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ADJUSTED BIOLOGICAL PARAMETERS AND SPAWNING BIOMASS CALCULATIONS FOR ALBACORE TUNA IN THE SOUTH PACIFIC, AND THEIR IMPLICATIONS FOR STOCK ASSESSMENTS

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Simon D. Hoyle¹

¹ Oceanic Fisheries Programme, Secretariat of the Pacific Community, BP D5, 98848 Noumea CEDEX, New Caledonia

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Introduction

Stock assessments for south Pacific albacore require estimates of a number of biological parameters that describe population dynamics, to use either as fixed values, initial (starting) values, or prior distributions. However, some of the estimates currently used are quite uncertain, either because the biological data are sparse or unavailable, or because analyses to estimate the parameters from data have not yet been carried out. Where no data are available, assumptions must be made, usually based on inferences from other stocks of the same or similar species. In this paper I re-estimate some biological parameters based on recent data, and examine the potential effects of improved data (sex ratio at age, maturity at age; natural mortality at age); and reconsider the base-case assumptions for unknown parameters (Langley and Hampton 2005) based on information from other tuna species (fecundity, spawning fraction, and egg viability at length).

The sex ratio observed in the catch changes with length for sexually mature fish in many tuna species, with the proportion of males generally increasing with size (e.g. yellowfin tuna in the Pacific (Cole 1980), bigeye tuna in the Pacific (Calkins 1980), Pacific bluefin tuna, Atlantic bluefin tuna, and southern bluefin tuna (Farley *et al.* 2007)). Albacore tuna are no exception, with males tending to predominate in catches of mature fish in the Pacific (Foreman 1980) and Atlantic oceans (Bard 1981) in (Alonso *et al.* 2005)). The increasing proportion of males with size may be due to higher natural mortality of sexually mature females than for males of the same age or size (Harley and Maunder 2003). The stress of reproduction may be higher for females than for males. Differential growth rate (e.g. Farley *et al.* 2007) or vulnerability provide complementary or alternative explanations.

Maturation is an interaction between the age and size of an individual. Some faster growing individuals can commence reproduction younger than slower growing individuals. To calculate the distribution of ages at maturity it is ideal to have information on length, age and fecundity for all individuals in a study. Typically, however, we have either length-at-age information or fecundity-at-length information, and we need to relate these two sources of data. In previous assessments (Fournier et al. 1998, Hampton and Fournier 2000, Hampton 2002, Labelle and Hampton 2003, Langley and Hampton 2005, Langley and Hampton 2006, Hoyle and Langley 2007), it has been assumed that some albacore reach maturity at five years of age and all by age six years (Ueyanagi 1957). This is the schedule of maturity at age used for Atlantic albacore (ICCAT 2007), based on observations at length, and may be consistent with Atlantic growth rates. However, the growth rate for south Pacific albacore, albeit uncertain, appears to differ from the Atlantic albacore stock. Age at maturity needs to be calculated in relation to region-specific maturity at length, and the best current estimate of the region-specific growth rate. In the South Pacific, female albacore mature at about 85 cm fork length (Murray 1994), as in the North

Pacific (Bartoo and Foreman 1994). In this paper, maturity is recalculated to take the most recent estimate of growth rate (Langley and Hampton 2006) into account.

Stock assessments for the WCPO and elsewhere (Langley and Hampton 2005, Hampton *et al.* 2005, Langley *et al.* 2007, ICCAT 2007) often report relative spawning potential in terms of spawning biomass ratio, defined as the product of numbers at age, weight at age, and maturity at age. However, if the goal of reporting spawning biomass is to address maintenance of reproductive potential, then it would be more accurate to report relative egg production. Egg production may be calculated as the product of numbers at age, maturity at age, proportion female at age, fecundity at age, and spawning fraction at age. Reporting egg production may have implications for stock status, since egg production may increase more rapidly with increasing length, than might biomass to egg production, since fecundity per gram increases rapidly with increasing length (Schaefer 1998, Itano 2000). The spawning fraction of yellowfin tuna also increases with length (Schaefer 1998).

