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# Estimating fishing and natural mortality rates for Pacific bluefin tuna (*Thunnus orientalis*) using electronic tagging data

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ABSTRACT

This paper presents estimates of fishing and natural mortality rates derived from a spatially- and seasonally structured Bayesian mark-recapture model for electronically tagged Pacific bluefin tuna (PBFT) (*Thunnus orientalis*). Fishing mortality rates (*F*) were estimated by age group, year, quarter and area and ranged between 0.02 and 1.92 quarter$^{-1}$ for the northeastern Pacific Ocean (EPO) and 0.18 and 0.54 quarter$^{-1}$ for the northwestern Pacific Ocean. Annual Fs in the EPO were on average 2–3 times higher than the estimated rate of natural mortality for Pacific bluefin tuna aged 2 and 3 and 4–6 times higher than the estimated rate of natural mortality for Pacific bluefin tuna aged 4 and older. The estimate of *M* for PBFT aged 5 and above (median 0.15 yr$^{-1}$, standard deviation = 0.10) was lower than the value currently used in the PBFT stock assessment (i.e. 0.25 yr$^{-1}$). In addition to estimating age-group specific natural mortality rates (*M*), the plausibility of alternative values for *M* was evaluated by fixing it at the age-specific schedules tested in the PBFT stock assessment and computing a Bayesian model selection criterion (the Deviance Information Criterion, DIC) for alternative *M* configurations. For models in which *M* was fixed, the lowest DIC was obtained for the *M* scenario that assumed the lowest value of *M* for PBFT aged 4 and above (i.e. 0.12 yr$^{-1}$).



## 1. Introduction

Pacific bluefin tuna (*Thunnus orientalis*) is a highly migratory species, having the largest home range of any tuna in the genus *Thunnus*. Pacific bluefin tuna, hereafter PBFT, are primarily distributed throughout the temperate waters of the northern Pacific Ocean but also range into the western South Pacific (Bayliff, 1994; Collette and Nauen, 1983). Two spawning areas are currently recognized; one in the southwestern North Pacific off Taiwan and the other in the Sea of Japan (Okiyama, 1974; Chen et al., 2006; Tanaka et al., 2007). PBFT in spawning condition have been taken in these waters in the months of April through August. Genetic structure has not been detected to date in PBFT, and one stock is currently recognized throughout the Pacific Ocean.

Commercial fisheries exist for PBFT throughout their range and are most intensive in the northwestern (WPO) and northeastern Pacific Ocean (EPO). Annual reported ocean-wide catches since the early 1950s have varied between 8000 and 35,000 tons (IATTC, 2005), averaging around 25,000 tons between 1950 and 1980 and 15,000 tons thereafter. Catches in the EPO have declined since the 1960s, although the last decade saw catches rapidly increase (Aires-da-Silva et al., 2007). Concomitantly, fishing effort in the EPO decreased between 1960 and 1990 but has rebounded since the late 1990s in concert with expansion of the PBFT ranching industry off Baja Mexico (Aires-da-Silva et al., 2007). PBFT are also exploited by a variety of fisheries in the WPO, including purse-seine, longline and gillnet fisheries (Bayliff, 2001).

A preliminary stock assessment was conducted for PBFT by the Inter-American Tropical Tuna Commission (IATTC) (Bayliff, 2001). However, the available catch and effort data and length-frequency data for the WPO were insufficient for calculation of abundance indices for the WPO or to conduct cohort analysis for the entire Pacific Ocean (Bayliff, 2001). A full stock assessment including updated catch and effort and length-frequency data for the WPO was conducted by the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC) in 2008 (Anon., 2008). Estimates of PBFT fishing mortality rates (*F*) in recent years were above fishing mortality levels corresponding to target reference points such as $F_{MSY}$ (the fishing mortality that would achieve maximum sustainable yield) (ISC, 2008).

The stock assessment for PBFT is subject to uncertainty about several basic life-history characteristics, foremost among them the rate of natural mortality, *M* (Bayliff, 2001). *M* is of primary importance in fish stock assessments as it determines potential

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maximum sustainable yield (MSY) (Beddington and Cooke, 1983; Beamesderfer and North, 1995) and a population's response to harvest. Higher rates of natural mortality are associated with more productive stocks and their ability to sustain higher harvest rates. However, for most exploited fish populations, *M* is typically difficult to estimate because it is not feasible to monitor natural deaths (Quinn and Deriso, 1999) and it is difficult to separate the effects of natural mortality, fishing mortality and recruitment in observations of fish abundance (Hightower et al., 2001; Hilborn and Walters, 1992). Moreover, methods available for the estimation of *M* for fish populations have onerous data requirements and assumptions that are not easily satisfied. For example, estimation of *M* using catch curve analysis (Ricker, 1975; Vetter, 1988) requires data from an unexploited or very lightly exploited population and when catch-at-age data become available, exploitation rates are typically non-negligible. In contrast, tagging experiments with sufficiently rigorous tagging design and high tag recovery rates are often not feasible in many instances (Walters and Martell, 2004).

*M* has commonly been identified as a key source of uncertainty in fish stock assessments (Lapointe et al., 1989; Hilborn and Walters, 1992). The treatment of age-specific *M*s as fixed parameters fails to capture this uncertainty, which could ultimately lead to loss of yield or overexploitation of the stock. Currently an age-specific vector for *M*, with *M* for ages 4 and above equal to 0.25 $yr^{-1}$ is used in the PBFT stock assessment. Lower values for *M* for fish of age 4 and older yielded estimates of the depletion of spawning biomass between 1952 and 2005 (<5%) and unfished spawning biomass (about 1.4 million tons) that were considered implausible by the working group (Anon., 2008; Aires-da-Silva et al., 2009). Currently, only the value of *M* for age-0 PBFT has been empirically derived using tagging data (Takeuchi and Takahashi, 2006). Values for fish of age 1 and older were derived using life-history based methods and estimates for southern bluefin tuna (*Thunnus maccoyi*) (Polacheck et al., 1997). However, when considered together, values for *M* of 0.25 $yr^{-1}$ and above with moderate to high fishing mortality rates for adult PBFT may be incongruous with their reported longevity (maximum age of 26 years, Shimose et al., 2009). More information on *M* for PBFT aged 4 and above may thus be useful to help reduce the substantial uncertainty associated with this parameter.

Tagging data can be informative with respect to rates of fishing and natural mortality. A major caveat to using tagging data is a requirement that the tag reporting rate is known or can be reliably estimated (Bacheler et al., 2009; Pollock et al., 1991, 2001). Telemetry has been applied to estimate natural mortality rates (mortality rates are inferred from transmitters that stop moving over successive time periods) (Hightower et al., 2001; Waters et al., 2005). More recently, tag return data (e.g. from archival or conventional tags) and telemetry data have been combined (Pollock et al., 2004; Bacheler et al., 2009) to provide information about both return rates and natural mortality rates.

State-space Bayesian tagging models (Michielsens et al., 2006; Kurota et al., 2009; Taylor et al., 2011) offer a powerful framework for analysis of tagging data and provide a statistically rigorous means to quantify uncertainty, accounting for both observation and process error (Wade, 2000; Michielsens et al., 2006). We extend this methodology to the analysis of electronic tagging data for PBFT. In this paper we seek to use electronic tagging data to examine age-group specific rates of natural mortality and seasonal movement patterns of PBFT. The use of a sequential Bayesian approach facilitates the flow of information from different data sources whereby the posterior from one analysis becomes the prior for the next (Michielsens et al., 2008). In the context of the current analysis, posterior probability density functions (pdfs) for seasonal movement rates from analysis of pop-up satellite archival tag (PAT) data were used as the prior for the archival tag model (Kurota et al., 2009). Our analysis additionally includes quarterly locations for archival tagged PBFT between the release and recapture locations, thereby using the additional spatial information available from the electronic tag data.

The quantitative integration of conventional and electronic tag data into spatially structured assessment models is opening the door to an improved understanding of the population dynamics of highly migratory species (Goethel et al., 2011). Integrating tagging data with other fisheries data (typically catch-at-age and catch-per-unit-effort data) has advanced stock assessment models for several species (e.g. sablefish (*Anoplopoma fimbria*) (Haist, 1998); yellowfin tuna (*Thunnus albacares*) (Hampton and Fournier, 2001) and Atlantic bluefin tuna (*Thunnus thynnus*) (Taylor et al., 2011)).

