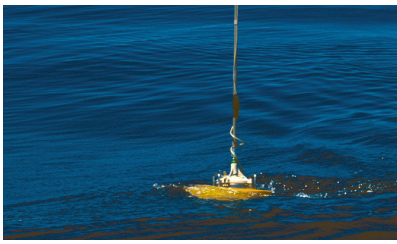
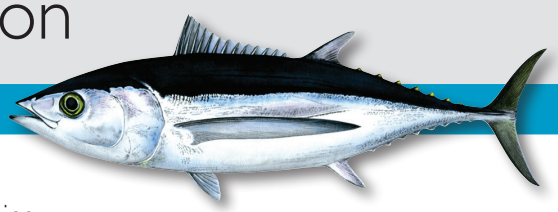
National Research
FLAGSHIPS
Wealth from Oceans

CSIRO



www.csiro.au

Population biology of albacore tuna in the Australian region



Marine and Atmospheric Research

FRDC Project No. 2009/012

Jessica H. Farley, Ashley J. Williams, Campbell R. Davies,
Naomi P. Clear, J. Paige Eveson, Simon D. Hoyle, Simon J. Nicol

Australian Government
Fisheries Research and Development Corporation

Western and Central Pacific Fisheries Commission

Australian Government
Australian Fisheries Management Authority

Population biology of albacore tuna in the Australian region

Jessica H. Farley[1,2], Ashley J. Williams[3], Campbell R. Davies[1,2], Naomi P. Clear[1,2], J. Paige Eveson[1,2], Simon D. Hoyle[3] and Simon J. Nicol[3]

July 2012

FRDC project 2009/012 Final Report

[1] Wealth from Oceans National Research Flagship

[2] CSIRO Marine and Atmospheric Research, Hobart, Australia

[3] Secretariat of the Pacific Community, Noumea, New Caledonia

Copyright and Disclaimer

© 2012 FRDC and CSIRO

Copyright Fisheries Research and Development Corporation and CSIRO Marine and Atmospheric Research 2011.

This work is copyright. Except as permitted under the Copyright Act 1968 (Cth), no part of this publication may be reproduced by any process, electronic or otherwise, without the specific written permission of the copyright owners. Information may not be stored electronically in any form whatsoever without such permission.

Disclaimer

The authors do not warrant that the information in this document is free from errors or omissions. The authors do not accept any form of liability, be it contractual, tortuous, or otherwise, for the contents of this document or for any consequences arising from its use or any reliance placed upon it. The information, opinions and advice contained in this document may not relate, or be relevant, to a readers particular circumstances. Opinions expressed by the authors are the individual opinions expressed by those persons and are not necessarily those of the publisher, research provider or the FRDC.

The Fisheries Research and Development Corporation plans, invests in, and manages fisheries research and development throughout Australia. It is a statutory authority within the portfolio of the federal Minister for Agriculture, Fisheries and Forestry, jointly funded by the Australian Government and the fishing industry.

Publisher: CSIRO Marine and Atmospheric Research, Castray Esplanade, Hobart, Tas, Australia.

National Library of Australia Cataloguing-in-Publication entry

Title: Population biology of albacore tuna in the Australian region / Jessica H. Farley ... [et al.].

ISBN: 9780643108462 (pbk.)

Series: FRDC Project ; no. 2009/012 Final Report.

Subjects: Albacore--Australia.
Albacore fisheries--Australia.
Fish populations--Estimates--Australia.

Other Authors/Contributors:
Farley, Jessica, 1968-
CSIRO. Marine and Atmospheric Research.

Dewey Number: 597.7830994

Contents

1. Non-technical summary 1
2. Acknowledgements 5
3. Background 6
4. Need 8
5. Objectives 9
5.1 Background to project objectives 10
5.1.1 Length-weight relationship 10
5.1.2 Age estimation 10
5.1.3 Growth 11
5.1.4 Reproduction 12
5.1.5 Maturity 13
6. Methods 14
6.1 Biological sampling program 14
6.2 Length-weight relationship 17
6.3 Annual age determination and validation 17
6.3.1 Otoliths 17
6.3.2 Fin spines 20
6.3.3 Precision 21
6.3.4 Age validation 23
6.4 Spatial variation in growth 25
6.5 Reproductive dynamics 28
6.5.1 Data collection 28
6.5.2 Female histological classification 29
6.5.3 Oocyte diameter 30
6.5.4 Spawning frequency and batch fecundity 34
6.6 Spatial variation in maturity 34
6.6.1 Data collection 34
6.6.2 Maturity analysis 35
6.6.3 Maturity ogive for the ETBF 36
7. Results and discussion 40
7.1 Length-weight relationship 40
7.2 Annual age determination and validation 42
7.2.1 Otolith reading and precision 42
7.2.2 Fin spine reading and precision 43
7.2.3 Comparison of structures 45
7.2.4 Age validation 46

7.2.5 Decimal age....52
7.2.6 Discussion....54
7.3 Spatial variation in growth....58
7.3.1 Growth modelling....58
7.3.2 Discussion....66
7.4 Reproductive dynamics....70
7.4.1 Size distribution and sex ratio....70
7.4.2 Gonad development....73
7.4.3 Spawning location and season....74
7.4.4 Time of spawning and POF degeneration....78
7.4.5 Spawning frequency....79
7.4.6 Batch fecundity....82
7.4.7 Discussion....83
7.5 Spatial variation in maturity....88
7.5.1 Catch composition....88
7.5.2 Maturity analysis....91
7.5.3 Maturity ogive for the ETBF....95
7.5.4 Discussion....98
8. Benefits....101
9. Further Developments....101
10. Planned Outcomes....103
11. Conclusions....105
12. References....108
13. Appendix A – Intellectual Property....124
14. Appendix B – Project staff....124

List of Figures

Figure 1. Map of the South Pacific Ocean indicating locations where sample of albacore were collected. 15

Figure 2. Images of transverse sections of sagittal otoliths under transmitted light showing clear opaque and translucent growth zones: #927 (a) and #2389 (b). Locations of the distal edges of the opaque zones counted are shown (white arrow) with a partially completed opaque zone at the margin of both otoliths (dark arrows). *FL* for #927 was 76 cm, and for #2389 was 89 cm. 19

Figure 3. Images of transverse sections of spine from 2 albacore: #692 (a and c) and #628 (b and d) at two magnifications. Fork length, spine diameter, zone counts for #692 and #628 were 105 cm, 6.36 mm and 12; and 68 cm, 3.67 mm, and 2 respectively. The zones counted are indicated by red dots at the transition between opaque (dark) and translucent (light) zones. It was estimated that 3 zones were obscured (not visible) in the core of # 692 based on the data in Table 9 (below) and this number was added to the number of visible zones to produce a final count of 12. 22

Figure 4. Histological sections of albacore ovaries showing examples of development classes, oocyte stages and postovulatory follicles. (A) unyolked oocytes in an immature ovary, (B) advanced yolked oocytes in a spawning capable ovary, (C) migratory nucleus oocyte in a spawning ovary, (D) hydrated oocytes in a spawning ovary, (E) <12 hour POF in a spawning ovary, (F) >12 hour POF in a spawning ovary. UY = unyolked, EY = early yolked, AY = advanced yolked, MN = migratory nucleus, H = hydrated, POF = postovulatory follicle. 31

Figure 5. Histological sections of albacore ovaries showing examples of development classes and maturity markers. (A) alpha and beta atresia in a regressed 1 ovary, (B) residual hydrated oocytes in a regenerating ovary, (C-F) late stage atresia (brown bodies). α = alpha atresia, β = beta atresia, RH = residual hydrated oocyte, EY = early yolked oocyte, BB = white arrows. 32

Figure 6. Map of ETBF indicating the designated areas used in the GLM analyses to standardize CPUE for albacore tuna by Campbell (2011). The number in brackets indicates the number of 1-degree squares associated with each area. Figure modified from Campbell (2011). Latitude areas 1 to 3 for statistical analysis of maturity are shown. 39

Figure 7. Weight-at-length data and fitted power curve for South Pacific albacore from Australian and New Zealand waters (n=1756). 40

Figure 8. Length-weight relationships for albacore in the South Pacific from published studies (see Table 8) 41

Figure 9. Age bias (left) and age difference (right) plots for comparisons of (a) counts by OR1 and OR2 (unadjusted, n=192), (b) counts by OR1 and OR2 (adjusted, n=191), and (c) counts from otolith and spines (n=292). Error bars are SE. 44

Figure 10. Transverse section of albacore otoliths injected with oxytetracycline (OTC). Fish no.1 (top) and Fish no.2 (bottom). Left: Location of the distal edges of the opaque zones (white arrow) counted under transmitted light with a partially completed opaque zone at the margin (dark arrow). Right: The OTC mark visible under ultraviolet light (white arrow).....47

Figure 11. Transverse section of albacore fin spines injected with oxytetracycline (OTC). Left: Fish no.1 with possible location of the OTC mark visible under ultraviolet light (white arrow). Right: Fish no.2, no OTC mark visible. 48

Figure 12. Mean monthly marginal increment ratio (MIR +/- 95% CI) for 2009 and 2010 in the western region. Data were pooled across age classes 4-6 years.....50

Figure 13. Mean monthly marginal increment ratio (MIR +/- 95% CI) for the western and eastern regions. Data were pooled across years and age classes. 50

Figure 14. Sectioned otoliths from four albacore demonstrating the annual cycle in opaque zone formation. The white arrows indicate distal edge of opaque zones counted, and the white arrows indicate if an additional opaque zone was forming at the otolith edge (not counted). A wide MIR is shown in otolith sampled in May (85.2) and a narrow MIR is shown in otolith sampled in July (41.7). The MIR then increased from July to December.....51

Figure 15. Marginal increment ratio (MIR) values by month for albacore (x). Mean monthly MIR values (●) +/-2 standard deviations (SD) are shown. Regression line is derived through the values of -2 SD of the mean MIR for December to March and +2 SD of the mean MIR for September to November (-----). The MIR values used to separate pre-and post increment otoliths for April to August are the fitted values from the regression line for these months (o). 53

Figure 16. Relationship between otolith weight and decimal age for albacore. 53

Figure 17. Length-at-age data and logistic growth models for female and male South Pacific albacore. Parameters of the models are presented in Table 12. 60

Figure 18. Predicted longitudinal trends in residual fork lengths from the logistic growth models for female (A) and male (B) South Pacific albacore. Dashed lines represent 2 standard deviations from the mean. Predictions from LMEs (dark lines) and GLMs (light lines) are shown. 64

