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**SENSITIVITY OF BIGEYE STOCK ASSESSMENT TO ALTERNATIVE
BIOLOGICAL AND REPRODUCTIVE ASSUMPTIONS.**

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Executive Summary

The outputs from mathematical and statistical models can be influenced by uncertainty in the estimates of the parameters used (known as parameter uncertainty) and to the methods and assumptions used to construct and link parameters in a model (known as structural uncertainty). Sensitivity analysis was applied to the current bigeye stock assessment to ascertain the influence of the structural assumptions on the reference point outputs of the model. The analysis examined the influence of alternative estimates of natural mortality, fecundity at length, spawning fraction at length and alternative maturity schedules. The effect of an alternative growth curve, and an alternative steepness assumption, were also assessed. The current stock assessment indicates that the fishing mortality exceeds F_{MSY} , and that the biomass is approaching MSY (Langley et al. 2008). The model is more strongly influenced by precision in CPUE and length frequency data than by the reproductive and growth parameters directly. This sensitivity analysis demonstrates that the model is also sensitive to the structural assumptions associated with estimation of the reproductive and growth parameters. Alternative estimates for all reproductive and growth parameters and natural mortality influenced the spawning biomass reference points ($SB_{current}/SB_{MSY}$ and $SB_{current}/SB_0$) typically by more than 10% and influenced biomass (B/B_{MSY}) and the $F_{multiplier}$ reference points by between 1 % and 5 %. The results support the need for further investment in knowledge acquisition to reduce the current level of uncertainty.

Introduction

Stock assessments of bigeye tuna have been routinely undertaken for the western and central Pacific Ocean (WCPO), eastern Pacific Ocean (EPO), and more recently Pacific-wide (Hampton et al. 2006, Hampton and Maunder 2006, IATTC 2004). In the WCPO, reference points (e.g. $F_{\text{current}}/F_{\text{MSY}}$, $SB_{\text{current}}/SB_{\text{MSY}}$, etc) are used by the members of the Western and Central Pacific Fisheries Commission (WCPFC) for evaluating that status of stocks in assessments. Recent stock assessments for bigeye indicate an increased probability that these reference points are being approached or exceeded to the extent that conservation measures may need to be considered to ensure long term sustainable of the fishery (Langley et al. 2008).

Stock assessments use models of the population dynamics of a species to estimate these reference points. As these models are simplifications of reality they are influenced by structural uncertainties (i.e. the choice of parameters used to describe biological processes, and the methods and assumptions used to combine these parameters together), and parameter uncertainties (the availability, precision and accuracy of information used to estimate each of these parameters). Consequently, understanding the influences of these uncertainties on the outputs of models is an important aspect of considering the actions to implement from a stock assessment.

In this paper we present the results from a sensitivity analysis of the reproductive parameters used in the 2008 bigeye stock assessment. The analysis specifically tests:

(1) The structural assumption that sex ratio is constant for all age classes.

In the standard bigeye assessment, sex ratio is assumed to be constant for all age classes. However, published (Schaefer et al. 2005, Sun et al. 2006) and unpublished observer data support the hypothesis that the proportion of females in the population declines with age and size. This “trend in sex ratio” hypothesis is assumed to be driven by differential natural mortality at age between the sexes, associated with the stress of reproduction. We estimated the level of differential natural mortality that would cause the observed changes in sex ratio, and estimated its effect on the pooled natural mortality at age of both sexes.

(2) The influence of parameter uncertainty for bigeye maturity schedule.

The schedule of bigeye maturity at age depends on the growth curve and data on bigeye maturity at length. Maturity at length may vary spatially, and sampling from a limited area off north Queensland, Australia, suggests a smaller length at 50% maturity in the Western Pacific than in the eastern Pacific (Farley *et al.* 2006, Schaefer *et al.* 2005). This smaller length at maturity is consistent with observations from the north-western WCPO (Sun *et al.* 2006). The values used in the previous WCPO bigeye stock assessment (Hampton et al. 2006) were derived from the eastern Pacific data (John Hampton personal communication). Mean length at age also tends to be lower in the Western Pacific (Aires-da-Silva and Maunder 2008, Hampton *et al.* 2005),.

It is unclear whether maturation of tunas is best regarded as a function of length or age (Schaefer 2001), but in other fish species both can be important (Heino *et al.* 2002). At an individual level, maturation may be influenced by growth history (Morita and Fukuwaka 2006), body condition (Grift *et al.* 2007), population density and environmental conditions (Policansky 1983). In addition, average age and size at maturation may change through time due to selection pressure from fishing.

We examined the effect of alternative assumptions about maturity by recalculating the MFCL maturity at age schedule. First, the schedule was recalculated based on observed maturity at length in the eastern Pacific and length at age from a preliminary version of the 2008 western Pacific stock assessment growth curve. Next, observed maturity at length in the western Pacific was used, and two alternative growth curves: the 2008 curve above, and the growth curve from the 2006 assessment. Finally, we applied the maturity schedule from the eastern Pacific.

(3) The structural assumption that spawning biomass as an indicator of reproductive output.

In the standard bigeye assessment, spawning biomass is used as an indicator of reproductive output. This assumes that the fecundity (combined with spawning fraction) is directly proportional to weight at age. However, reproductive potential should be estimated in terms of egg production, which may increase more rapidly than biomass with length. For example, for WCPO yellowfin tuna the exponent of the length-weight relationship is 2.94, while the exponent of the length-fecundity relationship is 3.27 (Itano 2000), indicating that large fish dedicate considerably more of their biomass to egg production. For bigeye in a relatively small area of the north-western WCPO, the exponent of the length-fecundity relationship has been found to be 4.419 (Sun *et al.* 2006), versus 3.025 for the length-weight relationship.

We investigated the sensitivity of the bigeye stock assessment to plausible levels of increasing fecundity at length by applying the length-fecundity relationship from the north-western Pacific (Sun *et al.* 2006).

In the standard bigeye assessment, spawning fraction is assumed to be uniform for all females. However, this assumption has not been examined for bigeye. The assumption has been examined for yellowfin tuna in the EPO, and the spawning fraction was found to increase with length (Schaefer 1998). We investigated the sensitivity of the bigeye stock assessment to a plausible increase in spawning fraction with length by applying the yellowfin spawning fraction at length relationship to bigeye.

In addition, the eggs of larger, older fish may be more viable than those of younger fish (e.g. Berkeley *et al.* 2004, Buckley *et al.* 1991, Marteinsdottir and Steinarsson 1998). Egg size increases with female size in yellowfin tuna (Margulies *et al.* 2007), but no relationship between tuna egg size and viability has been observed. More diversity of ages in the population may improve recruitment (e.g. Marteinsdottir and Thorarinnsson 1998). We investigated potential effects of increasing egg viability with age on the stock assessment for bigeye tuna.

