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Preliminary assessments of tuna natural mortality rates from a Bayesian Brownie-Petersen model

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Abstract

The natural mortality-at-age of three populations of Indian Ocean tunas (yellowfin, bigeye and skipjack) can be assessed through the use of a Brownie-Petersen model estimated from tagging and recapture experiments, commercial catch data and tag recovery estimates. The present paper focuses on eliciting a Bayesian version of this model from the RTTP-IO database, accounting for the differences of fishing pressure exerted by the main fleets. The rationale for choosing a Bayesian framework is that it offers a major treatment of uncertainties. The main sources of error in the data are highlighted and included in the model. , while the are updated using new growth curves for each species. These preliminary assessments provide new natural mortality curves that seem to be mostly decreasing over time, although they remain embued with non-negligible uncertainty.

Résumé

La mortalité naturelle de trois populations de thonidés de l'Océan Indien (albacore, patudo, listao) peut être estimée par l'entremise d'un modèle de Brownie-Petersen (BP), tirant parti de données de marquage-recapture, de données de prises commerciales et d'estimés des taux de retour des marques. Cet article se focalise sur l'information apportée par les données sélectionnées dans la base RTTP-IO sur les paramètres de mortalité naturelle d'un modèle BP bayésien. Le choix du cadre statistique bayésien répond ici à une volonté de mettre en lumière et traiter la majeure partie des incertitudes affectant les mécanismes de production des données. Les principales sources d'erreur sont donc prises en compte dans la modélisation, et notamment celles qui affectent les courbes de croissance. Les résultats préliminaires indiquent que les courbes de mortalité semblent suivre une forme décroissante, bien qu'elles restent affectées d'une incertitude dont une partie est due aux approximations numériques nécessaires à l'estimation.

1 Introduction

Assessing natural sources of mortality of tropical tunas is a major concern and an uneasy task since all the estimates of mortality can only be obtained from data depending on commercial fisheries (tag returns and catches), usually affected by many uncertainties. Understanding the mortality of juvenile, especially, is of particular interest since it underlies different exploitation strategies by various types of fisheries. In this regard, an additional difficulty is the mixing at young ages, in similar schools and habitats, of the Indian Ocean three species considered in the present paper: yellowfin (YFT; *Thunnus albacares*), bigeye (BET; *Thunnus obesus*) and skipjack (SKJ; *Katsuwonus pelamis*). Especially, Fonteneau & Pallares (2004) stressed the importance of testing the hypothesis that natural mortality of small tunas should be at similar levels as long as the three species are living in the same schools and in the same habitat.

The ability of mutiyear tagging models to allow the estimation of age- and year-specific survival of animal populations is now well documented and recognized (Seber, 1970; Brownie *et al.*, 1985; Latour *et al.*, 2001). Especially, they have been successfully used to analyse fisheries tagging data: as shown by Pollock *et al.* (1991) then Hoenig *et al.* (1998a), tag recovery rates can be converted to fishing exploitation rates provided information on tag retention, induced mortality and reporting rate is available. The formulation proposed by Brownie (Brownie *et al.*, 1985) has known several generalizations. Studied for multiple component fisheries by Brooks *et al.* (1998), it has been profitably strenghtened by incorporating statistically the observations of commercial catches by Pollock *et al.* (2002) in this same context. The comprehensive Brownie-Petersen (BP) framework of multiyear tagging experiment proposed by Polacheck *et al.* (2006) achieved to formalize the interplay between tagging and catch-at-age data. Furthermore it offers a precise view of the structural and numerical assumptions needed to get precise estimates of fishing and natural mortality parameters. Recently, this modelling was used by the IOTC, in parallel to standard population models (e.g., MULTIFAN-CL), to conduct preliminary survival studies on tuna populations (Eveson, 2011). Unknown parameters including natural mortality rates were estimated using a maximum likelihood (ML) approach.

The present article aims at providing an alternative preliminary assessment of these mortality rates using a Bayesian version of the BP model. Usually this framework allows for a better analysis of uncertainties affecting the model parameters (Low Choy *et al.*, 2009; Pasanisi *et al.*, 2012). In the context of tagging models, the estimation of uncertainty indicators as covariance matrix of estimators using standard ML theory often appears not relevant (Pollock *et al.*, 2002) and bootstrap techniques are usually prefered (Polacheck *et al.*, 1997). However, their validity remains based on asymptotic theory, the relevance of which being debatable when dealing with small time series. The Bayesian alternative offers a simulation-based method where all sources of variation and uncertainty are incorporated into the simulation procedure, as recommended by Pollock *et al.* (2002). Among others, Conn *et al.* (2008) have shown the relevance of this framework and the feasibility of estimation when dealing with models comparable to BP, involving similar urn mechanisms. Furthermore, providing posterior distributions for mortality rates rather than best-estimates can yield a first answer to the recommendations made by Fonteneau & Pallares (2004) in terms of sensitivity analysis, who suggested that stock assessments should be based on a wide range of biologically plausible levels of mortality-at-age rather than pointwise estimates only.

Nevertheless, strong assumptions (e.g., fixing some parameters) remain needed to ensure identifiability in BP models. Therefore the present article only aims at providing a first methodology of Bayesian estimation and establishing preliminary results. More precisely, the article is structured as follows. Section 2 described the modeling and its structuring hypotheses, including the nature of available data arising from the Regional Tuna Tagging

Project of the Indian Ocean (RTTP-IO), and the elicitation of prior distributions for the free parameters. Then Section 3 is devoted to conduct preliminary assessments of mortality rates through MCMC algorithms for the three species.

2 Material and methods

The fish population is assumed to be exploited by N fishing fleets. In the context of the three species described above, Indian Ocean fisheries are pooled in $N = 5$ separated fleets following consistent patterns of exploitation: Asian longliners (ALL), pooling Japan, Taiwan and Korean gears, French longliners (FLL) landing at La Réunion, South Asia Maldives (MDV) pole-and-liners and European purse seiners (EPS) landing mainly at Seychelles islands, Madagascar, Mauritius and in Spain. A separation is made between the purse seine fishery based on floating objects and fishing aggregating devices (EPS-FO-FAD) and the fishery on free schools (EPS-FS).

Quantities involved in BP models are tagging data and catches at age for each fleet. Tagging data used for the study were released during RTTP-IO between 2002 and 2010, and the same period is chosen to select commercial catch data. Each fleet (except FLL for which the catches are not known) is characterized by a good collection of catch data, with low discards (cf. Table 2 in IOTC (2010)).

A major prerequisite for handling BP models is the availability of age-length keys for each species. Growth curves providing such keys are estimated in the Appendix Appendix A. In the remainder of the paper, we denote $\omega_{a,\ell}^{(k)}$ the frequency of age a in an infinite population of fork length ℓ for the species k, for $a = a_0, \ldots, A$. In the present document $a_0 = 0.25$ and $A = 7$ years. Ages and time steps are considered in quarters of year, so that 28 age classes are considered.

