Times are changing, but has natural mortality? Estimation of mortality rates for tropical tunas in the western and central Pacific Ocean

Tom Peatman [a,b,*,1], Matthew T. Vincent [c,1], Joe Scutt Phillips [b], Simon Nicol [b,d]

[a] *Independent Consultant, Frome, United Kingdom*
[b] *Oceanic Fisheries Programme, Pacific Community, BP D5, 98848 Nouméa, New Caledonia*
[c] *NOAA National Marine Fisheries Service, Southeast Fisheries Science Center, 101 Pivers Island Rd, Beaufort, NC 28516, United States of America*
[d] *Centre for Conservation Ecology and Genomics, Institute for Applied Ecology, University of Canberra, Bruce, ACT 2617, Australia*

ABSTRACT

A variety of density-dependent and -independent processes have been proposed to influence natural mortality rates, potentially leading to variation through time. Processes of natural mortalities are rarely directly observed, making estimation of natural mortality rates difficult. Mark-recapture data allow estimation of total mortality rates, which can be separated into natural and fishing mortality with information on rates of tag reporting, tag shedding and tag-induced mortality. We fitted attrition models and length-based Brownie models to four decades of mark-recapture data from skipjack and yellowfin tuna in the Western and Central Pacific Ocean, a period representing a sustained expansion of associated fisheries in the region as well as rapid changes to the marine environment. The modelled dataset included c. 250,000 skipjack and 100,000 yellowfin tag releases, with 45,000 and 17,000 recoveries of skipjack and yellowfin respectively, released from 1977 to 2017. Increases in fishing mortality were detected over this time for both skipjack and yellowfin, with evidence of temporal changes in selectivity for yellowfin. Estimates of natural mortality were highest for the smallest size class and generally lower for larger sizes, though there was large uncertainty in the largest size groups due to lower sample sizes of tagged fish. There was no clear evidence of temporal changes in natural mortality rates for either species, though there was some evidence of changes in natural mortality for the smaller yellowfin size classes (< 61 cm). However, there was likely insufficient statistical power to test for plausible changes in natural mortality rates for yellowfin due to low precision of estimates during the earlier years of the tag dataset.

1. Introduction

Estimation of mortality rates in a population is one of the primary objectives of stock assessment models. Total mortality estimates are comprised of deaths due to anthropogenic harvest (fishing mortality) and other natural causes (natural mortality). Fishing mortality (*F*) is commonly estimated directly from catch and effort data, which are observed and recorded for many fisheries (Beverton and Holt, 1957). Examples of natural mortality processes include predation, starvation, senescence, nutrient deficiency, hypoxia, and red tides. Processes of natural mortality are rarely observed in marine ecosystems (Hampton, 2000) or are poorly recorded or measured; therefore, the rate of natural mortality is difficult to estimate within most stock assessments. The rate of natural mortality (*M*) is a parameter of interest in population

dynamics given its influence on estimation of stock size, productivity, and harvest rates (Clark, 1999; Pope et al., 2021). Values of *M* in a stock assessment are often derived from indirect methods (Kenchington, 2014; Pope et al., 2021); therefore, *M* is commonly a source of uncertainty in stock assessments (Punt et al., 2021). *M* is often calculated externally to stock assessment models based on life-history parameters and environmental variables (Pauly, 1980; Hoenig, 1983; Lorenzen, 1996; Griffiths and Harrod, 2007). However, these methods estimate average *M* across size/age, space, and time, which can lead to bias when applied in stock assessment models (Punt et al., 2021). These methods are frequently applied when direct estimates of natural mortality are not available.

Natural mortality is assumed to be temporally constant in most stock assessments due to the lack of direct estimates of this parameter. There are numerous processes that are hypothesised to cause changes in

natural mortality rates over time. Changes in environmental conditions can induce changes in density-independent *M* (Rountrey et al., 2014). Conversely, density-dependent *M* could be affected by a population's exposure to *F*, with subsequent impacts on numerous density-dependent effects including predation, food availability, disease, and life histories (Fournier, 1983; Jørgensen and Holt, 2013; Powers, 2014). Increased *F* can drive adaptations which may change *M* at age over time (Jørgensen and Fiksen, 2010). Some methods have attempted to estimate annual changes in natural mortality using random effects (Jiao et al., 2012) or predator diets (Collie et al., 2016), but these cases are rare. Unaccounted-for changes in natural mortality in a stock assessment may lead to biases in management quantities and could manifest as poor model diagnostics (e.g. high Mohn's rho).

Mark-recapture experiments enable estimation of total mortality for a population (e.g. Brownie et al., 1985), from which *F* and *M* can be separated. Robust estimates of *M* and *F* from these experiments depend on a sufficient number of recaptures from the fishery and accurate estimates of rates of tag-reporting, tag shedding and tagging induced mortality (Pine et al., 2003). Tag reporting rates can be estimated from high value tag returns (Pollock et al., 2002) or tag seeding experiments (Hampton, 1997). Tag shedding rates can be estimated by double tagging experiments (Hampton, 1997). Tag induced mortality is the most difficult to quantify, but can be observed for sessile species in holding tanks or laboratories. Estimates of tag induced mortality are more difficult for pelagic species such as tunas.

Mark-recapture data can be analysed by various models depending on the frequency of tag release events and other modelling assumptions. Size and age influences on natural mortality can be estimated when tagging data are combined with other sources of data, e.g. growth (Hampton, 2000), length (Hillary and Eveson, 2015), catch (Krause et al., 2020), or multiple tag types (Kurota et al., 2009; Whitlock et al., 2012). Tag attrition models (Kleiber et al., 1987; Hampton, 2000) are a general framework for analysing tagging data that can estimate mortality parameters, which in the simplest case are assumed constant over time. Conversely, length-based Brownie models (Hillary and Eveson, 2015) can be applied to sequential tag release events to estimate temporal fishing mortality parameters. These two methods have differing assumptions regarding the growth of fish; attrition models treat growth deterministically using a growth curve, whereas the length-based Brownie model uses a growth transition matrix. Application of these two methods on a common mark-recapture dataset could provide different estimates of natural mortality, which could have an influence on reference point estimates from a stock assessment.

Hampton (2000) applied a tag attrition approach to estimate the influence of size on the natural mortality of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) in the western and central Pacific Ocean. His analysis utilised a large mark-recapture data set collected during the 1990s as the purse-seine fishery in the region was developing (Leroy et al., 2015). Since this analysis, the purse-seine fishery in the western and central Pacific Ocean has expanded to become the largest globally, providing 1.8 million tonnes of skipjack and yellowfin in 2018 (SPC-OFP, 2021), representing 40 % of the global catch of these species (FAO, 2020). Mark-recapture experiments have continued to be implemented as a semi-fishery independent data source to monitor this fishery (Leroy et al., 2015). Additionally, tagging experiments for skipjack tuna were conducted in the 1970s and 80s that were not included in the analysis reported by Hampton (2000).

Here, we describe an analysis of three tagging programmes from the last four decades in the western and central Pacific Ocean to test the hypothesis that natural mortality in skipjack and yellowfin tuna has changed over time due to the combined effects of increasing *F* and the rapidly changing environmental conditions in this region (Bell et al., 2021). We applied tag attrition and length-based Brownie models to compare their ability to ascertain how *M, F,* and selectivity of skipjack and yellowfin tuna have changed over time.

2. Materials and methods

2.1. Tagging dataset

The modelled mark-recapture data in this paper consisted of skipjack tuna tagged during the Skipjack Survey and Assessment Programme (SSAP, 1977–1980), and skipjack and yellowfin tuna tagged during the Regional Tuna Tagging Project (RTTP, 1989–1992) and the Pacific Tuna Tagging Programme (PTTP, 2006-present). A variety of pole-and-line tagging platforms were used for the modelled dataset. Publicity campaigns and rewards for tag-finders have been used to incentivise reporting of tags, supported by an extensive network of tag recovery officers at ports of unloading and processors (Leroy et al., 2015). Tag seeding experiments have been used to estimate reporting rates for tag returns for the RTTP (Hampton, 1997) and PTTP (Berger et al., 2014). Double tagging experiments were analysed for the RTTP and PTTP to estimate tag shedding rates (Vincent et al., 2019a).

Tag releases were restricted spatially to the area 140°E to 165°E and 10°S to 5°N, leaving 10 % of SSAP skipjack releases, 40 % of RTTP releases of skipjack and yellowfin, and 70 % of PTTP releases of skipjack and yellowfin (Supplementary materials, Fig. S1 and S2). This spatial filtering was applied only to tag releases, with all corresponding tag recaptures included in the modelled dataset regardless of recapture location. This region accounted for a large portion of tuna catches in the western central Pacific Ocean by surface fisheries during the RTTP and PTTP, as well as the majority of tag releases in recent years. The modelled dataset consisted of 13,012 tag releases of skipjack during the SSAP, 53,433 tag releases from the RTTP (37,683 skipjack and 15,750 yellowfin) and 279,461 tag releases from the PTTP (196,528 skipjack and 83,113 yellowfin). The SSAP tags were released from October 1977 to June 1980, the RTTP tags were released from July 1989 to July 1992, and the PTTP released tags from August 2006 to November 2017. More recent PTTP release events were excluded to mitigate bias caused by delays in the reporting and processing of tag return data. Reported recaptures accounted for 13 % of skipjack SSAP releases, 10 % of skipjack and 15 % of yellowfin RTTP releases, and 19% of skipjack and 18 % of yellowfin PTTP releases. The distribution of release lengths by tagging programme are provided in the Supplementary materials (Fig. S3 and S4), along with the distribution of times at liberty of tag recoveries (Fig. S5 and S6). A cross-validation process is used to estimate the likely reliability of reported tag recapture dates and positions using a range of data sources including vessel monitoring systems and vessel logbooks (Leroy et al., 2015). The estimated accuracy of recapture date was ± 1 month or better for c. 90 % of the tag recaptures of RTTP and PTTP releases.

2.2. Analytical methods

2.2.1. Attrition models

Species-specific tag attrition models were fit to the combined SSAP, RTTP, and PTTP mark-recapture dataset, using the size-specific model of Hampton (2000). The estimated number of reported recaptures from release group *i* after *j* months at liberty, $\widehat{r}_{ij}$, is

$$\widehat{r}_{ij} = (1-\alpha)(1-\beta_i)R_i \exp\left[-\sum_{k=1}^{j-1}\left(F_{s(l_i,k)}+M_{s(l_i,k)}+\lambda\right)\right]$$
$$\times \frac{F_{s(l_i,j)}}{F_{s(l_i,j)}+M_{s(l_i,j)}+\lambda}\left[1-\exp\left(-F_{s(l_i,j)}-M_{s(l_i,j)}-\lambda\right)\right] \quad (1)$$

where α accounts for type-1 tag shedding, tag-induced mortality and incomplete reporting of tag recaptures, β_i is the proportion of (reported) recaptures missing recapture dates and which can't be included in the model, R_i is the number of releases of group *i*, l_i is the length of fish in release group *i* at release, $s(l_i,j)$ is the estimated size class of fish in release group *i* after *j* months at liberty, $F_{s(l_i,j)}$ and $M_{s(l_i,j)}$ are size class specific fishing and natural mortality rates, and λ is type-2 tag loss. Release group *i* was defined as a combination of fork length at release

(rounded down to the nearest integer) and release year-month.