Figure 19. Predicted longitudinal trends in growth model parameters L_∞ and k based on the logistic growth model for female (A and C) and male (B and D) South Pacific albacore (see Table 14 for model details). 65

Figure 20. Predicted growth curves in the west (150° E), central (185° E) and east (220° E) South Pacific Ocean based on predicted longitudinal trends in L_∞ and k for female (A) and male (B) South Pacific albacore. 66

Figure 21. Length-frequency distribution of female (bar) and male (line) albacore sampled in the regions A, B, and C of the southwest Pacific Ocean. 71

Figure 22. Length-frequency distributions of female albacore sampled in region A (green), B (red) and C (blue) between 10-25˚S. 71

Figure 23. Relation between gonad weight and *FL* for albacore in region A (green), B (red) and C (blue). 73

Figure 24. Relation between ovary weight and *FL* of albacore by reproductive state (regions combined). M = mature and I = immature. The regressing class includes classes 5, 6a and 6b (Table 6). The line represents a gonad index (GI) of 1.7 above which is assumed to indicate maturity by Ramon and Bailey (1996). 74

Figure 25. (a) Mean gonad index (n = 383) and (b) oocyte diameter (n = 154) for female albacore by MAGO stage for region A (black), region B (grey) and region C (white). AY = advanced yolked, MN = migratory nucleus and H = hydrated. Error bars are SE. 74

Figure 26. Sample locations of active (spawning and spawning capable) female albacore. Longitude is shown as degrees east. That is, 160˚W is shown as 200 (180-20) etc. Vertical lines indicate the division of the sampling area into region A (west of 175˚E), region B (175˚E to 155˚W) and Region C (east of 155˚W) for statistical analysis. 75

Figure 27. Mean monthly gonad index for (a) mature female (n=617) and (b) all male (n=895) albacore by region A (open circle), B (filled circle) and C (open square). Data were restricted to the spawning latitudes of 10-25˚S. Note that *GI* values are lower overall for males because the data used included both mature and immature fish. Error bars are SE. 76

Figure 28. Percent frequency of development classes of mature female albacore by month and region. Data were restricted to the spawning latitudes of 10-25˚S. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top. 77

Figure 29. Percent frequency of development classes of mature female albacore in region A by (a) 5-cm *FL* class in October to March, (b) age class in October to March, (c) month for 80-89 cm fish, and (d) month for 90-99 cm fish. Data were restricted to the spawning latitudes of 10-25˚S. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top. 78

Figure 30. Relationship between time of death and (a) most advanced oocytes (MAGO) stage and (b) assigned postovulatory follicle (POF) age. Most advanced oocytes stages are: 3=Advanced yolked, 4=migratory nucleus, 5=hydrated. Postovulatory follicle stages are: 1 = new, 2 = <12hours, 3 = >12 hours. 79

Figure 31. Relationship between (a) batch fecundity and *FL* and (b) relative batch fecundity (RBF) and spawning month of albacore (n=71). Regression lines shown in (b) are for all data (dotted line) and October to March (full line). 83

Figure 32. Sample locations of mature and immature female albacore. 89

Figure 33. Percent frequency of development classes by month and latitude west of 175˚E. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top. 90

Figure 34. Percent of females ≥ 70 cm *FL* by month with (a) alpha or beta stage atresia and (b) brown bodies and residual hydrated oocytes. 91

Figure 35. Predicted proportion of mature females by fork length at latitudes 10°S, 20°S, 30°S, and 40°S. Dashed lines represent 95% confidence intervals. 92

Figure 36. Predicted fork length at 50% maturity by latitude. Dashed lines represent 95% confidence intervals.....92

Figure 37. Predicted proportion of mature females by age at latitudes 10°S, 20°S, 30°S, and 40°S. Dashed lines represent 95% confidence intervals. 94

Figure 38. Predicted age at 50% maturity by latitude. Dashed lines represent 95% confidence intervals. 94

Figure 39. Predicted proportion of mature females by length in each latitudinal area of the ETBF. The shaded regions give approximate 95% confidence intervals. 96

Figure 40. Weights given to the predicted proportion of mature females in each of the 3 latitudinal areas, where the weights are the estimated proportion of females in a given 5-cm length class found in each of the 3 areas. 96

Figure 41. Results of proposed method to estimate a weighted maturity ogive for females in the ETBF region. Shown are: (i) the predicted proportion of mature females by length in each latitudinal area (as in Figure 39), and (ii) the predicted proportion of mature females by length +/- 2 standard errors across all areas (i.e., the weighted average of the area-specific curves). NOTE: the standard errors are underestimated because they do not include uncertainty in the weights (i.e., in the estimates of relative abundance of females by length in each area). 97

Figure 42. Comparison of the weighted maturity ogive, which should be representative of the female population for the whole ETBF, with the unweighted maturity ogive estimated directly from the sample data. The latter does not account for latitudinal differences in maturity and, therefore is not representative of the ETBF population because sampling was not done in proportion to abundance. 98

List of Tables

Table 1. Number of albacore sampled by year in each region. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. Albacore sampled in 2008 to 2011 were collected as part of the current project. 15

Table 2. Number of biological samples collected by region. Only fish that had at least one type of biological sample suitable for analysis and associated capture data are included. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. 17

Table 3. Number of albacore otoliths and fin spines sampled in each region that were selected for annual and daily age estimation. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. 18

Table 4. Number of albacore from which age estimates obtained for male, female and unknown sex individuals in each region of the south Pacific. High seas 1 refers to the waters between the Australian and New Caledonian EEZs, High seas 2 refers to the waters south of the Pitcairn Islands. 25

Table 5. Number of albacore with gonads analysed by region. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. 29

Table 6. Histological classification criteria for albacore. MAGO = most advanced group of oocytes, POF = postovulatory follicle. 33

Table 7. Number of female albacore with maturity status and decimal age obtained by region in the South Pacific. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. 35

Table 8. Regression coefficients for albacore length-weight (cm-kg) relationships in the South Pacific (sex combined). STCZ = Subtropical Convergence Zone, AS = American Samoa, LL = longline. * all fish with *FL* measured, not only those with *FL*-*W*. 41

Table 9. Mean diameter (mm) of the spine and the first three opaque zones used to "assign an age" to the first observed translucent band in sections with the core obscured. Measurements shown in bold were used to estimate the number of opaque zones potentially missing due to resorption before the first complete observed opaque zone. 45

Table 10. Analysis of variance comparing MIRs between 2009 and 2010 and among the four, five & six-year age classes in the western region. 49

Table 11. Analysis of variance comparing MIRs between the western and eastern regions. 49

Table 12. Parameter estimates (± standard error) from five candidate growth models fitted to length-at-age data for South Pacific albacore. Parameter estimates also given for the logistic model fitted separately to female and male length-at-age data. The small-sample bias-corrected form of Akaike's information criterion AIC_c are provided for each model fit, and Akaike differences Δ_i, and Akaike weights w_i are given for the fit of the five candidate models to all data. Note that the parameters *k* and *t* are defined differently in each model (see text for definitions), such that values are not comparable across models. 59

Table 13. Parameter estimates from the linear mixed effects (LME) and generalized linear models (GLM) fitted to the fork length residuals from the logistic growth models fitted to female and male South Pacific albacore length-at-age data. *R* is the residual fork length, α_{lon} is the effect of longitude (*lon*), β_{set} is the random effect of fishing set, and ε is the error term.....62

Table 14. Summary of growth models used to examine longitudinal variation in growth parameters *k* and L_∞ of female and male South Pacific albacore. L_∞ and *k* from the logistic model ($L_t = L_\infty(1+e^{-k(t-t_0)})^{-1}$) were modelled as linear or non-linear functions of longitude (*l*) where f_1 and f_2 are functions of the growth parameters and α_1 and α_2 describe the relationship between L_∞ and *l*, and β_1 and β_2 describe the relationship between *k* and *l*. The number of estimated model parameters (plus one for variance) (*K*), small-sample bias-corrected form of Akaike's information criterion AIC_c, Akaike differences Δ_i, and Akaike weights w_i are also given for each model fit.....63

Table 15. Predicted growth model parameter estimates in the west (150° E), central (185° E) and east (220° E) South Pacific Ocean based on predicted longitudinal trends in the growth parameters L_∞ and *k* for female and male South Pacific albacore. Common values of the growth parameter t_0 were used across regions for males and females. 63

Table 16. Sex ratio of albacore by region by 5-cm length class (lower value included). ‡ = $P < 0.05$ (females dominate), * = $P < 0.05$ (males dominate). Only shown where n > 5 for the length class.....72

Table 17. Spawning fraction (SF) of all mature females and those classed as active by month and region. Data were restricted to the spawning latitudes of 10-25˚S. SS = spawning season (shown in grey).....81

Table 18. Spawning fraction (n) of mature females by region, 5-cm *FL* class and age class for the months August to April. Only shown if n > 5. * = $P < 0.05$. Data were restricted to the spawning latitudes of 10-25˚S. 82

Table 19. Comparison of all length-based models with AICc weights greater than 1%. The integers associated with the first three columns represent the number of degrees of freedom in the cubic spline used to define the relationship of the parameters length, latitude, and longitude with maturity. Where no df are given,df=0, the parameter was not included in the model. 91

Table 20. Comparison of all age-based models with AICc weights greater than 1%. The integers associated with the first three columns represent the number of degrees of freedom in the cubic spline used to define the relationship of the parameters age, latitude, and longitude with maturity. Where df = 0, the parameter was modelled as a linear variable. Where no df are given, the parameter was not included in the model. 93

Table 21. Comparison of the best-fitting age-based model with the equivalent length-based model given the same dataset, using AICc. The integers associated with the column 2 represent the number of degrees of freedom in the cubic spline used to define the relationship between latitude and maturity. 95

1. Non-technical summary

2009/012	Population biology of albacore tuna in the Australian region

PRINCIPAL INVESTIGATOR: Jessica Farley
ADDRESS: CSIRO Marine and Atmospheric Research
Castray Esplanade
Hobart Tasmania 7000
Telephone: 03 6232 5222 Fax: 03 6232 5000

OBJECTIVES:

1. Collect biological samples (otoliths, spines, gonads & muscle) from albacore caught in the southwest Pacific in cooperation with AFMA, SPC and MFish using the sub-sampling regime designed in the tactical project[1].
2. Determine length-weight conversion factors for albacore in the ETBF
3. Depending on successful age validation, determine the age of 2000 albacore and investigate age-related stock parameters including catch-at-age and regional/sexual differentiation in growth
4. Determine reproductive-based stock parameters for South Pacific albacore including sex ratio statistics, maturity schedule(s), spawning fraction and batch fecundity (by size/age) using macroscopic and modern histological techniques
5. Provide key population biological parameters on age, growth, maturity and fecundity to harvest strategy and stock assessment scientists

[1] Farley and Dowling (2009)

OUTCOMES ACHIEVED TO DATE:

This is the first comprehensive study of albacore tuna population biology in the southern hemisphere. It has provided considerable new information on the population biology of albacore in the South Pacific, which will enable substantial improvement in the regional stock assessment scheduled for 2012, and ultimately the refinement and future implementation of the harvest strategy for albacore in the ETBF. The direct population parameters provided by this project will improve estimates of stock abundance and sustainable catch levels from regional stock assessments for albacore conducted by SPC and provide direct estimates of the biological reference points for the ETBF harvest strategy for albacore. Internationally, in addition to the direct contributions to the HS and regional stock assessment, the systematic and extensive coverage of the project may indirectly influence the direction of future research and monitoring on other target species to investigate the degree to which spatial variation evident for albacore may be reflected in these species. The project represents a direct contribution from Australia to the regional management arrangements and contributes to Australia's advocacy for the sustainable use of the resources. The project has achieved this by providing: length-weight conversion parameters, sex ratio statistics, validated age and longevity estimates, growth parameters by sex and region, reproductive parameters including spawning frequency and batch fecundity, and maturity ogives.