2.1 Population dynamics

For any species, the population dynamics are described by the classical following equations. Denote $P_{a,t}$ the number of individuals of age $a \in \{a_0, \ldots, A\}$ at time t. It is assumed that

$$P_{a+1,t+1} = S_{a,t} P_{a,t}$$

with $S_{a,t}$ the survival rate defined by

$$S_{a,t} = \exp\left(-\sum_{s=1}^{N} F_{a,t}^{s} - M_{a,t}\right), \tag{1}$$

where $F_{a,t}^{s}$ characterizes the instantaneous fishing mortality rate of the fishery $s \in 1, \ldots, N$ and $M_{a,t}$ denotes the instantaneous natural mortality rate. Consequently, the catch of individuals of age a at time t is defined by $C_{a,t} = \sum_{s=1}^{N} C_{a,t}^{s}$ where the catch attributable to fishery s is given by

$$C_{a,t}^{s} = \mu_{a,t}^{s} P_{a,t}$$

with $\mu_{a,t}^{s}$ the exploitation rate defined by (Ricker, 1975)

$$\mu_{a,t}^{s} = \frac{F_{a,t}^{s}}{M_{a,t} + \sum\limits_{s=1}^{N} F_{a,t}^{s}} (1 - S_{a,t}) \tag{2}$$

under the assumption that fishing effort is constant over the course of time step. It can be interpreted as the probability for an animal of age a present at time $t-1$ to be harvested by the fishery s until time t. The total probability for a fish of age a not to survive between times $t-1$ and t is

$$\sum_{s=1}^{N} \mu_{a,t}^{s} + \frac{M_{a,t}}{M_{a,t} + \sum\limits_{s=1}^{N} F_{a,t}^{s}} (1 - S_{a,t}) = 1 - S_{a,t}.$$

Since the species are jointly concerned with tagging and recapture, both processes induce correlations between the observations. To differentiate the quantities characterizing each species, an index $k \in \{1,2,3\}$ will be used along the paper when needed.

2.2 Tagging process

Denote $N_{\ell,t}$ the known number of fish of size ℓ tagged then released at time t. Define $\hat{N}^{(k)}_{\ell,t}$ as the *observed* number of fish of length ℓ of the species k tagged then released at time t. Then denote the observed frequency of species k released at time t

$$\hat{\kappa}^{(k)}_{\ell,t} = \frac{\hat{N}^{(k)}_{\ell,t}}{N_{\ell,t}}$$

This observed frequency never exactly fits with the true frequency $\kappa^{(k)}_{\ell,t}$, so that $\hat{N}^{(k)}_{\ell,t} \neq N^{(k)}_{\ell,t}$ the true value of fish from species k. Indeed, species can be erroneously attributed to tagged fish before release because of difficulties inherent in tagging processes and similarities between juveniles from different species. This specific error is likely to bias the relative comparison between the estimates of natural mortality of the three species if those tagged fish are not recaptured and their reported features never corrected. One has

$$\left\{\hat{\kappa}^{(k)}_{\ell,t}\right\}^{T}_{k\in\{1,2,3\}} = \Psi \cdot \left\{\boldsymbol{\kappa}^{(k)}_{\ell,t}\right\}^{T}_{k\in\{1,2,3\}} \tag{3}$$

with Ψ the transition matrix from the unbiased to the biased attribution frequencies. A good estimation of Ψ is given in Table 1. Consequently each $\kappa^{(k)}_{\ell,t}$ can be debiased by linear inversion. Denoting now $N^{(k)}_{a,t}$ the number of fish of age a of the species k tagged then released at time t, one has

$$N^{(k)}_{a,t} = \sum_{\ell} \omega^{(k)}_{a,\ell}\kappa^{(k)}_{\ell,t} N_{\ell,t}.$$

2.3 Tag-recapture data

For a given species, multiple cohorts of fish are simultaneously tagged. If all cohorts are modeled simultaneously, the mechanism of tagging recapture is described for one cohort only to alleviate the notations. Similarly, the notation k indicating the species is let only when needed Given $N_{a,t}$, the observed number of returns (of the species k) after j time steps by the fishery s is denoted $R^{s}_{a+j,t+j}$. Marginally, assuming that the fate of each tagged fish is independent,

$$R^{s}_{a+j,t+j} \sim \mathcal{B}_{inom}\left(N_{a,t}, \pi^{s}_{a+j,t+j}\right)$$

where $\pi^{s}_{a+j,t+j}$ is the conditional probability for a tag released at age a and year t to be returned by the fishery s after j time steps. A detailed description of the components of this probability follows. Consecutively, given a time period T after the release, and denoting

$$\begin{aligned}
\mathbf{R}_{\mathbf{a+T},\mathbf{t+T}} &= \left(R^{1}_{a+1,t+1},\ldots,R^{N}_{a+1,t+1},\ldots,R^{1}_{a+T,t+T},\ldots,R^{N}_{a+T,t+T}\right),\\
\boldsymbol{\pi}_{a+T,t+T} &= \left(\pi^{1}_{a+1,t+1},\ldots,\pi^{N}_{a+1,t+1},\ldots,\pi^{1}_{a+T,t+T},\ldots,\pi^{N}_{a+T,t+T}\right),\\
\mathbf{R}^{\Sigma}_{\mathbf{a+T},\mathbf{t+T}} &= \sum_{t=1}^{T}\sum_{s=1}^{N} R^{s}_{a+t,j+t},\\
\boldsymbol{\pi}^{\Sigma}_{a+T,t+T} &= \sum_{t=1}^{T}\sum_{s=1}^{N} \pi^{s}_{a+t,j+t},
\end{aligned}$$

then the joint distribution of all returns is

$$\left\{\mathbf{R}_{\mathbf{a+T},\mathbf{t+T}}, N_{a,t} - \mathbf{R}^{\Sigma_{\mathbf{a+T},\mathbf{t+T}}}\right\} \sim \mathcal{M}_{ult}\left(N_{a,t}\ ;\ \left\{\boldsymbol{\pi}_{a+T,t+T}, 1-\boldsymbol{\pi}^{\Sigma}_{a+T,t+T}\right\}\right).$$

A tagging recapture experiment can thus be described by a multinomial likelihood over the tagged catches of a given cohort. Since all cohorts are submitted to similar mechanisms of death in common time windows, they are clearly not independent. However, given the parameter vector $\boldsymbol{\theta}$ of all unknowns, which incorporates natural and fishing mortality parameters, the loglikelihood of tagging data for all cohorts is the sum of all multinomial loglikelihoods.