The number of electronic tags placed on PBFT has increased rapidly in the past decade with several archival and satellite tagging projects on both sides of the Pacific basin (Kitagawa et al., 2000, 2007; Boustany et al., 2010). In the EPO over 550 juvenile PBFT (primarily year classes 2 and 3) have been tagged with archival and pop-up satellite technologies, and a high archival tag recapture rate has resulted in a rich data set of over 58,000 tag days (Fig. 1), including track lengths exceeding 4 years (Kitagawa et al., 2007; Boustany et al., 2010; Block et al., 2011). These data provide new

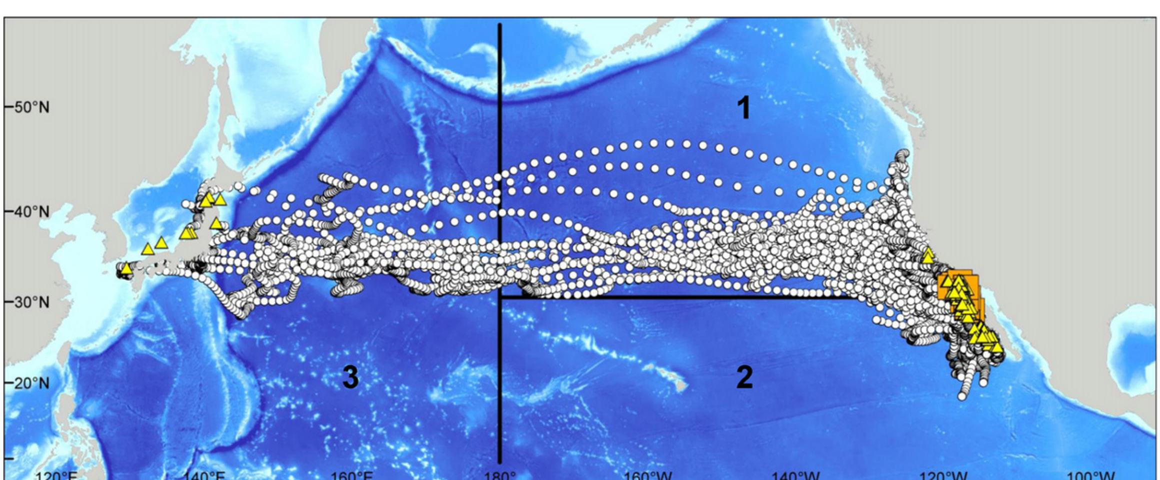


**Fig. 1.** Boxes used in the PAT (boxes 1 and 2) and archival (boxes 1–3) tag models for Pacific bluefin tuna. Release locations (orange squares), recapture locations (yellow triangles) and daily positions from a state-space model (white circles) for the archival tag data are overlaid.

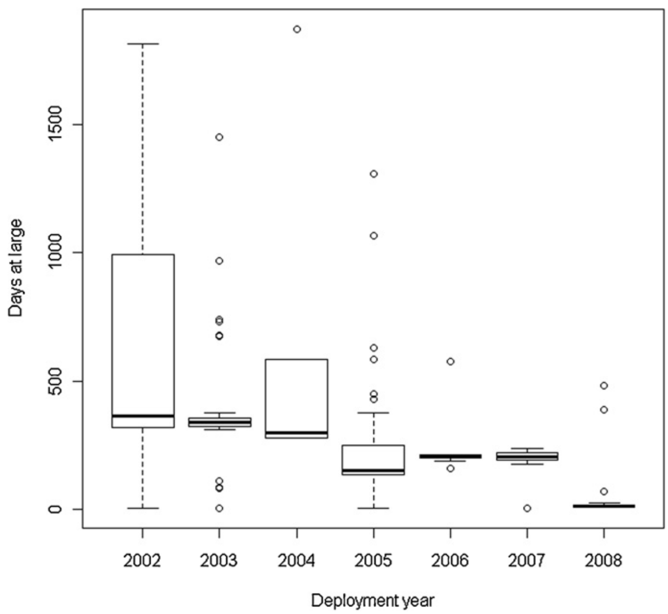


**Fig. 2.** Boxplot of days-at-large by deployment year for archival tagged Pacific bluefin tuna. Thick horizontal lines denote medians; the lower and upper limits of the boxes represent lower and upper quartiles. The dotted lines extend to the minimum and maximum values and open circles represent outliers (defined as values outside 3/2 times the interquartile range).

information on the migrations of PBFT and have revealed that PBFT in the EPO have predictable seasonal patterns of north-south movement that recur annually in the California Current in relationship to seasonal oceanographic changes (Kitagawa et al., 2007; Boustany et al., 2010; Block et al., 2011). The positional data also show that the California Current is retentive for young PBFT that migrate to the EPO, usually for one to four years with eventual return to the WPO along the North Pacific transition zone front (Boustany et al., 2010). Archival tagging experiments have also been carried out in the WPO, primarily to study ambient temperature preferences and migration patterns in young PBFT (Itoh et al., 2003a,b; Kitagawa et al., 2006, 2009).

This paper presents results from a novel tagging model based on EPO electronic tag data sets where fishing mortality rates were directly estimated from archival tag returns. With the relatively long times at large for electronically tagged PBFT, particularly in the early years of the study (2002–2004, Fig. 2) and the high recovery rates of tags, the tagging data should also be informative with respect to age-specific *M*s. The mark-recapture model is spatially structured and allows estimation of seasonal movement probabilities, which is desirable for robust estimation of exploitation rates for highly migratory fish such as tunas (Walters and Martell, 2004). Results are presented for informative and uninformative priors for age-group specific *M*s. The consistency of alternative candidate *M* vectors proposed for the PBFT stock assessment with the structure of the tagging data set was evaluated by computing the Deviance Information Criterion (DIC) for each fixed M-vector (Spiegelhalter et al., 2002; Bolker, 2008).

## 2. Materials and methods

### 2.1. Data

Electronic tagging data covering the period 2000–2009 were used in analyses described below. Tagging experiments, inclusive of deployments utilizing archival tags and pop-up satellite archival tags (PAT tags) were conducted under the Tagging of Pacific Pelagics (TOPP) Program (see Kitagawa et al., 2007; Boustany et al., 2010; Block et al., 2011). PAT tags ($N = 35$) were applied between 2000 and 2008 off the Baja California coast, with a maximum programmed time at large of 365 days. Pop-up satellite archival tags (several Wildlife Computers models, including PAT 2.0, 3.0 and Mk10) were attached to the PBFT using monofilament leaders with a shrink-wrap cover (Marcinek et al., 2001; Block et al., 2005). All tags were placed in the vicinity of the second dorsal fin region with a penetration of 8–10 cm.

Surgically implanted archival tags (Lotek, LTD 2310 series A–D) were deployed during cruises at sea off the coast of California and Mexico aboard the fishing vessel Shogun (Kitagawa et al., 2007; Boustany et al., 2010). Data used in the mark-recapture model comprise release location (vessel GPS) data for 523 surgically implanted archival tags released off the Baja California coast between 2002 and 2009. Recapture end point GPS locations were available for 270 archival tagged PBFT. Additionally, quarterly locations were obtained for archival tagged fish (in quarters intermediate between release and recapture) by finding the model area in which maximal occupancy (number of days) occurred during each quarter. Geolocation estimates of daily positions were obtained using light (longitude) and sea surface temperature (latitude) based algorithms (Teo et al., 2004). A state-space modeling approach (Jonsen et al., 2005; Block et al., 2011) was used to refine daily position estimates and quantify the uncertainty associated with the positions.

Curved lengths were measured in the tagging cradle for all electronically tagged fish. Ages were assigned (following conversion of curved length to straight length) using an inverse von-Bertalanffy equation with parameters taken from Shimose et al. (2009). The tagged tuna ranged in age (based on length) from 1 to 5 years at release.

## 3. Model structure

The Pacific Ocean was subdivided into three areas (boxes) for the purposes of the model. These areas correspond roughly to Japan and trans-Pacific (box 3); California (box 1) and Mexico (box 2) (Fig. 1). The boundary between the northern and southern boxes in the EPO was assigned such that an approximately equal number of releases occurred on either side of the boundary to facilitate estimation of movement rates between the EPO boxes. This division was also chosen as it coincides approximately with the southernmost limit of the USA's Exclusive Economic Zone (EEZ) in the Pacific Ocean and as such has relevance with regard to fishing dynamics and fishery management. The WPO box (box 3) was not used for the PAT model, since no releases or recoveries of PAT tags occurred in the WPO. We also note that in a few runs not reported below, slightly different configurations of the spatial boxes were applied to evaluate the sensitivity of results to different configurations. Estimates of movement parameters were similar, probably because most fish moved well beyond the current dividing line in their north-south migration. Both PAT and archival tag models follow the fate of cohorts of tagged fish released in a particular year, quarter and area. The archival tag model had additional age group structure (age-structure was not used in the PAT model owing to the relatively small number of tags modeled).

## 4. PAT model

The model of PAT tags included only those tags for which pop-up satellite tag location data were available (about 90%). This model was primarily used to estimate prior distributions for seasonal movement rates between two areas (north and south EPO, boxes 1 and 2). Fishing and natural mortality rates were not estimated in the PAT model. Few (<5) tags were known to have been recovered by fishers; the majority of tags used in this analysis were recovered as a result of release from fish at or close to a pre-programmed pop-up time. A vector of parameters describing the probability for a tag to pop-up x quarters earlier than its programmed pop-up date was used (Kurota et al., 2009) owing to the lack of information to clearly distinguish the state associated with tag release/recovery (e.g. tag popped-up after a natural mortality event, tag shed from a live fish etc.) in the data. This is just another way of expressing the probability of a tag popping up a given number of quarters after release. This formulation was adopted since it appears that the actual pop-up time is more likely to depend on the programmed pop-up time than the actual time (i.e. year and season of release). Tags that release before the scheduled time may also be of interest as these may be more likely to be shedding events.