Methods

The sensitivity analysis occurred in four parts (Table 1). Part 1 examined the inclusion of sex ratio in the calculation of reproductive parameters used in MFCL (model 1), its inclusion in the calculation of natural mortality (model 2), and the combination of both of these (model 3) in comparison to the early June version of the base case of the 2008 stock assessment (model 0). Model 3 became the reference model for part 2 of the sensitivity analysis as we consider that this model structure was a more complete description of the observed biology of bigeye, and because the assumed sex ratio and natural mortality affect the sensitivity of the model to other reproductive parameters.

Part 2 examine the sensitivity of the model to parameter uncertainty in the calculation of the mortality schedule used in MFCL. We tested the influence of applying the Coral Sea (model 4), EPO maturity at age (model 5) and EPO maturity at length (model 6) datasets.

Part 3 examined the structural sensitivity of assuming that spawning biomass was an indicator of reproductive output. Model 4 was used as the reference model for the same reasons as above: because we consider it a more complete description of the observed biology of western Pacific bigeye, and because the assumed maturity schedule affects the sensitivity of the model to other reproductive parameters. Adding fecundity at length (model 7) structure, spawning fraction at length (model 8) structure, and a combination of these (model 9) was tested. Model 9 was then used as the reference for part 4 as we also considered that this model was a more complete description of the reproductive biology of bigeye.

The final part of the analysis examined the inclusion of egg viability into the structure (model 10) and examined the sensitivity of model 9 to an alternative estimation of growth (model 11).

The sensitivity analysis used changes in B_{current} , B_{MSY} , MSY , $F_{\text{multiplier}}$, B/B_{MSY} , $\text{SB}_{\text{current}}/\text{SB}_{\text{MSY}}$, $\text{SB}_{\text{current}}/\text{SB}_0$ as it measures of influence and the fit statistics of the overall MFCL model to the CPUE and length frequency data. All model comparison were repeated for two alternate steepness estimates (0.957, 0.700) of the stock recruitment relationship.

Calculation of input values

1. Sex ratio at length and natural mortality at length

SPC observer data were examined to determine bigeye sex ratio at length in longline catches from bigeye stock assessment regions 3 and 4 of the Pacific. Data were cleaned by restricting the analysis to fish between 100 and 170 cm. A total of 24,222 sexed bigeye were in the dataset.

Differential natural mortality at age between the sexes was modelled by estimating the natural mortality parameters that gave the best fit to the sex ratio data. Following Harley and Maunder (2003), natural mortality M was modelled in three phases: (1) mortality the same for males and females, and declining from M^0 at the initial age (min age) at a rate of δ per time step to some breakpoint; (2) mortality M^1 constant and the same for males and females until females begin to mature; (3) constant mortality for males but higher mortality for mature females M^2 than for immature females. There may be a lag l between maturity and increasing mortality.

Natural mortality for males was:

$$(Eqn 0.1) \quad M_{M,a} = \begin{cases} M^0 & \text{for } a = a_{\min} \\ M_{M,a-1} - \delta & \text{for } a = a_{\min} + 1, \dots, a_{\text{break}} \\ M^1 & \text{for } a_{\text{break}} + 1, \dots, a_{\max} \end{cases}$$

$$\delta = \left(\frac{M^1 - M^0}{a_{\text{break}} - a_{\min}} \right)$$

For females, the full mortality schedule, given proportion mature φ_a , was:

$$(Eqn 0.2) \quad M_{F,a} = \begin{cases} M^0 & \text{for } a = a_{\min} \\ M_{F,a-1} - \delta & \text{for } a = a_{\min}, \dots, a_{\text{break}} \\ M^1(1 - \varphi_{a-l}) + M^2(\varphi_{a-l}) & \text{for } a = a_{\text{break}} + 1, \dots, a_{\max} \end{cases}$$

Length at age was used to convert sex ratio at length into sex ratio at age. The two alternative growth curves used were: the base case of the 2008 stock assessment (Langley et al. in prep), and the final growth curve from the 2006 bigeye stock assessment (Hampton et al. 2006). Length at age is modelled as

$$(Eqn 0.3) \quad L_a = L_1 + (L_A - L_1) \left[\frac{1 - e^{-K(a-1)}}{1 - e^{-K(A-1)}} \right]$$

where L_1 is the mean length at the first age, L_A is the mean length of the oldest age, and K is the von Bertalanffy growth coefficient (Kleiber et al. 2006). The standard deviation of length at age is calculated as

$$(Eqn 0.4) \quad sd.length_a = sda \cdot e^{-sdb \left(1 - 2 \frac{L_a - L_1}{L_{\max} - L_1} \right)}$$

Parameter values are given in Table 2

Given the assumed length at age and standard deviation of length at age, the proportion of fish age a in length class len , $p_{a,len}$, was calculated, using 1 cm length intervals. Expected sex ratios at length by sex were calculated as

$$(Eqn 0.5) \quad N_{sex,a} = N_{sex,a-1} e^{-M_{sex,a-1}}$$

$$(Eqn 0.6) \quad N_{sex,len} = \sum_a N_{sex,a} \cdot p_{a,len}$$

The parameters M^2 and lag l were estimated by optimising the fit of the expected to the observed sex ratio data, using the χ^2 distribution.

Since natural mortality and predicted sex ratio are affected by the maturity schedule and growth rate, natural mortality and sex ratio were re-estimated for each maturity schedule and growth rate examined in the sensitivity analysis.

2. Maturity schedules

The Queensland and eastern Pacific data give maturity at length, but Multifan-CL requires a schedule of maturity at age. Under the assumption that maturity is determined at length, we converted both Queensland and eastern Pacific maturity at length to maturity at age for each of the growth curves used (Table 1). Assuming maturity is a function of length, then for a given age,

$$p(mat) = \sum_{len} p(len) \cdot p(mat | len). \text{ The distribution of length at age is determined by the growth curve}$$

(Eqn 0.3) and standard deviation of length at age (Eqn 0.4). Proportion mature at length was calculated as

$$mat_{len} = \frac{e^{\alpha+\beta \cdot len}}{1+e^{\alpha+\beta \cdot len}}, \text{ where } a = -12.1141 \text{ and } b = 0.1183 \text{ (Farley et al. 2003).}$$

Proportion mature at length for EPO fish was calculated as $mat_{len} = \left(1 - (1 - \psi_l) \cdot e^{-\kappa_l(len-v_l)}\right)^{\frac{1}{1-\psi_l}}$, where $\psi_l = 3.37057$, $\kappa_l = 0.167734$, and $v_l = 138.201$ (Schaefer et al. 2005).