In addition, although somewhat speculative in the case of tunas, the eggs of larger, older fish may be more viable than those of younger fish. Such maternal effects have been observed for a number of fish species (Buckley *et al.* 1991, Marteinsdottir and Steinarsson 1998, Berkeley *et al.* 2004, Francis *et al.* 2007). If this is the case for albacore tuna, spawning potential would more accurately approximated by the product of total egg production at age (as calculated above) and total egg viability at age. Egg size increases with female size in yellowfin tuna (Margulies *et al.* 2007), and larger eggs are more viable in some species (e.g. Buckley *et al.* 1991, Trippel 1998). However, there do not appear to have been any investigations into the relationship between egg size and viability for tuna species. In addition, greater diversity of ages in the population may improve recruitment (e.g. Marteinsdottir and Thorarinsson 1998).

Throughout this paper, the use of the term 'spawning biomass' refers to the adult biomass that is traditionally used in stock assessments. 'Spawning potential' refers to potential egg production (i.e. the number of eggs per produced per female for each age/size class) and 'reproductive potential' refers to the product of egg production and egg viability.

The objectives of this paper are to re-estimate biological parameters based on recent data, examine how improved data might affect the stock assessment, and reconsider the base-case assumptions for unknown parameters based on information from other tuna species.

Methods

SPC observer data were examined to determine South Pacific albacore sex ratio at length in longline catches from the south Pacific. These data were only collected if individual albacore could be sexed through macroscopic inspection of the gonads by observers, which depended on the fishery and its on-board processing facilities/capability.

Data were cleaned by removing fish less than 80cm as female albacore have not been reported to mature at sizes less than 80 cm FL. Fish larger than the maximum length reported for albacore (i.e. 130 cm FL) were also omitted; fish above this size are

likely to be mislabelled yellowfin and bigeye. Before 1997 few albacore were sexed by observers, and temporally and spatially consistent sex data are only available after 2002. Most sex data for albacore were collected from the area bounded by 5°S and 25°S, and 145°E to 135°W (Table 1), the area where most of the albacore longline fishery operates. A total of 23,711 sexed albacore were in the dataset.

	Long E						Long W									
Lat	145	150	155	160	165	170	175	180	175	170	165	160	155	150	145	220
5 S	125	64	21	12	2	0	1	1	0	0	1	0	1	76	701	9
10S	85	175	25	13	1	283	412	0	351	1036	2113	0	1594	2930	3200	600
15S	241	316	25	274	374	33	31	445	768	0	0	26	1063	1068	148	499
20S	0	4	524	1320	409	9	8	234	244	0	0	32	265	733	695	91

Table 1: Number of sexed fish included in the analysis by latitude and longitude

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^l 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:

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

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

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

Length at age was used to convert sex ratio at length into sex ratio at age. The growth curve from the base case of the 2006 stock assessment (Langley and Hampton 2006) was used, with length at age 20 $L_{max} = 104.48$ FL, Brody growth coefficient k = 0.2144. year⁻¹, and length at age 1 of $L_1 = 44.056$ FL, and no deviations from the growth curve for the younger age classes (Kleiber *et al.* 2006). The standard deviation of length at age $sd.length_a = sda \cdot e^{-sdb \left(1-2\frac{L_a-L_1}{L_{max}-L_1}\right)}$, where sda = 3.55 and sdb = 0.22.

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. Expected sex ratios at length by sex were calculated as

(0.3)
$$N_{sex,a} = N_{sex,a-1} e^{-M_{sex,a-1}}$$

(0.4)
$$N_{sex,len} = \sum_{a} N_{sex,a} \cdot p_{a,len}$$

The parameters M^2 and lag *l* were estimated by optimising the fit to the sex ratio data.

Relative egg production at age was estimated as the product of sex ratio, maturity, batch fecundity, and spawning fraction. These values are all generally estimated from observations at length, and must be translated into age based on a growth curve. Reliable data on fecundity at length and spawning fraction at length for albacore were unavailable so, for the purposes of examining the potential impact of biological information for albacore, the values for yellowfin tuna were used (Schaefer 1998, Itano 2000).

Given the basis of the data collection, alternative growth curves required changes to schedules for maturity and natural mortality at age.

