Drag forces were thought to have been responsible for differences in tag shedding rates between different tag types observed by Fabrizio et al. (1996). Bacterial infection has also been thought to increase tag shedding rates in some tagging studies (see e.g., Jones 2003). Higher rates of infection in tuna farms might also be related to higher rates of tag shedding by SBT estimated to occur in the tuna farms. The rate that SBT shed their tags also varies depending on the skill of the tagger (Hearn et al. 1991), but this alone does not explain the differences in shedding rates between the open ocean and tuna farms.

The rate of tag shedding by SBT on tuna farms during the 2000s study was considerably higher than during the 1990s study. When the tuna farming industry began in Port Lincoln in the early 1990s, tuna pens were situated within Boston Bay along the western (near shore) side of Boston Island. From the year 2000 onwards, leases for tuna farms were instead situated further offshore in the Spencer Gulf. The extent of biofouling of tags would be expected to have been lower in the deeper offshore sites than in the more protected sites nearshore (K. Rough, Australian Southern Bluefin Tuna Industry Association, Port Lincoln, South Australia, personal communication, 2013). This being the case, if biofouling was the cause of higher tag shedding rates on farms, higher shedding rates on farms would have been expected during the 1990s than the 2000s. Our analyses suggest the opposite, which suggests factors other than biofouling might contribute to elevated tag shedding rates on tuna farms.

The modelled data include a considerable number of recoveries sourced from the ocean that do not spend any time in tuna farms (i.e., $t_F = 0$; see Table 1). It might be expected that these recoveries are responsible for the more precise estimation of the ocean retention parameters β_O and λ_O compared with the corresponding farm retention parameters and that perhaps these recoveries are required for the estimation of all model parameters. However, we fitted the same model to the farm recoveries only (i.e., recoveries with $t_F = 0$ were excluded) and got quite similar parameter estimates that were only slightly less precise. The two-stage model can be fitted to double-tag recovery data when the data include no single-stage recoveries. Even without the ocean recoveries, the ocean tag retention parameters β_O and λ_O are estimated more precisely than the farm retention parameters recoveries, β_F and λ_F. We conclude this additional precision is because of the much greater contrast in observed times in ocean compared with times on farm. We also point out that while the individual farm retention parameters are somewhat imprecise, the farm retention curves (Figs. 5*b* and 5*d*) are quite precisely estimated.

Weibull models are commonly used in reliability analysis to model the expected lifetimes of mechanical components. A desirable characteristic of the Weibull model is its ability to model the lifetimes of components with increasing, decreasing, or constant hazard rates despite having only two parameters (Duchateau and Janssen 2008, p. 23). The flexibility and parsimony of the Weibull model would seem to make it well suited to the problem of estimating tag shedding rates in tagging studies of fish. The flexibility of Weibull models is notable because the tag shedding models most often fitted to double-tagging data, essentially those described by Hampton and Kirkwood (1990), are unable to model increasing tag shedding rates. Despite their apparent suitability for modelling tag shedding, Weibull models have seldom been used for this purpose (but see Barker et al. 2002).

The analysis described relies upon a number of assumptions common to most analyses of double-tag recovery data. One of the most important is the assumption that the shedding of any tag occurs independently of all other tags. Beverton and Holt (1957) suggested that some circumstances might result in a double-tagged fish shedding both tags at the same time, inducing positive dependence in shedding probabilities at the fish level. Positive dependence in tag shedding at the fish level would lead to more double-tag recoveries (and zero tag recoveries) for a given tag shedding rate than would be expected under the assumption of independence of tag shedding. Looked at another way, in the presence of positive dependence in tag shedding probability at the fish level, estimates of tag shedding rates based on the ratio of double-tag to single-tag recoveries assuming independence of tag shedding will be negatively biased. Dependence in shedding of ear tags by black bears (*Ursus americanus*) has been observed (Diefenbach and Alt 1998). Bears were tagged in each ear and were also tattooed. The permanent tattoo enabled individuals that had shed both tags to be identified. The inability to identify fish recaptured after shedding both tags makes estimating dependence in tag shedding more difficult in a large-scale study of a commercially harvested fish species. It is conceivable that departures from independence in tag shedding might be more problematic on tuna farms than in the open ocean. For instance, tag shedding rates are likely to be higher in some grow-out pens than in others. Dependence in tag shedding on tuna farms could be investigated, for example, by double-tagging all fish released into an experimental grow-out pen and observing the number of fish that retained zero, one, and two tags at the end of the study period.