Expanding the description made by Pollock *et al.* (2002), the tag recovery probability $\pi^s_{a+j,t+j}$ can be precised as follows:

$$\pi^s_{a+j,t+j} = \alpha \cdot \delta^s_{a+j,t+j} \cdot \lambda^s_{a+j,t+j}.$$

(a) α is the probability that an animal survives any initial tag shedding and initial tag-induced mortality (so-called instantaneous retention-survival rate). Denoting $Q_{a,j}$ the probability of a tag being retained after j time steps for a fish released at age a, then $\alpha = Q_{a,0}$. The calibration of the tag shedding probability $1 - Q_{a,j}$, expressing continuous tagging mortality or loss, is detailed in Appendix Appendix B.

(b) $\delta^s_{a+j,t+j}$ is the probability that a tagged fish released at age a and time t be captured after j time steps by the fishery s:

$$\delta^{s,(k)}_{a+j,t+j} = \zeta^{s,(k)}_{a+j,t+j} \cdot \nu^{s,(k)}_{a+j,t+j},$$

where:

- $\zeta^s_{a+j,t+j}$ is the conditional probability that the tagged fish is mixed with the non-tagged population targeted by the fishery s after j time step. In the application considered here, following recent IOTC recommendations (IOTC, 2009; Langley *et al.*, 2010), the mixing of tagged and non-tagged fish is assumed to be certain after 3 months ($j \geq 1$ and $\zeta^s_{a+j,t+j} = 1$), therefore the animals tagged at time t are expected to experience the same fishing mortality than previously tagged or non-tagged animals. In § 3.1, supplementary details are given about the careful data selection needed to validate this mixing hypothesis, which is a major assumption of tag-recovery models, outlined by Brownie *et al.* (1985) and Pollock *et al.* (1991). Hoenig *et al.* (1998b) have indeed highlighted that the violation of this assumption can lead to seriously biased mortality estimates.
- $\nu^s_{a+j,t+j}$ is the conditional probability that a fish of age a at time t be catched after $j \geq 1$ time steps by the fishery s:

  $$\nu^s_{a+j,t+j} = \mu^s_{a+j,t+j} \left[\prod_{k=0}^{j-1} S_{a+k,t+k} \right].$$

  To account for continuous tagging mortality or loss, equations (1) and (2) must be modified in

  $$S_{a+k,t+k} = \exp(-\beta) \exp\left(-\sum_{s=1}^{N} F^s_{a+k,t+k} - M_{a+k,t+k} \right),$$

  $$\mu^s_{a,t} = \frac{F^s_{a,t}}{M_{a,t} + \sum\limits_{s=1}^{N} F^s_{a,t} + \beta} (1 - S_{a,t})$$

  with β the continuous shedding rate (cf. Appendix B).

(c) $\lambda^s_{a+j,t+j}$ is the conditional probability of a recovered tagged fish being reported if it is captured by fishery s after j time steps. This probability depends on three processes: (a) the tag detection on a harvested fish ; (b) the probability that a detected tag be reported ; (c) the reporting error due to the possible misidentification of the harvested species. Available information on the $\lambda^s_{a+j,t+j}$ is described beneath.

2.4 Reporting rate data

For each species, tag reporting rates were recently estimated by Hillary *et al.* (2008) for the purse-seine fleet based in Seychelles and Carruthers *et al.* (2012) for European purse-seiners, Maldivian pole-and-liners and French longliners. Using a generalized linear-logistic regression based on discrete tagging of harvested fish by scientific observers and voluntary skippers between 2004 and 2007, Hillary *et al.* (2008) produced couples of estimates $(\hat{\lambda}^s_t, \hat{\sigma}^s_{\lambda_t})$ which were mostly explained by a year effect. Updated after 2007, the stability of results (Figure 1) allows to predict an average reporting rate of 95% for the three species confounded in the most recent years. Since no detail is available about the reporting rates by stevedores at other locations in the Indian Ocean, these results are assumed to be relevant for European purse-seiners in general.

In Carruthers *et al.* (2012), similar estimates were computed for the full period 2002-2010 (Table 4). Similarly, species and age are second-order explicative variables, and are therefore not accounted for in the present modelling. The reporting rate of Asian longliners considered here is a mixture of Japan (J), Korean (K) and Taiwanan (Tw) LL reporting rates given in Carruthers *et al.* (2012), weighted by the relative capturability of each fishery. This capturability is estimated by

$$\gamma^{(s)} = \frac{1}{t_1 - t_0} \sum_{t=t_0}^{t_1} \frac{T^{(s)}_{mt}}{\sum\limits_{i \in \{J,K,Tw\}} T^{(i)}_{mt}}$$

where $T^{(s)}_{mt}$ is the total weight of catches at time step t annually observed between 2002 and 2010, given in the RTTP-IO database. One has $\gamma^{(T)} = 61\%$, $\gamma^{(J)} = 35\%$ and $\gamma^{(K)} = 4\%$. These proportions are detailed by species in Table 3.

The estimates of tag reporting rates are furthermore submitted to identification errors. Despite the correction of the tagging error described at § 2.2, two species can still be confounded during the collect of tags after recapture with a small probability (estimated to 2.7%) and in case of confusion, this error was found to be rather symmetrical ($\sim$ 50% of choosing among the two other species), unlike the tagging error. Renaming $\hat{\lambda}^s_t$ in $\hat{\lambda}^{s(k)}_t$ with the species index $k \in \{1,2,3\}$, one replace $\hat{\lambda}^{s(k)}_t$ by the unbiased estimation $\tilde{\lambda}^{s(k)}_t$ defined by the linear problem

$$\left\{\hat{\lambda}^{s(k)}_t\right\}^T_{k\in\{1,2,3\}} = \Psi^{-1} \cdot \Lambda \cdot \left\{\tilde{\lambda}^{s(k)}_t\right\}^T_{k\in\{1,2,3\}}$$

where the transition matrix Λ is estimated in Table 1. Consequently, each $\tilde{\lambda}^{s(k)}_t$ can be computed by linear inversion.

Finally, the incorporation of reporting rates estimates with their estimated standard deviation into the Bayesian model is made as follows. It is assumed that a good approximation of the distribution of $\hat{\lambda}_t$, defining a likelihood of tag reporting rates, is

$$\hat{\lambda}^s_t | \lambda^s_t \sim \mathcal{N}(\lambda^s_t, \hat{\sigma}^s_t)$$

where λ^s_t is the true reporting rate. If a more accurate distribution of $\hat{\lambda}^s_t$ should lay on a urn mechanism involving a binomial distribution, as explained in Polacheck *et al.* (2006), this practical Gaussian choice appears relevant with respect to the shape of posterior distributions of $\hat{\lambda}^s_t$ obtained by Carruthers *et al.* (2012) and appears furthermore justified by the Bayesian central limit (Bernstein-von Mises) theorem. It is truncated over $[0,1]$ in practice since $\hat{\lambda}^s_t$ is a fraction. A non-informative uniform prior is also implemented for λ^s_t.