This is the most comprehensive study of albacore tuna population biology undertaken in the southern hemisphere, and it has contributed markedly to the body of knowledge of the biology, life-history traits and population dynamics of the species. The primary objectives of the project were to (i) undertake a large-scale biological sampling program across the southwest Pacific in collaboration with international partners, (ii) collect length and weight data to obtain a conversion equation for management and stock assessment purposes for the Eastern Tuna and Billfish Fishery (ETBF), (iii) sample otoliths (small bones found in the inner ear) to estimate age and growth; and (iv) collect gonads to examine sex ratio, reproduction and maturity. In addition, muscle tissue samples were collected from fish caught in Australia and New Zealand for potential future research.

The biological sampling program was successively implemented with the support of international collaborators and the fishing industry. In total, 3385 albacore were sampled from Australia in the west, to south of the Pitcairn Islands in the east. The total number of albacore sampled since the initial AFMA-funded pilot project[2] in November 2006 is 3824. By processing the material collected and analysing the data, we estimated several key biological parameters for albacore and investigated variation in these parameters across the region.

The study found that albacore caught in the ETBF are in better condition on average (greater weight for length) than albacore caught previously in the Australian region (1987-97) or other regions of the South Pacific. The lack of comprehensive studies on albacore length-weight relationships in the South Pacific, however, makes it difficult to determine if the increase in condition of ETBF albacore is a widespread trend occurring across the South Pacific, or a more localised phenomenon.

We present validated estimates of age for albacore based on counts of annual growth zones in otoliths. The periodicity of the (opaque) growth zones counted was verified by a combination of direct and indirect methods, which indicated that the growth zones form over the austral summer and are completed by autumn to winter. The longevity of albacore was found to be at least 14 years. We consider that age estimates from otoliths are more accurate than those from fin spines, and recommend the use of validated counts for sectioned otoliths as the preferred method for providing age-based parameters for assessment and management advice for albacore.

Based on the validated age estimates obtained, we examined spatial variation in growth of albacore across 90° of longitude in the South Pacific Ocean from the east coast of Australia to Pitcairn Islands. We found evidence for significant variation in growth between sexes and across longitudes. The growth rates were similar between sexes up until age 4, after which the growth for males was on average greater than that for females, with males reaching an average maximum size more than 8 cm larger than

[2] Farley and Clear (2008)

females. The different growth rates between sexes may be responsible for the observed dominance of male among fish greater than 95 to 100 cm fork length. Growth rates were also consistently greater at more easterly longitudes than at westerly longitudes for both females and males. The determinants of the longitudinal variation in growth of albacore remain unclear, but variation in oceanography, particularly the depth of the thermocline, may affect regional productivity and therefore play a role in modifying growth of South Pacific albacore.

This study significantly improved our understanding of the reproductive dynamics of albacore over a broad spatial range in the South Pacific. We found that spawning is synchronised between 10 and 25ºS during the austral summer. We confirmed that albacore spawn during the early hours of the morning and that they are capable of spawning daily, although spawning occurs on average every 1.3 days during peak spawning months. The number of eggs released per spawning averaged 1.2 million oocytes. Although we were not able to sample females monthly in the region east of 175˚E, we found no evidence of large variations in the reproduction or spawning dynamics of females across the southwest Pacific Ocean. Our research, however, showed that the proportion of females mature-at-length varied significantly with latitude in the Australian region, and that this variation was due to different geographic distributions of mature and immature fish during the year. A method is proposed to account for the latitudinal variation in maturity. Preliminary results showed that the predicted age at which 50% of an age class were sexually mature was 4.5 years, and the predicted age at 100% maturity was age 7. These estimates are younger than those currently used in the harvest strategy or stock assessment.

Overall, the suite of life-history traits examined will significantly improve the quality of biological inputs to the 2012 stock assessment for albacore and directly aid further refinement of the ETBF Harvest Strategy for albacore.

Keywords: Albacore tuna, Eastern Tuna and Billfish Fishery, South Pacific Ocean, age, growth, reproduction, spawning, maturity.

2. Acknowledgements

There are many people we would like to acknowledge. Within Australia, we are especially grateful to Eastern Tuna and Billfish Fishery industry members and skippers, and the recreational fishing clubs, who kindly allowed us to sample their catch. We also acknowledge the port samplers in Australia including Glen Cuthbert, Steve Hall (AFMA Observer coordinator), Kevin Williams (W W Fisheries) and Mitch Zischke. Thanks also to MFish and the New Zealand Observer Program for their assistance with sampling the NZ troll fishery, and Lynda Griggs especially for coordinating the shipment of samples to Australia. We also gratefully acknowledge the many people for their assistance with biological sampling from the Pacific Island Countries and Territories including the observers and observer coordinators for carrying out the sampling program, and the skippers and crew of the longline fishing fleets for allowing observers to collect biological samples, and finally to those who coordinated the shipments of frozen material to Australia especially Caroline Sanchez and Marlo Hosken (Secretariat of the Pacific Community; SPC). In additions, we thank Kyne Krusic-Golub (Fish Ageing Services) and Dong Lou (James Cook University) for sectioning the otoliths and fin spines. We also thank Mitch Zischke, Thor Carter and Tonya Van Der Velde (CSIRO) for processing biological material in the laboratory, cleaning and archiving hardparts, and preparing histological sections of gonads. The work was funded by the CSIRO Wealth from Oceans Flagship, FRDC Project 2009/012 with co-funding (catch contribution) from DAFF, AFMA, and the Western and Central Pacific Fisheries Commission (WCPFC). The Pacific Island Countries and Territories (PICT) component of this project is supported under SPC's SCIFISH project which is funded by the 9th European Development Fund (Overseas Countries and Territories component). Biological samples collected prior to the current project are also included in some of the analyses, and those samples were collected through separate CSIRO Wealth from Oceans Flagship, AFMA (No. 2006/826) and FRDC (TRF project 2008/075) funded projects.

3. Background

Distribution and migration

Albacore tuna, *Thunnus alalunga,* are distributed in tropical, sub-tropical, and temperate waters between approximately 10-50°N and 5-45°S globally. Separate northern and southern stocks are assumed to exist in the Pacific Ocean based on their spatial distribution and different spawning times and locations (Hampton, 1999; Ramon and Bailey, 1996; Nishikawa *et al.*, 1985). Albacore is considered one of only four tuna species that are truly migratory and undertake seasonal migrations to specific feeding and spawning areas (along with southern, Pacific and Atlantic bluefin tunas) (Schaefer, 2001). The life cycle and migration routes of albacore in the South Pacific, however, are poorly understood. Spawning is thought to occur when surface water temperatures exceed 24ºC, predominantly between 10-25ºS in the western and central regions to about 140°W (Ueyanagi, 1957; Nishikawa *et al.*, 1985; Schaefer, 2001; Anon, 2006). Juveniles at age 1 year are caught well south of the spawning latitudes in waters at approximately 40˚S and in the subtropical convergence zone (to approximately 130°W). These fisheries predominantly catch juveniles and sub-adults up to ~80-90 cm from December to April. It has been suggested that juveniles remain south of 30°S and do not return to the sub-tropics and tropics until they mature (Jones, 1991; Murray, 1994; Labelle and Hampton, 2003; Chen *et al.*, 2005). Catch rates of albacore in the sub-tropics usually peak in December–January and May–July suggesting they migrate seasonally between the tropics and sub-tropics possibly following specific temperature isotherms (Langley, 2003; Chen *et al*., 2005; Langley and Hampton, 2005). The separation of life history stages with latitude also occurs in the Indian Ocean and has been linked to distinct ocean current systems (Chen *et al*., 2005).

Catches and stock assessments

Albacore currently comprises 6% of the global tuna catch (ISSF, 2011). In the South Pacific, albacore have been targeted by longline fleets since the early 1950s, and catches have increased from 20,000-30,000 t per annum in the mid-1980s to 60,000-70,000 t per annum in the mid-2000s (Hoyle, 2011). The annual catch of albacore in Australia's Eastern Tuna and Billfish Fishery (ETBF) increased from approximately 500 tonnes in the late-1990s and early-2000s, to 2,591 tonnes in 2006 as a number of domestic

longliners switched from targeting broadbill swordfish (shallow setting) to targeted albacore tuna fishing (deep setting). In 2007, this higher catch level was maintained (1,916 t) and "deep set" fishing expanded from the initial northern grounds, where targeted fishing was focussed, to as far south as Ulladulla. As a result of this, development, albacore has become an important target species and is likely to remain so given developing European and US markets for value added fresh product and a proposal for specialized onshore processing facilities in Mooloolaba. In 2010, the catch of albacore in the ETBF declined to 867 tonnes (Woodhams *et al*., 2011).