The length of fish in release group i after j months at liberty, $\widehat{L}_{ij}$, was estimated using the von Bertalanffy growth curve

$$\widehat{L}_{ij} = l_i + (L_\infty - l_i)[1 - \exp(-kj/12)] \tag{2}$$

where L_∞ and k are the parameters for maximum length and growth rate respectively. Skipjack growth parameters were taken from Vincent et al. (2019b), and converted appropriately for use with the annual von Bertalanffy growth curve (i.e. an L_∞ and k of 80.3 cm and 0.848 year^{-1} respectively). Yellowfin growth parameters were taken from Eveson et al. (2020), using the parameters from the integrated growth model fitted to mark-recapture data and high readability otoliths (i.e. an L_∞ and k of 158.9 cm and 0.349 year^{-1} respectively). The estimated lengths of tagged fish, $\widehat{L}_{ij}$, were then mapped to size classes, $s(l_i, j)$, and their corresponding mortality rates. Five size classes were used for skipjack models (21–40, 41–50, 51–60, 61–70, ≥ 71 cm), with eight size classes used for the yellowfin models (21–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100, ≥ 101 cm). Tag release groups were tracked for 48 months and tags recaptured after this point were considered to be unrecovered.

Type-I tag shedding was assumed to be 0.07 (Vincent et al., 2019a), with tag-induced mortality assumed to be 0.07 (Berger et al., 2014). Reporting rates were assumed to be 0.58 for all tagging programmes, based on analyses of tag seeding experiments undertaken during both the RTTP (Hampton, 1997) and PTTP (using methods described in Peatman et al., 2020). This resulted in an α of 0.498. β_i was estimated for each release group, with a mean of 0.02 for the skipjack and yellowfin models. Type-II tag shedding (λ) was assumed to be zero (Vincent et al., 2019a).

Analyses of tagging data are generally used to make inferences on a wider population of interest, which requires assuming that the tagged fish are mixed with, and representative of, the wider population. Tag releases are less likely to be fully mixed shortly after release and so may experience differing levels of fishing mortality than the wider population which could result in biased estimates of natural mortality and fishing mortality rates. To mitigate this bias, a mixing period was defined in which fishing mortality rates (F'_{im}) were set such that estimated recaptures were equal to observed recaptures. This was implemented as per Hampton (2000), by setting predicted recaptures ($\widehat{r}_{im}$) equal to observed recaptures (r_{im}) and solving Eq. (1) for each combination of mixing period month m and release group i. The length of the mixing period was selected using AIC (Akaike, 1974), with candidate mixing periods of 0–4 months.

The parameters M_s, F_s and F'_{im} were then estimated by minimising the multinomial negative log likelihood function

$$\sum_i \left[\left(R_i - \sum_j r_{ij} \right) \ln \left(1 - \frac{\sum_j \widehat{r}_{ij}}{R_i} \right) + \sum_j r_{ij} \ln \left(\frac{\widehat{r}_{ij}}{R_i} \right) \right] \tag{3}$$

where r_{ij} is the reported recaptures from release group i after j months at liberty. Approximate 95 % confidence intervals were obtained from the Hessian.

It was assumed that both natural mortality and fishing mortality rates remained constant within each of the tagging programmes for a given size class. We tested for differences in natural mortality and fishing mortality rates among tagging programmes by fitting models with either programme-specific mortality rates or mortality rates shared among programmes. This resulted in four treatments of mortality rates for each species: programme-specific M_s and F_s; shared M_s and programme specific F_s; programme-specific M_s and shared F_s; and shared M_s and F_s. Additionally, temporal changes in mortality rates during the PTTP were assessed by splitting the PTTP data into two effective tagging programmes, 'PTTP-early' with releases from 2006 to 2009 and 'PTTP-late' with releases from 2011 to 2017. The treatment with most support from the tagging dataset was selected by AIC.

We note that initial model runs with time-varying fishing mortality within tagging programmes, calculated as the product of size-specific catchabilities and reported purse seine effort, had less support than equivalent models with time-invariant fishing mortality and were not considered further. Skipjack M_s for the 41–50 cm and 51–60 cm size classes were shared for SSAP mark-recapture data when including tagging-programme-specific natural mortality rates, as initial model runs were not able to obtain robust estimates of M_s for the 41–50 cm size class. Similarly, yellowfin M_s for the 51–60 and 61–70 cm size classes were shared, as was M_s for the 71–80 and 81–90 cm size classes, when fitting to RTTP mark-recapture data with programme-specific natural mortality rates.

The sensitivity of mortality rate estimates to assumed growth rates was assessed by refitting the selected models with alternative assumed growth curves. The 'high' growth scenario from Vincent et al. (2019b) $L_\infty = 87.8$ cm, $k = 0.839$ year^{-1}) was used for skipjack. For yellowfin, we used the growth curve fitted to high readability otoliths and daily age readings from Farley et al. (2020) $L_\infty = 150.3$ cm, $k = 0.442$ year^{-1}).

Comparisons of observed and predicted recoveries were undertaken against release year-quarter, months at liberty, and release length, to assess model fits. Model fits were considered adequate for the selected mixing periods (Supplementary materials, Fig. S7). Following Hillary and Eveson (2015), standardised residuals were extracted and used to calculate overdispersion factors. There was no indication of extra-multinomial overdispersion.

2.2.2. Length-based Brownie models

Length-based Brownie mark-recapture models (Hillary and Eveson, 2015) were fit to the data for each species and tagging programme using quarterly (3 months) time steps. This method requires a growth transition matrix (Punt et al., 1997) that was derived using the species-specific growth curves used in the attrition method, with a standard deviation of length at age for skipjack of 3.40 estimated from the stock assessment model (Vincent et al., 2019b). The standard deviation for yellowfin was calculated based on the median of the size class using the equation $\sigma_s = 9.23\exp\left(-0.38 \left(1 - 2 \frac{\mu_s - 41.03}{153.98 - 41.03} \right) \right)$, which was estimated by the 2020 yellowfin stock assessment (Vincent et al., 2020). These growth transition matrixes were created for a quarterly time step using the size classes and growth curves described for the attrition model for both species and both growth curves described above (see Supplementary materials, Tables S1–S4). Transition matrixes were calculated using the midpoint of each size class, except for the smallest size class which used the mean length of tag releases in this size class. The smallest size class was treated differently as releases in this size class were larger on average than the midpoint of this length range and so would be more likely to transition to the next size class. This consideration was possible as fish do not grow into the smallest size class. Models were fit to the data assuming a mixing period of either 1 or 2 quarters for each tagging programme separately for both species.

Many of the same assumptions made by the attrition model were also used for the Brownie model. The Type-I and Type-II tag shedding, tag induced mortality, and reporting rates described above were used in this model. Corrections to the number of tags released based on unusable tag returns were conducted outside of the model for each quarterly release event by size class. Due to the requirement of temporally adjacent release events to estimate model parameters, the PTTP was further filtered to only include the time period 2006–2014, because after this time period there were too many temporal gaps between release events.

To explain the equations used in the Brownie mark-recapture we define the variables that are used:

$T_{t,s}$: number of tagged fish alive at the beginning of time t in size class s.

t_0: time period of initial tag release.

$\tilde{s}$: size class of initial release of tag.

R_t: observed number of reported recaptures at time t from a specific

tagging event.

$\widehat{R}_t$: model predicted number of recaptured tags at time t from a specific tagging event.

γ: probability of surviving and retaining a tag in the quarter of release (process that accounts for immediate tag shedding and tagging mortality).

φ: probability of detecting a recaptured tag (reporting rate).

$F_{t,s}$: fishing mortality in time period t and size class s that was modelled by the separable equation of a length-based selectivity (η_s) and a temporal fishing mortality (f_t): $F_{t,s} = \eta_s f_t$.

M_s: natural mortality in size class s.

$\xi_{t,s} = \frac{F_{t,s}}{F_{t,s}+M_s} * \left(1 - \exp\left(-F_{t,s}+M_s\right)\right)$: harvest rate at time t in size class s.

$\phi_{t,s}$: proportion of tagged fish in length class s and time t from a specific tagging event.

$\Delta_{x,y}$: Growth transition matrix probability from length class x to length class y.

π_t: probability of survival to the end of period t.

p_t: probability of recapture in time period t.

τ: negative binomial variance parameter estimated by parameter O; $\tau = 1 + e^O$.

We reduced the number of parameters needed to fit the model by allowing perfect fit to the recaptured tags during the mixing period, but corrected for non-reporting. The model also accounted for tag losses due to shedding and tag induced mortality by reducing the number of tags alive at the beginning of the period after release. The equation used to calculate the number of tags alive at the beginning of the quarter after release was:

$$T_{t_0+1,s} = \gamma T_{t_0,s}\widetilde{\Delta}_{s,s}e^{-M_s} - \frac{R_{t_0}}{\varphi} \quad (4)$$

If the model assumed a mixing period of 2 quarters then the tags that survived to the beginning of the second quarter after release was calculated by:

$$T_{t+1,s} = \sum_k \left(T_{t,k} - \frac{\phi_{t,k}R_t}{\gamma}\right)\Delta_{k,s}e^{-M_k},$$
$$\text{where } \phi_{t,k} = T_{t,k}\bigg/\sum_s T_{t,s} \quad (5)$$

For all quarterly time steps after the assumed mixing period of 1 or 2 quarters, the number of tags alive at the beginning of the next time step was calculated using estimated fishing and natural mortality parameters from the model and the growth transition matrix:

$$T_{t+1,s} = \sum_k T_{t,k}\Delta_{k,s}e^{-M_k-F_{t,k}} \quad (6)$$

The probability of surviving during the mixing period was calculated as follows: $\pi_{t+1} = \pi_t\frac{\sum_s T_{t+1,s}}{\sum_s T_{t,s}}$ where $\pi_{t=0} = 1$. After the mixing period, the survival probability was modelled by: $\pi_{t+1} = \pi_t\sum_s\phi_{t,s}e^{-M_s-F_{t,s}}$. The probability of recapture in time t was calculated from the survival probability, the harvest rate, and the reporting rate:

$$p_t = \pi_{t-1}\sum_s\phi_{t,s}\varphi\xi_{t,s} \quad (7)$$

This probability of recapture in time t was then multiplied by the initial number of tags released for the specific release event to estimate the number of recaptured tags in period t:

$$\widehat{R}_t = T_{t_0,s}\widetilde{p}_t \quad (8)$$

To fit the model to the data we assumed that the number of tags returned from a single tagging event at time t was distributed by a negative binomial with an estimated level of variance (overdispersion,

τ). For a specific tag event release group let $a = \frac{\widehat{R}_t}{\tau-1}$ and $b = \log(a + \widehat{R}_t)$, then the negative log-likelihood for the negative binomial ignoring constants can be calculated as:

$$\Theta = \sum_t (ab + R_t b) - (a*\log(a) + R_t\widehat{R}_t) - \Gamma(a+R) + \Gamma(R+1) + \Gamma(a) \quad (9)$$

where Γ is the log-gamma function.