2.5 Commercial catch data

Urn mechanisms similar to those monitoring the returns of tags applies to catch-at-age production. The catch $C^s_{a+j,t+j}$ taken by the fishery s is such that, marginally,

$$C^s_{a+j,t+j} \sim \mathcal{B}\left(P_{a,t}, \nu^s_{a+j,t+j}\right).$$

And similarly, using the same kind of notations, one has

$$\left\{\mathbf{C}_{\mathbf{a+T,t+T}}, P_{a,t} - \mathbf{C}^{\sum}_{\mathbf{a+T,t+T}}\right\} \quad \sim \quad \mathcal{M}\left(P_{a,t}\ ;\ \left\{\boldsymbol{\nu}_{a+T,t+T}, 1-\boldsymbol{\nu}^{\sum}_{a+T,t+T}\right\}\right).$$

However, this multinomial likelihood characterizes the true catches-at-age. In reality, various uncertainties occur in the observational process and, additioned to those that may emanate from model assumptions, usually dominate this uncertainty (Polacheck *et al.*, 2006). For this reason, most BP studies lays on the catch likelihood emanating from this process (Eveson *et al.*, 2009; Eveson, 2011). Following a common practice in tag-recapture models, a Gaussian distribution is assumed over the catch estimates $\left\{\hat{\mathbf{C}}_{\mathbf{a+T,t+T}}\right\}$:

$$\hat{C}^s_{a+j,t+j} \quad \sim \quad \mathcal{N}\left(\nu^s_{a+j,t+j}P_{a,t}, (\sigma^s_{a+j,t+j})^2\right).$$

Polacheck *et al.* (2006) have detailed why catch CVs cannot be estimated in a reliable way for usual BP models from tagging and catch data. Thus it has become common to set a large value for $\sigma^s_{a+j,t+j}$ (typically such that $\mathrm{CV}[\hat{C}^s_{a+j,t+j}] \in [30\%, 40\%]$). Indeed, Polacheck *et al.* (2006) showed the BP model results remain rather insensitive to this value. For the present preliminary assessments, a 30% CV was chosen.

2.6 Assumption on mortality rates

Natural mortality rates. Following the practice of most tuna stock assessments worldwide, it is assumed that the natural mortality rate can differ between ages, but not between cohorts ($M_{a,t} = M_a$). Most of previous works involving a BP model have usually placed no hypothesis on the form of M_a to account for all uncertainties (Polacheck *et al.*, 2006; Eveson *et al.*, 2007; Eveson, 2011). However, some analytical simplifications are often assumed to avoid too much model complexity, identifiability issues or irrealistic estimations, as constant rates for young and old ages, respectively (Fonteneau & Pallares, 2004; IOTC, 2010), or linear interpolation (Polacheck *et al.*, 2006).

Nonetheless, we deliberately choose not to follow an analytical approach fitting with the common idea that M is strongly correlated with various life history parameters, such as growth rate, age at sexual maturity, etc. (Vetter, 1988; Hampton, 1992; Chen & Watanabe, 1989). Rather, we adopt a more flexible, versatile modelling of $M(a)$, independent of the growth curve, that may fit with the variety of shape constraints noticed in previous works for the mapping $a \mapsto M(a)$. Especially, Fonteneau & Pallares (2004) highlighted that bigeye tuna mortality seems not to always obey the traditional U-shaped curve (Siegfried & Sansó, 2009; Brodziak *et al.*, 2011), according to which, after a fast decrease of $M(a)$ at the first ages, a senescence phenomenon starts after the age a_1 sexual maturity (Fig. 3 in Fonteneau & Pallares (2004)). An alternative is the W-shaped curve (Fig. 4 in Fonteneau & Pallares (2004)), involving a second peak of mortality in a_2 usually attributed to the occurence of first spawning.

Two possible approaches have been preliminary explored to model $M(a)$. The first one was analytical, based on cubic splines (Bartels *et al.*, 1998), the parameters of which being submitted to prior constraints. It was found to give some unrealistic estimations. The second approach is non-analytical but based on placing *conditional prior constraints* directly on the components of $M(a)$ in the following way:

$$\begin{aligned}
M(a_0) &\sim \mathcal{U}_{[M_{0\,\min}, M_{0\,\max}]},\\
M(a_0+1)|M(a_0) &\sim \mathcal{U}_{[M_{1\,\min}, M(a_0)]},\\
M(a_0+2)|M(a_0+1) &\sim \mathcal{U}_{[M_{2\,\min}, M(a_0+1)]},\\
&\ \ \dots
\end{aligned}$$

such that the common convex form of the mortality be assumed for youngest ages. A constant prior is assumed from the postulated age when senescence begins such that both $U-$ and $W-$shaped curves be possible. Moreover, to diminish the dimension of the estimation problem in these preliminary assessments, the natural mortality is assumed to be constant per year, except for year 0 (between 0.25 and 1 year). For all species relevant magnitudes for the bounds ($M_{i\,\min}, M_{i\,\max}$) can be found in Fonteneau (2003); Fonteneau & Pallares (2004); Fonteneau (2011).

Fishing rates. Different fishing rates characterize the fleets for reasons mixing technical and behavioral particularities. To avoid overparameterization a *separability assumption* (Doubleday, 1976; Fournier & Archibald, 1982) is needed. Following classical assumptions made in MULTIFAN-CL models and the formulation proposed by Hoenig *et al.* (1998a) for multiyear tagging models, it is assumed that

$$\log F^s_{a,t} \quad = \quad \log F^s_t + \log \varsigma^s_a$$

where ς^s_a is the selectivity-at-age characterizing the fishery s. In the model, fishing rates F^s_t are free parameters while ς^s_a are fixed. Considering that $\exp(-F^s_t)$ can be interpreted as a survival probability, a non-informative uniform prior on this probability implies that a reference prior is $F^s_t \sim \mathcal{E}(1)$.

The ς^s_a for each species have been estimated using the approach proposed by Restrepo *et al.* (2007). Selectivities were originally estimated for YFT using MULTIFAN-CL (Langley *et al.*, 2011), for BET using ASPM (Nishida & Rademeyer, 2011) or Virtual Population Analysis (VPA ; Zhu *et al.* (2011)), and for SKJ using SS3 (Kolody *et al.*, 2011). In the present paper they have been recalculated as follows. First they have been translated in smooth selectivities-at-length with the help of the growth curves used by these authors and cubic spline interpolation (Bartels *et al.*, 1998), then retranslated to selectivities-at-age using the growth curves given in Appendix A. The selectivity estimated for the baitboats of the MFCL region 2 was used for the Maldivian pole and liners. The selectivity for all longliners for the period 1972-2010 was constant across regions and used for the Japanese longliners. Finally, the selectivity estimated for the purse seiners on free-swimming and log-associated sets in the MFCL region 2 were used since most of the purse seine catch comes from this area. Final selectivity curves are plotted on Figures 3 to 5.