The current regional stock assessment for South Pacific albacore indicate that the stock is not overfished and that overfishing is not occurring (Hoyle, 2011). The stock assessment, however, uses many biological parameters that are either uncertain or assumed (Hoyle, *et al*., 2008; Hoyle, 2011). The Western and Central Pacific Fisheries Commission (WCPFC) noted in 2005 that "there are critical biological uncertainties for south Pacific albacore....and that these should be addressed in order to inform the next full stock assessment" (Anon, 2005). In particular, it was noted that revised estimates of size and age compositions, sex ratios, growth parameters, maturity rates, maximum longevity, and natural mortality were needed. It is important to note that the inputs required for decreasing the uncertainties in the regional stock assessments will also be important for refining the harvest strategy for albacore in the ETBF. The harvest strategy uses reference points in the decision rule that are based on reproductive characteristics of the stock (i.e. Spawner Biomass Per Recruit). The uncertainty in the current stock assessment is one of the reasons that the albacore harvest strategy was considered the least reliable of the five target species of the ETBF (Kolody *et al.*, 2010).

Project development

The rapid increase in the catch of albacore in the ETBF in 2006 raised concerns about the long-term sustainability of the Australian fishery (since localised depletion of albacore has been observed in several Pacific island nations) and highlighted the pressing need to implement a Harvest Strategy. At that time, the state of knowledge about albacore in Australian waters was not sufficient to quantify its productivity in the development of the harvest strategy. Thus for meeting the long-term sustainability requirements of the fishery, there was a pressing need to initiate research to address key

biological uncertainties such as age-at-maturity, growth rates, and mortality to determine target reference levels, consistent with the Commonwealth Harvest Strategy Policy.

In response to this, a feasibility study was undertaken in 2007 to investigate the size, age and reproduction of albacore caught by the fishery (Farley and Clear, 2008). The project provided preliminary descriptions of a number of key biological parameters such as length-weight conversions, sex ratios, age, growth, maturity and fecundity. The project also made several recommendations including that substantially more biological samples were required to undertake research on direct ageing and reproduction to address key biological uncertainties for albacore. In late 2008, an 8-month FRDC tactical research fund sampling project was undertaken to meet the need for size data and continue the collection of biological samples in the ETBF with additional direct funding from the Western and Central Pacific Fishery commission (WCPFC) (Farley and Dowling, 2009). That project was followed by the current study to finalise the collection of biological samples and undertake the analysis. The projects were complemented by studies being undertaken at the Secretariat of the Pacific Community (SPC) (SCIFISH project) including sampling albacore across the southwest Pacific, as well as otolith microchemistry work and tagging studies to address the need for information on stock structure.

4. Need

In 2005, the Ministerial Directive to AFMA included the requirement to develop harvest strategies for all Commonwealth fisheries. The proxies for the reference points for the ETBF Harvest Strategy require estimates of several biological parameters, including size/age-at-maturity, growth rates, fecundity and mortality (Campbell *et al.*, 2007). In particular, the spawner-per-recruit reference points require estimates of size-at-maturity and mortality. As noted previously, the estimates of these parameters are taken from the SPC's regional stock assessment, which in turn are either uncertain or assumed.

In 2008, the stock assessment model for South Pacific albacore was revised and "the cumulative effect of these changes was to reduce the biomass estimates and raise the fishing mortality estimates compared to previous assessments" (Hoyle *et al.*, 2008). Although there was still significant uncertainty in the model, the assessment provided a more pessimistic view of stock size and MSY (1/3 of the volume) compared to the 2006 assessments. Such significant changes in stock assessment outputs highlighted the requirement for accurate assessments of albacore and the ensuing need for revised biological data. Subsequent stock assessments (2008, 2009 and 2011) provided updated estimates of stock size and MSY, but there remained considerable uncertainty. Research on biological parameters such as sex ratio, maturity, growth by sex, fecundity, and spawning fraction were recommended. The current project addressed that need and maximized the value of complimentary studies undertaken at SPC.

5. Objectives

1. Collect biological samples (otoliths, spines, gonads & muscle) from albacore caught in the southwest Pacific in cooperation with AFMA, SPC and MFish using the sub-sampling regime designed in the tactical project.
2. Determine length-weight conversion factors for albacore in the ETBF
3. Depending on successful age validation, determine the age of 2000 albacore and investigate age-related stock parameters including catch-at-age and regional/sexual differentiation in growth
4. Determine reproductive-based stock parameters for South Pacific albacore including sex ratio statistics, maturity schedule(s), spawning fraction and batch fecundity (by size/age) using macroscopic and modern histological techniques
5. Provide key population biological parameters on age, growth, maturity and fecundity to harvest strategy and stock assessment scientists

5.1 Background to project objectives

5.1.1 Length-weight relationship

The length-weight relationship of albacore caught in the South Pacific is an important input to the regional stock assessment as it is used to convert catches in weight into catches in numbers. It can also provide information on relative condition of fish (Le Cren, 1951). Very few estimates of length-weight relationship parameters are available for albacore in the Australian region. Hence it was important to provide an accurate and representative estimate of this relationship and any consistent regional variation in it.

5.1.2 Age estimation

Tuna support several of the largest pelagic fisheries in the world (Majkowski, 2007). To determine the status of the fished stocks and provide management advice, routine stock assessments of the target species are undertaken periodically. Many of these stock assessments use age-structured models requiring estimates of length-at-age, age-at-maturity, and age-specific natural mortality (FAO, 2001) yet validated age estimation methods across the full age range of many of these important species are not available. Many tuna stock assessments often use analysis of length-frequency and tagging data to estimate growth parameters. However, there is considerable uncertainty in growth parameter estimates using these methods because of the limited size range of fish included and the inadequacies inherent in some of the methods (Farley *et al.*, 2006). Studies over the past decade, however, have shown that tuna otoliths exhibit annual growth checks that can be consistently and unambiguously interpreted and provide a valuable source of length-at-age data (Clear *et al.*, 2000; Farley *et al.*, 2003; Neilson and Campana, 2008; Griffiths *et al.*, 2009) as a basis for estimation of population parameters.

The direct age of albacore has been estimated using a variety of hard parts including scales, vertebrae, otoliths and fin spines; the latter two are the most commonly used to estimate daily and annual age respectively (Davies *et al.,* 2008a). A difficulty in using fin spines for estimating annual age is that vascularisation of the core can obscure the early growth zones in older fish. This loss of growth zones has been overcome to some

extent in some tuna species by estimating the positions of the early zones on younger fish (Hill *et al.*, 1989). This method is yet to be validated in albacore.

5.1.3 Growth

Knowledge of the growth of individuals is essential for understanding the processes shaping populations and for managing exploited fish species (Gulland, 1988). Many stock assessment models require estimates of growth to estimate current and unexploited biomass, and to identify fishing mortality rates that will achieve specific management objectives (Hilborn and Walters, 1992). Information about growth variation among groups of individuals is useful for defining stock assessment structure, and can be more important for the assessment than the growth estimates themselves.

Estimates of growth are typically derived from information on the size and age of individuals or from tag-recapture studies (Haddon, 2001). Collecting sufficient data across an entire stock to obtain reliable estimates of growth can be difficult and expensive. Therefore, estimates of growth are often drawn from a single location or averaged across multiple locations without consideration of spatial variation in growth (Hilborn and Walters, 1992; Punt, 2003).

Variation in growth between populations can result from genotypic variation or from plastic phenotypic responses to variation in local environmental factors such as temperature and food availability (Weatherley and Gill, 1987). Spatial variation in growth is a common feature of demersal fish populations and has been observed at multiple scales ranging from patch reefs on the same reef (<1km) (Pitcher, 1992; Gust *et al*., 2002) to thousands of kilometres across an ocean basin (Meekan *et al*., 2001; Robertson *et al*., 2005). Many demersal species display a metapopulation structure (Kritzer and Sale, 2006), with spatial separation of adult sub-populations linked to varying degrees by a pelagic larval stage, and spatial variation in growth is expected. However, the metapopulation paradigm might not be applicable to highly mobile pelagic species such as tunas which typically do not have a strong association with benthic habitat and are assumed to exhibit a continuous distribution as a result of high mobility as adults. There have been no comprehensive studies of spatial variation in

growth within a stock for large pelagic species, although Farley *et al*. (2006) demonstrated a difference in growth of bigeye tuna between stocks in the Pacific and Indian Oceans. Therefore, it remains unclear whether the spatial variation in growth observed for many demersal species is evident in stocks of pelagic migratory species such as tuna that are assumed to move at the scale of ocean basins.

There have been numerous studies of albacore growth throughout their distribution, most of which have estimated growth parameters from modal analysis of length-frequency data, tag-recapture experiments or age estimates from scales, vertebrae or spines (e.g. Laurs and Wetherall, 1981; Labelle *et al*., 1993; Megalofonou, 2000; Santiago and Arrizabalaga, 2005; Lee and Yeh, 2007). Very few studies have used increment counts in otoliths to estimate age and growth of albacore over their entire lifespan, perhaps due to the perceived difficulty of interpreting annual increments in tuna otoliths. However, as noted in above, otoliths have been shown to be a reliable structure for estimating age for tunas (Clear *et al.*, 2000; Farley *et al*., 2006; Neilson and Campana, 2008; Griffiths *et al*., 2010). These studies have provided a foundation for the use of otoliths to estimate age-based population parameters for tropical and temperate tuna.

5.1.4 Reproduction

Despite the long history of exploitation for albacore and general knowledge of its life-history, there are few quantitative estimates of size- or age- specific reproductive parameters for albacore in the South Pacific Ocean. A common assumption in many fishery assessments is uniformity in population dynamics across the entire distribution of the stock, or sufficiently rapid mixing that any substantial variation is not important for assessment purposes (Punt, 2003). Currently many of the estimates of reproductive parameters that are integrated into the stock assessment model for albacore in the South Pacific Ocean (Hoyle, 2011) are derived from studies of other stocks or tuna species (Hoyle *et al*., 2008). Analyses examining the sensitivity of the assessment outputs to these estimates demonstrate that small changes in these parameter estimates have a substantial influence on the value of important reference points for management advice, such as the size and level of depletion of the spawning biomass (Hoyle *et al*., 2008).

Consequently, potential differences in the population biology between stocks of albacore in the Pacific (i.e. north versus south) and other oceans may have substantial implications for South Pacific stock assessments, the fishery and management.