Seasonal (quarterly) probabilities of movement from area $j$ to area $k$ ($p_{jk}$) were estimated, with the probability of residency equal to $1 - p_{jk}$. Movement in any time step was assumed to be independent of all prior locations except that in the previous time step. Beta prior pdfs (the conjugate prior for binomial data) were placed on seasonal movement probabilities in the PAT model.

A Dirichlet prior pdf (the conjugate prior for multinomial data) was placed on the probability for a tag to pop-up $\times$ quarters earlier than its programmed pop-up date, with equal probabilities for each quarter. The number of tags that popped off in each time and area cell was assumed to follow a negative binomial distribution. The negative binomial distribution has a variance no less than its mean, and can describe the overdispersion or clustering of recapture events. It therefore provides an appropriate representation in situations where random mixing of fish in space does not occur, so that recapture events are not independent. The suitability of a Poisson versus negative binomial observation error model for the pop-up tag data was addressed using a likelihood ratio test. This indicated that the PAT recovery data are over-dispersed relative to a Poisson distribution ($\chi^2 = 84$ on 1 degree of freedom, $p < 0.001$).

## 5. Archival tag model

Fishing mortality rates were estimated by area group, where annual patterns in fishing mortality were estimated for the northeastern Pacific Ocean (boxes 1 and 2, Fig. 1) (EPO) and the northwestern Pacific Ocean (box 3, Fig. 1) (WPO). 94% of recaptured archival tags were recovered in the EPO boxes, so this analysis is intended primarily to estimate fishing and natural mortality rates for the EPO.

### 5.1. Movement

The archival tag model comprised three boxes (with a northwestern Pacific box in addition to the two northeastern Pacific boxes used in the PAT model). The posterior beta pdfs for season-specific movement rates in the eastern Pacific Ocean from analysis of PAT tag data were used to parameterize the Dirichlet prior for movement rates between the EPO areas in the archival tag model. Posterior correlations between estimated movement parameters from the PAT model were low (maximum absolute pairwise correlation of 0.30). We therefore chose not to include information about correlations between movement parameters when formulating the prior for the archival tag analysis. Seasonal movements from areas 1 and 2 (the EPO) to area 3 (the WPO) were assigned one third of the total prior probability for movements originating in those areas. Parameters describing seasonal movement rates out of the WPO box were set equal to 0.

For archival tag data, quarterly locations for the entire time at large were used to inform estimates of movement parameters for recaptured and reported tags. For this purpose, an additional (multinomial) likelihood component was added to describe the probability of observing a certain number of tags in each area at time $t$ (where $t$ is intermediate between the quarters of release and recapture), given the predicted distribution of tagged animals at that time.

### 5.2. Fishing and natural mortality rates

Three age groups were used for estimation of $M$ (ages 2 and 3, group 1; age 4, group 2; ages 5+ group 3). This grouping was used because attempts at estimation with parameters stratified by actual ages indicated over-parameterization (no updating of priors for $F$ and $M$ parameters for some ages). The grouping adopted was the most disaggregated in terms of the number of age groups that still resulted in an adequate amount of updating of priors. Process error was included in age group specific survival rates; this was implemented through the use of an error term with variance dependent on the length of the model time step (Michielsens et al., 2006). A symmetric uniform distribution centered around 1 was used to model process error in survival rate: the quarterly process error was bounded between 0 and $e^Z$ (where $Z$ is the total mortality rate), the latter to ensure that the number of tagged fish could not increase between subsequent time steps.

The suitability of a Poisson versus negative binomial observation error model for the recapture data was addressed using a likelihood ratio test. This indicated that the recapture data are highly overdispersed and a negative binomial observation model is thus a better candidate than the Poisson distribution $\chi^2 = 993$ on 1 degree of freedom, $p < 0.001$.

$F$s in the EPO areas were not disaggregated by fleet or gear type, since a high proportion (88%) of the tags was recovered by the Mexican purse seine fishery. In order to avoid estimation of too many $F$ parameters, within-year $F$s were estimated by area group, quarter and age group, and an annual $F$ multiplier was estimated which was applied to within-year $F$s in a given year (i.e. the within-year seasonal pattern was assumed to be the same across years for the EPO and WPO respectively) (Eq. (1i)). The $F$ multiplier in the first year in the time series (2002) was set equal to 1 (Eq. (1ii)); estimated $F$ multipliers for subsequent years are thus relative to the 2002 value:

$$F_{tot\,y,g(a),s,h(k)} = F_{g(a),s,h(k)}\phi_{y,h(k)} \quad (1i)$$

$$\phi_{2002,h(k)} = 1 \quad (1ii)$$

where $F_{g(a),s,h(k)}$ is the quarterly fishing mortality rate for fish in age group $g$ in season $s$ and area group $h$. Area group 1 corresponds to the EPO areas (boxes 1 and 2), while area group 2 corresponds to the WPO (box 3) and $\phi_{y,h(k)}$ is the annual $F$ multiplier for year $y$ and area group $h$.

The prior applied to within-year $F$s in the EPO (areas 1 and 2) implied a seasonal pattern; a lognormal prior was placed on quarterly $F$s with lower medians for the winter seasons (quarters 1 and 4) relative to the summer (quarters 2 and 3) (Table 1). Note that we use the median as the key statistic for central tendency of priors and posteriors throughout since this is the conventional statistic for the lognormal distribution which is applied extensively in this analysis. Moreover, the use of the median rather than the mean has become common practice in many Bayesian stock assessments since among other things it is easier to interpret than the mean. Due to a lack of information regarding the possible seasonality of WPO fisheries (area 3), a prior that implied equal $F$ for all quarters was placed on WPO within-year $F$s (Table 1). Priors for $F$ multipliers in the EPO between 2003 and 2006 were based on the ratios of estimates of annual fishing effort in this region to estimated fishing effort in 2002 (Aires-da-Silva et al., 2007). Priors for EPO $F$s were further specified such that the annual $F$s implied encompassed estimated values for annual $F$s corresponding to different fixed schedules

**Table 1**
Prior probability density functions for estimated parameters in the Bayesian mark-recapture model for Pacific bluefin tuna: see equations in population dynamics section for definitions. $M$ is in units of $yr^{-1}$, $F$s are in units of $quarter^{-1}$.

| Model | Parameter | Prior | Prior median |
|---|---|---|---|
| PAT | $\psi$ | Dirichlet[] | Equal prior probabilities |
| PAT | $p$ | Beta(1,1) | 0.50 |
| Archival | $F_{EPO\ (winter)}$ | Lognormal($-3.00,0.45^2$) | 0.05 |
| Archival | $F_{EPO\ (summer)}$ | Lognormal($-1.0, 0.45^2$) | 0.37 |
| Archival | $F_{WPO}$ | Lognormal($-1.50, 0.50^2$) | 0.22 |
| Archival | $\phi_{EPO,2003}$ | Lognormal($0.05,0.60^2$) | 1.04 |
| Archival | $\phi_{EPO,2004}$ | Lognormal($0.58,0.60^2$) | 1.79 |
| Archival | $\phi_{EPO,2005}$ | Lognormal($0.33,0.60^2$) | 1.39 |
| Archival | $\phi_{EPO,2006}$ | Lognormal($0.81,0.60^2$) | 2.24 |
| Archival | $\phi_{EPO,2007–2009}$ | Lognormal($0,0.60^2$) | 1.00 |
| Archival | $\phi_{WPO,2003–2009}$ | Lognormal($0,0.60^2$) | 1.00 |
| Archival | $M_1$ base-case | Lognormal($-0.91,0.63^2$) | 0.40 |
| Archival | $M_2$ base-case | Lognormal($-1.38,0.63^2$) | 0.25 |
| Archival | $M_3$ base-case | Lognormal($-1.60,0.63^2$) | 0.20 |
| Archival | $M_1$ [a] | Uniform(0.01,1.5) | 0.75 |
| Archival | $M_2$ [a] | Uniform(0.01,1.5) | 0.75 |
| Archival | $M_3$ [a] | Uniform(0.01,1.5) | 0.75 |
| Archival | $p$ | Dirichlet[] | Posterior medians from PAT model |
| Archival | $\lambda_{EPO}$ | Beta(2,2) | 0.50 |
| Archival | $\lambda_{WPO}$ | Beta(2,2) | 0.50 |
| Archival | $\gamma$ | Beta(1.25,19) | 0.05 |

[a] Prior used in sensitivity analysis.

for $M$ from ISC's assessment model (Table 2) (Aires-da-Silva et al., 2009).

Owing to concerns about the proximity of releases to fishing effort in some years, $F$s were also estimated using a data set that excluded recaptures and releases that occurred in the same quarter.

Lognormal priors placed on $M$s for the 3 age groups used in the archival tag model were moderately informative and were specified to be consistent with values used in the PBFT stock assessment—the prior median for age group 1 (ages 2 and 3) was 0.40 $yr^{-1}$ with a 95% credibility interval of 0.12–1.38 $yr^{-1}$. The prior placed on $M$ for age group 2 (age 4) had a lower median (0.25 $yr^{-1}$). This is the value for $M$ for age 4 PBFT that is currently used in ISC's stock assessment; this prior had a 95% credibility interval of 0.07–0.86 $yr^{-1}$. A lower prior median of 0.20 $yr^{-1}$ was used for the age 5+ (age group 3) $M$, since $M$ can generally be assumed to decrease with size (e.g. Lorenzen, 2000; Hampton, 2000). This prior had a 95% credibility interval of 0.06–0.69 $yr^{-1}$. As a sensitivity analysis, the model was also run with uniform priors for $M$ for all 3 age groups (Table 1).