The updated maturity schedule was re-parameterised in seven stages to examine potential contributions of different assumptions about reproduction. First, the sensitivity of the model to information on sex ratio was examined in two stages: a) spawning potential at age was adjusted to account for sex ratio, and b) natural mortality was adjusted as described above. Second, the sensitivity of the model to better information on maturity at age was examined by adjusting the maturity schedule to match the growth rate. Third, sensitivity to information on fecundity at length, which may increase faster than weight at length, was examined by adjusting the base case maturity schedule to reflect the rate at which WCPO yellowfin fecundity increases with size. Fourth, sensitivity to information on spawning fraction at length was examined by adjusting the maturity schedule to reflect the relationship seen for EPO yellowfin. Fifth, sensitivity to egg viability increasing with age was examined by increasing relative reproductive potential with fish age by an arbitrary value of 20% per year.

Scenario	rep sex ratio	M at age	Maturity at age	Fec at age	Sp. frac. at length	Viability at age
Base	Ν	const	Mat series 1	wt	const	const
1a. rep sex r	Y	const	Mat series 1	wt	const	const
1b. M sex r	Ν	series 1	Mat series 1	wt	const	const
1c. combined sr	Y	series 1	Mat series 1	wt	const	const
2. mat growth	Y	series 1	Mat series 2	wt	const	const
3. fecundity@L	Y	series 1	Mat series 2	yft	const	const
4. sp.frac@L	Y	series 1	Mat series 2	wt	yft	const
5. viability@A	Y	series 1	Mat series 2	wt	const	+20%/yr
6. comb 2	Y	series 1	Mat series 2	yft	yft	const
7. comb 3	Y	series 1	Mat series 2	yft	yft	+20%/yr

 Table 2: Scenarios run to examine the sensitivity of model outcomes to alternative biological parameters.

The base case used the standard approach, with maturity 0 for ages 1 to 4 years, 0.5 for age 5 years, and 1.0 for all older ages (Langley and Hampton 2005). The adjusted maturity schedule used maturity 0 for ages 1 to 4 years, 0.2, 0.5, 0.8, for ages 5, 6, and 7, and 1.0 for ages 8+.

Fecundity at length was modelled as $fec_{age} = \alpha . age^{\beta}$, where $\alpha = 2.934 \text{ x}10\text{-}4$ and $\beta = 3.2673$.

Spawning fraction at length was modelled as $fraction_{age} = y_{\infty} \left(1 - e^{-y_k \cdot (age - y_0)} \right)$, where $y_{\infty} = 0.742$, $y_k = 0.046$, and $y_0 = 54.892$.

Results

The sex ratio data from the northern area of the longline fishery targeting south Pacific albacore were pooled (Table 1). The proportion of males in the catch increased with length (Figure 1).



Figure 1: Numbers by sex at length for aggregated observer data

Mid	F	М	total	Proportion
Length				male
82	38	35	73	0.479
86	387	218	605	0.360
90	1461	1353	2814	0.481
94	2170	3220	5390	0.597
98	2036	4653	6689	0.696
102	1015	4083	5098	0.801
106	236	1862	2098	0.888
110	87	603	690	0.874
114	25	127	152	0.836
118	16	42	58	0.724
122	б	29	35	0.829
126	2	б	8	0.750
	Mid Length 82 86 90 94 98 102 106 110 114 118 122 126	MidF823886387901461942170982036102101510623611087114251181612261262	MidFMLength383582382189014611353942170322098203646531021015408310623618621108760311425127118164212262912626	MidFMtotalLength5383573823835738638721860590146113532814942170322053909820364653668910210154083509810623618622098110876036901142512715211816425812262935126268

Table 3: Albacore sex	x ratio by	length from	longline	observer	data
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Given the growth curve and distribution of length at age (Langley and Hampton 2006), the modified maturity curve, an assumed initial sex ratio of 0.5, and M¹ of 0.4516.yr⁻¹, the model was fitted to the sex ratio at length data (Figure 2). Lags of l = 0 to 5 years were trialled, with l = 3 giving the best χ^2 value (Figure 3). M² was estimated to be 0.727.yr⁻¹ per year (Figure 4, Table 4). The model showed good fit to the ascending arm of the distribution where sample sizes were high. There appeared to



be some positive bias for fish less than about 90 cm FL, suggesting the possibility that sex ratio is less than 50% male in this size range. Some bias was also evident among fish over 112 cm FL.