5.1.5 Maturity

Accurate estimates of length- or age-at-maturity for female fish are important life history parameters required for assessing a stock and particularly for estimating spawning stock biomass (SSB) or reproductive potential (SPR). Estimates of maturity are typically obtained by examining ovaries using macroscopic or histological techniques to determine maturity status of individuals, and applying statistical models to determine the proportion mature as a function of length or age (Chen and Paloheimo, 1994). It is generally acknowledged that maturity ogives can vary spatially and temporally and this variability needs to be understood and accounted for in assessment models (Hilborn and Walters, 1992). Spatial variability in maturity can be due to differences in growth rates of a species in different geographic areas, providing evidence for stock structure within a population (Begg and Cadrin, 2009). However, variability can also result from geographic distributions of mature and immature fish which may bias the estimated maturity ogive towards one status or the other, depending on the nature of the distribution of sampling effort. For instance, estimates of length at 50% maturity will be lower for fish sampled in spawning areas than for fish sampled elsewhere if only mature fish migrate to spawning areas and immature fish do not. As a result, the estimated maturity ogive will represent the spawning component of the stock rather than the whole population (Schmitt & St-Pierre, 1997). Similarly, sampling of only spawning aggregations will bias the maturity ogive towards mature fish (Murua, *et al*., 2003). Hence, it is important to account for potential spatial variability in maturity through a well-designed sampling program and when estimating a population ogive from the resulting maturity data. If this is not possible, it is important to incorporate the potential for this variation in the stock assessment (i.e., by exploring models that allows for different maturity ogives across space and over time).

There are no quantitative estimates of size- or age-at-maturity of albacore tuna for the South Pacific (Schaefer, 2001). Estimates of minimum size at maturity for females

range between 82 cm and 90 cm *FL* (Ueyanagi, 1957; Otsu and Uchida, 1959; Bard, 1981; Ramon and Bailey, 1996; Chen *et al*., 2010). Albacore stock assessments in the Pacific, Atlantic and Indian Oceans all assume that 50% maturity is reached at age five and full mature at age six (Hillary, 2008; ICCAT, 2010; ISC, 2010; ICCAT, 2011; Hoyle, 2011). In the Mediterranean, 50% maturity is estimated at 66 cm *FL* and age two or three years depending on the growth curve used (Anon, 2011). It is recognised that improved estimates of maturity using modern histological methods and validated ageing techniques are required (Schaefer, 2001). This requires a large-scale sampling program that encompasses the full geographic range of the stock, an adequate number of samples of the size range over which the transition to maturity occurs, and appropriate histological criteria to identify the maturity status (Murua *et al*., 2003). The use of appropriate histological criteria is especially important for females sampled after the spawning season when the ovaries of mature but resting females may appear immature using macroscopic techniques. Underestimating the proportion of mature females would positively bias the maturity ogive and potentially result in an underestimation of SSB or SRP.

6. Methods

6.1 Biological sampling program

A large-scale biological sampling program was undertaken across the southwest Pacific Ocean. In total, 3577 albacore were sampled between 2008 and 2011 (current project) and 3826 since November 2006 (Table 1). Material collected in the current project was obtained from fish caught off Australia, New Zealand, New Caledonia, Fiji, Tonga, American Samoa, Cook Islands, French Polynesia, and in high seas waters west of New Caledonia and south of the Pitcairn Islands (Figure 1). Very good industry cooperation was integral to the success of the sampling program.

Table 1. Number of albacore sampled by year in each region. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands. Albacore sampled in 2008 to 2011 were collected as part of the current project.

Region	2006	2007	2008	2009	2010	2011	Total
American Samoa				19	411		430
Australia	4	216	31	644	678		1573
Cook Islands					190		190
Fiji				52	157	22	231
French Polynesia				176	196		372
High seas 1				31	59		90
High seas 2					82		82
New Caledonia				194	42		236
New Zealand		29	160	72	227	1	489
Tonga					133		133
Total	4	245	191	1188	2175	23	3826

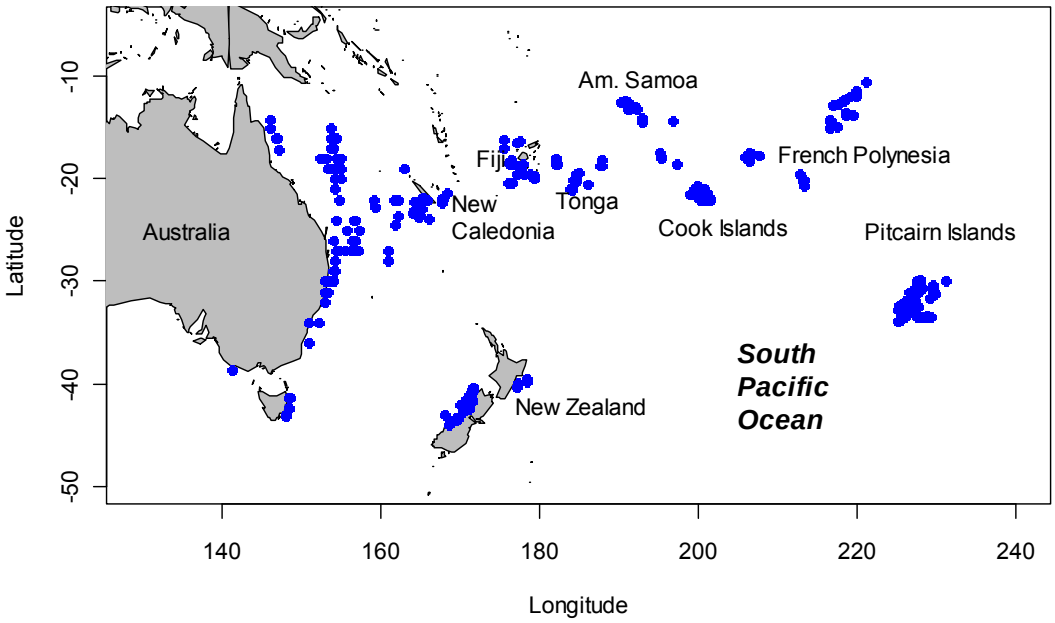


Figure 1. Map of the South Pacific Ocean indicating locations where sample of albacore were collected. Note that longitude is shown as degrees East, thus 200 is 160°W.

Within Australia, fish were sampled from the Eastern Tuna and Billfish longline fishery (ETBF) and the recreational fishery. Sampling in the ETBF was predominantly undertaken in port, from fish caught along most of the mainland coast of Australia between 14°S and 37°S. Fish sampled from the recreational fishery were caught

between 37°S and 44°S. In New Zealand, albacore were also sampled in port from the domestic troll fishery as well as during chartered tagging operations. An additional two fish that had been injected with oxytetracycline (OTC) on a known date were sampled in New Zealand. Albacore sampled from all other regions across the southwest Pacific were collected either by observers on longline fishing vessels or directly by the fishing crew of longline fishing vessels.

The majority of fish sampled were measured to the nearest cm (fork length; *FL*) apart from 87 fish sampled in Fiji that were measured to the nearest (lower) 5-cm. These fish were not included in analyses where 1-cm data were required. In addition, reliable length data were not available for 82 fish sampled south of Pitcairn Island. However, accurate weight data were available for these fish, so the relationship between whole weight and *FL* was used to estimate *FL* for these individuals (see Section 7.1). Whole weight (*W*) was measured to the nearest 0.1 kg for most fish sampled in Australia, New Zealand. Capture information including location and date were obtained for all fish while additional information such as time of death (with immediate sampling) were obtained for a subset 71 females caught in the Cook Islands and American Samoa.

The primary objective of the biological sampling program was to collect sagittal otoliths and gonads from each fish with length measured, and to collect dorsal spines where possible. Muscle samples were also collected from fish caught in Australia and New Zealand. All biological material was processed a CSIRO Laboratories in Brisbane or Hobart. Otoliths and spines were cleaned, dried and archived in CSIRO's 'Hardparts' collection. Gonads were trimmed of fat, weighed to the nearest 0.1 g (if whole) and sex determined. Previous studies found no significant difference in the size of oocytes sampled along the length of the ovary, but did find a significant difference between the core and periphery of an ovary cross-section (Otsu and Uchida, 1959). Given this, a full cross section or core subsample was removed from one lobe of each gonad and preserved in 10% buffered formalin for potential histological examination. Muscle tissue samples were archived in a -10°C freezer. Table 2 shows the number of biological samples obtained by region since 2006. Of the samples collected, subsets were selected for analysis as detailed in Sections 6.3 to 6.6 below.

Table 2. Number of biological samples collected by region. Only fish that had at least one type of biological sample suitable for analysis and associated capture data are included. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands.

Region	Gonads	Otoliths	Spines	Muscle
American Samoa	404	420	270	
Australia	1457	1479	1540	1447
Cook Islands	186	168	175	
Fiji	224	125	0	
French Polynesia	363	326	0	
High seas 1	89	30	89	
High seas 2	9	74	62	
New Caledonia	226	221	54	
New Zealand	450	527	374	321
Tonga	133	127	131	
Total	3541	3497	2695	1768

6.2 Length-weight relationship

The relationship between *FL* and *W* was estimated using a power function of the form $W = a \times FL^b$ where *a* is the coefficient of the power function and *b* is the exponent indicating isometric growth when equal to 3. Weight-at-length data were available only from Australia and New Zealand, although the size range of fish from New Zealand was limited mostly to individuals <70 cm *FL*. Therefore, the *FL*-*W* relationship was compared between males and females within Australia and New Zealand using an analysis of covariance (ANCOVA) with *FL* as the covariate of *W*. A second ANCOVA was then used to compare the *FL*-*W* relationship between Australia and New Zealand using a common length range for each region. Length and weight data were log-transformed for the analysis to satisfy the assumption of linearity.

6.3 Annual age determination and validation

6.3.1 Otoliths

A total of 2120 sagittal otoliths were selected from albacore sampled between January 2009 and December 2010 (43 to 133 cm fork length; *FL*) (Table 3). The left or right otolith was selected randomly from each fish (with preference given to undamaged

otoliths) and weighed to the nearest 0.1mg if complete. No significant difference in otolith weight was detected between left and right pairs (paired *t*-test, d.f. = 151, P = 0.19), suggesting that either otolith could be used for age estimation.

All otoliths were embedded in clear casting polyester resin. Four serial transverse sections were cut from 2002 otoliths (one section including the primordium) while a single transverse section, incorporating the primordium, was cut from the remaining 118 otoliths. All sections were mounted on glass slides with resin and polished to 400 µm following the protocols developed for southern bluefin tuna (Anon, 2002). Opaque (dark) and translucent (light) zones were visible along the ventral 'long' arm of each otolith section viewed under transmitted light on a Leica Wild stereo microscope (Figure 2). These zones together are considered as one growth increment. The number of opaque zones was counted using the techniques developed for southern bluefin and bigeye tunas (Anon., 2002; Farley *et al.*, 2006). All sections prepared from an otolith were assessed before a count was assigned. Opaque zones at the terminal edge of the otolith were counted only if a translucent edge was visible after the zone. A confidence score of zero (no pattern) to five (no doubt) was assigned to each reading.