### *5.3. Tag reporting rate*

Separate reporting rates were estimated for fisheries operating in the EPO and WPO. While it is generally not proper to develop priors with knowledge of the data, the use of slightly informative priors for archival tag reporting rates was felt to be justified since a very high proportion of tags have been recaptured for some deployment years (>70%) providing a minimum threshold for the reporting rate. Because we lacked independent information about WPO and EPO reporting rates we chose to apply the same prior pdf in both areas. A moderately informative beta prior with median 0.50, 2.5th percentile 0.10 and 97.5th percentile of 0.90 was therefore used for archival tag reporting rates in the EPO and WPO (Table 1).

**Table 2**
Alternative scenarios for age-specific rates of natural mortality ($yr^{-1}$). Scenarios taken from Aires-da-Silva et al. (2009).

| $M$ schedule | Age 1 | Age 2 | Age 3 | Age 4 | Age 5+ |
|---|---|---|---|---|---|
| 2006 | 0.8 | 0.4 | 0.25 | 0.25 | 0.25 |
| 2008 base case | 0.46 | 0.27 | 0.2 | 0.12 | 0.12 |
| Ishigaki | 0.39 | 0.25 | 0.25 | 0.25 | 0.25 |

### *5.4. Tagging-induced mortality*

A fairly informative prior was placed on the probability of mortality resulting from archival tag implantation ($\gamma$, Table 1). This prior had a median of 0.05, which was felt to be justified because of the high recapture rates and since observations in captive tanks utilizing similar procedures do not result in significant mortality.

### *5.5. Evaluations of the plausibility of alternative M schedules*

For evaluations of alternative assumptions about the $M$-at-age vector, $M$ was simply fixed to represent natural mortality rate scenarios used in ISC sensitivity analyses (Aires-da-Silva et al., 2009). These are listed in Table 2. Since the Ishigaki WP04 and WG scenarios are fairly similar, only the Ishigaki WG schedule was used in evaluations, hereafter referred to as "Ishigaki".

The Deviance Information Criterion, DIC (Spiegelhalter et al., 2002) is a measure of model fit based on the trade-off between the fit of the data to the model and the complexity of the model. DIC is defined analogously to AIC as:

$$DIC = D(\bar{\theta}) + 2p_D \tag{2}$$

where $D(\bar{\theta})$ is the deviance with the likelihood substituted with the probability of the data given the posterior mean of the parameter values $\bar{\theta}$.

$$D(\bar{\theta}) = -2\ \log(p(\text{data}|\bar{\theta})) \tag{3}$$

and $p_D$ is an estimate of the effective number of parameters (a measure of model complexity):

$$p_D = E_{\theta|y}[D] - D(E_{\theta|y}[\theta]) = \bar{D} - D(\bar{\theta}) \tag{4}$$

i.e. the posterior mean deviance minus the deviance evaluated at the posterior mean of the parameters. The model with the smallest DIC is estimated to best predict a replicate dataset of the same structure as that observed. DIC differences of 5–10 indicate that one model is clearly better than another, while differences of more than 10 are sufficient to remove the inferior model from consideration (Spiegelhalter et al., 2002; Bolker, 2008).

## 6. Population dynamics

For notational simplicity, subscripts for year, season and area of release are omitted from the following equations. The subscripts below refer to the year, season and area for the current quarter at large.

## 7. PAT tags

In the equations that follow, $S$ denotes the number of seasons (4), while $J$ denotes the number of areas (2) in the PAT tag model. The number of tagged fish in area $k$ with tags programmed to pop-up after $l$ quarters at large in year $y$ and season $s$, in the first quarter at large (i.e. the quarter of release) is given by:

$$N_{k,l,y,s} = R_{j,l,y,s} p_{s,j,k} \tag{5}$$

where $R_{j,l,y,s}$ is the number of tagged fish released in area $j$ in year $y$ and season $s$ programmed to pop-up after $l$ quarters at large and $p_{s,j,k}$ is the probability of movement from area $j$ to area $k$ in season $s$.

The number of PAT tags that pop-up or were shed from a fish in year $y$, season $s$ and area $k$, $t$ quarters before the programmed number of quarters at large $l$ is given by:

$$P_{k,l,y,s,t} = N_{k,l,y,s}\psi_t \tag{6}$$

where $\psi_t$ is the probability that a PAT tag pops-up $t$ quarters early.

For quarters following the quarter of release, the number of PAT tagged fish at the end of season $s$ in year $y$ and area $k$ with tags programmed to pop-up after $l$ quarters at large is given by the number in the previous time step minus the number that released during the previous time step:

$$N_{k,l,y,1} = \sum_{j=1}^{J} (N_{j,l,y-1,S} - P_{j,l,y-1,S,t})p_{s,j,k} \quad s = 1 \tag{7i}$$

$$N_{k,l,y,s} = \sum_{j=1}^{J} (N_{j,l,y,s-1} - P_{j,l,y,s-1,t})p_{s,j,k} \quad s > 1 \tag{7ii}$$

## 8. Archival tags

In the equations that follow, $S$ denotes the number of seasons (4), while $J$ denotes the number of areas (3) in the archival tag model. The archival tag model describes the survival, movement and capture of archival tagged fish. The number of tagged fish of age a in area $k$ in year $y$ and season $s$, in the first quarter at large (i.e. the quarter of release) is given by:

$$N'_{a,y,s,k} = \sum_{j=1}^{J} R_{a,y,s,j} \quad p_{s,j,k}(1-\gamma) \tag{8}$$

where $R_{a,y,s,j}$ is the number of tagged fish of age $a$ released in area $j$ in year $y$ and season $s$, and $p_{s,j,k}$ is the probability of movement from area $j$ to area $k$ in season $s$. $\gamma$ is the fraction of fish dying from injuries induced by tagging (applied only to newly tagged and released fish).

The number of tagged fish of age $a$ surviving at the beginning of season $s$ in year $y$ and area $k$ is given by:

$$N_{a,y,s,k} = N'_{a-1,y-1,S,k} e^{-(M_{g(a-1)}+F_{g(a-1),S,h(k)}\phi_{y-1,h(k)})}\varepsilon_{g(a-1)} \quad S{=}1 \tag{9i}$$

$$N_{a,y,s,k} = N'_{a,y,s-1,k} e^{-(M_{g(a)}+F_{g(a),s-1,h(k)}\phi_{y,h(k)})}\varepsilon_{g(a)} \quad S{>}1 \tag{9ii}$$

where $Mg(a)$ is the rate of natural mortality for fish in age group $g$, scaled to the quarterly time step, $F_{g(a),s,h(k)}$ is the quarterly fishing mortality rate for fish in age group $g$ in season $s$ and area group $h$. Area group 1 corresponds to the EPO areas (boxes 1 and 2), while area group 2 corresponds to the WPO (box 3). $\phi_{y,h(k)}$ is the annual $F$ multiplier for year $y$ and area group $h$ and $e^{-(M_{g(a)}+F_{g(a),s-1,h(k)}\phi_{y,h(k)})}$ is the quarterly survival rate. $\varepsilon_{g(a)}$ represents process error in survival for age group $g$. A symmetrical uniform distribution centered around 1 was used for the process error term (see Michielsens et al., 2006 for details). This formulation allows scaling of the process error variance according to the size of the time step and the total mortality rate $Z$.

The number of tagged fish of age $a$ in area $k$ in year $y$ and season $s$ is given by:

$$N'_{a,y,s,k} = \sum_{j=1}^{J} N_{a,y,s,j}p_{s,j,k} \tag{10}$$

The predicted number of recaptured tagged fish of age $a$ in year $y$, season $s$ and area $k$, $C_{a,y,s,k}$ is given by:

$$C_{a,y,s,k} = N'_{a,y,s,k}\frac{F_{g(a),s,h(k)}\phi_{y,h(k)}}{M_{g(a)+}F_{g(a),s,h(k)}\phi_{y,h(k)}} \times (1 - e^{-(M_{g(a)+}F_{g(a),s,h(k)}\phi_{y,h(k)})})\lambda_{h(k)} \tag{11}$$

where $\lambda_{h(k)}$ is the average fraction of archival tags that are reported in area group $h$.

The number of reported and recaptured tags in each quarter, area and age group was assumed to follow a negative binomial distribution. A parameterization of the negative binomial probability density function for the number of recaptures given parameter vector $\theta$ in terms of the mean $C_{a,y,s,k}$ and overdispersion parameter $\tau$ was used (Hilborn and Mangel, 1997). WinBUGs code for this parameterization was provided by Samu Mantyniemi, University of Helsinki.

$$p(O_{a,y,s,k}\,|\theta) = \frac{\Gamma(\tau + O_{a,y,s,k})}{\Gamma(\tau)O_{a,y,s,k}!}\left(\frac{\tau}{\tau + C_{a,y,s,k}}\right)^{\tau}\left(\frac{C_{a,y,s,k}}{C_{a,y,s,k}+\tau}\right)^{O_{a,y,s,k}} \tag{12}$$

where $O_{a,y,s,k}$ is the observed number of reported recaptures for fish of age $a$ in year $y$, season $s$ and area $k$.