Figure 2: Sex ratio (proportion male) predicted with natural mortality model.



Figure 3: χ^2 values for lags of 0 to 5 years between maturity and increased female natural mortality.



Figure 4: Male, female, and joint schedules for natural mortality (M) at age.

Age	M male	M female	M joint	
(years)				
0	0.4516	0.4516	0.4516	
1	0.4516	0.4516	0.4516	
2	0.4516	0.4516	0.4516	
3	0.4516	0.4516	0.4516	
4	0.4516	0.4516	0.4516	
5	0.4516	0.4516	0.4516	
б	0.4516	0.4516	0.4516	
7	0.4516	0.4516	0.4516	
8	0.4516	0.5067	0.4791	
9	0.4516	0.5894	0.5186	
10	0.4516	0.6721	0.5512	
11	0.4516	0.7272	0.5613	
12	0.4516	0.7272	0.5437	
13	0.4516	0.7272	0.5276	
14	0.4516	0.7272	0.5134	
15	0.4516	0.7272	0.5012	
16	0.4516	0.7272	0.4910	
17	0.4516	0.7272	0.4825	
18	0.4516	0.7272	0.4757	
19	0.4516	0.7272	0.4703	

Table 4: Male, female, and joint schedules for natural mortality (M) at age.



Figure 5: Schedules of relative reproductive output at age used in stock assessment model sensitivity analyses. Combination 2 included both fecundity at age and spawning frequency at age. Combination 3 included combination 2 and egg viability at age. See Table 2 for details of scenarios.

Schedules of relative reproductive output for each scenario were calculated based on sex ratio, fecundity, spawning frequency, and egg viability at age (Figure 5).

Results from the scenarios run in the MFCL stock assessment are reported in Table 5 with reference point results for the base case given in absolute terms, and those for the first three scenarios as offsets from the base case. The 'sex ratio + female M' scenario is used as the reference case (i.e. the reported proportional offsets are from this scenario) for the four scenarios that involve higher reproductive output by older fish, and for the two scenarios that combine those effects. Finally, the two combination scenarios are also reported as offsets from the base case. The term 'latest' refers to the final year's estimate. The term 'curr' or 'current' refers to an average over the 4 years 'latest-4' to 'latest-1'. Recruitment estimates differed very little among the scenarios (Figure 6).

Substituting in the natural mortality curve derived from the sex ratio data increased the MSY-related parameters MSY, Bzero, Bmsy, Fmsy, and SBmsy by between 3% and 17%, and raised the F multiplier by 5%. Higher natural mortality implies greater productivity (refs). Changing the sex ratio at age [describe nature of the change] reduced estimates of spawning biomass, but increased the F multiplier by 7%. Changing the sex ratio [describe nature of the change] reduced the spawning biomass estimate more heavily where fishing pressure was lower and there were more old fish in the population, so that SBzero was reduced most (12%) followed by SBlatest (8%) and SBmsy (5%).

The four scenarios involving higher reproductive output by older fish (updated maturity schedule, yellowfin tuna fecundity at length relationship, yellowfin tuna spawning fraction at length relationship, and egg viability at age relationship) all resulted in lower estimates of the F multiplier (i.e. a multiplier indicating the level of increase or decrease in fishing mortality required to achieve maximum sustainable yield (MSY)) than for their reference scenario (with higher female M and observed sex ratio) by 16%, 24%, 19%, and 37% respectively. Combining the first three relationships reduced the F multiplier by 28% below the reference scenario. Adding the egg viability effect reduced the F multiplier 43% below the reference scenario. In comparison with the base case, the combined effects reduced the F multiplier by 20% without egg viability and 37% with the egg viability effect.