The model for skipjack tuna using the SSAP data could not estimate the overdispersion factor of the negative binomial model as it tended towards a value of 1. Therefore, we estimated the fishing mortality and natural mortality parameters using a negative log-likelihood multinomial function. The likelihood function ignoring scaling factors was calculated by:

$$\Theta = -\sum_t\left[R_t\log(p_t) + \left(T_{t_0,s}\widetilde{} - \sum_t R_t\right)\log\left(1 - \sum_t p_t\right)\right] \quad (10)$$

The likelihood was summed over tag release groups and minimised by estimating natural mortality for each size class, a separable fishing mortality, and the overdispersion parameter (when applicable). The fishing mortality at length (selectivity, η_s) for both species was parameterised such that the 41–50 cm size class was fixed to equal 1 and the other selectivity parameters were estimated to be between 0 and 1. This scaled the temporal estimates of fishing mortality for each of the length classes, with $F_{t,s} = f_t\eta_s$. Models were fit with a combination of assumptions of constant natural mortality or length based natural mortality and fishing mortality modelled as constant, length based, time based or both length and time based. The PTTP model was further tested for different selectivity and natural mortality rates separated in the first quarter of 2011, which are referred to as PTTP-early and PTTP-late. Models were selected using AIC and approximate 95% confidence intervals were obtained from the Hessians. For the yellowfin tuna model, the estimation of independent selectivity and natural mortality parameters for size classes 71–80, 81–90, 91–100, and $\geq$ 101 cm was not supported by AIC, thus these length classes were modelled by a single shared parameter. Similarly, the estimation of the selectivity parameters for the skipjack SSAP and yellowfin RTTP were not supported by AIC and thus only a temporal fishing mortality parameter was estimated (Table 2). Model fits were considered adequate for the models selected by AIC (Supplementary materials, Fig. S9 and S10).

3. Results

3.1. Attrition models

3.1.1. Skipjack

The selected mixing period for the candidate skipjack models was 2 months (Table 1). The separation of the PTTP into two effective tagging programmes was supported by AIC, with the most support for programme-specific M_s and F_s parameters, followed by shared M_s and programme-specific F_s (ΔAIC = 234.0; Table 1). The estimated relationships between skipjack M_s and size were broadly consistent for all tagging programmes. Skipjack M_s was highest for the smallest size class (21–40 cm), decreasing as size increased to 51–60 cm, then displaying an increasing trend with further increases in size (Fig. 1a). However, there were apparent differences in M_s among tagging programmes for some size classes; M_s was relatively low for the 41–50 cm size class during the SSAP, high for the 61–70 cm size class during the PTTP, and low for the $\geq$ 71 cm size class during the PTTP. Additionally, there were apparent differences in M_s within the PTTP, with higher estimates of M_s during 'PTTP-late' for all but the 41–50 cm size class. Skipjack F_s estimates during the PTTP were higher than those during the RTTP for all size classes, and lowest for the SSAP for all size classes. Skipjack F_s estimates during the PTTP displayed a decreasing trend with increasing length for the 41–50 cm, 51–60 cm and 61–70 cm size classes. There were apparent differences in F_s within the PTTP, with higher F_s in the

Table 1
AIC and ΔAIC values for skipjack and yellowfin attrition models with selected mixing period lengths for: programme-specific M_s and F_s, shared M_s and programme specific F_s, programme-specific M_s and shared F_s, and, shared M_s and F_s. ΔAIC values are also provided relative to the lowest AIC for each species (model provided in bold). Models with programme-specific M_s or F_s were fitted with: separate parameters for the 'PTTP-early' (releases from 2006 to 2009) and 'PTTP-late' (2011–2017), denoted Split PTTP = TRUE; and, parameters held constant during the PTTP, denoted Split PTTP = FALSE.

Species	M_s and F_s treatment	Split PTTP?	Mixing period (months)	AIC	ΔAIC
Skipjack	**Programme-specific M_s and F_s**	**TRUE**	**2**	**399,435.2**	**0.0**
	Shared M_s and programme-specific F_s	TRUE	2	399,669.3	234.0
	Programme-specific M_s and shared F_s	TRUE	2	400,083.5	648.2
	Programme-specific M_s and F_s	FALSE	2	399,679.0	243.7
	Shared M_s and programme-specific F_s	FALSE	2	399,827.8	392.6
	Programme-specific M_s and shared F_s	FALSE	2	400,221.4	786.1
	Shared M_s and F_s	FALSE	2	400,945.8	1510.6
Yellowfin	**Programme-specific M_s and F_s**	**TRUE**	**1**	**173,783.1**	**0.0**
	Shared M_s and programme-specific F_s	TRUE	1	173,830.7	47.7
	Programme-specific M_s and shared F_s	TRUE	2	174,067.5	284.4
	Programme-specific M_s and F_s	FALSE	1	174,156.3	373.2
	Shared M_s and programme-specific F_s	FALSE	1	174,154.5	371.4
	Programme-specific M_s and shared F_s	FALSE	2	174,391.1	608.1
	Shared M_s and F_s	FALSE	2	174,748.7	965.6

21–40 cm and 51–60 cm size classes during 'PTTP-late'. Skipjack F_s estimates during the RTTP were highest for the 41–50 cm and 51–60 cm size classes, and lowest for the 61–70 cm and $\geq$ 71 cm size classes. Skipjack F_s estimates during the SSAP demonstrated a decreasing trend with increasing size. Estimates of F_s for the 21–40 cm size class were imprecise for the RTTP due to the low numbers of estimated tags at liberty, and associated recoveries, in this size class after the end of the mixing period. There were 11 release groups during the SSAP (corresponding to 50 tags) with skipjack estimated to be in the 21–40 cm size class outside of the mixing period. Of these 50 tags, there was one reported recovery which was estimated to be 40 cm. As such, there was insufficient information to obtain robust estimates of M_s and F_s during the SSAP for the 21–40 cm size class, and these parameters were not included in Fig. 1a (M = 5.6, F = 1.9). Estimates of skipjack M_s and F_s with the alternative growth curve were broadly equivalent in magnitude and displayed similar relationships with size (Supplementary materials, Fig. S8a). Estimates of M_s for the smallest size classes were increased with the alternative growth curve. The alternative growth curve reduced the within-PTTP variability in F_s. Estimates of F_s for the $\geq$ 71 cm size class increased for the SSAP and RTTP, and decreased for both 'PTTP-early' and 'PTTP-late'. However, estimates of M_s for the 51–60 cm size class (RTTP) and the 61–70 cm size class (RTTP and PTTP-late) were close to zero.
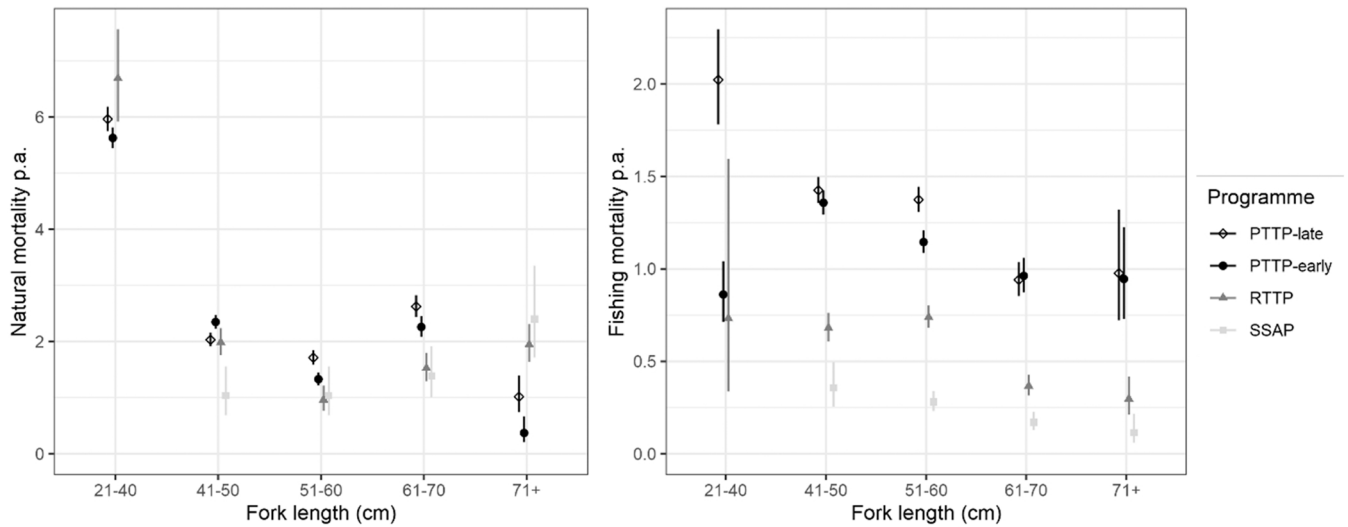
3.1.2. Yellowfin

The selected mixing period for yellowfin tuna models depended on the treatment of mortality rate parameters, with a mixing period of 1 month for models with programme specific F_s and a mixing period of 2 months for models with F_s shared between tagging programmes (Table 1). The separation of the PTTP into two effective tagging programmes was supported by AIC, with the most support for programme-specific M_s and F_s parameters followed by shared M_s and programme-specific F_s (ΔAIC = 47.7; Table 1). Estimated yellowfin M_s displayed a relationship with size that was similar to skipjack, with the highest M_s for the smallest size class and larger size classes, with lower rates of M_s for intermediate sizes (Fig. 1b). There were apparent differences in M_s within the PTTP, with higher M_s during 'PTTP-late' for the 51–60 cm size class, and lower M_s for the 91–100 cm size class. Yellowfin F_s estimates were higher during the PTTP than the RTTP for all size classes. Yellowfin F_s during the RTTP were relatively constant with increasing lengths from 21–40 cm to 81–90 cm, before decreasing. Yellowfin F_s estimates during the PTTP were highest for the 21–40 cm and 41–50 cm size classes, then decreased with increasing sizes up to 81–90 cm, with a potential increasing trend as lengths increased further. F_s was estimated to be higher in the early years of the PTTP than the later years, particularly for the 41–50 cm and 51–60 cm size classes. Estimates of yellowfin M_s and F_s with the alternative growth curve were broadly equivalent in magnitude and displayed similar relationships with size (Supplementary materials, Fig. S8b). Estimates of M_s and F_s for the larger size classes during 'PTTP-late' were more consistent with those from 'PTTP-early'. However, estimates of M_s for the 51–60 cm size class (RTTP) and the 61–70 cm size class (RTTP and PTTP-late) were close to zero.