The alternative assumption, that maturity is determined at age, was examined by fitting a maturity-at-age schedule that would give the observed maturity-at-length in the eastern Pacific. This assumes that maturity would occur at the same ages in the Western and Central Pacific. A model of numbers at age was developed based on the IATTC growth curve and total mortality at age (Aires-da-Silva and Maunder 2008). The model allows for the fact that observed numbers at length, and hence maturity at length, is affected by fishing mortality and natural mortality.

Maturity at length was calculated as follows:

$$mat_{len} = \frac{\sum_a (mat_a \cdot N_{a,len})}{\sum_a N_{a,len}}, \text{ where } mat_a = \left(1 - (1 - \psi_a) \cdot e^{-\kappa_a(len-v_a)}\right)^{\frac{1}{1-\psi_a}}.$$

The parameters ψ_a , κ_a , and v_a were estimated by fitting to the EPO proportions mature at length.

3. Fecundity at length

The standard fecundity schedule used the length weight relationship to predict fecundity at age. The alternative schedule applied the bigeye length-fecundity relationship estimated from data collected near the Philippines (Sun et al. 2006), $fecundity = a \cdot length^b$, with $a = 8.815 \times 10^{-4}$ and $b = 4.419$.

4. Spawning fraction

The standard spawning fraction schedule used constant spawning fraction at age. The alternative schedule applied the EPO yellowfin spawning fraction at length relationship (Schaefer 1998),

$$fraction_{length} = y_{\infty} \left(1 - e^{-y_k \cdot (length - y_0)}\right), \text{ with } y_{\infty} = 0.742, y_k = 0.046, \text{ and } y_0 = 54.892.$$

5. Viability at age

The standard spawning fraction schedule used constant egg viability with age. The alternative schedule used a 5% increase per age in quarters.

Results

The consequences of the tested models on relative reproductive output from MFCL are presented in Figure 1. Reproductive output commenced between quarters 5 and 10 and peaked between quarters 15 and 30. All demonstrated senescence in reproductive outputs except for model 0 and model 2.

1. Inclusion of sex ratio in the calculations of reproductive parameters and natural mortality at length

Estimates of natural mortality for each of the alternative growth curves are provided in Figure 2.

Estimates of sex ratio for each of the alternative growth curves are provided in Figure 3.

The inclusion of sex ratio in the calculation of reproductive parameters increased the $SB_{current}/SB_{MSY}$ estimate by 6% and $SB_{current}/SB_0$ by 22% when steepness was 0.957 and had little or no effect on the other reference points (Table 4). Stronger influences were observed when steepness was 0.7, a decrease in B_{MSY} of 5% and increases in $F_{multiplier}$ (7%), B/B_{MSY} (4%), $SB_{current}/SB_{MSY}$ (14%), and $SB_{current}/SB_0$ (23%) were observed (Table 5). The overall fit of the Multifan-CL model was improved when sex ratio data was included (Table 3).

The inclusion of sex ratio in the calculation of reproductive parameters increased the $F_{multiplier}$ (5%), $SB_{current}/SB_{MSY}$ estimate by 5% and $SB_{current}/SB_0$ by 4% when steepness was 0.957 and had little or no effect on the other reference points (Table 4). When steepness was 0.7, influences were $\leq 3\%$ (Table 5).

The combined effect increased the $F_{multiplier}$ by 7%, $SB_{current}/SB_{MSY}$ estimate by 10% and $SB_{current}/SB_0$ by 25% when steepness was 0.957. All other reference points were changed by $\leq 4\%$. When steepness was 0.7, B_{MSY} was decreased by 6%, and increases of $F_{multiplier}$ (10%), B/B_{MSY} (7%), $SB_{current}/SB_{MSY}$ (17%), and $SB_{current}/SB_0$ (26%) were observed (Table 5).

2. Maturity schedules

Estimates of the maturity schedule for each of the alternative growth curves and maturation data's are provided in Figure 4. The use of the WPO (Farley et al. 2006) dataset increased the $SB_{current}/SB_{MSY}$ estimate by 12% and $SB_{current}/SB_0$ by 41% when steepness was 0.957 (Table 4). The EPO maturity at age (Maunder et al. 2007) had no detectable influence. Little or no influence was detected for the EPO maturity at length dataset (Schaefer et al. 2005), except for $SB_{current}/SB_0$ where a 4% decrease was observed.

When steepness was 0.7, a decrease in B_{MSY} of 8% and increases in $F_{multiplier}$ (11%), B/B_{MSY} (8%), $SB_{current}/SB_{MSY}$ (28%), and $SB_{current}/SB_0$ (42%) were observed (Table 5). No influence was detected for the EPO maturity at age dataset (Maunder et al. 2007). Little or no influence was detected for the EPO maturity at length dataset (Schaefer et al. 2005), except for $SB_{current}/SB_0$ where a 5% decrease was observed.

3. Including fecundity and spawning fraction at length structure

The alternative fecundity at length relationships are presented in Figure 5. When steepness was 0.957, both $SB_{\text{current}}/SB_{\text{MSY}}$ (8%), and SB_{current}/SB_0 (22%) were influenced (Table 4). Little or no influence on the other reference points was detected (Table 4). When steepness was 0.7, B_{MSY} decreased by 6% and the $F_{\text{multiplier}}$ (6%), B/B_{MSY} (4%), $SB_{\text{current}}/SB_{\text{MSY}}$ (17%), and SB_{current}/SB_0 (23%) increased (Table 5).

The alternative fecundity at length relationships are presented in Figure 6. When steepness was 0.957, both $SB_{\text{current}}/SB_{\text{MSY}}$ (11%), and SB_{current}/SB_0 (37%) were influenced (Table 4). Little or no influence on the other reference points was detected (Table 4). When steepness was 0.7, B_{MSY} decreased by 7% and the $F_{\text{multiplier}}$ (10%), B/B_{MSY} (7%), $SB_{\text{current}}/SB_{\text{MSY}}$ (26%), and SB_{current}/SB_0 (38%) increased (Table 5).

The combined effect of including structure to both the fecundity and spawning fraction increased both $SB_{\text{current}}/SB_{\text{MSY}}$ (7%), and SB_{current}/SB_0 (19%) when steepness was 0.957 (Table 4). When steepness was 0.7, B_{MSY} decreased by 4% and the $F_{\text{multiplier}}$ (5%), B/B_{MSY} (4%), $SB_{\text{current}}/SB_{\text{MSY}}$ (15%), and SB_{current}/SB_0 (19%) increased (Table 5).

4. Including egg viability structure

When Stock recruitment steepness of 0.957 was examined decreases $SB_{\text{current}}/SB_{\text{MSY}}$ (6%), and SB_{current}/SB_0 (21%) were observed (Table 4). When steepness was 0.7, B_{MSY} increased by 6% and the $F_{\text{multiplier}}$ (8%), B/B_{MSY} (5%), $SB_{\text{current}}/SB_{\text{MSY}}$ (15%), and SB_{current}/SB_0 (22%) decreased (Table 5). Little or no influence on the other reference points was detected (Table 4, Table 5).