A multinomial likelihood was used for quarterly positions for recaptured and reported archival tags, for quarters intermediate between release and recapture. In each time step the number of recaptured tags in each area was subtracted from the number of tags at large in that area. Movement between the three areas in each time step was assumed to be governed by the movement parameters $p_{s,j,k}$. The likelihood for the number of tags on live fish in areas 1–3 is therefore:

$$p(t_{a,s,1}, t_{a,s,2}, t_{a,s,3}|\pi_{a,s,1}, \pi_{a,s,2}, \pi_{a,s,3}) = \frac{T_{a,s}!}{t_{a,s,1}!t_{a,s,2}!t_{a,s,3}!}\pi_{a,s,1}^{t_{a,s,1}}\pi_{a,s,2}^{t_{a,s,2}}\pi_{a,s,3}^{t_{a,s,3}} \tag{13}$$

where $t_{a,s,k}$ is the observed number of tags on fish of age $a$ in season $s$ and area $k$; $T_{a,s}$ is the total number of tags on fish of age $a$ in season $s$, and $\pi_{a,s,k}$ is the probability that a tagged fish of age $a$ is in area $k$ in season $s$.

Bayesian mark-recapture models were implemented using WinBUGS (Bayesian inference using Gibbs sampling) software, version 1.4 (http://www.mrc-bsu.cam.ac.uk/bugs). To avoid basing inference on early draws from the Markov chain, which are still influenced by the starting values and thus may not be representative of the target posterior density function, the initial sequence of draws is usually discarded (referred to as "burn-in"). In this analysis, two chains were run, and convergence to the posterior distribution was assessed by applying the Gelman–Rubin diagnostic (Gelman and Rubin, 1992) and Monte Carlo error statistic (Spiegelhalter et al., 2003) leading the first 25,000 samples to be discarded. Statistics for model parameters were based on the first 10,000 samples after burn-in.

## 9. Results

This study examined the data set originating from deployment of 523 tags between August 2002 and October 2009. Over 270 archival tagged PBFT were recaptured during the study; recovery rates of archival tagged fish were substantial, varying between 43 and 75% by deployment year excluding the final year of the study (Table 3, final column). A summary of release and recapture numbers by year is given in Table 3. The mean time at liberty for archival tagged PBFT was 600 days; times at liberty decreased steadily over the study period (Fig. 2). This decline in part reflects the fact that later tagged cohorts have not had so much time to be recaptured, although the high recapture rates (e.g. 2005, 2008, Table 3) indicate that times at liberty have really decreased. Based on age-at-release (modal age 3 years) and time at liberty, ages at recovery varied between 2 and 9 years, with approximately 37% of recaptures falling into age group 1 (ages 2 and 3), 45% in age group 2 (age 4), and 18% in age group 3 (ages 5 and above). The age frequencies of releases and recaptures from the tagging experiment are shown in Fig. 3.

**Table 3**
Summary of archival tag release and recapture numbers by year and area for Pacific bluefin tuna. The final column contains recovery percentages by deployment year.

| Year | Releases | | | Recaptures | | | % recoveries by release year |
|---|---|---|---|---|---|---|---|
| | Box 1 | Box 2 | Box 3 | Box 1 | Box 2 | Box 3 | |
| 2002 | 35 | 53 | 0 | 1 | 3 | 0 | 52 |
| 2003 | 0 | 103 | 0 | 3 | 19 | 1 | 74 |
| 2004 | 8 | 0 | 0 | 6 | 64 | 2 | 75 |
| 2005 | 109 | 0 | 0 | 21 | 25 | 5 | 67 |
| 2006 | 67 | 0 | 0 | 9 | 29 | 1 | 19 |
| 2007 | 23 | 0 | 0 | 10 | 3 | 2 | 43 |
| 2008 | 106 | 1 | 0 | 55 | 5 | 1 | 63 |
| 2009 | 18 | 0 | 11 | 0 | 2 | 3 | 3 |

## 10. PAT tags

PAT tags were deployed most often in the third quarter (around two thirds). The estimated probabilities for a tag to pop-up and report in a given quarter showed that tags had the highest probability of releasing during the programmed quarter (Fig. 4). Tags were more likely to pop-up before than after the programmed quarter. The probability of releasing and surfacing 2 or 3 quarters before the programmed pop-up date was high (54%), while there was a low probability for tags to release after the programmed pop-up date (8%) (Fig. 4).

Priors for seasonal movement rates between the north and south EPO were updated by the PAT data, although the information in the tagging data did not lead to large reductions in prior standard deviations for most seasonal-specific movement vectors. Residency (remaining in the same area) was prevalent for most combinations of season and originating area (Table 4). Notable exceptions to this were northward movement (from area 2 to 1) between the third and fourth quarters and southward movement (from area 1 to 2) between the fourth and first quarters.

## 11. Archival tags

Priors for season-specific movement rates from the PAT model were further updated by the archival tagging data. The following results are shown for the base case model with informative priors for age group specific natural mortality rates $M_{g(a)}$ and tag reporting rates (Table 1) unless otherwise stated.

Informative priors for age group specific *M*s were updated by the tagging data, particularly for ages 5+ (age group 3, Fig. 5a). The estimated posterior median *M* for ages 2 and 3 (age group 1) was substantially higher than that for ages 5+ (0.40 $yr^{-1}$ versus 0.15 $yr^{-1}$ (Fig. 5a). The posterior median *M* for age group 2 was intermediate between these values (0.19 $yr^{-1}$). When an uninformative uniform prior was used (median 0.75 $yr^{-1}$), the posterior for ages 2 and 3 was fairly diffuse (median 0.72 $yr^{-1}$); however, posteriors for age 4 (age group 2) and ages 5+ (age group 3) showed more updating (medians of 0.43 $yr^{-1}$ and 0.13 $yr^{-1}$, respectively) (Fig. 5b).

Priors for archival tag reporting rates were also updated, particularly that for the EPO (Fig. 6), to yield posterior pdfs with means of 0.74 (EPO) (standard deviation of 0.10) and 0.62 (WPO) (standard deviation of 0.17).

The prior for the fraction of tagging-induced mortalities was updated slightly by the archival tag data to a more precise beta distribution with a mean and standard deviation of 0.04, relative to the prior mean of 0.06 and standard deviation of 0.05.

Estimates of within-year quarterly *F*s revealed a strong seasonal pattern to the EPO fishery, with much higher rates of recapture occurring in the second quarter, and to a lesser extent the third quarter, relative to the first and fourth quarters (Fig. 7a). Maximal within-year quarterly *F* values for each age group occurred in the second quarter, with the exception of age group 1 and area 2, for which the maximum *F* occurred in the third quarter (Fig. 7a). Total quarterly *F*s for the EPO (the product of the estimated within-year fishing mortality rate and *F* multiplier) ranged between 0.02

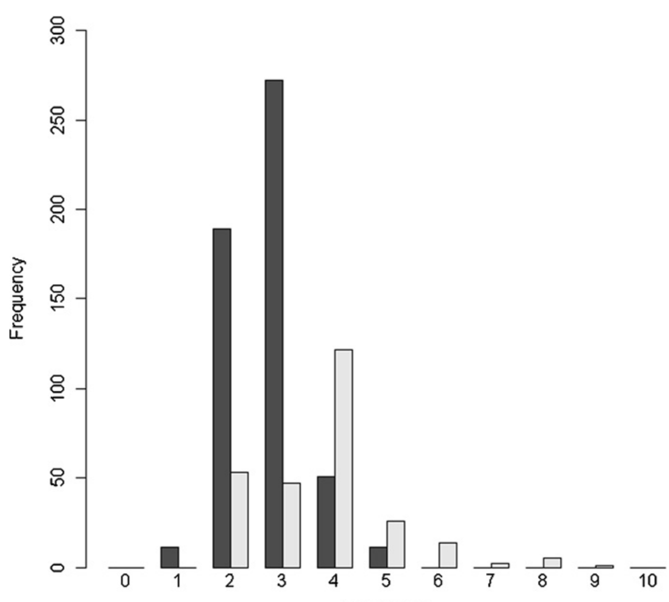


**Fig. 3.** Age frequencies of released (dark bars) and recaptured (light bars) archival tagged Pacific bluefin tuna.

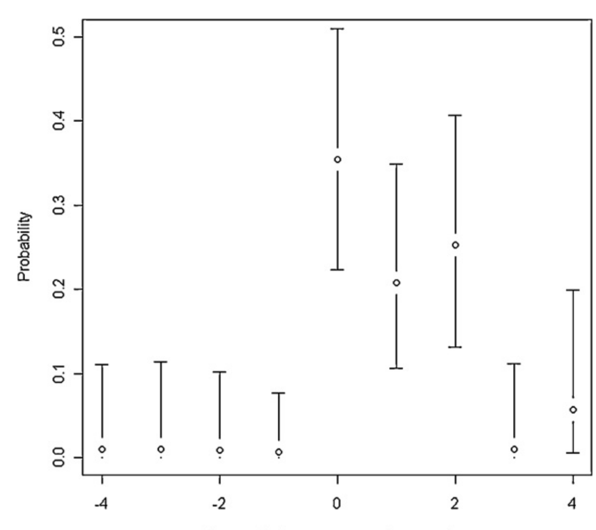


**Fig. 4.** Median and 95% probability intervals for the probability that a pop-up satellite archival tag surfaces and reports × quarters earlier than its programmed pop-up date.