3.2. Length-based Brownie models

3.2.1. Skipjack

Models selected by AIC for skipjack tuna modelled fishing mortality with both temporal (f_t) and length based (η_s) parameters for all programmes, except the SSAP where only temporal (f_t) parameters were selected (Table 2). Length-based natural mortality was chosen by AIC for all tagging programmes. The PTTP tagging data were best modelled by estimating separate selectivity and natural mortality size bin parameters for the PTTP early and PTTP late periods. There was also support for models where natural mortality was assumed temporally constant during the PTTP, but selectivity was separated in 2011 (ΔAIC = 2.6 and 8.6 with a mixing period of 1 and 2 quarters respectively). Natural mortality estimates for skipjack differed slightly among the tagging programmes and mixing period but generally estimated the highest rate for the smallest size class (Fig. 2 - top left panel). The exception to this was the skipjack SSAP programme with a higher natural mortality for the $\geq$ 71 cm group, but the estimates were very uncertain. The estimate of natural mortality from the PTTP early period was marginally higher than the PTTP late period for size classes 41–50 cm and $\geq$ 71 cm, but was lower for 61–70 cm. M estimates from models with mixing periods of 1 and 2 quarters for the PTTP were consistent with one another for most size classes. Natural mortality for the largest size class from the PTTP late period was estimated to be practically zero for both mixing periods. Estimates of M from the RTTP were highest for the smallest size class, and then decreased with larger size classes. The uncertainty surrounding the natural mortality estimates were generally larger for the PTTP compared to the RTTP and was the largest for the SSAP at the smallest and largest size classes. The selectivity at length for the first size class was estimated to be either fully selected for the PTTP with a mixing period of 1 quarter, or 0 for the PTTP mixing period of 2 quarters and the RTTP models (Fig. 2 - top right panel). For the 51–60 cm size class, the PTTP-early selectivity at length was estimated to be higher compared to the PTTP-late, but the opposite occurred for the 61–70 cm and $\geq$ 71 cm
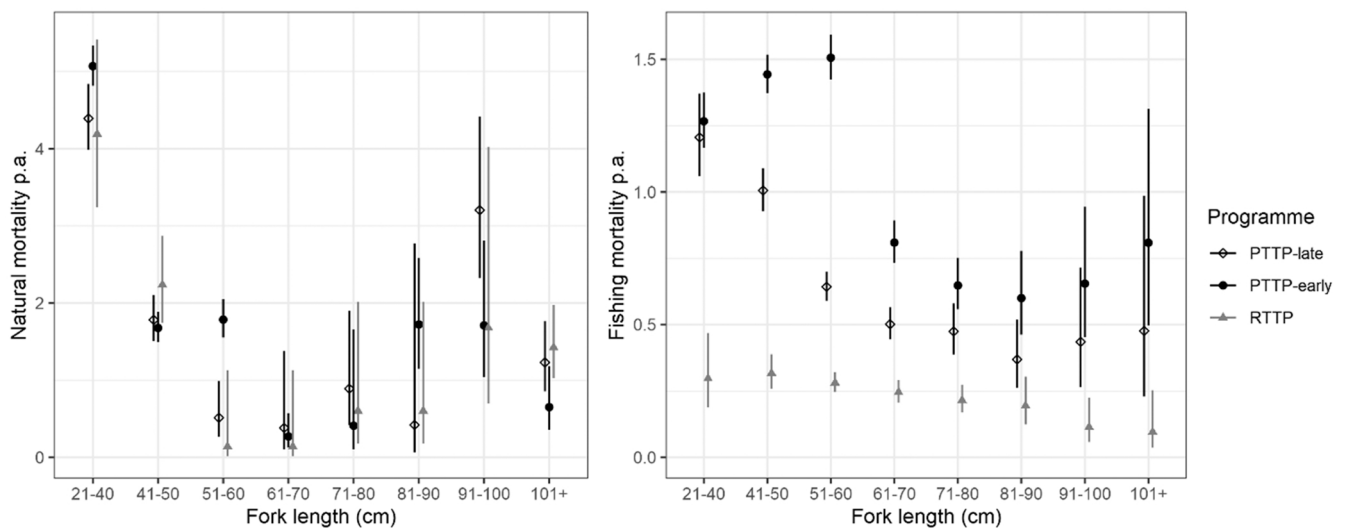
a) Skipjack

b) Yellowfin

Fig. 1. Estimated M_s and F_s parameters and 95 % confidence intervals for a) the skipjack attrition model with programme-specific M_s and F_s and a mixing period of 2 months, and b) the yellowfin attrition model with shared M_s and programme-specific F_s and a mixing period of 1 month. For both skipjack and yellowfin, the PTTP was split into two effective tagging programmes: the PTTP-early with releases from 2006 to 2009; and, the PTTP-late with releases from 2011–2017. There was insufficient data to reliably estimate M_s and F_s for 21–40 cm skipjack during the SSAP (see text), and so these parameters are not included in the plot ($M = 5.6$, $F = 1.9$).

size classes and was higher for a mixing period of 1 quarter compared to 2 quarters in most cases. Selectivity in the largest size group was relatively small for both mixing periods for the RTTP and PTTP-early. The SSAP model did not estimate selectivity parameters and thus were equal for all lengths. Estimates of temporal fishing mortality were highly uncertain for one or two time periods in the RTTP and SSAP (Fig. 2 - bottom panel). Both the SSAP and RTTP estimated the temporal fishing mortality in the last time step at the upper bound of the model. Temporal fishing mortality estimates for the PTTP also became more uncertain between time steps 14 and 20 and then after time step 28, when there were no tag release events. Fishing mortality estimates were the highest at the end of the time series for the PTTP, but estimates were highly uncertain with only a few tags recaptured. The estimate of over-dispersion (τ) of the tag returns was highest for the PTTP with a mixing period of 1 quarter (8.29), followed by a mixing period of 2 quarters

(5.69). The RTTP models estimated lower overdispersion in the model with a mixing period of 1 quarter (1.70) than a mixing period of 2 quarters (2.22). The SSAP model could not estimate the overdispersion in the negative binomial model because it was estimated to be close to 1 and thus we used the multinomial distribution, which is equivalent to an overdispersion equal to 1. Estimates from the alternative growth followed similar trends with highest mortality rates for the smallest size class which generally decreased with increasing size (Supplementary materials, Fig. S11). Estimates of M for size classes 51–60 and 61–70 cm were marginally lower for the alternative growth, but estimates of selectivity and temporal fishing mortality for the PTTP were more uncertain.

3.2.2. Yellowfin

    The length-based Brownie models for yellowfin selected by AIC

Table 2

AIC and ΔAIC values for sets of Brownie models with different combinations of approaches to modelling *M* and *F* and mixing periods. *M* was modelled as constant *M*, length-based *M*, and length-based *M* estimated separately for the PTTP-early and PTTP-late periods ('Separated Length M'). *F* was modelled as constant *F*, temporal *F*, length-based *F*, both temporal and length-based *F* ('both F'), and both temporal and length-based *F* estimated separately for the PTTP-early and PTTP-late periods ('Separated Both F'). Models fitted to the same dataset and which can be compared against one another are separated by horizontal black lines, with the model with the lowest AIC in bold. Models with a ΔAIC less than 10 are presented in the Supplementary materials (Figs. S13–S20).

Species	Programme	Mixing period	M Model	F Model	AIC	ΔAIC
Yellowfin	RTTP	1	Length M	Constant F	908.93	46.52
Yellowfin	RTTP	1	Length M	Length F	910.01	47.6
Yellowfin	**RTTP**	**1**	**Length M**	**Temporal F**	**862.4**	**0.00**
Yellowfin	RTTP	1	Length M	Both F	868.25	5.85
Yellowfin	RTTP	1	Constant M	Constant F	935.29	72.88
Yellowfin	RTTP	1	Constant M	Length F	929.38	66.98
Yellowfin	RTTP	1	Constant M	Temporal F	896.75	34.34
Yellowfin	RTTP	1	Constant M	Both F	901.04	38.64
Yellowfin	RTTP	2	Length M	Constant F	688.97	18.34
Yellowfin	RTTP	2	Length M	Length F	691.37	20.74
Yellowfin	**RTTP**	**2**	**Length M**	**Temporal F**	**670.63**	**0.00**
Yellowfin	RTTP	2	Length M	Both F	677.11	6.48
Yellowfin	RTTP	2	Constant M	Constant F	711.78	41.15
Yellowfin	RTTP	2	Constant M	Length F	706.15	35.53
Yellowfin	RTTP	2	Constant M	Temporal F	701.79	31.17
Yellowfin	RTTP	2	Constant M	Both F	707.11	36.48
Yellowfin	PTTP	1	Length M	Constant F	3785.33	222
Yellowfin	PTTP	1	Length M	Length F	3784.55	221.21
Yellowfin	PTTP	1	Length M	Temporal F	3607.08	43.74
Yellowfin	PTTP	1	Length M	Both F	3580.19	16.86
Yellowfin	PTTP	1	Constant M	Constant F	4113.00	549.66
Yellowfin	PTTP	1	Constant M	Length F	4080.22	516.88
Yellowfin	PTTP	1	Constant M	Temporal F	3982.04	418.71
Yellowfin	PTTP	1	Constant M	Both F	3964.32	400.99
Yellowfin	PTTP	1	Separated Length M	Both F	3574.10	10.76
Yellowfin	**PTTP**	**1**	**Length M**	**Separated Both F**	**3563.34**	**0.00**
Yellowfin	PTTP	1	Separated Length M	Separated Both F	3563.83	0.50
Yellowfin	PTTP	2	Length M	Constant F	3142.78	146.05
Yellowfin	PTTP	2	Length M	Length F	3144.62	147.89
Yellowfin	PTTP	2	Length M	Temporal F	3028.30	31.57
Yellowfin	PTTP	2	Length M	Both F	3014.37	17.64
Yellowfin	PTTP	2	Constant M	Constant F	3413.56	416.83
Yellowfin	PTTP	2	Constant M	Length F	3420.55	423.83
Yellowfin	PTTP	2	Constant M	Temporal F	3350.57	353.85
Yellowfin	PTTP	2	Constant M	Both F	3353.6	356.87
Yellowfin	PTTP	2	Separated Length M	Both F	3002.98	6.25
Yellowfin	**PTTP**	**2**	**Length M**	**Separated Both F**	**2996.73**	**0.00**
Yellowfin	PTTP	2	Separated Length M	Separated Both F	2997.92	1.19
Skipjack	SSAP	1	Length M	Constant F	8699.74	506.10
Skipjack	SSAP	1	Length M	Length F	8665.46	471.83
Skipjack	**SSAP**	**1**	**Length M**	**Temporal F**	**8193.63**	**0.00**
Skipjack	SSAP	1	Length M	Both F	8200.00	6.37
Skipjack	SSAP	1	Constant M	Constant F	8742.79	549.15
Skipjack	SSAP	1	Constant M	Length F	8704.61	510.98
Skipjack	SSAP	1	Constant M	Temporal F	8219.91	26.28
Skipjack	SSAP	1	Constant M	Both F	8202.52	8.89
Skipjack	SSAP	2	Length M	Constant F	4635.18	146.58
Skipjack	SSAP	2	Length M	Length F	4633.76	145.15
Skipjack	**SSAP**	**2**	**Length M**	**Temporal F**	**4488.60**	**0.00**
Skipjack	SSAP	2	Length M	Both F	4494.70	6.10
Skipjack	SSAP	2	Constant M	Constant F	4704.65	216.05
Skipjack	SSAP	2	Constant M	Length F	4649.66	161.06
Skipjack	SSAP	2	Constant M	Temporal F	4512.24	23.64
Skipjack	SSAP	2	Constant M	Both F	4495.28	6.68
Skipjack	RTTP	1	Length M	Constant F	1316.43	144.53
Skipjack	RTTP	1	Length M	Length F	1316.96	145.06
Skipjack	RTTP	1	Length M	Temporal F	1191.93	20.02
Skipjack	**RTTP**	**1**	**Length M**	**Both F**	**1171.90**	**0.00**
Skipjack	RTTP	1	Constant M	Constant F	1367.56	195.66
Skipjack	RTTP	1	Constant M	Length F	1346.48	174.57
Skipjack	RTTP	1	Constant M	Temporal F	1285.80	113.90
Skipjack	RTTP	1	Constant M	Both F	1254.26	82.36
Skipjack	RTTP	2	Length M	Constant F	1006.63	108.37
Skipjack	RTTP	2	Length M	Length F	1010.62	112.37
Skipjack	RTTP	2	Length M	Temporal F	912.96	14.71
Skipjack	**RTTP**	**2**	**Length M**	**Both F**	**898.25**	**0.00**