3 Preliminary assessments of natural mortality rates

3.1 Treatment of RTTP-IO data

Two populations of tags were removed from the number of releases N considered at any release event: (a) the tags that are immediatly recaptured within the considered period of non-mixing (assumed to be 3 months for each species) ; and (b) the tags that were recaptured by other fishing fleets than those considered in the present paper. The correction of the tagging error described in § 2.2 is only applied to released tags that were not recovered and for which the placement were not fully reliable.

3.2 Statistical estimation

The statistical estimation of the parameters is based on the product of three likehoods emanating from all observational processes carrying main uncertainties: the sampling arising from the tag recovery process (§ 2.3), the reporting process itself (§ 2.4) and the observation of catches (§ 2.5). The free parameters of the model are the fishing rates F^s_t, the natural mortality components, the true tag reporting rates and the population of tagged cohorts at first age of tagging. Informative priors were elicited for (F^s, M, λ) (especially λ) and weakly informative uniform priors were chosen for the cohort population on the log scale. The Bayesian BP model was implemented and tested in OpenBUGS (Lunn *et al.*, 2009) and JAGS (Plummer, 2003) languages. The second software was found to be more suitable to run Gibbs posterior sampling in acceptable time (3 4 days per experiment). MCMC experiments were conducted using a minimum number of 40,000 iterations and the convergence of chains to the stationary posterior distribution was managed and checked using the Brooks-Gelman diagnostic (Brooks & Gelman, 1998) implemented in the `CODA` software (Plummer *et al.*, 2006). Approximate posterior areas of highest density for $M(a)$ are plotted on Figures 6 to 8. If these preliminary curves remain imbued with much sampling uncertainty which could encompass a variety of forms, they seem to be mostly decreasing over time.

4 Discussion

These preliminary assessments must be first confirmed by several simulation studies, then strengthened with sensitivity analyses. The present results remain too crude to test statistically the hypothesis that at youngest ages the species share natural mortality features, as it is expected to be since they live in same schools. Refining the model and improving the computational aspects of the estimation will help to do so. The sensitivity analyses must be conducted by varying the most critical aspects of the model: reporting rates for Asian fishing fleets, priors over natural mortality components. The huge computational work needed to carry out both kind of analyses appears clearly as a limiting factor of the study. Nonetheless, it is important to test the identifiability and the posterior robustness with respect to several combinations of (somewhat arbitrary) prior constraints, as assuming a constant natural mortality rate per year to diminish the dimension of the problem, even if it is likely that this hypothesis should help to improve the assessment of natural mortality rates at first ages. These studies should besides focus on how the mortality at-age evolves with the growth, and if a clear correspondence can be established with each growth curve, as in **?**.

Several technical points could be improved in future studies. The mixing of tagged and untagged fish could be better accounted for. In this paper, it was considered that only a quarter of year (trimester) is enough to ensure that catch of tagged fish are not unbiased by a slow mixing of the two populations. Nonetheless, Langley *et al.* (2011) recently recommended to use yearly time steps rather than one quarter to increase the quality of mixing. The robustness of results could be tested by selecting the tagging data followig this more cautious hypothesis.

In a more long-term perspective, another research avenue is accounting for sexual dimorphism in growth, as summarized in IOTC (2010) (§ 3.4.3). Testing if the natural mortality curves between males and females statistically differ could be helpful to improve the population assessment models and to adjust the exploitation policies. Finally, the spatialization of the BP model including multiple component fisheries, initiated by Eveson *et al.* (2009), would be a major theme of research.

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Appendix A Age-length keys

Recent IOTC works (Eveson & Million, 2008a; Fonteneau & Gascuel, 2008) have demonstrated that the growths of YFT and BET follow multi-stanza patterns instead of classical von Bertalanffy curves. On the contrary, this classical approach was found relevant for SKJ by various studies (IOTC, 2010). The estimated growth curves used in this paper, affected with uncertainty, are plotted on Figure 2.

YFT: Eveson & Million (2008a) showed the relevance of a von Bertalanffy-log K (VB-log K) model (Laslett *et al.*, 2002). Massiot-Granier *et al.* (2010) proposed a VB-log K model which was found coherent with the two-stanza growth model (Fonteneau, 2008) used in the current YFT stock assessment produced by MULTIFAN-CL (IOTC (2010), § 4.4.1) but somewhat differing from the results previously obtained by Eveson & Million (2008b):

$$\ell(a|\boldsymbol{\theta}_Y) = L_\infty \left\{ 1 - \exp\left(-k_2[a-a_0]\right) \left[\frac{1+\exp(-\beta'_Y(a-a_0-\alpha'_Y))}{1+\exp(\beta_Y\alpha'_Y)} \right]^{-(k_2-k_1)/\beta'_Y} \right\} \tag{4}$$

where the parameter vector $\boldsymbol{\theta}_Y = (L_\infty, a_0, k1, k2, \alpha'_Y, \beta'_Y)$ is considered random and ℓ is given in centimeters while a is given in years. A Bayesian study conducted in Dortel *et al.* (2012) allows to estimate the posterior distribution of $\boldsymbol{\theta}_Y$ given otolith and modal progress data (capture frequencies) collected through the RTTP-IO before September 2010, independently of the tagging data used in the present paper for estimating the BP model.

BET: Similarly to YFT, strong evidences support the use of a VB-log K model (Eveson & Million, 2008a). Following the same kind methodology and similar data than for the YFT case, the posterior distribution of $\boldsymbol{\theta}_Y$ was estimated in (Dortel *et al.*, 2012). However, the lack of data in the upper tail of the curve leads to higher uncertainty levels from age 3.75 years.

SKJ: A von Bertalanffy-Fabens model (favored by Eveson & Million (2008a)) was recently fitted by Gaertner *et al.* (2011) from tagging-recapture RTTP-IO data released between 2005 and 2007. Their estimates were found consistent with the range of growth estimates obtained in various studies of the world's oceans.