The four scenarios involving higher reproductive output by older fish all tended to lower, in comparison with the reference case, the estimate of recent spawning biomass compared to its level in the absence of fishing. This is because they imply a greater proportion of spawning biomass supplied by old fish, which are proportionally more affected by targeted longline fishing pressure than younger fish. For the same reason, these scenarios also gave lower estimates of spawning biomass at MSY / virgin spawning biomass.



Figure 6: Recruitment estimates for all scenarios plotted over one another, showing minimal effect from alternative scenarios for reproductive potential.

Table 5: Reference point based results of scenarios. The base case is reported in absolute terms. The first three and the final two scenarios are reported as proportional offsets from the base case. The other six scenarios are reported as proportional offsets from the 'sex ratio + female M' scenario. The term 'latest' refers to the final year's estimate. The term 'curr' or 'current' refers to an average over the 4 years 'latest-4' to 'latest-1'.

	Scenario 0. Base case	Offset from base case Offset from 'Sex ratio + female M'								Offset from base		
		1.	11.	1.	2	2	4	5	C	7	case	0
		Ta. Sex	10. Female	IC. Sex ratio	2. Undated	3. Fecundity	4. Snawning	э. Egg viability	0. All	7. All	8. All	9. All
	Duse cuse	ratio	M	+ female	maturity	at age	fraction at	at age	effects	effects	effects	effects
			higher	Μ	schedule	C	age	increases 20% / year	but egg viability		but egg viability	
MSY	193900	1.02	1.09	1.11	0.95	0.91	0.94	0.88	0.90	0.82	1.00	0.91
Bzero	2243000	1.00	1.06	1.06	1.00	1.00	1.00	1.00	1.00	1.00	1.06	1.06
Bmsy	1122000	1.00	1.06	1.05	1.03	1.05	1.04	1.06	1.06	1.08	1.11	1.14
Fmsy	0.173	1.02	1.03	1.05	0.92	0.87	0.90	0.84	0.85	0.75	0.90	0.80
SBzero	844400	0.88	1.08	0.96	0.81	0.75	0.78	0.46	0.73	0.28	0.70	0.27
SBlatest	475470	0.92	1.10	1.02	0.74	0.65	0.70	0.37	0.62	0.21	0.63	0.21
SBmsy	131400	0.95	1.17	1.12	0.68	0.57	0.63	0.32	0.53	0.17	0.60	0.18
Blatest / Blatest.Fzero	0.897	1.00	1.01	1.01	1.00	1.00	1.00	1.00	1.00	1.00	1.01	1.01
SBcurr / SBcurr.Fzero	0.802	1.06	1.02	1.08	0.96	0.92	0.95	0.85	0.91	0.79	0.98	0.85
SBlatest / SBlatest.Fzero	0.776	1.08	1.03	1.10	0.94	0.89	0.92	0.79	0.87	0.69	0.95	0.76
SBcurr / SBzero	0.622	1.01	1.00	1.01	1.01	1.01	1.01	0.98	1.01	0.96	1.02	0.97
SBcurr / SBmsy	3.99	0.93	0.93	0.87	1.20	1.33	1.24	1.43	1.37	1.65	1.19	1.43
Bmsy / Bzero	0.500	1.00	1.00	1.00	1.03	1.05	1.04	1.05	1.06	1.08	1.05	1.08
SBmsy / SBzero	0.156	1.09	1.08	1.17	0.84	0.76	0.81	0.69	0.73	0.58	0.86	0.68
Fmsy / Fcurr												
(Fmultiplier)	26.5	1.07	1.05	1.11	0.84	0.76	0.81	0.69	0.72	0.57	0.80	0.63
Steepness	0.894	1.00	1.00	1.00	1.01	1.01	1.01	1.01	1.01	1.01	1.01	1.01

Discussion

As demonstrated here, reference points based on spawning potential can differ significantly from those based on spawning biomass. Sustainable fisheries depend on continued reproductive output, and it is largely for this reason that stock assessments report relative spawning biomass, and related parameters, as stock status indicators or reference points. However, on this basis spawning potential is a more appropriate indicator of sustainability than is spawning biomass, since it includes age-related and sex-related effects on reproductive output.