Table 2 (*continued*)

Species	Programme	Mixing period	M Model	F Model	AIC	ΔAIC
Skipjack	RTTP	2	Constant M	Constant F	1022.86	124.6
Skipjack	RTTP	2	Constant M	Length F	1024.34	126.08
Skipjack	RTTP	2	Constant M	Temporal F	969.16	70.90
Skipjack	RTTP	2	Constant M	Both F	957.11	58.85
Skipjack	PTTP	1	Length M	Constant F	3512.39	159.81
Skipjack	PTTP	1	Length M	Length F	3441.62	89.04
Skipjack	PTTP	1	Length M	Temporal F	3417.57	64.99
Skipjack	PTTP	1	Length M	Both F	3358.4	5.82
Skipjack	PTTP	1	Constant M	Constant F	3865.18	512.6
Skipjack	PTTP	1	Constant M	Length F	3807.80	455.21
Skipjack	PTTP	1	Constant M	Temporal F	3757.97	405.38
Skipjack	PTTP	1	Constant M	Both F	3720.79	368.2
Skipjack	PTTP	1	Separated Length M	Both F	3361.59	9.01
Skipjack	PTTP	1	Length M	Separated Both F	3355.07	2.48
Skipjack	**PTTP**	**1**	**Separated Length M**	**Separated Both F**	**3352.58**	**0.00**
Skipjack	PTTP	2	Length M	Constant F	2764.82	120.00
Skipjack	PTTP	2	Length M	Length F	2742.14	97.33
Skipjack	PTTP	2	Length M	Temporal F	2692.01	47.19
Skipjack	PTTP	2	Length M	Both F	2657.74	12.92
Skipjack	PTTP	2	Constant M	Constant F	2999.93	355.11
Skipjack	PTTP	2	Constant M	Length F	2982.22	337.4
Skipjack	PTTP	2	Constant M	Temporal F	2923.65	278.83
Skipjack	PTTP	2	Constant M	Both F	2927.89	283.08
Skipjack	PTTP	2	Separated Length M	Both F	2653.70	8.88
Skipjack	PTTP	2	Length M	Separated Both F	2653.46	8.64
Skipjack	**PTTP**	**2**	**Separated Length M**	**Separated Both F**	**2644.82**	**0.00**

assumed that natural mortality was modelled by size-class specific parameters for the first 4 size classes and then a shared parameter for the 4 largest size classes (Table 2). AIC selected models with fishing mortality parameterised with only temporal (f_t) parameters for the RTTP, but parameterised with both length (η_s) and temporal (f_t) parameters for the PTTP. The lowest AIC values for models of the PTTP data were obtained where natural mortality was assumed temporally constant, but selectivity was separated in 2011. However, there was strong support for models where both natural mortality and selectivity were separated in 2011 (ΔAIC = 0.5 and 1.2 with a mixing period of 1 and 2 quarters respectively). Natural mortality estimates for yellowfin tuna from a length-based Brownie model were most uncertain for intermediate length classes (51–60 cm and 61–70 cm; Fig. 3 - top left panel). Similar to skipjack, yellowfin was estimated to have the highest natural mortality at the smallest size class and *M* generally declined with larger size. Natural mortality was estimated to be higher during the RTTP compared to the PTTP for all length classes except the smallest. Estimates of natural mortality were relatively similar between mixing periods for the programmes. Selectivity was only estimated for the PTTP and was held constant for the RTTP (Fig. 3 - top right panel). Selectivity was estimated to be close to 1 for the smallest size class, except for the early period with a mixing period of 1 quarter where the estimate was close to 0. Selectivity parameters for the PTTP-late period with a mixing period of 2 quarters were more uncertain. For a mixing period of 2 quarters the PTTP late selectivity was estimated close to zero for the length bin of 51–60 cm but much higher for the 61–70 cm bin. Selectivity for the early period was higher than the late-PTTP for the 51–60 cm and 61–70 cm size classes but was lower for ≥ 71 cm. Temporal fishing mortality of yellowfin for the RTTP was estimated to be highly uncertain for time steps 16 through 18 after the first release, close to 0 for quarters 19–22, but at the upper bound for the 23rd time step (Fig. 3 - bottom panel). Estimates of fishing mortality from the PTTP were more uncertain with a mixing period of 2 quarters than estimates from the model with a mixing period of 1 quarter. Estimates of fishing mortality were much higher for the PTTP compared to the RTTP, where estimates from the PTTP with a mixing period of 1 quarter were generally the most certain estimates, except the last time step. Estimates of overdispersion from the tagging data were consistent with the trends observed for skipjack, with higher values for the PTTP with a mixing period of 1

quarter (3.47) compared to 2 quarters (2.69), and higher values for the PTTP relative to the RTTP (1 quarter = 1.22, 2 quarters = 1.12). Estimates from the alternative growth model for yellowfin had the same general trends in natural mortality with minor changes in selectivity and slightly lower temporal fishing mortality estimates (Supplementary materials, Fig. S12).

4. Discussion

A variety of density-dependent and -independent processes have been proposed to influence natural mortality, potentially leading to variation through time. However, natural mortality rates are currently assumed to be time-invariant in stock assessment models of skipjack and yellowfin tuna in the western and central Pacific Ocean (WCPO). In this study, we fitted tag attrition and Brownie models to the WCPO mark-recapture dataset to assess temporal changes in natural mortality rates during a period of sustained expansion of the industrial fisheries targeting tropical tunas in the region. This expansion and change in fishing technologies within the industrial fisheries is reflected by the higher estimates of fishing mortality (*F*) during the PTTP in comparison to the earlier tagging programmes. There was no clear evidence of significant changes in natural mortality rates of skipjack and yellowfin tuna during the past four decades.

We applied both the tag attrition and Brownie approaches to include the influence that the different assumptions of each methodology have on the estimation of mortalities. The Brownie model typically performs well when there are multiple release events (Polacheck et al., 2010). In a length-based setting, this requires multiple release events for each size class. However, this experimental design aspect has not been a consistent feature in the three Pacific tagging programmes. The tag attrition model is not reliant on such design aspects (Polacheck et al., 2010) and consequently provided a point of reference for comparison.

Considerable uncertainty in natural mortality estimates remained for some strata using both modelling approaches. The yellowfin models presented here had relatively imprecise estimates of *M*, particularly when fitted to the RTTP dataset using both tag-attrition and Brownie models. Similarly, the length-based Brownie model for the yellowfin RTTP dataset did not have sufficient information to inform η_s and thus assumed constant selectivity. The Brownie models for yellowfin tuna
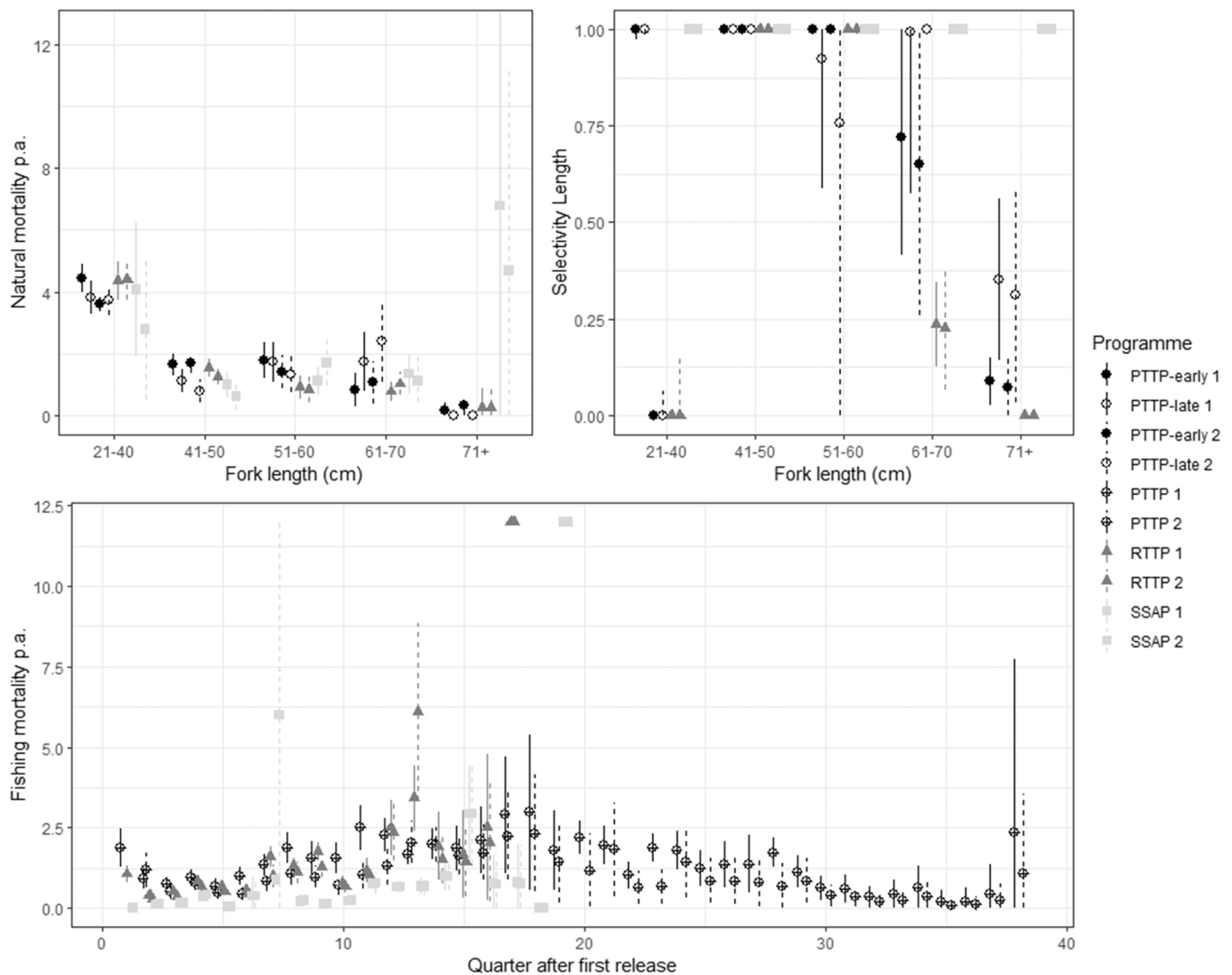
Fig. 2. Estimated M_s, f_t, and η_s and 95 % confidence intervals from length-based Brownie models chosen by AIC (see Table 2) for skipjack tuna in the western Pacific Ocean for three tagging programmes with either 1 or 2 mixing quarters. The natural mortality and selectivity for length bins in the PTTP were modelled as separate parameters before and after 2011, indicated by PTTP-early and -late.