When applied to the conversion of fish fork length to fish age, it is needed to define $\omega^{(k)}_{a,\ell}$ the frequency of age a in an infinite population of fork length ℓ for the species k. Given a length ℓ, the most probable age is estimated by

$$a^*(\ell) \quad = \quad \arg \max_{x\in\{a_0,\dots,A\}} \omega^{(k)}_{x,\ell}.$$

Consider a fish of any length ℓ of the species k with unknown age. Then $\omega^{(k)}_{i,\ell}$ can be interpreted as the limit probability that the age a of the fish is i given that ℓ is a given class $C_{\ell,\epsilon}$ of measure $\epsilon \rightarrow 0$. Bayes' rule implies that

$$\omega^{(k)}_{i,\ell} \quad = \quad K_\ell \cdot P\left(\ell(a) \in C_{\ell,\epsilon} | a = i\right)$$

with K_ℓ a normalization factor due to the constraint $\sum_{i=a_0}^{A} \omega^{(k)}_{i,\ell} = 1 \ \forall (k,\ell)$. Practically, an estimation of $\omega^{(k)}_{i,\ell}$ can be provided by $f^{(k)}_i(\ell)/\sum_{a=a_0}^{A} f^{(k)}_a(\ell)$ where $f^{(k)}_i$ is the density function of all lengths that can be sampled given age i from (4) and the distribution of $\boldsymbol{\theta}_Y$. In the present paper, Gaussian kernel estimation was used to assess the frequencies $\omega_{i,\ell}^{(k)}$ using 50,000 sampled lengths for each age, from 10cm to 250cm at the minimal precision level of 0.1cm (corresponding to the precision level of tagging data). Two final remarks can be made:

1. The implemented age-length relationships are used to estimate the most probable age given an *observed* length. This can be done by adding the effect of the observational noise (reading error) when sampling the length-at-age to estimate the ω:

   $$\ell^*(a|\boldsymbol{\theta}_Y) \quad = \quad \ell(a|\boldsymbol{\theta}_Y) + \epsilon_a$$

   with $\epsilon_a \sim \mathcal{N}(0, \phi^2)$. A unique standard deviation of $\phi = 3$ cm was used in the present paper, which was estimated from repeated tagging experiments (cf. Dortel *et al.* (2012)).

2. It is more convenient to establish the age of a tagged fish by estimating the age at release using a growth curve then adding the time at liberty, rather than using directly the growth curve at the time of recapture. Although the measurement noise is larger before release than at recapture, the uncertainty affecting the growth curves and their flatteting at oldest ages makes the age conversion more hazardous in practice.

Appendix B Tag shedding

Shedding rates can be divided in two types (Wetherall, 1982) and are usually estimated from double tagging experiments. Type-1 refers to immediate tag shedding/mortality and failure to report recovered tags, while Type-2 pertains to continuous tag shedding/mortality (for instance attributable to the tag itself, emigration processes away fishing grounds, etc.). We do not use here the method proposed by Hillary *et al.* (2008) who considered a partition of the time-at-liberty and estimated the tag retention probability for each element of this partition, but the simpler approach favored by (among others) Gaertner and Hallier (2008, 2009). They analysed 27,850 double tags with 4,650 recoveries collected between 2006 and 2009, during the RTTP-IO. The results revealed that a simple constant tagging rate is enough to explain each kind of shedding, independently of time and locations of tagging cruises. Consistently with other results obtained from large-scale tropical tuna tagging projects and after testing several models, the authors estimated the probability of a tag being retained at time j after release by

$$Q_{a,j} \ = \ Q_j \quad = \quad \alpha \exp(-\beta j) \tag{5}$$

with parameters $(\alpha, \beta) \in [0,1] \times I\!R^+$ updated in 2012 and given in Table 2 for the three species. Considering a time step in quarters, the value β is divided by 4 in the computations.

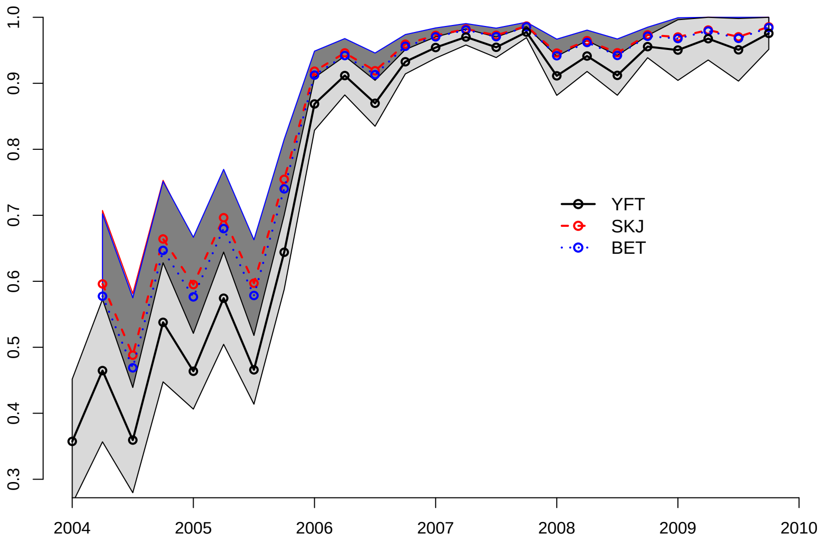


Figure 1: Estimated reporting rates (with 95% confidence intervals) for purse-seine fishery unloaded by stevedores in Seychelles (Victoria harbour), based on Hillary *et al.* (2008). BET and SKJ share similar confidence areas.