The stock recruitment relationship (SRR) also requires an index of potential reproductive output, and in this context spawning potential is clearly more appropriate than spawning biomass. Using spawning potential rather than spawning biomass barely changes historical estimates of recruitment, which are very strongly determined by the size and catch rate data. However, if a stock-recruitment relationship is modelled, then using spawning potential will change the relationship between fishing mortality and future expected average recruitment. This is a significant change, since it alters yield-related reference points such as the F multiplier.

Consistent language and modelling approaches among stock assessments will help stakeholders understand the implications of reference points, and make comparisons among regions. The terms 'spawning biomass', 'spawning stock biomass', 'adult biomass', and (occasionally) 'spawning potential' are variously used in stock assessments by the IATTC, IOTC, and ICCAT to refer to the quantities that I have termed 'spawning potential (S)' and 'spawning biomass (SB)'. However, the quantity that the IATTC generally model and report is spawning potential (Aires-da-Silva and Maunder 2007, Maunder 2007), whereas IOTC (IOTC 2006) and ICCAT (ICCAT 2007) models mostly use spawning biomass.

Given the high steepness (Table 5) (Mace and Doonan 1988) of the SRR in the albacore stock assessment, changing the reproductive parameters was not expected to affect the F multiplier so strongly. Steepness of 0.89 suggests a stock that is very robust to fishing pressure. It implies that at 20% of the maximum spawning potential, average recruitment would be 89% of the average recruitment at maximum spawning potential. However, note that S_{MSY}/S_{ZERO} is very low at 0.156 in the base case, and further reduced by a factor of 0.86 (i.e. 0.134) when all reproductive effects but egg viability are included. In comparison, for WCPO and EPO yellowfin, SB_{MSY}/SB_{ZERO} and S_{MSY}/S_{ZERO} are 0.31 and 0.37 respectively. Albacore's low relative spawning potential at MSY makes predicted yield at MSY, and hence the F multiplier, unusually sensitive to changes in spawning potential. It must be noted that for WCPO and EPO bigeye SB_{MSY}/SB_{ZERO} and S_{MSY}/S_{ZERO} are 0.18 and 0.22 respectively. This suggests that research to improve the estimates of biological parameters for bigeye may also be rewarding.

Estimates of stock sustainability and yield- or MSY-related parameters depend strongly on the assumed SRR. Tuna stocks are often assumed to have an SRR with high steepness. A prior distribution of 0.867 ± 0.027 is used in the albacore assessment (Langley and Hampton 2006), and the stock assessment's posterior estimate of 0.894 suggests that the data imply a higher value. However, determining the relationship between stock and recruitment is made difficult by a great deal of natural variation. Recruitment also affects stock size, so that long term time series effects on recruitment (e.g. environmental effects a.k.a. regime changes) positively bias the steepness estimate. Steepness is therefore very difficult to estimate within a single stock assessment. A lower steepness value may be consistent with the data for tunas in general (Myers *et al.* 1999).

Assumptions of using spawning potential, not biomass.

Using only the potential output of eggs assumes that the availability of males to fertilise them is not a limiting factor. This appears to a reasonable assumption for tunas in general (Yund 2000), and perhaps particularly for tunas given the male bias in sex ratio, although it may not be the case for all marine species (see Gascoigne and Lipcius 2004).

Assumptions in calculation of the component parameters

The sex ratio data suggests a strong increase in natural mortality for mature females. When added to the model it changes the natural mortality schedule quite dramatically. Changing the base level of natural mortality (M^1) or the juvenile natural mortality trend (based on M^0) would not alter the post-maturity shape of the curve. In these analyses, the base level of natural mortality was held constant at 0.4516.yr⁻¹, the value estimated in the 2006 assessment. Further assessments should be carried out to estimate M^1 , which may result in a lower value base value, implying a longer-lived and therefore less productive stock. Natural mortality for albacore is often assumed to be between 0.3 and 0.4, but has been variously estimated between 0.17 and 0.6 (Hampton 1990, Fournier *et al.* 1998, Bertignac *et al.* 1999, IATTC 2000).