Table 3. Number of albacore otoliths and fin spines sampled in each region that were selected for annual and daily age estimation. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands.

EEZ	Otolith annual age	Fin spine annual age	Otolith daily age
American Samoa	208		
Australia	709	99	50
Cook Islands	168		
Fiji	121		
French Polynesia	248		
High seas 1	66	13	
High seas 2	74	43	
New Caledonia	218	16	
New Zealand	184	44	18
Tonga	124	19	
Total	2120	234	68

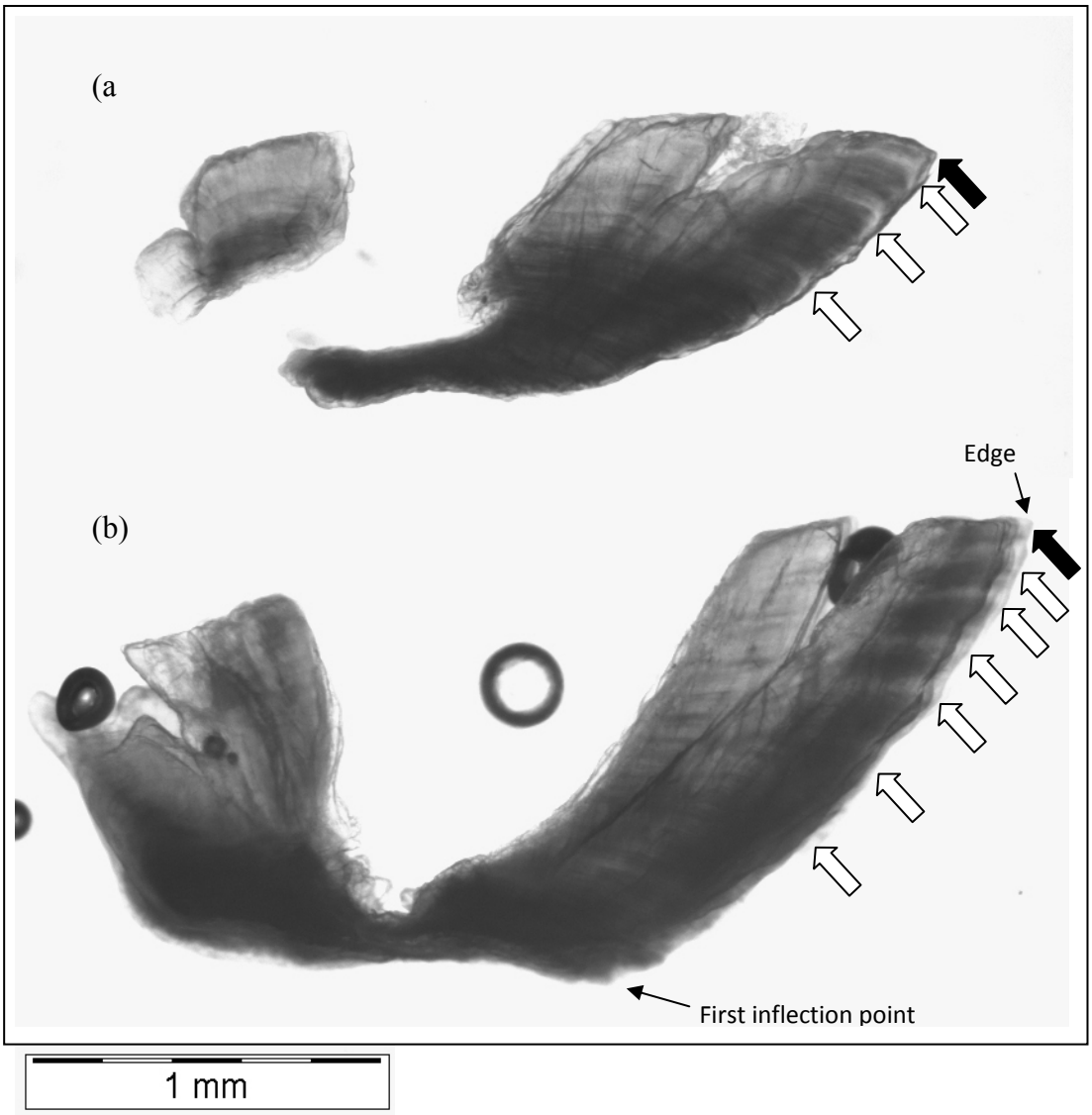


Figure 2. Images of transverse sections of sagittal otoliths under transmitted light showing clear opaque and translucent growth zones: #927 (a) and #2389 (b). Locations of the distal edges of the opaque zones counted are shown (white arrow) with a partially completed opaque zone at the margin of both otoliths (dark arrows). *FL* for #927 was 76 cm, and for #2389 was 89 cm.

Otoliths were read at least two times by the same reader (OR1) without reference to the previous reading, size of fish or capture date. If the successive readings were in agreement, this estimate was used as the final count for the otolith. However, if the readings differed, a further reading was conducted with knowledge of the previous readings to decide on a final count and confidence score. If no obvious pattern could be seen in the otolith section, a count was not made.

Marginal increment measurements were made to determine the relative state of completion of the last opaque zone. Measurements were made on sectioned otoliths along the same axis that counts were made. The distance from the outer edge of the two most recently completed opaque zones to the edge of the otolith was measured. From these measurements, the marginal increment ratio (MIR) was calculated as the state of completion of the marginal increment as a percentage (%) of the previous increment (i.e. relative marginal increment). For otoliths with only one opaque zone, the absolute marginal increment was measured. These measurements were taken on all otoliths with clear increments at the terminal edge, although the measurements were probably most accurate for age classes one to five where the width of individual opaque zones is still relatively large. Measurements were made using an image-analysis system; images were acquired with an Olympus F-view II digital camera mounted on the Leica Wild stereo microscope connected to a PC computer. AnalySIS 3.2 (Soft Imaging System) was used to take the measurements.

To assess the consistency of otolith interpretation, a second reader (OR2) read 10% of the otoliths. OR2 was experienced in reading sectioned southern bluefin tuna otoliths, but not albacore otoliths. OR2 received limited training in otolith interpretation via annotated otolith images and a learning set of 85 otoliths. Each of the otoliths was then read twice by OR2 and a final count estimated. An edge classification was assigned as either narrow (marginal increment < 30% complete) or wide (marginal increment > 30% complete) for otoliths with counts > two years of age.

6.3.2 Fin spines

To compare age estimates from different hardparts of the same fish, fin spines were selected from a subsample of 234 fish. Spines were selected based on fish length and sex from several sampling locations (Table 3). The spines were sectioned using the protocols of Rodriguez-Marin *et al.* (2007). Sections were cut starting at $d/2$, where d is the diameter of the fin spine above the “hollows”. Several serial cross sections 500 µm thick were made from this position. The sections were embedded in clear casting polyester resin and mounted on glass slides with resin.

As with otoliths, opaque (dark) and translucent (light) zones were visible across the sectioned spine when viewed under transmitted light on an Olympus BX51 compound microscope at a low magnification (Figure 3). The translucent zones were observed in different forms: fine or thick single zones, and double or triple translucent zones that were separated by narrow opaque zones. Multiple translucent zones were considered to belong to the same zone if the distance between them was less than the distance to the preceding and subsequent translucent zone, and the translucent zones converged at the vertex of the spine (Megalofonou, 2000; Santiago and Arrizabalaga, 2005).

To be consistent with the otolith reading, the number of opaque zones observed was counted only if a translucent edge was visible after the zone. In an attempt to account for inner opaque zones in larger fish that may have been obscured by resorption or extra vascularisation, the diameter of opaque zones in younger fish was used to assign a count to the first observed opaque band in sections of larger fish. This assigned count was added to the number of subsequent opaque zones observed to obtain a total count.

The spines were read at least twice by the same reader (OR3), without reference to the previous readings, size of fish or date of capture, or to the otolith-based counts. The reading protocol was identical to that used for otoliths and a final count of opaque zones with a confidence score was obtained for each spine section. If no obvious pattern could be seen in the spine section, estimate count was not recorded. MIR measurements and calculations were made as for otoliths above. The diameter of the section to the outer edge of the last two opaque zones and to the edge of the spine was measured.

6.3.3 Precision

The precision of readings (intra- and inter-reader consistency) was assessed using the index average percent error (IAPE) (Beamish and Fournier, 1981). Age-bias plots were used to detect systematic disagreement between age estimates obtained from otoliths and spines (Campana *et al.*, 1995) and a paired *t*-test used to compare the age estimates obtained from otoliths and spines.