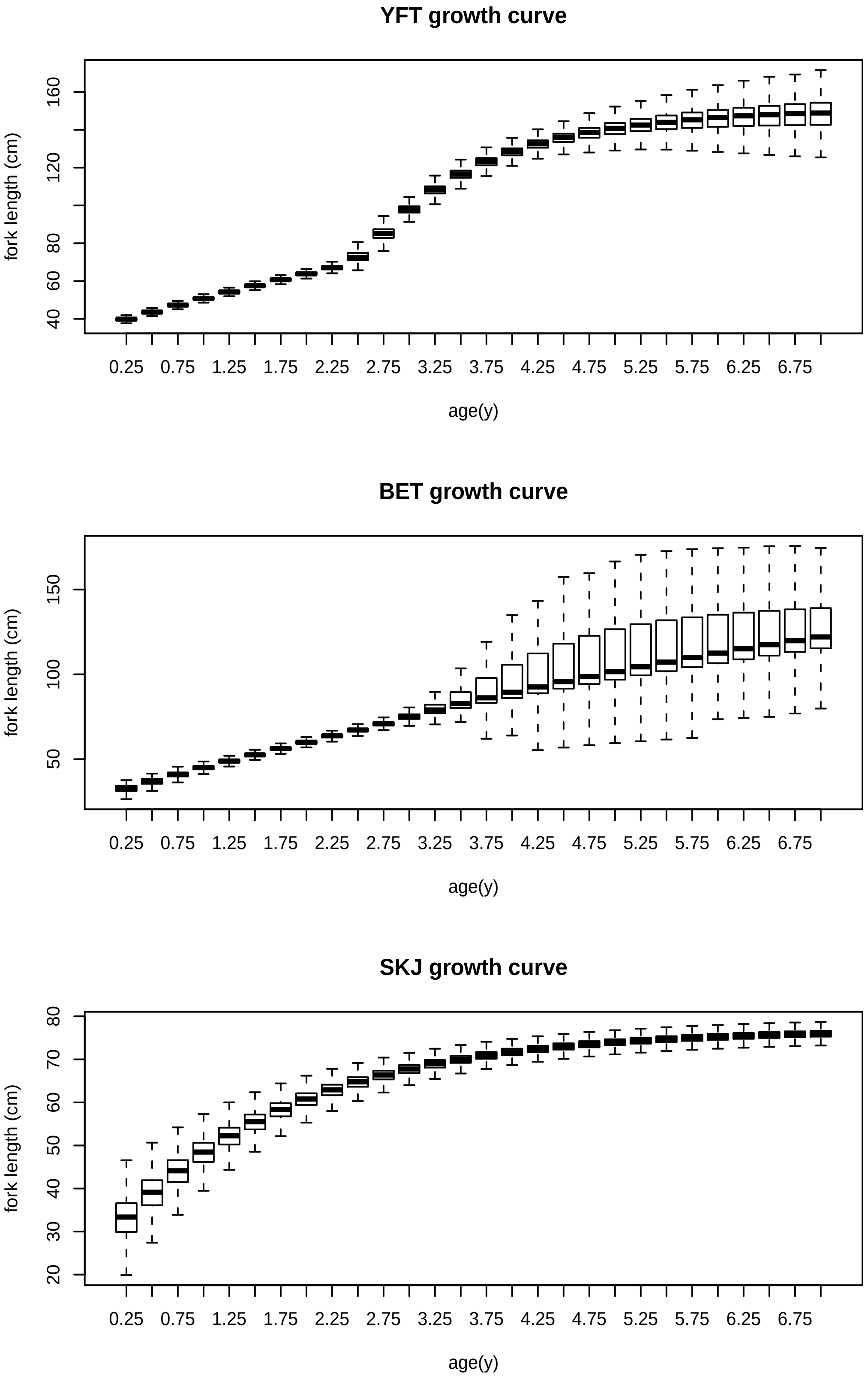


Figure 2: Growth curves for the three species.

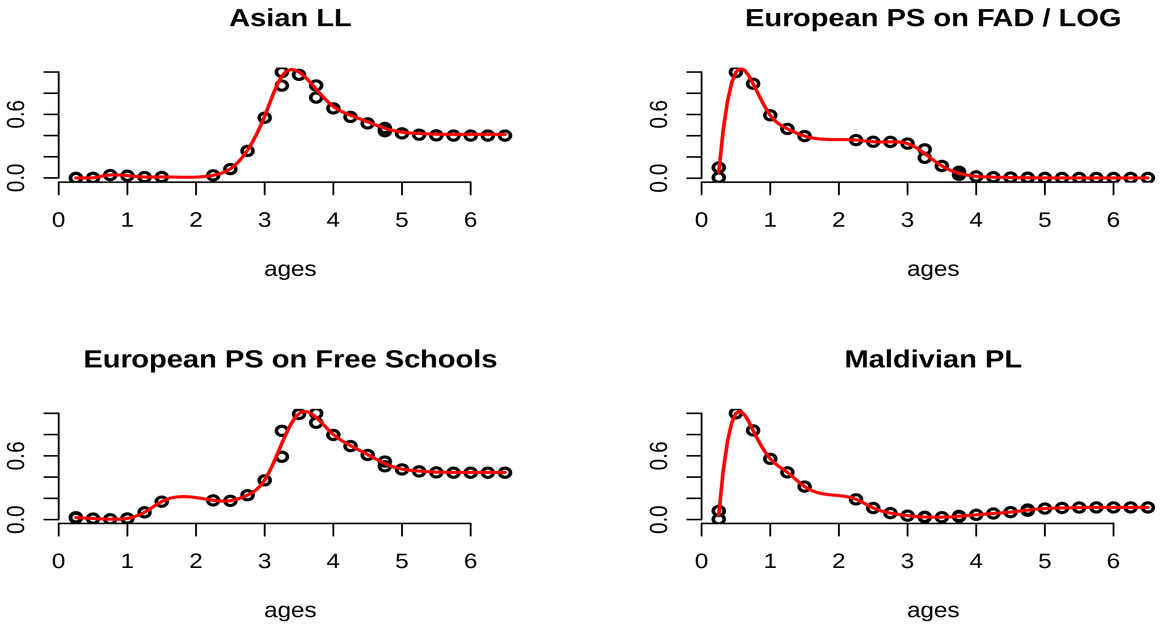


Figure 3: Selectivity-at-age for the yellowfin.

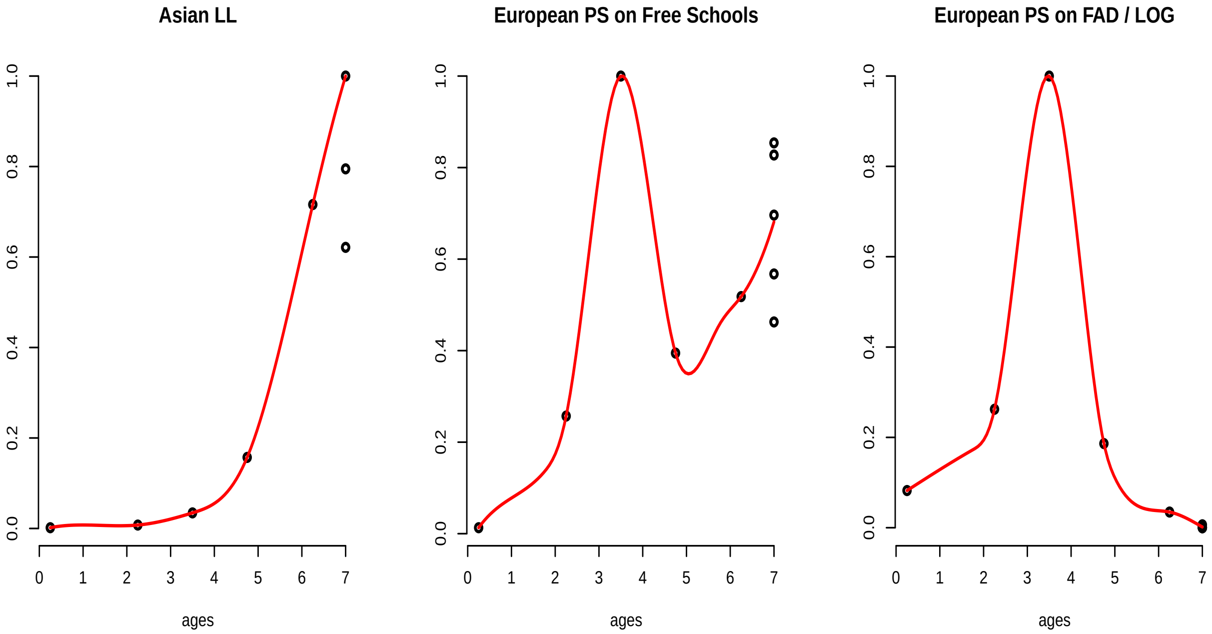


Figure 4: Selectivity-at-age for the bigeye.