5. Sensitivity to alternative growth

No influence on the other reference points was detected when applying the final 2006 stock assessment growth curve (Table 4, Table 5).

Discussion

The current stock assessment indicates that the fishing mortality exceeds F_{MSY} , and that the biomass is approaching MSY (Langley et al. 2008). The stock assessment is more strongly influenced by precision in CPUE and length frequency data than by the reproductive and growth parameters directly. This sensitivity analysis however demonstrates that the model is also sensitive to the structural assumptions associated with estimation of the reproductive and growth parameters. Alternative estimates for all reproductive and growth parameters and natural mortality influenced the spawning biomass reference points ($SB_{\text{current}}/SB_{\text{MSY}}$ and SB_{current}/SB_0) typically by more than 10% and influenced biomass (B/B_{MSY}) and the $F_{\text{multiplier}}$ reference points by between 1 % and 5 %.

All MSY-related reference points are affected by changing the components of spawning biomass (growth, natural mortality, maturity, fecundity, sex ratio, spawning fraction, and egg viability), via the stock recruitment relationship (SRR). At different levels of relative spawning biomass, relative recruitment is assumed to change according to the SRR. Thus, a stronger SRR (0.7) makes the model more sensitive to changes in spawning biomass than a weaker SRR (0.957). The spawning biomass-related reference points experience an additional impact, due to the change in the relative spawning biomass itself.

Our analysis indicates that adding more biological realism to the reproductive parameters is warranted. The inclusion of sex ratio and size structure upon fecundity and spawning fraction was influential on the estimation of the reference points, particularly those associated with overfishing ($SB_{\text{current}}/SB_{\text{MSY}}$ and SB_{current}/SB_0). This result suggests that adding such structure should improve the accuracy and precision of future stock assessments of bigeye. Data availability to parameterise such a structured model however would need to be considered. Our results support the need for further investment in knowledge acquisition to reduce current levels of uncertainty. The parameter uncertainty examined in the spawning

schedule exerted strong influence on the spawning biomass reference point. The data used was from the extremes of longitude and a couple of latitudes and it is likely that similar differences also occur for other attributes such as spawning fraction and fecundity. Furthermore, there is no information available for the central Pacific regions or at higher latitudes. Knowledge acquisition in these regions would provide the opportunity to add this spatial structure to the MFCL model. The biological studies on reproductive parameters in the WCPO have occurred on the western boundary of region 3 and northern boundary of region 5. Since the MFCL base case indicates that a large proportion of the reproduction of bigeye occurs in region 3, applying the WCPO data appears more appropriate than applying EPO derived data.

References

Aires-da-Silva, A. and Maunder, M. N. (2008). Status of bigeye tuna in the Eastern Pacific Ocean.)

Berkeley, S. A., Chapman, C., and Sogard, S. M. (2004). Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**, 1258-1264.

Buckley, L. J., Smigielski, A. S., Halavik, T. A., Caldarone, E. M., and Burns, B. R. (1991). Winter flounder *Pseudopleuronectes americanus* reproductive success. 11. Effects of spawning time and female size on size, composition and viability of eggs and larvae. *Marine Ecology Progress Series* **74**, 125-135.

Farley, J. H., Clear, N. P., Leroy, B., Davis, T. L. O., and McPherson, G. (2006). Age, growth and preliminary estimates of maturity of bigeye tuna, *Thunnus obesus*, in the Australian region. *Marine & Freshwater Research* **57**, 713-724.

Farley, J., Clear, N., Leroy, B., Davis, T., and McPherson, G. (2003). Age and growth of bigeye tuna (*Thunnus obesus*) from the eastern and western AFZ. No. Report No. 2000/100 (CSIRO Marine Research, Fisheries Research and Development Corporation, and Queensland Government, Department of Primary Industries.)

Grift, R. E., Heino, M., Rijnsdorp, A. D., Kraak, S. B. M., and Dieckmann, U. (2007). Three-dimensional maturation reaction norms for North Sea plaice. *Marine Ecology Progress Series* **334**, 213-224.

Hampton, J., Kleiber, P., Langley, A., Takeuchi, Y., Ichinokawa, M., and Maunder, M. (2005). Stock assessment of bigeye tuna in the western and central Pacific Ocean, with comparisons to a Pacific wide assessment. *WCPFC SCI SA WP-2*.

Hampton, J., Langley, A., and Kleiber, P. (2006). Stock assessment of bigeye tuna in the western and central Pacific Ocean, including an analysis of management options. *WCPFC SC2 SA WP-2*, Manila.

Harley, Shelton and Maunder, Mark N. (2003). A simple model for age-structured natural mortality based on changes in sex ratios. IATTC, 4th Meeting of the Scientific Working Group, La Jolla, USA, May 19-21 2003.

Heino, M., Dieckmann, U., and God, O. R. (2002). Measuring probabilistic reaction norms for age and size at maturity. *Evolution* **56**, 669-678.

Itano, D. G. (2000). 'The Reproductive Biology of Yellowfin Tuna (*Thunnus Albacares*) in Hawaiian Waters and the Western Tropical Pacific Ocean: Project Summary.' (University of Hawaii, Joint Institute for Marine and Atmospheric Research.)

Kleiber, P., Hampton, J., and Fournier, D. A. (2006). MULTIFAN-CL User's Guide.

Margulies, D., Suter, J. M., Hunt, R., Olson, R. J., Scholey, V. P., Wexler, J. B., and Nakazawa, A. (2007). Spawning and early development of captive yellowfin tuna (*Thunnus albacares*). *Fishery Bulletin - National Oceanic and Atmospheric Administration* **105**, 249.

Marteinsdottir, G. and Steinarsson, A. (1998). Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology* **52**, 1241-1258.

Marteinsdottir, G. and Thorarinsson, K. (1998). Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1372-1377.

Morita, K. and Fukuwaka, M. (2006). Does size matter? The effect of growth history on probabilistic reaction norm for salmon maturation. *Evolution* **60**, 1516-1521.

Policansky, D. (1983). Size, Age and Demography of Metamorphosis and Sexual Maturation in Fishes 1. *Integrative and Comparative Biology* **23**, 57-63.

Schaefer, K. M. (1998). Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Bulletin. Inter-American Tropical Tuna Commission*. **Vol. 21**. 205-272.

Schaefer, K. M. (2001). Reproductive biology of tunas. In *Tuna physiology, ecology, and evolution*. Vol. 19. *Fish Physiology*. (Eds BA Block and ED Stevens.) pp, 225-270.

Schaefer, K. M., Fuller, D. W., and Miyabe, N. (2005). Reproductive biology of bigeye tuna (*Thunnus obesus*) in the eastern and Central Pacific Ocean. *Inter-American Tropical Tuna Commission Bulletin* **23**, 1-31.