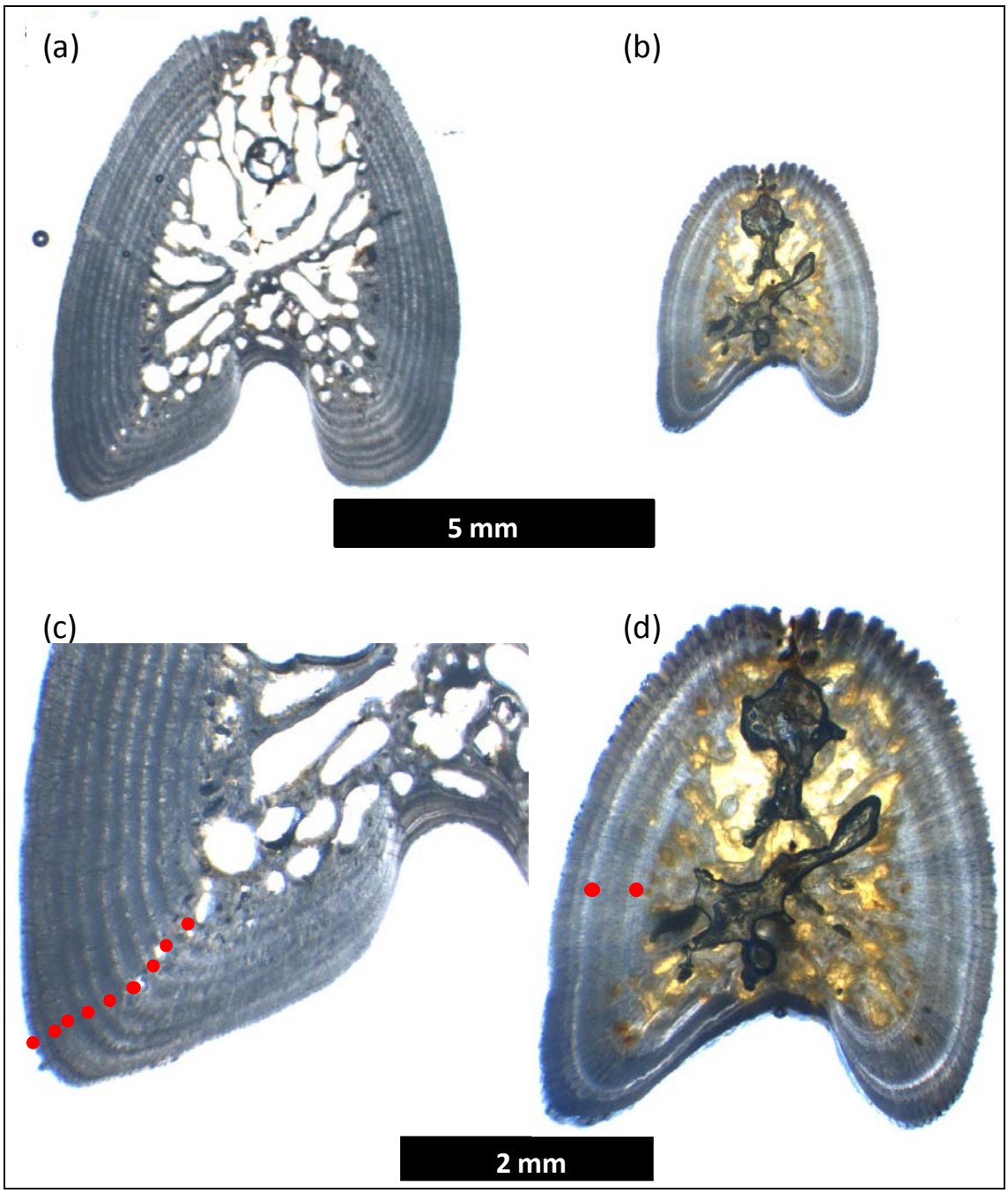


Figure 3. Images of transverse sections of spine from 2 albacore: #692 (a and c) and #628 (b and d) at two magnifications. Fork length, spine diameter, zone counts for #692 and #628 were 105 cm, 6.36 mm and 12; and 68 cm, 3.67 mm, and 2 respectively. The zones counted are indicated by red dots at the transition between opaque (dark) and translucent (light) zones. It was estimated that 3 zones were obscured (not visible) in the core of # 692 based on the data in Table 9 (below) and this number was added to the number of visible zones to produce a final count of 12.

6.3.4 Age validation

Location of the first annual increment

To estimate the location of the first opaque growth zone in otoliths, micro-increment analysis and annual ageing was undertaken for 68 juveniles ranging in size from 43 to 56 cm *FL* sampled in the months of January to April (Table 3). Initially, 18 pairs of otoliths were selected and one transverse section incorporating the primordium was prepared from each. For micro-increment analysis, the sections were attached to microscope slides using Crystalbond thermoplastic glue and ground with wet 1,200 grit sandpaper and polished with water and aluminium powder (0.3 mm) until the primordium was reached and the section was approximately 75-100 μm thick. For annual ageing, the sections were prepared as above but were polished to a thickness of 400 μm. For micro-increment analysis, the number of (assumed) daily increments was counted by OR2 under high magnification on a dissecting microscope. Counts were made from the primordium to the terminal edge of the otolith long the ventral arm of the section. Measurements were taken from the first inflection point to the 365th increment (age one year; Y1) and to the edge of the otolith (Figure 2). For annual ageing, a measurement was made from the first inflection point to the outer edge of the first opaque zone and to the edge of the otolith by OR1. Comparisons were made between the location of the 365th micro-increment and the opaque zone on the sister otoliths.

Transverse sections were then prepared from a further 50 otoliths for microincrement analysis. The number of (assumed) daily increments visible in each section was counted and the distance from the first inflection point to the otolith edge measured by OR2. Each section was then examined by OR1 and if an opaque increment was visible, the distances from the first inflection point to the outer edge of the first opaque zone and to the edge of the otolith were measured.

Direct validation

As part of SPC's SCIFISH project, a mark-recapture experiment was conducted for albacore in New Zealand waters. A total of 1457 albacore (44 to 100 cm *FL*) were captured by troll fishing in Jan-Mar 2009, and 92 albacore (52 to 97 cm *FL*) captured by

longline fishing in Apr-May 2010. Each fish was given an injection of oxytetracycline (OTC; 200 mg/ml) at an approximate dosage of 25-50 mg/kg body weight using a 40 mm 18-gauge needle in an automatic syringe injected deeply within the muscle tissue under the first dorsal fin. Each fish was also tagged with a conventional plastic tip 140 mm PDAT Hallprint™ dart tag.

Two OTC marked fish were recaptured from which the otoliths and fin spines were collected. Four serial transverse sections were prepared for one otolith from each pair using the methods described above for annual age estimation. Five serial sections were prepared for each spine using the methods described above. Without knowledge of time at liberty, the total number of opaque zones and the number of zones after the OTC mark was counted by OR1 and OR3 for each otolith and spine respectively.

Indirect validation

Marginal increment ratio analysis was undertaken as an indirect method of validation of the periodicity of opaque zone formation in otoliths. MIR data were divided into a western region (west of 180° E) and eastern region (east of 180° E) for comparison of broad spatial scale variation in increment formation. Mean MIR for each region, age class (count) and month were estimated to examine annual, spatial and age-specific patterns in opaque increment formation. There were several months in 2009 and 2010 when sample sizes were low or when no samples were collected, particularly in the eastern region. A single, orthogonal analysis of region × year × month × age was not possible because of this uneven distribution of the data. Accordingly, separate fixed factor analyses of variance (ANOVA) were used to test for the effects of year, region and age on MIR, and their interaction with month. The first ANOVA tested for the effect of year (2009, 2010) and age for age classes four, five and six years in the western region to determine whether the timing of opaque increment formation varied between years and age classes. A second ANOVA tested for the effect of region for both years and all age classes combined to determine whether the timing of opaque increment formation varied between regions. Significant interactions between any factor and month were explored using Bonferroni adjusted pairwise comparisons to determine in which months differences in MIR occurred.

6.4 Spatial variation in growth

For analysis of growth, estimates of annual age were obtained for 1899 albacore of known sex sampled in 2009 and 2010 (Table 4). We used an information theoretic, multi-model inference approach to determine the optimal growth model for albacore (Katsanevakis and Maravelias 2008). We fitted length-at-age data to a set of five candidate models commonly used for teleosts which included the von Bertalanffy (VBGM) (von Bertalanffy, 1938), Gompertz (Gompertz 1825), Logistic (Ricker 1975) and Richards (Richards, 1959), and the generalised growth model proposed by Schnute and Richards (1990) of which all the other models are special cases. The form of the VBGM was:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}) \quad (1)$$

where L_t is the fork length at age t, L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year^{-1}), and t_0 is the age at which fish have a theoretical length of zero.

Table 4. Number of albacore from which age estimates obtained for male, female and unknown sex individuals in each region of the south Pacific. High seas 1 refers to the waters between the Australian and New Caledonian EEZs, High seas 2 refers to the waters south of the Pitcairn Islands.

Region	Female	Male	Unknown sex	Total
American Samoa	72	122		194
Australia	455	219	4	678
Cook Islands	41	111		152
Fiji	15	92	1	108
French Polynesia	103	123		226
High seas 1	49	11		60
High seas 2	8	9	55	72
New Caledonia	85	105	7	197
New Zealand	89	82	3	174
Tonga	53	55		108
Total	970	929	70	1969

The Gompertz and Logistic models are both three parameter sigmoidal curves that assume that the growth rate decreases exponentially with size. They typically characterize growth well where growth is relatively slow early in life (Griffiths *et al*., 2010). The form of these models was:

Gompertz $$L_t = L_\infty e^{-e^{-k(t-t_0)}} \quad (2)$$

Logistic $$L_t = L_\infty (1+e^{-k(t-t_0)})^{-1} \quad (3)$$

where L_∞ is the mean asymptotic length, k is the rate of exponential decrease of the relative growth rate with age (year^{-1}), and t_0 is the age at the inflection point of the curve.

The four parameter sigmoidal Richards model is equivalent to the generalised VBGM proposed by Pauly (1979) and the form used here was:

$$L_t = L_\infty (1+1/p) e^{-k(t-t_0)})^{-p} \quad (4)$$

where L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year^{-1}), t_0 is the age at the inflection point of the curve, and p is a dimensionless parameter.

The five parameter Schnute-Richards model was proposed as an omnibus approach to modelling fish growth and is useful for modelling growth where the relationship between length and age is allometric (Quinn and Deriso, 1999). The form of the Schnute-Richards model was:

$$L_t = L_\infty (1+\delta e^{-kt^\nu})^{1/\gamma} \quad (5)$$

where L_∞ is the mean asymptotic length, k is a relative growth rate parameter (year$^{-\nu}$) and δ, γ and ν are dimensionless parameters for which particular values provide special cases equivalent to models (1) to (4).

The five candidate models were fitted to albacore length-at-age data using non-linear least squares in R version 2.13.2 (R Development Core Team, 2011. We evaluated the relative support for each model using Akaike's Information Criteria for small sample sizes (AIC_c: Burnham and Anderson, 2002). Models with an AIC_c value within two of that calculated for the best approximating model (lowest AIC_c) were considered to describe the data equivalently well (Burnham and Anderson, 2002). The Akaike weight, w_i (Burnham and Anderson, 2002), of each model i was calculated to quantify the plausibility of each model, given the data and the set of five models using:

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{k=1}^{5} \exp(-0.5\Delta_i)} \quad (6)$$

where $\Delta_i = AIC_{c,min} - AIC_{c,i}$. The Akaike weight is considered as the weight of evidence in favour of model *i* being the actual best model of the available set of models.

We evaluated support for sex-specific growth curves by comparing the AICc from the best fit model for all data to that from the same model fitted separately to male and female data. This comparison indicated substantial support for separate growth curves for females and males. Accordingly, separate growth models for females and males were used to evaluate support for longitudinal variation in albacore growth across the South Pacific Ocean.