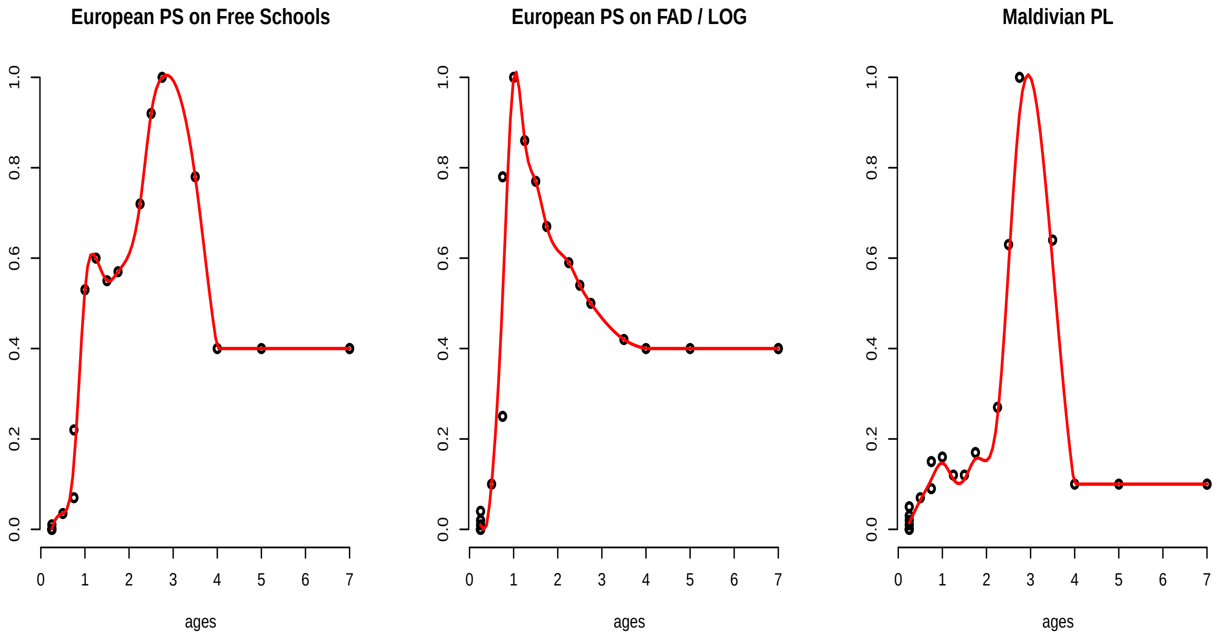
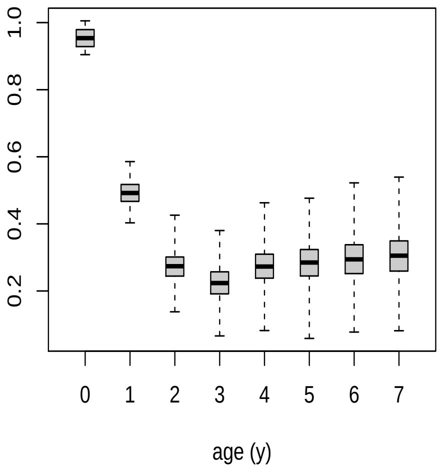


Figure 5: Selectivity-at-age for spikjack.



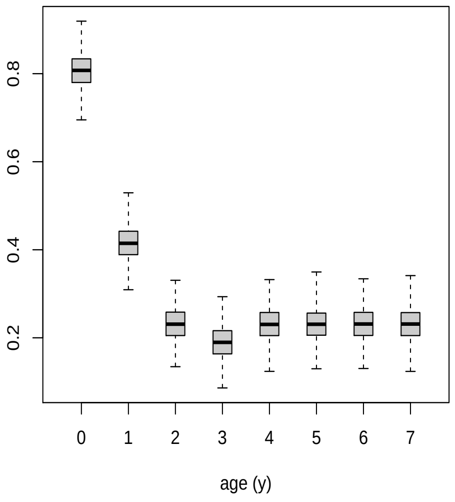


Figure 6: Preliminary assessment of YFT natural mortality-at-age.

Figure 7: Preliminary assessment of BET natural mortality-at-age.

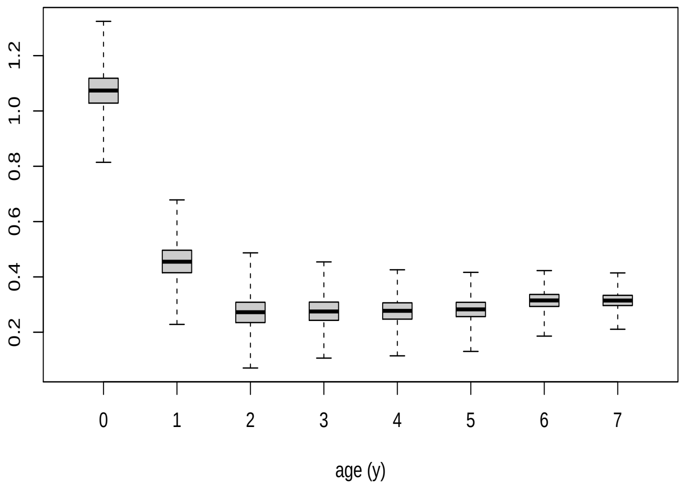


Figure 8: Preliminary assessment of SKJ natural mortality-at-age.

	Ψ				Λ		
	B	Y	S		B	Y	S
B	97.92	1.85	0.23	B	97.33	1.93	0.73
Y	1.68	97.92	0.40	Y	1.84	97.33	0.83
S	0.39	1.69	97.92	S	1.25	1.42	97.33

Table 1: Inter-species transition matrices (Ψ, Λ) for the species attribution frequency at tagging (left) and at recapture.

	α	β (year^{-1})
SKJ	0.993 (0.0040)	0.029 (0.007)
YFT	0.977 (0.0056)	0.039 (0.010)
BET	0.993 (0.0036)	0.017 (0.005)

Table 2: Parameters of the tag retention equation (5) estimated by Gaertner & Hallier (2009) for skipjack (SKJ), yellowfin (YFT) and bigeye (BET) tunas, updated in 2012. Conservative standard deviations (between parenthesis) are computed from bootstrapped confidence intervals given by the authors. Results are consistent with those obtained in Hillary *et al.* (2008) using a different method.

	SKJ	YLF	BET
JPN	44%	37%	25%
KOR	53%	57%	72%
TWN	3%	6%	3%
	100%	100%	100%

Table 3: Observed relative capturability for Asian longliners, per species.

s	$\hat{\lambda}_T^{(s)}$	$\hat{\sigma}_T^{(s)}$
EPS-FS / EPS-LS	93.99%	0.55%
ALL	3.77%	0.51%
FLL	5.50%	2.06%
MDV	23.84%	0.46%

Table 4: Reporting rate estimates per fishing fleet in most recent years, from Carruthers *et al.* (2012), for all tuna species.