Sun, Chi-Lu, Chu, Su-Ling, and Yeh, Su-zan. (2006). Reproductive biology of bigeye tuna in the Western and Central Pacific Ocean. Western and Central Pacific Fisheries Commission, Scientific Committee, Second Regular Session. -22. Manila, Philippines. **WCPFC-SC2-2006/BI WP-1**.

Table 1: Scenarios run for biological sensitivity analysis

Scenario	rep sex ratio	M at age series	Maturity series	Fecundity at length	Spawning fraction at length	Egg viability	Growth
Base	No	EPO (Hampton et al. 2006)	EPO (Hampton et al. 2006)	Proportional to weight	constant	constant	June 2008 base case
PART 1							
i. Reproduction sex ratio	Yes	As above	As above	As above	As above	As above	As above
ii. M sex ratio	No	sex ratio @ length	As above	As above	As above	As above	As above
Combination of i, ii	Yes	As above	As above	As above	As above	As above	As above
PART 2							
iii. Maturity growth	Yes	As above	WPO (Farley et al. 2006)	As above	As above	As above	As above
vii (b). EPO mat@A	Yes	As above	EPO (Maunder et al. 2007)	As above	As above	As above	As above
vii (c). EPO mat@L	Yes	As above	EPO (Schaefer et al. 2005)	As above	As above	As above	As above
PART 3							
iv. Fecundity@L	Yes	As above	As above	WPO (Sun et al. 2006)	As above	As above	As above
v. Sp.frac@L	Yes	As above	As above	Proportional to weight	Yellowfin (Itano 2000)	As above	As above
Combination of iii, iv, v	Yes	As above	As above	WPO (Sun et al. 2006)	As above	As above	As above
PART 4							
vi. Viab@A	Yes	As above	As above	As above	As above	5% increase per age quarter	As above
vii (a). Alt growth	Yes	As above	WPO (Farley et al. 2006)	As above	As above	constant	Final growth from 2006 stock assessment

Table 2: Parameters of the two growth curves

	base case 2008	final 2006
L_A	173.257	186.678
K	0.07677	0.06327
L_I	20	19.928
sda	6.719	5.444
sdb	0.7315	0.5479

Table 3: Comparison of model fit under different scenarios

SR steepness	Model	gradient	npars	obj fnt	Objective offset
0.957	Base	0.00095	5642	1246175.5	0
0.957	Model 1	0.00096	5642	1246175.7	0.2
0.957	Model 2	0.00059	5642	1246162.7	-12.8
0.957	Model 3	0.00066	5642	1246162.8	-12.6
0.957	Model 4	0.00096	5642	1246163.0	-12.4
0.957	Model 5	0.00052	5642	1246163.0	-12.5
0.957	Model 6	0.00086	5642	1246163.0	-12.5
0.957	Model 7	0.00090	5642	1246162.9	-12.5
0.957	Model 8	0.00052	5642	1246162.8	-12.7
0.957	Model 9	0.00069	5642	1246162.3	-13.1
0.957	Model 10	0.00077	5642	1246162.3	-13.2
0.957	Model 11	0.00050	5642	1246161.3	-14.2
0.7	Steepness	0.00074	5642	1246168.9	0.0
0.7	Model 1	0.00098	5642	1246170.9	2.0
0.7	Model 2	0.00043	5642	1246157.1	-11.8
0.7	Model 3	0.00059	5642	1246158.9	-10.0
0.7	Model 4	0.00075	5642	1246161.2	-7.7
0.7	Model 5	0.00073	5642	1246160.3	-8.6
0.7	Model 6	0.00065	5642	1246160.9	-7.9
0.7	Model 7	0.00060	5642	1246160.1	-8.8
0.7	Model 8	0.00061	5642	1246158.2	-10.7
0.7	Model 9	0.00054	5642	1246159.5	-9.4
0.7	Model 10	0.00092	5642	1246158.4	-10.5
0.7	Model 11	0.00091	5642	1246157.1	-11.8

Table 4: Comparison of reference points for runs with base case steepness of 0.957.

	Base	Rep sex ratio	M sex ratio	Comb. 1	Mat growth	EPO mat@A	EPO mat@L	Fec@L	Sp.frac@L	Comb. 2	Viab@A	Alt growth
	Model 0	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11
Bcurrent	339348	339057	345610	345309	344838	345530	345966	345003	344877	345039	345367	345286
Bmsy	253300	249800	251400	248000	242400	247700	248400	244400	242900	244800	248700	244800
MSY	16040	16130	16290	16380	16490	16390	16380	16440	16480	16430	16340	16440
Fmult	0.6772	0.6907	0.7079	0.7218	0.7438	0.7237	0.7222	0.7354	0.7419	0.7337	0.7177	0.7349
b/bmsy	1.3397	1.3573	1.3747	1.3924	1.4226	1.3950	1.3928	1.4116	1.4198	1.4095	1.3887	1.4105
SBcurr/SBmsy	1.1364	1.2016	1.1926	1.2541	1.4004	1.2570	1.2422	1.3497	1.3906	1.3403	1.2553	1.3425
SBcurr/SB0	0.2440	0.2982	0.2527	0.3060	0.4314	0.3074	0.2923	0.3735	0.4182	0.3638	0.2863	0.3634

		Relative to base case			Relative to Combination 1						Relative to Combination 2	
Bcurrent	339348	1.00	1.02	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Bmsy	253300	0.99	0.99	0.98	0.98	1.00	1.00	0.99	0.98	0.99	1.02	1.00
MSY	16040	1.01	1.02	1.02	1.01	1.00	1.00	1.00	1.01	1.00	0.99	1.00
Fmult	0.6772	1.02	1.05	1.07	1.03	1.00	1.00	1.02	1.03	1.02	0.98	1.00
b/bmsy	1.3397	1.01	1.03	1.04	1.02	1.00	1.00	1.01	1.02	1.01	0.99	1.00
SBcurr/SBmsy	1.1364	1.06	1.05	1.10	1.12	1.00	0.99	1.08	1.11	1.07	0.94	1.00
SBcurr/SB0	0.2440	1.22	1.04	1.25	1.41	1.00	0.96	1.22	1.37	1.19	0.79	1.00

Table 5: Comparison of reference points for runs with steepness of 0.7.