were also unable to provide reasonable estimates for fishing and natural mortality rates for size classes greater than 71 cm individually. This lack of precision precluded a robust investigation of temporal variation in natural mortality for yellowfin, with likely insufficient statistical power to detect plausible changes. The Brownie models did provide some evidence of a reduction in yellowfin M for the 41–50 and 51–60 cm size classes between the RTTP and PTTP, and an increase in M for the 21–40 cm size class. However, the 95% confidence intervals generally overlapped and these differences were not seen in the attrition models for this species.

Both the attrition and Brownie models estimate natural mortality averaged across time within each tag programme. It is possible that small temporal changes in M are not detected due to this assumption. However, attempting to estimate finer-scale within-programme temporal changes in M would likely have led to increased uncertainty in estimates, further complicating determination of whether temporal changes have occurred. The small variations in estimated M among tagging programmes could be due to differences in reporting rates, tag shedding, or tag mortality that were not accounted for by the single rate applied to all three tagging programmes. There is no clear evidence for temporal changes in reporting rates or tag shedding rates across the tagging programmes modelled here. However, there have been

indications of a potential reduction in tag reporting rates after 2015, though this is uncertain (Peatman, 2020).

Time-varying natural mortality can have significant implications for stock assessments and their estimated parameters. However, allowing M to vary within an assessment has implications on the estimation of other parameters due to the increased flexibility afforded to the model and can cause difficulty in setting reference points (Legault and Palmer, 2016). Despite the uncertainty in some of the strata in our analyses presented here, neither approach suggests strong evidence for a change in M across the large-scale tagging programmes of the previous four decades.

Fishing-pressure driven phenotypic plasticity in fish populations is widely accepted for its potential to cause changes in length-at-age and length-at-maturity (Law, 2000). The particularities of the fishing gears or spatial concentration of this pressure may also influence M (Jørgensen and Fiksen, 2010), for example the targeting of individuals whilst resting leading to selection of more bold traits in a population (Claireaux et al., 2018). This could be the case with increased catch of tropical tunas associating with floating objects over the time-period of our study (Leroy et al., 2013). However, while fishing mortality appears to have increased for both species and most size classes, we do not detect a corresponding change in M accompanying this increased fishing pressure using the methods outlined here. This indicates that the current
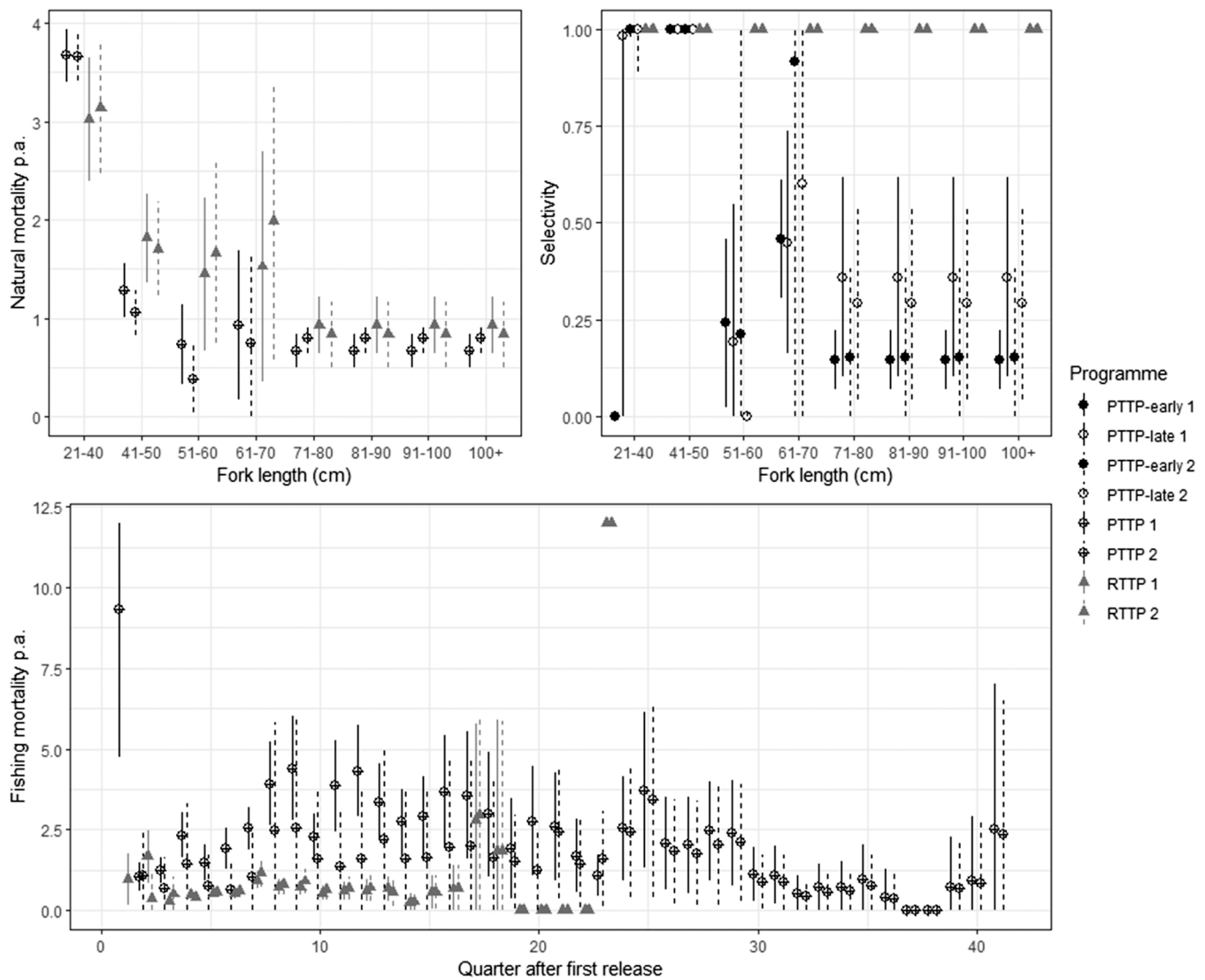
Fig. 3. Estimated M_s, f_t, and η_s and 95 % confidence intervals from length-based Brownie models chosen by AIC (see Table 2) for yellowfin tuna in the western Pacific Ocean for two tagging programmes with either 1 or 2 mixing quarters. Selectivity for size bins for the PTTP were modelled as separate parameters before and after 2011 (PTTP- early and late), but natural mortality was best modelled as temporally constant (PTTP).

assumption of temporally constant values of M within stock assessments of WCPO skipjack and yellowfin tuna is appropriate.

Our estimates of fishing mortality do suggest a change in selectivity through time for yellowfin from both analyses. The relative fishing mortality rates for individuals in the size classes up to 51–60 cm (attrition models) and 61–70 cm (Brownie models) were higher during the PTTP compared with the RTTP. This increase in fishing mortality for yellowfin smaller than 70 cm may reflect increasing catches from the purse seine fishery, particularly sets on schools associated with FADs and other floating objects, which capture relatively small individuals. The apparent increase in PTTP F for the largest yellowfin size classes in the attrition model estimates could reflect the second modal peak in size compositions from free school purse seine sets during the PTTP, driven by recoveries of large tagged fish at liberty for long periods of time. However, the estimated increase in F for large yellowfin is relatively imprecise and not detected by the Brownie models. The selectivity estimates suggest that the fishing mortality may be highly dome-shaped with the highest mortality for lengths between 30 and 60 cm, which is consistent with length frequency data from the purse seine fishery. The apparent change in selectivity over time could be due to an increase in fishing mortality from the purse seine fishery, or a change in the

proportion of free school and associated sets. Equally, it could reflect a change in the selectivity of the purse seine fisheries, which may warrant further investigation in future WCPO yellowfin assessments.

Hampton (2000) identified size-related variability in natural mortality rates of skipjack and yellowfin. The attrition analyses presented here demonstrate similar relationships between size and M, with the highest rates for the smallest size class, lower rates for intermediate size classes, and potentially increasing rates for the largest size classes. The Brownie models also detected similar trends of M with size for small to intermediate size classes of skipjack and yellowfin, though with limited (skipjack) or no (yellowfin) evidence of increasing M for the largest size classes. The apparent inconsistencies in trends in mortality rates for the largest size classes may be due to the majority of recaptures of large tagged fish originating from individuals at liberty for long periods, rather than from tag releases of large individuals directly. As such, the estimates of mortality rates for the larger size classes are more dependent on the assumed growth model and estimated mortality rates of smaller size classes. In the case of the Brownie model, the yellowfin growth transition matrix caused fish in the 71–80 cm size class to remain at that size 33 % of the time, or transition to the 81–90 cm size class and the 91–100 cm size class 42 % and 15 % of the time, respectively

(Supplementary materials, Table S2). In combination with the lack of tag releases of large size classes, this resulted in insufficient information in the mark-recapture data set to differentiate mortality rates between the largest size classes with the length-based Brownie model. Even with the deterministic growth used in the attrition model, the decrease in data for these size classes suggests that the increase in estimated *M* of large yellowfin tuna is uncertain.