The initial sex ratio was assumed to be 0.5, but the proportion male was observed to be lower than this among fish less than about 90cm. This suggests that the hypothesis of slower female growth rate should be investigated further, since it would result in more females in smaller size classes. However, a similar effect would be produced if small males were more likely than small females to be designated 'indeterminate' sex. Male albacore may mature at a larger size than females on average (Foreman 1980, Murray 1994), although males can mature at much smaller sizes (Murray 1994). There is likely to have been variation in the ability to assign sex correctly among the observers who provided these data.

The apparent recovery of proportion female for the very largest fish, over 110 cm, may be due to an increased proportion of mislabelled yellowfin and bigeye, since there are so few albacore of this size. The effect appears consistent across several size classes. Of the 54 females larger than 100 cm FL in the data set, 22, enough to account for much of the discrepancy, came from 9 sets in a 2x2 degree area in the winter of 2006. Observer error is probably responsible. A real biological effect seems unlikely. Similar recovery in proportions has not been observed in analyses of yellowfin or bigeye data (Hoyle unpublished).

All data north of 25° S were included in the sex ratio analysis. This was the area for which the best and most consistent data series was available, and the purpose of the analysis was to determine the sex ratio at length in the population. Spawning appears to occur primarily in the November-February period north of 20° S (Murray 1994), and variation in sex ratios may occur in association with spawning.

The sex ratio data were pooled here; determining the contributions of the various sources of variation was beyond the scope of the analysis. Preliminary investigations suggested that sex ratios vary with (at least) the interactions of 5 degree square, season, and year, although no consistent patterns were apparent. Additional variation appears to occur among sets, which suggests sex ratio variation on a small spatial and

temporal scale. A hierarchical analysis, or appropriate accounting for overdispersion, is likely to be necessary to model the data. Given the variation among sets, the true effective sample sizes will be much lower than those presented in Table 1. These sources of variability, and the scale of the population, must be considered when designing research to estimate reproductive parameters. Further statistical analyses of such data will be needed to clarify this question.

Two of the relationships used in this paper were inferred from yellowfin tuna, due to lack of data for albacore. These were the assumption that fecundity of albacore increases more than proportionally with weight, and the assumption that spawning frequency increases with size. Fecundity has been found to increase with size in albacore (Saito 1973), although one study found no such relationship (Wu and Kuo 1993). There is evidence of multiple spawning in albacore (Otsu and Uchida 1959) but no information of the relationship between spawning frequency and size.

Nevertheless, whether fecundity increases or perhaps even decreases relative to biomass, should not distract from the point that the current assumption (that it is precisely proportional to weight) is influential. The question needs to be resolved through biological research.

The 2008 stock assessment

Introducing the sex ratio data to the stock assessment reduced the influence of old age classes on the assessment, because both the changed sex ratio and the higher M for older fish reduced the numbers of old females in the population. This makes the stock assessment results more optimistic. Introducing the fecundity, spawning frequency, and updated maturity data had the opposite effect.

Based on the results presented here, sex ratio, maturity, and M at age will be included in the base case of this year's south Pacific albacore stock assessment. The approach used in previous assessments will be included as a sensitivity analysis. The assumed relationships between spawning frequency and fecundity at age will not be included in the base case. This is because reliable data on spawning frequency or fecundity at age are not available from any albacore population.

For yellowfin and bigeye however, sex ratio, maturity, spawning frequency, and fecundity at length data are available for either or both of the WCPO and EPO stocks. There is a case for including these, and updated M at age relationships, in the base case for new assessments of both species. Doing so may not substantially change the estimates of stock status, but will result in more biologically realistic stock assessments. Ideally such parameters derived from other stocks should be included as prior distributions (Hilborn and Liermann 1998), but in Multifan-CL (Fournier *et al.* 1998, Kleiber *et al.* 2006) and most other stock assessment models this is not feasible for the components of spawning potential.

Egg viability is potentially influential for tuna stock assessments, and future research in this area should be prioritised to determine support for the egg viability - age hypothesis. However, including the egg viability at age relationship in the stock assessment would be premature. There is no evidence that albacore, or indeed any tuna species, produce more viable eggs as they age. However, neither is there evidence that they do not.

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