	Base Model 0	Rep sex ratio Model 1	M sex ratio Model 2	Comb. 1 Model 3	Mat growth Model 4	EPO mat@A Model 5	EPO mat@L Model 6	Fec@L Model 7	Sp.frac@L Model 8	Comb. 2 Model 9	Viab@A Model 10	Alt growth Model 11
Bcurrent	350762	348717	355013	352921	349308	353065	353976	350599	349607	350883	353293	351183
Bmsy	340200	324400	335700	320700	295100	320100	323700	305600	297500	307600	326000	307700
MSY	13790	14110	13870	14190	14540	14190	14110	14350	14500	14310	13960	14310
Fmult	0.4375	0.4679	0.4509	0.4813	0.534	0.4826	0.4755	0.5091	0.5284	0.5048	0.466	0.5051
b/bmsy	1.0310	1.0750	1.0575	1.1005	1.1837	1.1030	1.0935	1.1472	1.1752	1.1407	1.0837	1.1413
SBcurr/SBmsy	0.7513	0.8582	0.7767	0.8812	1.1284	0.8852	0.8574	1.0281	1.1063	1.0091	0.8589	1.0105
SBcurr/SB0	0.2293	0.2821	0.2363	0.2881	0.4103	0.2895	0.2747	0.3531	0.3973	0.3436	0.2678	0.3433
	Relative to base case				Relative to Combination 1						Relative to Combination 2	
Bcurrent	350762	0.99	1.01	1.01	0.99	1.00	1.00	0.99	0.99	0.99	1.01	1.00
Bmsy	340200	0.95	0.99	0.94	0.92	1.00	1.01	0.95	0.93	0.96	1.06	1.00
MSY	13790	1.02	1.01	1.03	1.02	1.00	0.99	1.01	1.02	1.01	0.98	1.00
Fmult	0.44	1.07	1.03	1.10	1.11	1.00	0.99	1.06	1.10	1.05	0.92	1.00
b/bmsy	1.03105	1.04	1.03	1.07	1.08	1.00	0.99	1.04	1.07	1.04	0.95	1.00
SBcurr/SBmsy	0.75127	1.14	1.03	1.17	1.28	1.00	0.97	1.17	1.26	1.15	0.85	1.00
SBcurr/SB0	0.23	1.23	1.03	1.26	1.42	1.00	0.95	1.23	1.38	1.19	0.78	1.00