**Table 4**
Prior and posterior means and standard deviations for season-specific movements rates for Pacific bluefin tuna in the PAT and archival tag models. Modal movement rates originating in a given area and season are bolded.

| Quarter | Originating area | Destination area | PSAT prior mean | PSAT prior SD | PSAT posterior mean | PSAT posterior SD | Archival posterior mean (start and endpoints only) | Archival posterior SD (start and endpoints only) | Archival posterior mean | Archival posterior SD |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 0.50 | 0.29 | 0.35 | 0.24 | 0.11 | 0.11 | 0.35 | 0.04 |
| 1 | 1 | 2 | 0.50 | 0.29 | **0.65** | 0.24 | **0.87** | 0.12 | **0.63** | 0.05 |
| 1 | 1 | 3 | – | – | – | – | 0.02 | 0.03 | 0.01 | 0.01 |
| 1 | 2 | 1 | 0.50 | 0.29 | 0.32 | 0.24 | 0.24 | 0.26 | 0.23 | 0.12 |
| 1 | 2 | 2 | 0.50 | 0.29 | **0.68** | 0.24 | **0.57** | 0.33 | **0.75** | 0.12 |
| 1 | 2 | 3 | – | – | – | – | 0.19 | 0.24 | 0.02 | 0.03 |
| 2 | 1 | 1 | 0.50 | 0.29 | **0.52** | 0.28 | **0.95** | 0.05 | **0.58** | 0.04 |
| 2 | 1 | 2 | 0.50 | 0.29 | 0.48 | 0.28 | 0.02 | 0.04 | 0.36 | 0.04 |
| 2 | 1 | 3 | – | – | – | – | 0.02 | 0.03 | 0.07 | 0.03 |
| 2 | 2 | 1 | 0.50 | 0.29 | **0.53** | 0.23 | 0.15 | 0.10 | 0.07 | 0.04 |
| 2 | 2 | 2 | 0.50 | 0.29 | 0.47 | 0.23 | **0.84** | 0.10 | **0.91** | 0.04 |
| 2 | 2 | 3 | – | – | – | – | 0.01 | 0.02 | 0.02 | 0.02 |
| 3 | 1 | 1 | 0.50 | 0.29 | **0.60** | 0.20 | **0.89** | 0.11 | **0.91** | 0.08 |
| 3 | 1 | 2 | 0.50 | 0.29 | 0.40 | 0.20 | 0.08 | 0.10 | 0.08 | 0.07 |
| 3 | 1 | 3 | – | – | – | – | 0.03 | 0.04 | 0.01 | 0.02 |
| 3 | 2 | 1 | 0.50 | 0.29 | 0.50 | 0.22 | **0.61** | 0.16 | **0.90** | 0.03 |
| 3 | 2 | 2 | 0.50 | 0.29 | 0.50 | 0.22 | 0.36 | 0.16 | 0.10 | 0.03 |
| 3 | 2 | 3 | – | – | – | – | 0.03 | 0.03 | 0.00 | 0.01 |
| 4 | 1 | 1 | 0.50 | 0.29 | 0.49 | 0.13 | **0.77** | 0.25 | **0.75** | 0.04 |
| 4 | 1 | 2 | 0.50 | 0.29 | **0.51** | 0.13 | 0.19 | 0.25 | 0.24 | 0.04 |
| 4 | 1 | 3 | – | – | – | – | 0.03 | 0.04 | 0.00 | 0.01 |
| 4 | 2 | 1 | 0.50 | 0.29 | **0.64** | 0.25 | **0.61** | 0.32 | **0.69** | 0.08 |
| 4 | 2 | 2 | 0.50 | 0.29 | 0.36 | 0.25 | 0.30 | 0.30 | 0.30 | 0.08 |
| 4 | 2 | 3 | – | – | – | – | 0.10 | 0.13 | 0.01 | 0.02 |

and 1.92. Estimated *F* multipliers for the EPO showed an increasing trend between 2003 and 2006, followed by a decrease up to 2009; EPO *F* multipliers in 2005 and 2006 were significantly higher than that in 2003 (based on non-overlapping 95% probability intervals) (Fig. 8). 95% posterior probability intervals were fairly wide for some years (e.g. 2006 and 2008, Fig. 8).

Around 6% of all recaptured archival tags were recovered in the WPO. The archival tag data were much less informative about *F*s in the WPO, with wide posterior probability intervals and little updating of priors for *F*s and *F* multipliers (Figs. 7b and 8). Estimated quarterly *F*s for the WPO ranged between 0.18 and 0.53 (Fig. 7b). The annual pattern in WPO F multipliers was fairly flat, with a modest (non-significant) increase in 2005 and 2006. Posterior correlations between *F* and *M* were low, with a maximum absolute pairwise correlation of 0.05. Median annual total *F*s (total quarterly *F*s (the product of the estimated within-year *F* and *F* multiplier) summed over the year) are shown in Fig. 9. These reflect the interannual patterns of estimated *F* multipliers. Annual *F*s ranged

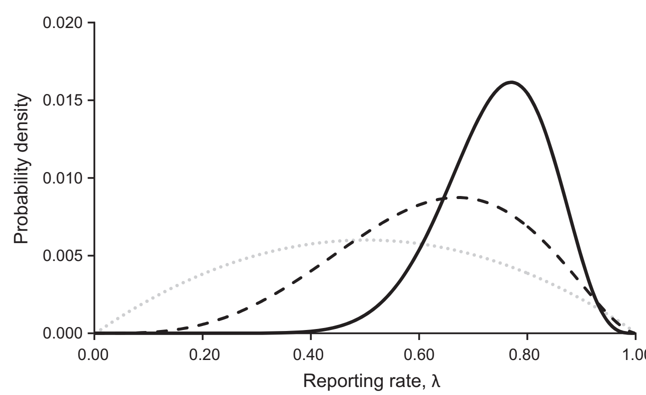


**Fig. 6.** Prior (dotted grey line) and posterior probability density functions for archival tag reporting rates in the EPO (solid black line) and WPO (dashed black line).

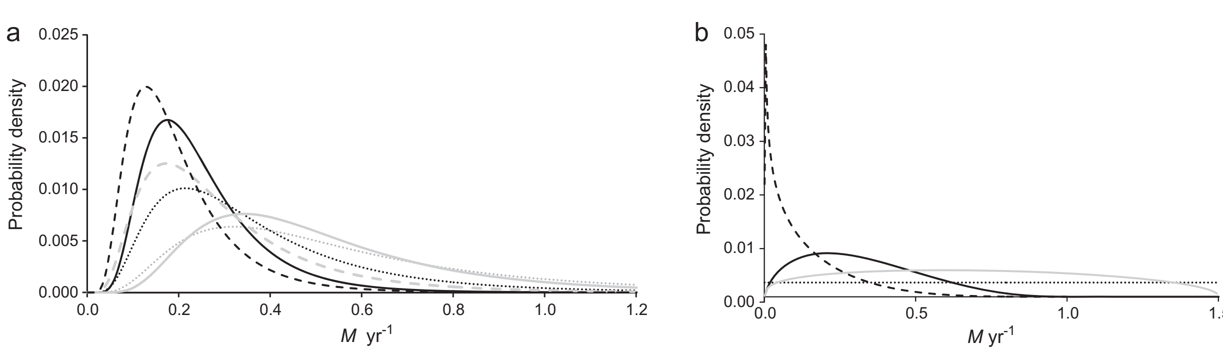


**Fig. 5.** (a) Prior and posterior probability density functions (pdfs) for natural mortality rates for three age groups. Age group 1 (ages 2 and 3), dotted light grey line (prior), solid light grey line (posterior); age group 2 (age 4), dotted black line (prior) and solid black line (posterior); age group 3 (ages 5+), dashed grey line (prior) and dashed black line (posterior). (b) Posterior probability density functions (pdfs) for natural mortality rates for three age groups estimated using a uniform prior. Age group 1 (ages 2 and 3), solid grey line; age group 2 (age 4), solid black line; age group 3 (ages 5+), dashed black line. The dotted black line denotes the uniform prior pdf.