We also make the common assumption that double-tag recoveries and single-tag recoveries are reported with the same probability. Hampton (1997) considers the possibility that sometimes only one tag might be returned from a double-tag recovery so that a proportion of double-tag recoveries are incorrectly recorded as single-tag recoveries. In other situations, double-tag recaptures might be detected with higher probability (Björnsson et al. 2011). For a number of reasons, we believe it is reasonable to assume single-tag and double-tag recoveries of SBT are reported with similar probability. Firstly, a financial reward is offered for the return of each tag. Secondly, most recoveries are sourced from the farm sector where the same contractors that monitor the transfer of juveniles from the tow cages to the grow-out pens also encourage tuna farm operators to return tags and explain the protocols for returning tags. The operators of the tuna farms are likely to recapture large numbers of tags during tagging studies so that differences in the financial incentive of returning a double-tag recovery as opposed to a single-tag recovery are unlikely to be a major factor in determining the probability a particular recovery is reported. Tag recoveries from longline vessels are likely to be sourced either from onboard observers or from vessels where tag return protocols are well understood. Finally, as a high-value fish, SBT are individually handled so that all retained tags are likely to be detected at the time of longline capture or harvest from farms.

As well as the more common assumptions required for modelling of double-tag recovery data, the two-stage aspect of the model we describe required a further assumption that the farm retention curve was independent of the length of time the fish previously spent in the open ocean. This assumption could be tested by comparing observed and predicted proportions of single-tag and double-tag recoveries sourced from farms, grouped by time in ocean. This is slightly complicated for Bernoulli data, where each recovery has a different expected value and is beyond the scope of this paper.

Since the model we have described is not hierarchical, a similar two-stage tag retention model could have alternatively been fitted by maximum likelihood. However, there are some advantages to modelling tag shedding in a Bayesian framework. For example, estimates of uncertainty in derived quantities such as the proportion of tags shed and the proportion of fish that shed both tags prior to recapture can be obtained as functions of the posterior distributions of the model parameters. To our knowledge, Bayesian modelling of tag shedding data at exact recovery times has not been described previously.

A two-stage tag retention model might be applicable to tagging studies of other species that are fattened after wild capture, such as Atlantic bluefin tuna (*Thunnus thynnus*; Mylonas et al. 2010), but realistically the scope for application of this type of model is limited. On the other hand, the basic approach that we have described including the Weibull process model can be used to analyse double-tag recovery data more generally by setting $t_F = 0$ in the process model (eq. 3). Furthermore, a variety of alternative reliability functions (also called survivor functions) are used in time-to-event and survival analysis. These can be fitted within the framework we have described by substituting the appropriate reliability function in place of the Weibull reliability function given in eq. 1.

Planted tag experiments (Hearn et al. 2003) were carried out during the 2000s study to facilitate estimation of tag reporting rates from the farm sector. Most of the SBT used in the tag planting experiments were double-tagged. It might be expected that these data could have been used to estimate tag shedding rates in farms more simply. However, additional modelling (not included here) indicated that planted tags were shed at an even higher rate than the regular tags in on-farm enclosures. Higher shedding rates of planted tags in farms might be due to type 1 shedding of these tags upon release into the on-farm enclosures. It is also possible that higher shedding rates among planted tags were related to differences in tagger skill between the technicians that carried out the tag seeding and those that tagged fish released into the ocean. However, all taggers, including contractors that attached the planted tags, were fully trained. A more complete analysis of reporting rates accounting for shedding of planted tags is among future work being considered. In any case, tags recovered from the tag seeding experiment were excluded from this analysis.

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