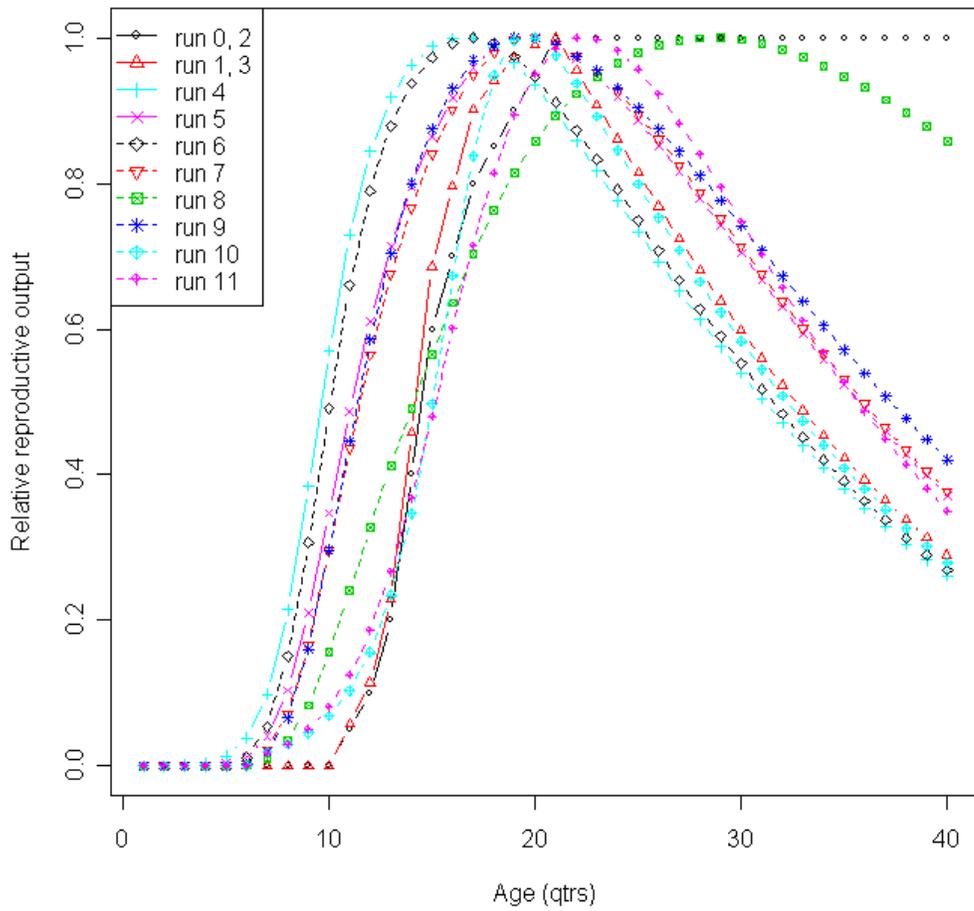


Figure 1: Relative combined reproductive output

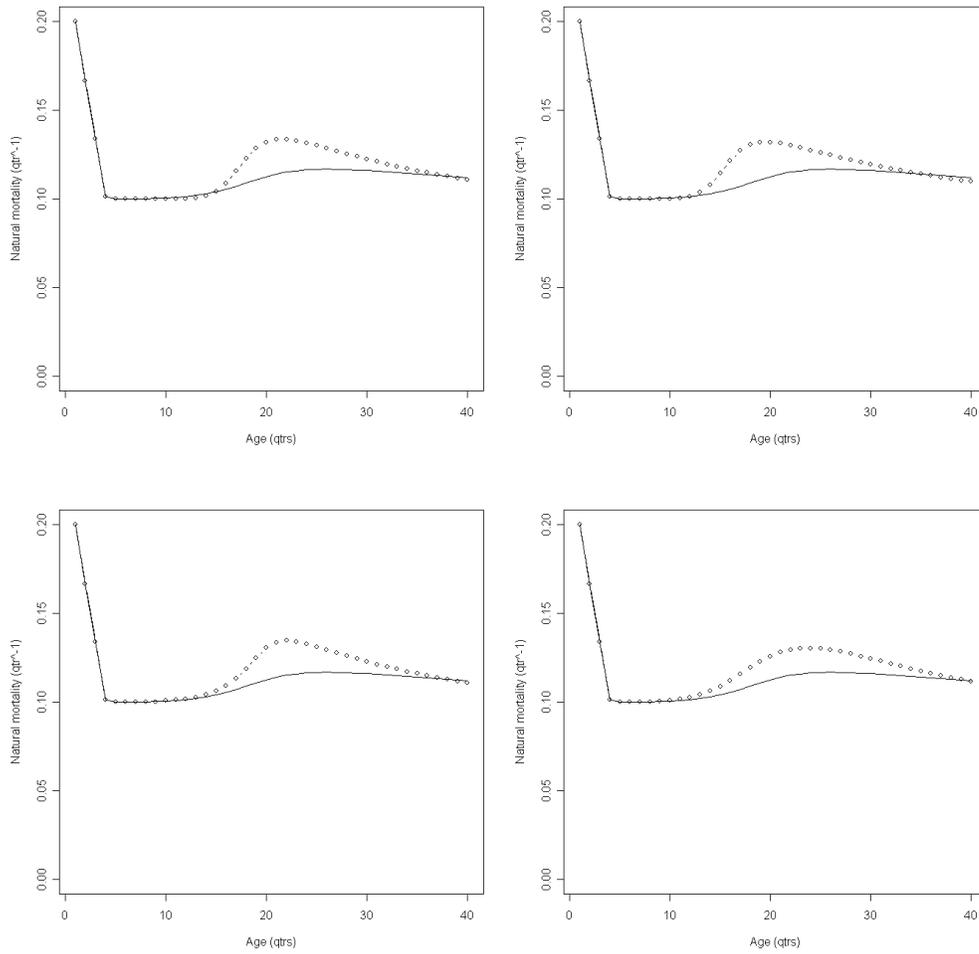


Figure 2: Natural mortality at age for a) North Queensland data with 2008 growth curve b) North Queensland data with 2006 growth curve c) EPO maturity at age assumption with 2008 growth curve d) EPO maturity at length assumption with 2008 growth curve.

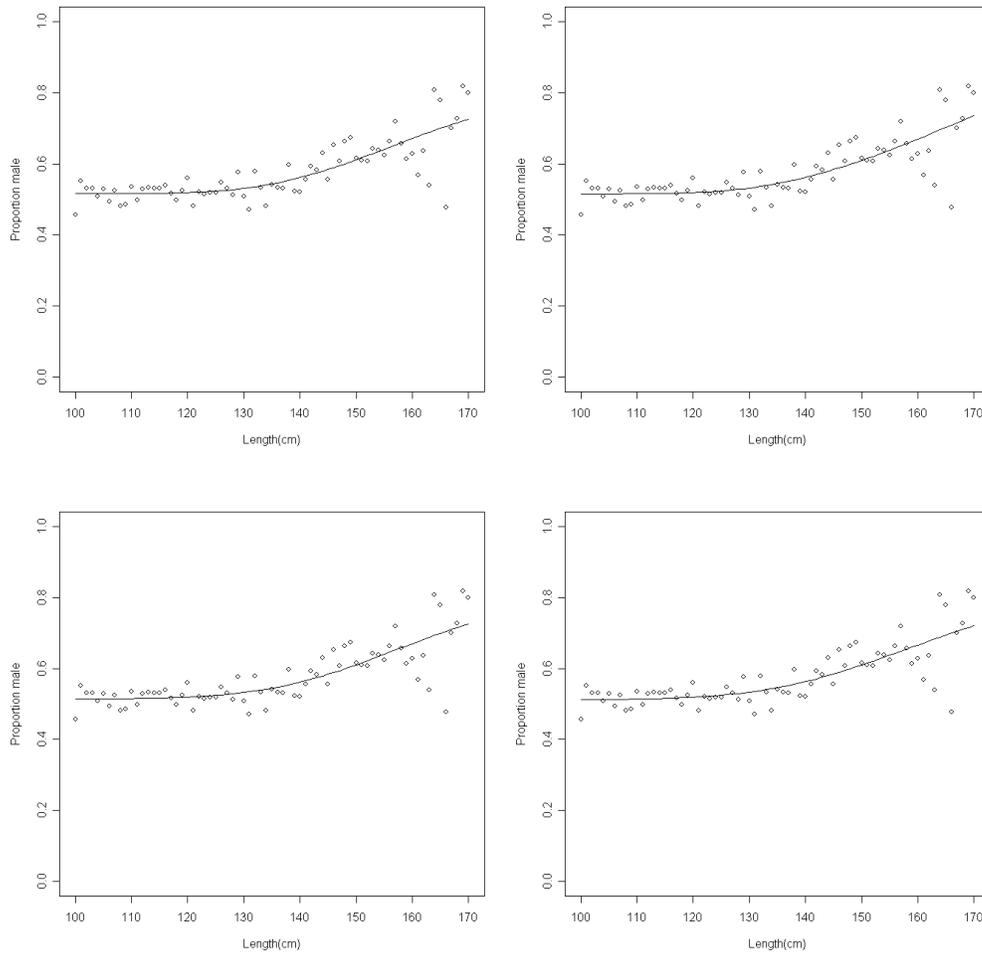


Figure 3: Fit to sex ratio at age data for a) North Queensland data with 2008 growth curve b) North Queensland data with 2006 growth curve c) EPO maturity at age assumption with 2008 growth curve d) EPO maturity at length assumption with 2008 growth curve.