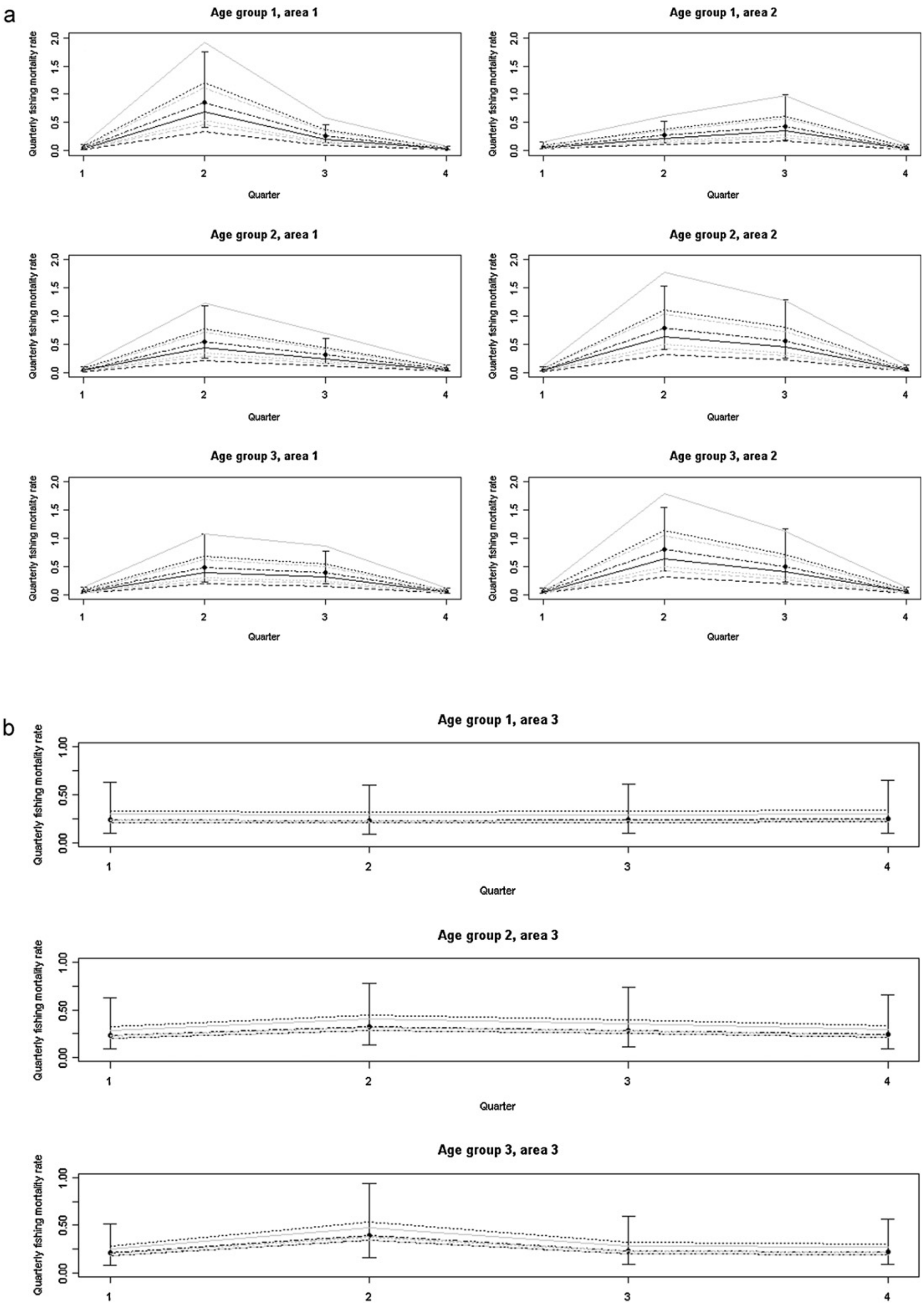


**Fig. 7.** (a) Quarterly fishing mortality rates in the EPO. Solid black line, 2002; dashed black line, 2003, dot-dash black line, 2004; dotted black line, 2005; solid grey line, 2006; dashed grey line, 2007; dot-dash grey line, 2008; dotted grey line, 2009 (the 95% posterior probability interval is shown for 2004). (b) Quarterly fishing mortality rates in the WPO. Solid black line, 2002; dashed black line, 2003, dot-dash black line, 2004; dotted black line, 2005; solid grey line, 2006; dashed grey line, 2007; dot-dash grey line, 2008; dotted grey line, 2009 (the 95% posterior probability interval is shown for 2004).

between approximately 0.5 and 3 in the EPO and 0.75–1.5 in the WPO, Figs. 7–9.

Total quarterly *F*s estimated from a model in which releases and recaptures occurring in the same quarter were excluded revealed that most quarterly *F* estimates were unaffected. All of the estimated quarterly *F*s except for seven differed by less than 10% from the estimate corresponding to the complete data set. Of these seven, where estimated *F*s differed by 10% or more, four occurred in quarter 3 and three occurred in quarter 2. However, there were no significant differences in quarterly *F* estimates from the two models, based on non-overlapping 95% posterior probability intervals.

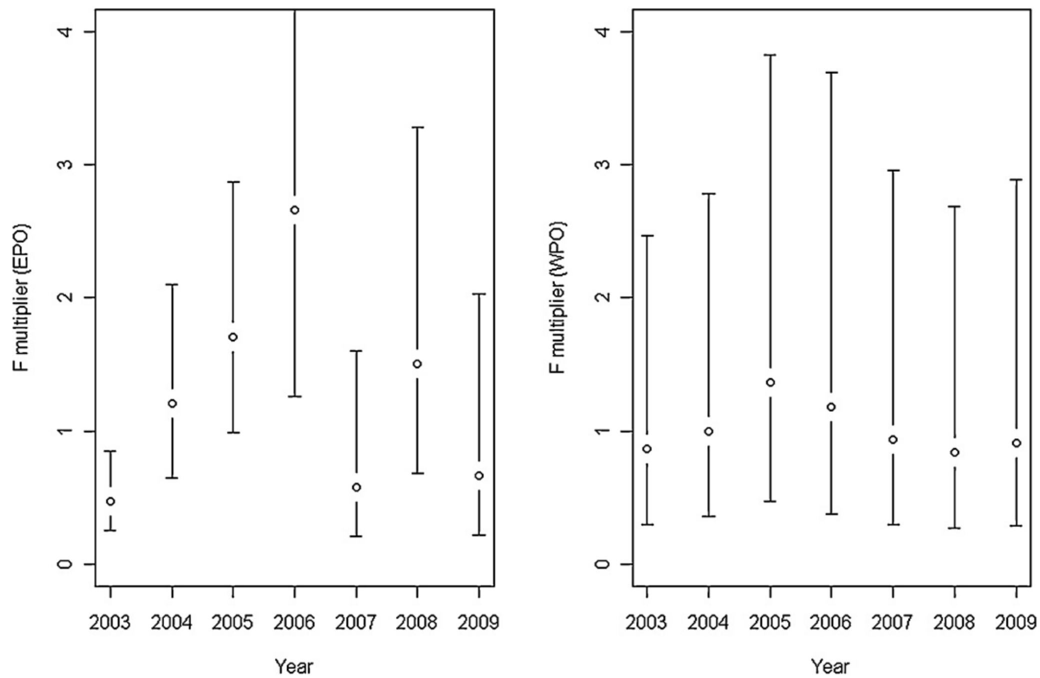


**Fig. 8.** Annual multipliers for fishing mortality rates in the EPO (left panel) and WPO (right panel) with 95% posterior probability interval from 2003 to 2009.

As with the PAT posteriors, estimated movement rates were highest for residency for over half of the season and area of origination combinations (Table 4). However, the seasonal pattern of north-south movement, with southward movement from area 1 to area 2 between quarters 4 and 1 (winter), and northward movement from area 2 to area 1 in late summer (between quarters 2 and 3 and 3 and 4) became more apparent. For purposes of comparison, posterior means and standard deviations are also shown from a model that included information on movement from release and recapture locations only (columns 8 and 9). Adding information on intermediate quarterly locations for each recaptured tag resulted in marked improvements in the precision of estimated movement rates (Table 4). The highest rate of east to west movement occurred between quarters 2 and 3 (Table 4).

Delta DICs (the DIC for model *i* minus the lowest DIC value for the set of models considered) for alternative fixed *M* scenarios are shown in Table 5. The model with the 2008 base case *M* scenario had the lowest DIC (delta DIC of 0) of the 3 fixed *M* scenarios evaluated, meaning that this *M* schedule would best predict a replicate dataset of the same structure as that observed (Table 5). The Ishigaki schedule, with an age 2 *M* of 0.25 had a marginally lower DIC than that for the 2006 schedule, with an age 2 *M* of 0.40 (Table 5).