Hampton (2000) also detected increased rates of skipjack *M* for the ≥ 71 cm size class during the RTTP. This feature was not consistently detected by the attrition and Brownie skipjack models, with low rates of *M* for ≥ 71 cm skipjack during the PTTP for both modelling approaches. This apparent decrease in *M* may be due to the increase in recaptured tags that were at liberty for long periods during the PTTP. It is unclear whether such long times-at-liberty are genuine, or due to errors in reported recovery date, e.g. anecdotal claims that fishermen use tags as a currency while at sea and potentially fabricate the date of recapture when tags are finally reported. Alternatively, the increase in sample size of tags released in the PTTP compared to the RTTP and SSAP could have led to the increase in observation of these rare long-lived fish. However, the observation of tags of long liberty recovered at the same time as numerous tags recovered shortly after release lends support to the former hypothesis, due to the size-based schooling behaviour of tuna.

Estimates of natural mortality for the 21–40 cm size class from the attrition models were consistently higher than their equivalents from the Brownie models for both skipjack and yellowfin. This may be due to the difference in the time steps between the attrition and Brownie models, where the later exposes individuals to the 21–40 cm natural mortality rate for longer due to the quarterly time step. Additionally, errors in reported recovery dates may have introduced bias in the attrition model estimates, given the use of a relatively short, monthly, time-step which was used to facilitate comparison with Hampton (2000). The quarterly time step of the length-based Brownie model is consistent with the time step used in the most recent skipjack (Vincent et al., 2019b) and yellowfin tuna (Vincent et al., 2020) stock assessments.

The attrition models presented here can be viewed as a simplification of the Brownie modelling approach, in which variability and uncertainty in growth was ignored and temporal variation in *F* ignored, or constrained. The Brownie models detected temporal variation in fishing mortality rates within tagging programmes, which in some cases was stronger than apparent variability in fishing mortality rates by size (Table 2). Tag attrition models with fishing mortality parameterised as a function of size-specific catchabilities and purse seine effort had worse likelihoods than their time-invariant *F* equivalents. This difference in interpretation between the two modelling approaches is likely due to the relatively inflexible parameterisation of time-varying *F* in the attrition models relative to the less constrained approach implemented in the Brownie models. Comparisons between the modelling approaches suggests that the precision of the attrition model parameter estimates was substantially overestimated, which is likely to have been partially a result of ignoring variability in growth rates. This could result in type-I errors when testing for temporal changes in natural mortality rates; the apparent support for variation in natural mortality rates among tagging programmes, as well as variation during the PTTP, from the attrition models should be viewed in this context. Of the models presented here, the Brownie models appear the more appropriate choice for the analysed mark-recapture dataset.

There are numerous factors in this study that could potentially lead to biased estimates of parameters. Estimates of quarterly *F* from the Brownie model are likely only reliable when there are recaptures from multiple release events, which is not the case for many of the fishing mortality estimates later in the PTTP and RTTP time series or the SSAP. Uncertainty in recapture dates of tags could potentially smooth over temporal variability in fishing mortality estimates and cause bias in quarterly estimates of *F*. Tag releases may not be fully mixed with the wider population at the end of the assumed mixing period and thus may not represent the rates experienced by the population at large (Kolody

and Hoyle, 2015). Alternatively, the schooling behaviour of tunas may impede mixing of tagged fish with the overall population that are represented by the catch, particularly as fishers target schools and aggregations in this fishery. Additionally, there is the potential for high variability in the reporting of tags across the WCPO dependent on the local awareness of the tagging programme, the country of recovery, the number of tags recovered, fishers' views about reporting tags, and other factors which cannot be accounted for by these models. Therefore, recaptures of tagged fish within a school may be overdispersed relative to a random distribution of tags in the population and may not represent temporal variability in the fishing mortality on the population. Not accounting for changes in reporting rates, if they occur, could potentially lead to biases in fishing or natural mortality estimates.

Overdispersion is a common modelling concern for mark-recapture data which is difficult to address. Overdispersion is the presence of variation in data that is higher than assumed by the modelled distribution. The negative binomial distributions used in the Brownie models were parameterised to estimate the overdispersion rate relative to the Poisson distribution. The variance of residuals from the attrition models did not suggest overdispersion relative to the multinomial distribution. However, the length-based Brownie model estimated overdispersion for the PTTP and RTTP, though the level in the latter was relatively low. The skipjack stock assessment estimated the overdispersion of all mark-recapture data used in the model (SSAP, RTTP, PTTP, and Japanese Tagging Programme) at a level of 2.96, which is slightly less than the average of the three tagging programmes in this study (Vincent et al., 2022). The increase in overdispersion estimated for the PTTP could be an artefact of the increase in sample size of the latter tagging programme increasing estimability of this parameter. Alternatively, this higher overdispersion in the PTTP could reflect slower rates of mixing relative to the other tagging programmes, which could lead to higher variability in recapture rates of tagged fish. A lower proportion of tag releases were made on free schools during the PTTP (24 % of modelled skipjack releases) compared with earlier tagging programmes (e.g. 52 % for modelled RTTP releases), with a corresponding increase in tag releases from schools associated with drifting FADs and other objects. This may make PTTP releases more vulnerable to recapture in the purse seine fishery shortly after release.

Concerns of un-modelled dynamics that lead to overdispersion go hand in hand with concerns that tags are not fully mixed with the population and thus not representative of the dynamics in the region. The proposed solution to allow sufficient mixing with the population to occur, is to extend the time period after which tag returns contribute to the likelihood. However, if a mixing period of 2 quarters is assumed, the majority of information for the smallest two size classes, which are also the most exploited, is lost because few fish are estimated to remain in these size classes due to the high growth rate of tuna. This is a difficult conundrum to resolve when analysing tagging data, either in isolation or using integrated stock assessment models for skipjack and yellowfin tuna in the WCPO, which requires further investigation. Simulation analyses could be used to explore the degree to which tagged fish are likely to have mixed with the wider population and the implications on mark-recapture based estimates of mortality rates based on plausible assumptions regarding movement dynamics (e.g. Scutt Phillips et al., 2018). Such simulations could also inform the experimental design of future tagging efforts in the region (Lauretta and Goethel, 2017).

Recent stock assessments of skipjack and yellowfin tuna in the western and central Pacific Ocean have treated natural mortality differently between the two species. For skipjack, natural mortality at age was estimated within the stock assessment using a cubic spline informed by catch length compositions and tagging data. The stock assessment estimated an instantaneous natural mortality rate in the first year of life of 2 year^{-1} (Vincent et al., 2022). This was within the range of estimates for *M* for the different tagging programmes and mixing periods from the skipjack Brownie length-based models for a 30 cm tagged fish (1.60–2.38), and 27–38 % lower than estimates from the

attrition models (2.56–3.24). The shape of the natural mortality curve at age from the skipjack assessment model depended on the mixing period assumed but was estimated to be highest for the youngest age, decreased until 1.5–2 years and then increased for the oldest ages. Conversely, natural mortality at age for the WCPO yellowfin stock assessment was fixed at an externally estimated vector derived from assumed values of juvenile and baseline M along with proportions of females in catches (Harley and Maunder, 2003; Vincent et al., 2020). A range of values of M were also generated from a meta-analysis of estimates based on life-history characteristics and theory (Piner and Lee, 2011), and used to assess the sensitivity of model outputs to assumed natural mortality rates. The estimates of M from the meta-analysis were substantially lower, leading to lower estimates of depletion rates which were considered less plausible. The estimates of M presented here, informed by the PTTP dataset, support the higher rates of natural mortality which were used to generate management advice. Future assessments of yellowfin tuna in the WCPO should consider using estimates from this analysis to inform assumed values of M.

In conclusion, the analysis presented here suggests that fishing mortality on skipjack and yellowfin tuna in the WCPO has increased since the late 1970s but with no clear evidence of temporal changes in natural mortality. Estimates of length-based natural mortality are highest for the smallest length class, but differences among the larger size classes are difficult to detect as a result of growth variability and limited data availability for these sizes. Overdispersion is higher in the PTTP relative to the other tagging programmes and may be a result of the sampling design which has focused on tagging aggregations of tuna associated with floating objects, alongside the targeting and technological changes in the fishery which occurred in parallel. Our results suggest that additional analysis of the mixing of tag releases with the population is needed to address concerns that estimated natural and fishing mortality rates may not be representative of the overall population. The results also highlight the uncertainty in estimating natural and fishing mortality rates for large size classes from tropical tuna mark-recapture data.

CRediT authorship contribution statement

Tom Peatman: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Matthew Vincent:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Joe Scutt Phillips:** Conceptualization, Writing – original draft, Writing – review & editing. **Simon Nicol:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

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

Data Availability

The data are available on request, and through SPC's web tagging data system (https://www.spc.int/webtagging).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106463.

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control. 19 (6), 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Bell, J.D., Senina, I., Adams, T., Aumont, O., Calmettes, B., Clark, S., Dessert, M., Gehlen, M., Gorgues, T., Hampton, J., Hanich, Q., Harden-Davies, H., Hare, S.R., Holmes, G., Lehodey, P., Lengaigne, M., Mansfield, W., Menkes, C., Nicol, S., Ota, Y., Pasisi, C., Pilling, G., Reid, C., Ronneberg, E., Sen Gupta, A., Seto, K.L., Smith, N., Taei, S., Tsamenyi, M., Williams, P., 2021. Pathways to sustaining tuna-dependent Pacific Island economies during climate change. Nat. Sustain. 4, 900–910. https://doi.org/10.1038/s41893-021-00745-z.

Berger, A.M., McKechnie, S., Abascal, F., Kumasi, B., Usu, T., Nicol, S., 2014. Analysis of Tagging Data for the 2014 Tropical Tuna Assessments: Data Quality Rules, Tagger Effects, and Reporting Rates. Technical Report WCPFC-SC10-2014/SA-IP-06. Majuro, Republic of the Marshall Islands. Available: ⟨https://meetings.wcpfc.int/node/8636⟩.

Beverton, R., Holt, S., 1957. On the dynamics of exploited fish populations. Fish. Investig. 19, 1–533.

Brownie, C., Anderson, D.R., Burnham, K.P., Robson, D.S., 1985. Statistical Inference from Band Recovery Data: A Handbook, 156. US Fish Wildl. Resour. Publ., Washington D.C.

Claireaux, M., Jørgensen, C., Enberg, K., 2018. Evolutionary effects of fishing gear on foraging behavior and life-history traits. Ecol. Evol. 8 (22), 10711–10721. https://doi.org/10.1002/ece3.4482.

Clark, W.G., 1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. Can. J. Fish. Aquat. Sci. 56 (10), 1721–1731. https://doi.org/10.1139/f99-085.

Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K., Werner, F.E., 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish Fish. 17 (1), 101–125. https://doi.org/10.1111/faf.12093.