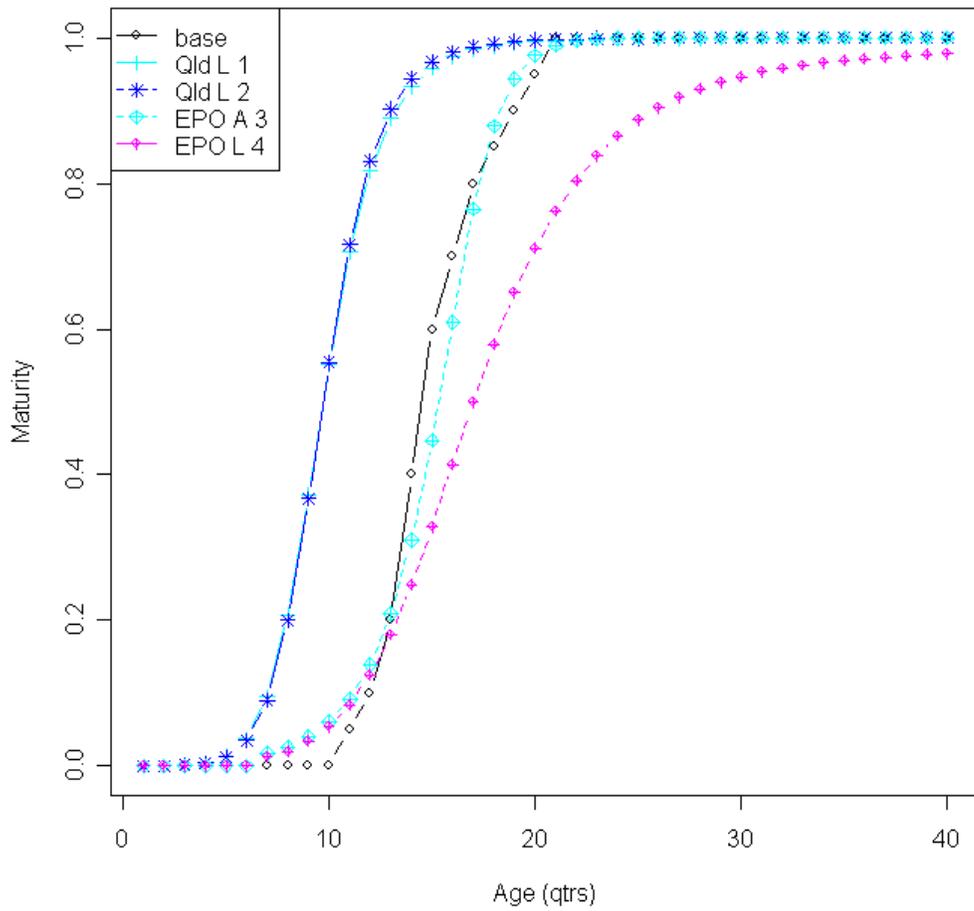


Figure 4: Relative maturity

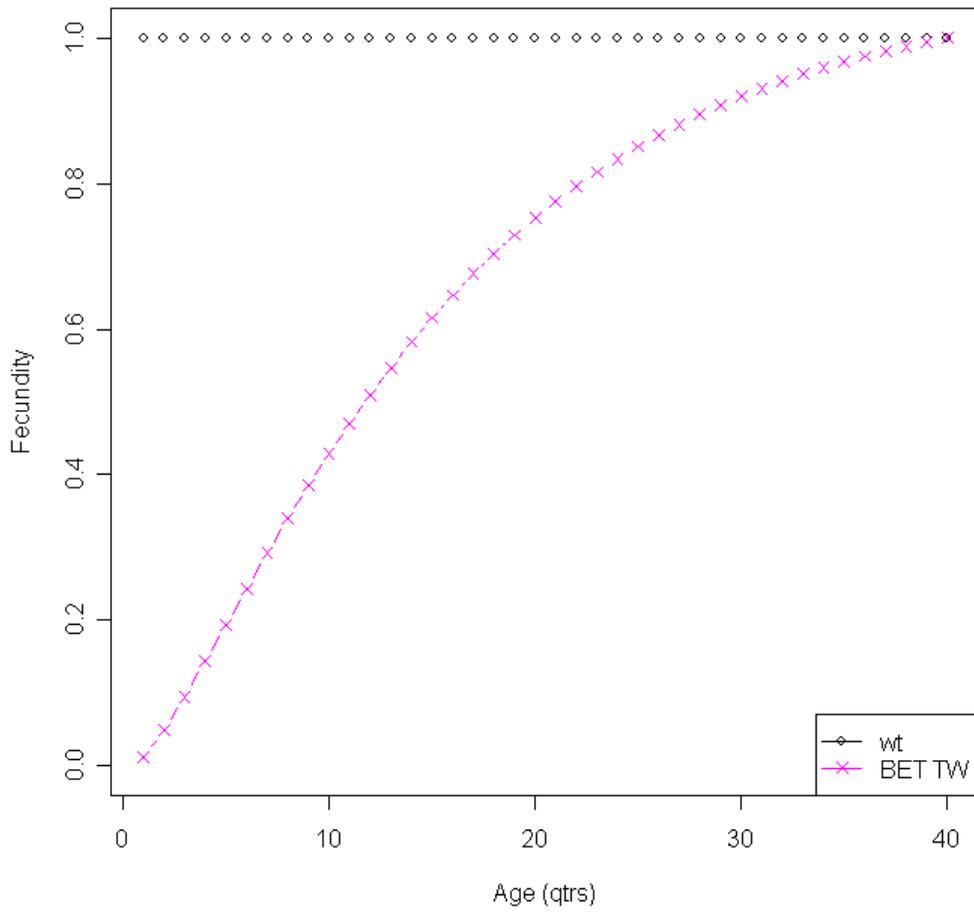


Figure 5: Relative fecundity

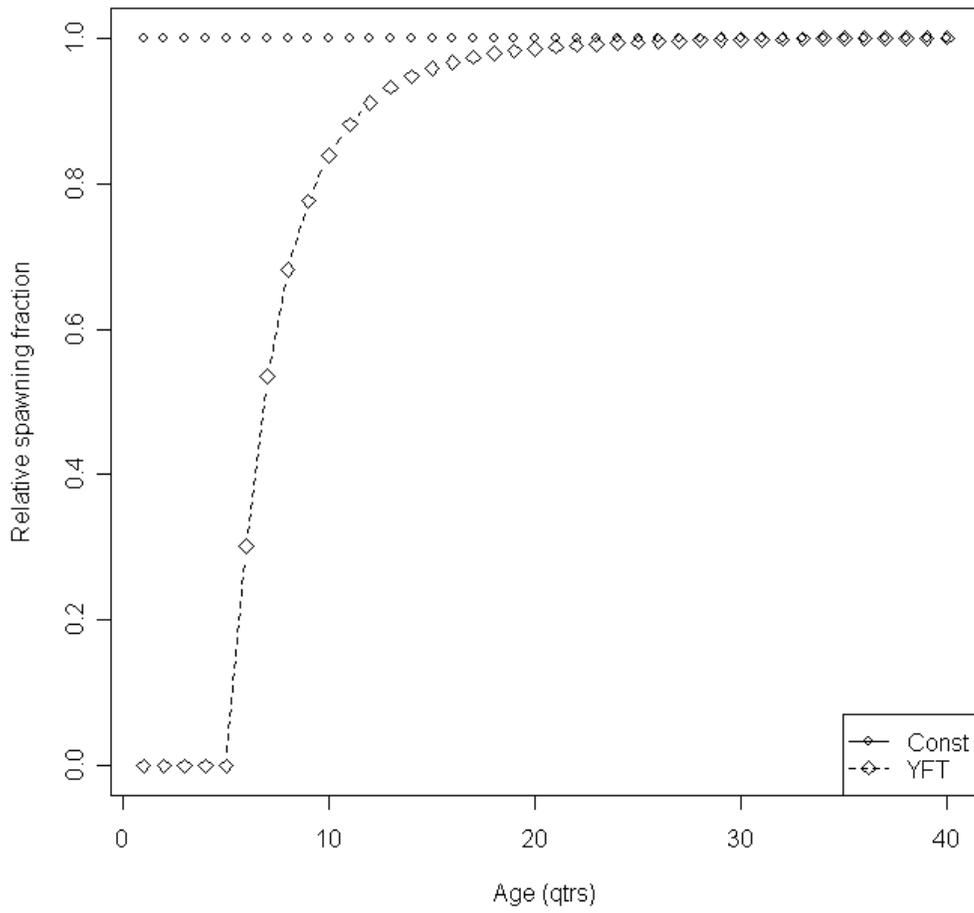


Figure 6: Relative spawning fraction