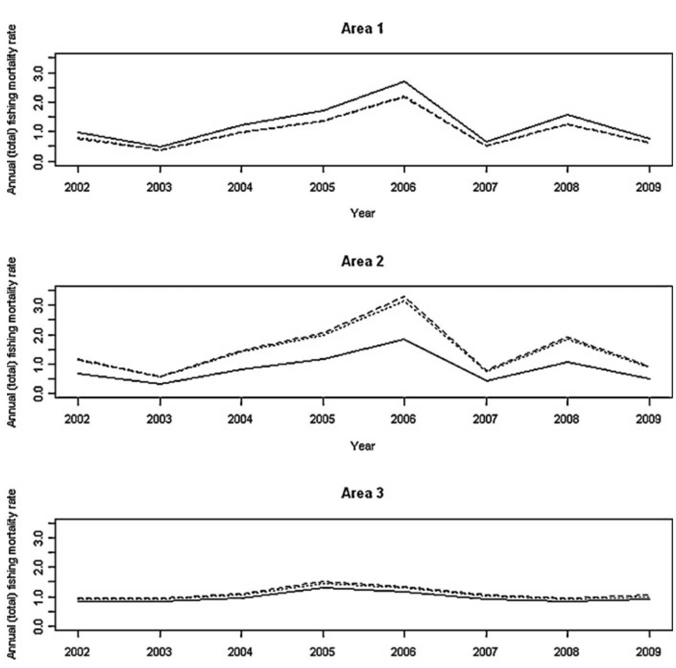


**Fig. 9.** Estimated annual total fishing mortality rates by year, 2002 to 2009 for areas 1–3. Solid line age group 1, dashed line, age group 2, dotted line, age group 3.

## 12. Discussion

Electronic tagging data provide new opportunities for improving our understanding of the spatial and temporal components of fish population dynamics. They offer information on the movements, stock structure, life history and feeding ecology of tunas (e.g. Bestley et al., 2009; Kurota et al., 2009; Boustany et al., 2010) at finer spatial scales than were previously possible. While numerous papers have examined foraging ecology or diving behaviors, relatively few have used electronic tagging data to improve stock assessment models (Kurota et al., 2009; Taylor et al., 2011). In this paper we examine Bayesian sequential state-space modeling techniques for the utilization of electronic tagging data to develop a spatially structured model for estimation of fishing and natural mortality rates and seasonal movement rates of PBFT.We used a spatial model because this should result in less biased estimates of *F* (i.e. relative to a non-spatial model); for example, the spatial model accounts for the differing abundances and recapture rates

**Table 5**
Delta DIC values for fixed natural mortality rate schedules for Pacific bluefin tuna in the eastern Pacific Ocean.

| *M* schedule | Delta DIC |
|---|---|
| 2006 | 2.91 |
| 2008 base case | 0.00 |
| Ishigaki | 1.80 |

of tagged PBFT in different quarters and areas which will affect estimates of *F*. A growing number of stock assessments of highly migratory species like other species of bluefin tunas make use of spatially structured models (e.g. Kurota et al., 2009; Taylor et al., 2011). This may be appropriate for a number of reasons including accounting for differential habitat use by different life-history stages, or populations, and understanding implications of habitat loss or modification as well as describing the spatial reach of fishing fleets and governance structures (national boundaries). Use of spatially structured models may also be desirable for evaluation of spatial management options (e.g. seasonal closure of spawning areas).

The seasonal movement patterns estimated in this analysis were consistent with patterns of movement described elsewhere (e.g. Kitagawa et al., 2007; Boustany et al., 2010). The spatial box model utilized here captured the movements of PBFT that were tagged primarily in the third quarter off the coast of Baja Mexico and subsequently moved northward. The northward movement is thought to be associated with increasing surface water temperatures and a decrease in upwelling and associated production (Block et al., 2011). PBFT achieve their most northerly locations along the western coast of North America late in the fourth quarter and move southward or offshore in winter months (first quarter). Sequential updating of the prior distributions for seasonal movement rates was evident from the progressive reduction in the standard deviations from the PAT prior through the PAT posterior to the archival tag data posterior (Table 4). The movement rates estimated with the archival tag data demonstrate one of the key advantages of electronic tag data over conventional tag data, namely that if geolocation is feasible, a data set that is much more informative about movement rates can be generated, resulting in improved precision of movement rate estimates. In addition, locations obtained by geolocation are independent of fisheries and should therefore constitute a less biased source of information about the spatial distribution of fish populations than recapture locations, which will to some extent be affected by the spatial distribution of fishing effort.

Rates of annual fishing mortality for PBFT of ages 2–3 (age group 1) estimated using archival tagging data were consistent with previously reported estimates from a scenario that assumed the 2008 *M* schedule, but were otherwise somewhat higher than estimates from other analyses (e.g. Aires-da-Silva et al., 2009). Estimated annual *F*s for age 4 PBFT were considerably higher than estimates reported elsewhere, even relative to previous estimates obtained with the 2008 *M* schedule (around 0.4, Aires-da-Silva et al., 2009).

Mark-recapture data can be valuable for estimation of *M* when tag recovery rates are high and reporting rates are known or estimable which is the case for PBFT in the WPO. We have thus presented the first empirical estimates of *M* for PBFT aged 2 and above. Although the experiment in which the data analyzed in this paper were collected was not designed for the purpose of estimating *M*s, the high tag recovery rate combined with long times at large achieved, particularly in the early years of the experiment make these data informative with respect to *M*. The relatively high reporting rate estimates in this study probably reflect the fact that a significant financial reward ($500) was offered for return of archival tags, resulting in an exceptionally high tag return rate. The archival tagging data analyzed in this study appeared to be fairly informative with respect to the *M*s for PBFT of age 4 and ages 5+ (ages groups 2 and 3), but less so about the M for PBFT of ages 2 and 3 (age group 1). This probably results from the higher proportion of tags recaptured by age for older ages at release, meaning that there is more information available about *M* from the distribution of times at large for older fish. Using an uninformative prior on *M* with a median of 0.75 $yr^{-1}$ still yielded a posterior with a relatively low median of 0.13 $yr^{-1}$ for PBFT aged 5+ (age group 3); conversely, the posterior median estimate of *M* for ages 2 and 3 (age group 1) showed little updating with a posterior median (0.72 $yr^{-1}$), close to the prior median.

Posterior median estimates of *M* for ages 4 and above were lower than values used in recent stock assessments (e.g. ISC, 2009), although the median for age group 3 (ages 5+) was comparable to *M* in the 2008 assessment (0.12 $yr^{-1}$ for ages 4+). The posterior median for ages 2 and 3 (age group 1) using an informative prior was comparable to age 1 *M* values assumed in ISC's scenarios. There were posterior probabilities of 60% and 76% that *M*s for age groups 2 (age 4) and 3 (ages 5+) were less than 0.25 $yr^{-1}$, the value currently used in the PBFT stock assessment for ages 4 and above. The corresponding percentages for the uniform *M* priors were 41% (age group 2) and 82% (age group 3). It should be noted that the possibility of there being different reporting rates of recovered tags in the WPO than in the EPO and having relatively little data with which to accurately estimate the WPO reporting rate could cause bias in estimates of *M* since the posterior for the WPO reporting rate would be more strongly influenced by its prior. However, mark-recapture models that assumed lower fixed values for age 4+ *M* were also found to be more consistent with the tagging data (Table 5).

Estimates of *M* provide potential information on *F*s in the EPO. *F* and *M* are typically negatively correlated, since a higher (lower) number of recaptures could be explained by a higher (lower) *F* or lower (higher) *M*. Interestingly, very low absolute values for the correlation between *F* and *M* were obtained in this study. This is in part due to the ability to estimate the EPO reporting rate reasonably precisely with these data (posterior CV of 0.14). The tag reporting rate is key in partitioning mortality into its fishing and natural components in a mark-recapture context. The updating of the informative prior for the archival tag reporting rate indicates that there was information about this parameter in the tagging data. This is likely to result from the high recovery rates achieved in the PBFT tagging program (Table 3).

Although assuming a lower value of *M* for older fish (age 4+ $M = 0.12\,yr^{-1}$) in the PBFT stock assessment resulted in estimates of unfished spawning stock biomass and depletion estimates that were considered implausible (Aires-da-Silva et al., 2009), this apparent inconsistency may arise from other features of the assessment that will tend to give low SSB and correspondingly higher depletion estimates. For example, all else being equal, conditioning on an estimate of current abundance or biomass, assuming a greater level of density-dependent compensation in recruitment will lead to a lower estimate of historic abundance/biomass (e.g. Walters et al., 2006). The PBFT stock assessment used by the ISC assumes a steepness of 1 implying that recruitment is independent of spawning stock size and on average constant down to the very smallest spawning stock levels. This assumption and the current application of higher values for *M*, if incorrect could cause a downwards bias in estimates of unfished stock biomass and upwards bias in depletion estimates making the population appear to be less depleted and more resilient to exploitation than it actually is.

There are several ways in which this analysis could be extended and improved upon. Future models could incorporate quarterly fishing effort or catch data (as a proxy for effort), which would improve fishing mortality estimates. Additionally, conventional tagging data could be added to the model in order to gain more information about, e.g. age specific, rates of movement and natural and fishing mortality. More data are needed on rates of movement from the WPO and EPO and vice versa; collaborative analysis of pooled tagging data sets from both sides of the Pacific Ocean in the future would help to achieve this.

In the light of the results from this study, it may be instructive to look further into estimating age-specific *M*s using electronic tagging data. Using empirical estimates of age-specific *M*s would help to reduce potential bias in stock reconstructions from the PBFT stock assessment, while accounting for the uncertainty associated with estimates of *M* would be more consistent with a precautionary approach. Moreover, integrating tagging data into the stock assessment model for PBFT should improve the accuracy of estimated fishing mortality rates and abundance. This would be desirable in the context of effective regulation of fishing effort for Pacific bluefin tuna fisheries.

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