Eveson, P., Vincent, M., Farley, J., Krusic-Golub, K., Hampton, J., 2020. Integrated Growth Models from Otolith and Tagging Data for Yellowfin and Bigeye Tuna in the Western and Central Pacific Ocean. Technical Report WCPFC-SC16-SA-IP-03. Online. Available: ⟨https://meetings.wcpfc.int/node/11699⟩.

FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action. Rome. ⟨https://doi.org/10.4060/ca9229en⟩.

Farley, J., Krusic-Golub, K., Eveson, P., Clear, N., Roupsard, F., Sanchez, C., Nicol, S., Hampton, J., 2020. Age and Growth of Yellowfin and Bigeye Tuna in the Western and Central Pacific Ocean from Otoliths. Technical Report WCPFC-SC16-SA-WP-02. Online. Available: ⟨https://meetings.wcpfc.int/node/11692⟩.

Fournier, D., 1983. An analysis of the Hecate Strait Pacific cod fishery using an age-structured model incorporating density-dependent effects. Can. J. Fish. Aquat. Sci. 40 (8), 1233–1243. https://doi.org/10.1139/f83-140.

Griffiths, D., Harrod, C., 2007. Natural mortality, growth parameters, and environmental temperature in fishes revisited. Can. J. Fish. Aquat. Sci. 64 (2), 249–255. https://doi.org/10.1139/f07-002.

Hampton, J., 1997. Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean. Fish. Bull. 95 (1), 68–79 (Available: ⟨https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/1997/951/hampton.pdf⟩).

Hampton, J., 2000. Natural mortality rates in tropical tunas: size really does matter. Can. J. Fish. Aquat. Sci. 57 (5), 1002–1010. https://doi.org/10.1139/f99-287.

Harley, S.J., Maunder, M.N., 2003. A Simple Model for Age-structured Natural Mortality Based on Changes in Sex Ratios. Technical Report SAR-4-01. Inter-American Tropical Tuna Commission, La Jolla, California, USA. https://www.iattc.org/GetAttachment/0fe29bd2-8606-4b90-bb1b-4975529ca0da/Age%20structured%20natural%20mortality.

Hillary, R.M., Eveson, J.P., 2015. Length-based Brownie mark-recapture models: derivation and application to Indian Ocean skipjack tuna. Fish. Res. 163, 141–151. https://doi.org/10.1016/j.fishres.2014.06.004.

Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82 (1), 898–903. https://spo.nmfs.noaa.gov/content/empirical-use-longevity-data-estimate-mortality-rates.

Jiao, Y., Smith, E.P., O'Reilly, R., Orth, D.J., 2012. Modelling non-stationary natural mortality in catch-at-age models. ICES J. Mar. Sci. 69 (1), 105–118. https://doi.org/10.1093/icesjms/fsr184.

Jørgensen, C., Fiksen, Ø., 2010. Modelling fishing-induced adaptations and consequences for natural mortality. Can. J. Fish. Aquat. Sci. 67 (7), 1086–1097. https://doi.org/10.1139/F10-049.

Jørgensen, C., Holt, R.E., 2013. Natural mortality: its ecology, how it shapes fish life histories, and why it may be increased by fishing. J. Sea Res. 75, 8–18. https://doi.org/10.1016/j.seares.2012.04.003.

Kenchington, T.J., 2014. Natural mortality estimators for information-limited fisheries. Fish Fish. 15 (4), 533–562. https://doi.org/10.1111/faf.12027.

Kleiber, P., Argue, Kearney, R.E., 1987. Assessment of Pacific skipjack tuna (Katsuwonus pelamis) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44 (6), 112–1134. https://doi.org/10.1139/f87-135.

Kolody, D., Hoyle, S., 2015. Evaluation of tag mixing assumptions in western Pacific Ocean skipjack tuna stock assessment models. Fish. Res. 163, 127–140. https://doi.org/10.1016/j.fishres.2014.05.008.

Krause, J.R., Hightower, J.E., Poland, S.J., Buckel, J.A., 2020. An integrated tagging and catch-curve model reveals high and seasonally-varying natural mortality for a fish population at low stock biomass. Fish. Res. 232, 105725 https://doi.org/10.1016/j.fishres.2020.105725.

Kurota, H., McAllister, M.K., Lawson, G.L., Nogueira, J.I., Teo, S.L., Block, B.A., 2009. A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic bluefin tuna (Thunnus thynnus). Can. J. Fish. Aquat. Sci. 66 (2), 321–342. https://doi.org/10.1139/F08-197.

Lauretta, M.V., Goethel, D.R., 2017. The robustness of Brownie tag return models to complex spatiotemporal dynamics evaluated through simulation analysis. Can. J. Fish. Aquat. Sci. 74 (11), 1845–1861. https://doi.org/10.1139/cjfas-2016-0291.

Law, R., 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57 (3), 659–668. https://doi.org/10.1006/jmsc.2000.0731.

Legault, C.M., Palmer, M.C., 2016. In what direction should the fishing mortality target change when natural mortality increases within an assessment? Can. J. Fish. Aquat. Sci. 73 (3), 349–357. https://doi.org/10.1139/cjfas-2015-0232.

Leroy, B., Scutt Phillips, J., Nicol, S., Pilling, G.M., Harley, S., Bromhead, D., Hoyle, S., Caillot, S., Allain, V., Hampton, J., 2013. A critique of the ecosystem impacts of drifting and anchored FADs use by purse-seine tuna fisheries in the Western and Central Pacific Ocean. Aquat. Living Resour. 26 (1), 49–61. https://doi.org/10.1051/alr/2012033.

Leroy, B., Nicol, S., Lewis, A., Hampton, J., Kolody, D., Caillot, S., Hoyle, S., 2015. Lessons learned from implementing three, large-scale tuna tagging programmes in the western and central Pacific Ocean. Fish. Res. 163, 23–33. https://doi.org/10.1016/j.fishres.2013.09.001.

Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. 49 (4), 627–642. https://doi.org/10.1111/j.1095-8649.1996.tb00060.x.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES J. Mar. Sci. 39 (2), 175–192. https://doi.org/10.1093/icesjms/39.2.175.

Peatman, T., 2020. Analysis of Tag Seeding Data and Reporting Rates for Purse Seine Fleets. Technical Report WCPFC-SC16-2020/SA-IP-04. Online. Available: ⟨https://meetings.wcpfc.int/node/11700⟩.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J., Rice, J.A., 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28 (10), 10–23. https://doi.org/10.1577/1548-8446(2003)28[10:AROTMF]2.0.CO;2.

Piner, K., Lee, H., 2011. Meta-analysis of Striped Marlin Natural Mortality. Technical Report, ISC/11/BILLWG-1/10. Available: ⟨http://isc.fra.go.jp/pdf/BILL/ISC11_BILL_1/ISC11BILLWG1_WP10.pdf⟩.

Polacheck, T., Eveson, J.P., Laslett, G.M., 2010. Classifying tagging experiments for commercial fisheries into three fundamental types based on design, data requirements and estimable population parameters. Fish Fish. 11, 133–148. https://doi.org/10.1111/j.1467-2979.2010.00360.x.

Pollock, K.H., Hoenig, J.M., Hearn, W.S., Calingaert, B., 2002. Tag reporting rate estimation 2: use of high-reward tagging and observers in multiple-component fisheries. N. Am. J. Fish. Manag. 22 (3), 727–736. https://doi.org/10.1577/1548-8675(2002)022<0727:TRREUO>2.0.CO;2.

Pope, J.G., Gislason, H., Rice, J.C., Daan, N., 2021. Scrabbling around for understanding of natural mortality. Fish. Res. 240, 105952 https://doi.org/10.1016/j.fishres.2021.105952.

Powers, J.E., 2014. Age-specific natural mortality rates in stock assessments: size-based vs. density-dependent. ICES J. Mar. Sci. 71 (7), 1629–1637. https://doi.org/10.1093/icesjms/fst226.

Punt, A.E., Kennedy, R.B., Frusher, S.D., 1997. Estimating the size-transition matrix for Tasmanian rock lobster. Mar. Freshw. Res. 48 (8), 981–992. https://doi.org/10.1071/MF97017.

Punt, A.E., Castillo-Jordan, C., Hamel, O.S., Cope, J.M., Maunder, M.N., Ianelli, J.N., 2021. Consequences of error in natural mortality and its estimation in stock assessment models. Fish. Res. 233, 105759 https://doi.org/10.1016/j.fishres.2020.105759.

Rountrey, A.N., Coulson, P.G., Meeuwig, J.J., Meekan, M., 2014. Water temperature and fish growth: otoliths predict growth patterns of a marine fish in a changing climate. Glob. Change Biol. 20 (8), 2450–2458. https://doi.org/10.1111/gcb.12617.

Scutt Phillips, J., Gupta, A.S., Senina, I., van Sebille, E., Lange, M., Lehodey, P., Hampton, J., Nicol, S., 2018. An individual-based model of skipjack tuna (Katsuwonus pelamis) movement in the tropical Pacific ocean. Prog. Oceanogr. 164, 63–74. https://doi.org/10.1016/j.pocean.2018.04.007.

SPC-OFP, 2021. Estimates of Annual Catches in the WCPFC Statistical Area. Technical Report WCPFC-SC17-2021/ST-IP-01. Online. Available: ⟨https://meetings.wcpfc.int/node/12537⟩.

Vincent, M., Pilling, G., Hampton, J., 2022. Assumptions influencing the estimation of natural mortality in a tag integrated statistical model for western and central Pacific Ocean skipjack. Manuscript submitted for publication.

Vincent, M., Pilling, G., Hampton, J., 2019b. Stock Assessment of Skipjack Tuna in the WCPO. Technical Report WCPFC-SC15-2019/SA-WP-05, Pohnpei, Federated States of Micronesia. Available: ⟨https://meetings.wcpfc.int/node/11230⟩.

Vincent, M., Aoki, Y., Kiyofuji, H., Hampton, J., Pilling, G., 2019a. Background Analyses for the 2019 Stock Assessment of Skipjack Tuna. Technical Report WCPFC-SC15-2019/SA-IP-04. Pohnpei, Federated States of Micronesia. Available: ⟨https://meetings.wcpfc.int/node/11239⟩.

Vincent, M., Ducharme-Barth, N., Hamer, P., Hampton, J., Williams, P., Pilling G., 2020. Stock Assessment of Yellowfin Tuna in the Western and Central Pacific Ocean. Technical Report WCPFC-SC16-2020/SA-WP-04. Online. Available: ⟨https://meetings.wcpfc.int/node/11694⟩.

Whitlock, R.E., McAllister, M.K., Block, B.A., 2012. Estimating fishing and natural mortality rates for Pacific bluefin tuna (Thunnus orientalis) using electronic tagging data. Fish. Res. 119–120, 115–127. https://doi.org/10.1016/j.fishres.2011.12.015.