Evidence for longitudinal variation in length-at-age was examined using generalised linear models (GLM) and linear mixed-effects models (LME) to model the effects of longitude on the residual length-at-age data from the growth models for males and females. The relationship between the residuals and longitude was explored by modelling longitude as a linear and non-linear (cubic spline with 2 or 3 degrees of freedom) variable in both the GLM and LME. AIC_c was used to determine whether there was support for including longitude in the models and, if so, which functional form for the relationship between the residuals and longitude was best supported by the data. Fishing set was modelled as a random effects term in the LME models because multiple individual fish were often sampled at the same time from a single location and, therefore, not all samples were independent. Results from LMEs and GLMs were compared graphically to evaluate the effects of the non-independent sampling. To determine whether samples collected at higher latitudes from New Zealand and Australia confounded the longitudinal analyses for all data, the same analyses were conducted on a subset of the length-at-age data from latitudes north of 25°S. Longitudinal variation in the pattern of albacore growth was explored by including additional parameters in the growth models for females and males. The growth parameters L_∞ and k were expected to be more affected by longitude than other growth parameters. Accordingly, L_∞ and k were modelled as linear or non-linear functions of longitude in the best-fit growth models for females and males, and fitted to length-at

age data using least squares. AIC_c and Akaike weights were used to determine whether there was support for including longitude in the growth models and, if so, which functional form for the relationship between each growth parameter and longitude was best supported by the data. To estimate the magnitude of variation in growth of albacore that could be expected across the longitudinal range of samples collected in this study, we calculated the predicted growth parameters from the best-fit growth models that incorporated parameters for longitude, and plotted the resulting growth curves, for the central (185° E), west (150° E) and east (220° E) longitudes of the study area.

6.5 Reproductive dynamics

6.5.1 Data collection

Gonads were collected from 3327 albacore in the current project. To provide as comprehensive data coverage as possible, female reproductive data collected in a pilot study in Australia (see Farley and Clear, 2008) were combined with the current data (n=361). The pilot project included fish landed in ports that were not sampled in the current project. Table 5 shows the number of albacore analysed by region and sex. To examine longitudinal variation in reproductive dynamics, the sampling area was divided into three regions to obtain a similar number of samples for each region in the spawning latitudes: region A is west of 175˚E; region B is from 175˚E to 155˚W and region C is east of 155˚W (see Figure 26; Section 7.4). The longitude 175˚E and 155˚W lines were taken as a convenient boundary between sampling areas. Gonad index (*GI*) was calculated as: $GI = GW/FL^3 \times 10^4$, where GW is gonad weight (g) and *FL* is fork length in cm. Sex ratio was calculated and chi-square tests were used to test for differences from an expected ratio of 1:1. Estimates of annual age were obtained for 951 females sampled between January 2009 and December 2010.

Table 5. Number of albacore with gonads analysed by region. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands.

EEZ	Female	Male	Total
American Samoa	163	241	404
Australia	641	855	1496
Cook Islands	55	131	186
Fiji	41	160	201
French Polynesia	165	198	363
High seas 1	21	9	30
High seas 2	3	6	9
New Caledonia	104	122	226
New Zealand	264	185	449
Tonga	70	63	133
Total	1527	1970	3497

6.5.2 Female histological classification

Ovaries from females ≥70 cm *FL* (n=1219) were selected for histological analysis as this size was well below the minimum size at maturity (~80 cm) previously estimated for albacore. Tissue samples were embedded in paraffin and standard histological sections prepared (cut to 6 μm and stained with Harris' haematoxylin and eosin). Ovaries were classified using criteria similar to those developed for northern anchovy (Hunter and Macewicz, 1980; 1985a; 1985b), skipjack tuna (Hunter *et al.*, 1986), yellowfin tuna (Itano, 2000; Schaefer, 1998), bigeye tuna (Schaefer *et al.*, 2005), and southern bluefin tuna (Farley and Davis, 1998) based on:

1. The most advanced group of oocytes (MAGO) present (Figure 4A-F): unyolked, early yolked, advance yolked, migratory nucleus, and hydrated
2. The presence and approximate age of postovulatory follicles (POF's) (Figure 4E-F): absent, new (stage 1), <12 hours (stage 2), 12-24 hours (stage 3). The ages of POFs were estimated based on criteria developed for skipjack, bigeye and yellowfin tunas (Hunter *et al.*, 1986; Nikaido *et al.*, 1991; Schaefer, 1996).
3. The level of alpha atresia of advance yolked oocytes (Figure 5A): absent, <50%, 100%
4. The presence/absence of beta stage atresia (Figure 5A).
5. The presence/absence of maturity markers indicating previous ovary development. The maturity markers used were (i) residual hydrated oocytes which may be

encapsulated by connective tissue (Figure 5B), and (ii) very late stages of atresia (gamma/delta) (Figure 5C-F) which are a yellow-orange-brown colour and are often referred to as melano-macrophage centres or brown bodies (Saidapur, 1978; Hunter and Macwicz, 1985b; Ravaglia and Maggese, 1995).

The maturity status and reproductive class of each female was determined based on the criteria given in Table 6. Females were classified as mature by the presence of yolked oocytes (advanced, migratory nucleus or hydrated), atresia of yolked oocytes (alpha or beta stage) and/or maturity markers in the ovary. Immature fish were characterised by the presence of unyolked or early yolked oocytes in the ovary and no atresia or maturity markers. Histological analysis of ovaries removed the potential high rate of misclassification using macroscopic staging methods, and all histological sections were read at least twice before a reproductive class was assigned.

6.5.3 Oocyte diameter

To determine if longitudinal variation existed in the size of the most advanced group of oocytes, up to 30 sections were randomly selected from ovaries with advanced yolked or migratory nucleus oocytes from each region (A to C). Sufficient ovaries were available in all three regions only for the months of October to December. Insufficient ovaries with hydrated oocytes were available in all regions for comparison. For each section, the diameter of five oocytes in the MAGO was measured using an Olympus F-view II digital camera mounted on the Leica Wild stereo microscope and AnalySIS 3.2 software, and the mean oocyte diameter calculated for each ovary.

Figure 4. Histological sections of albacore ovaries showing examples of development classes, oocyte stages and postovulatory follicles. (A) unyolked oocytes in an immature ovary, (B) advanced yolked oocytes in a spawning capable ovary, (C) migratory nucleus oocyte in a spawning ovary, (D) hydrated oocytes in a spawning ovary, (E) <12 hour POF in a spawning ovary, (F) >12 hour POF in a spawning ovary. UY = unyolked, EY = early yolked, AY = advanced yolked, MN = migratory nucleus, H = hydrated, POF = postovulatory follicle.

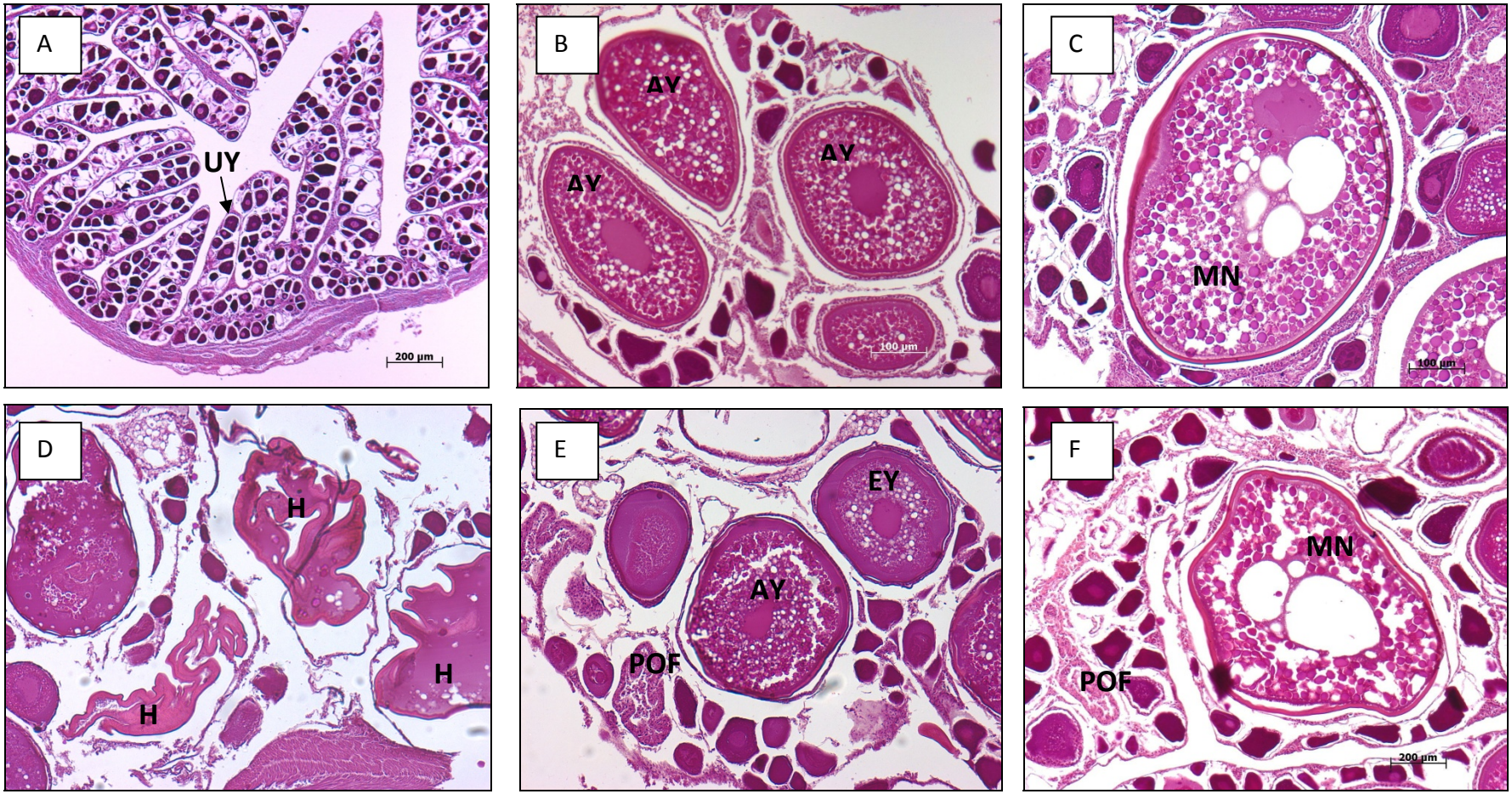


Figure 5. Histological sections of albacore ovaries showing examples of development classes and maturity markers. (A) alpha and beta atresia in a regressed 1 ovary, (B) residual hydrated oocytes in a regenerating ovary, (C-F) late stage atresia (brown bodies). α = alpha atresia, β = beta atresia, RH = residual hydrated oocyte, EY = early yolked oocyte, BB = white arrows.

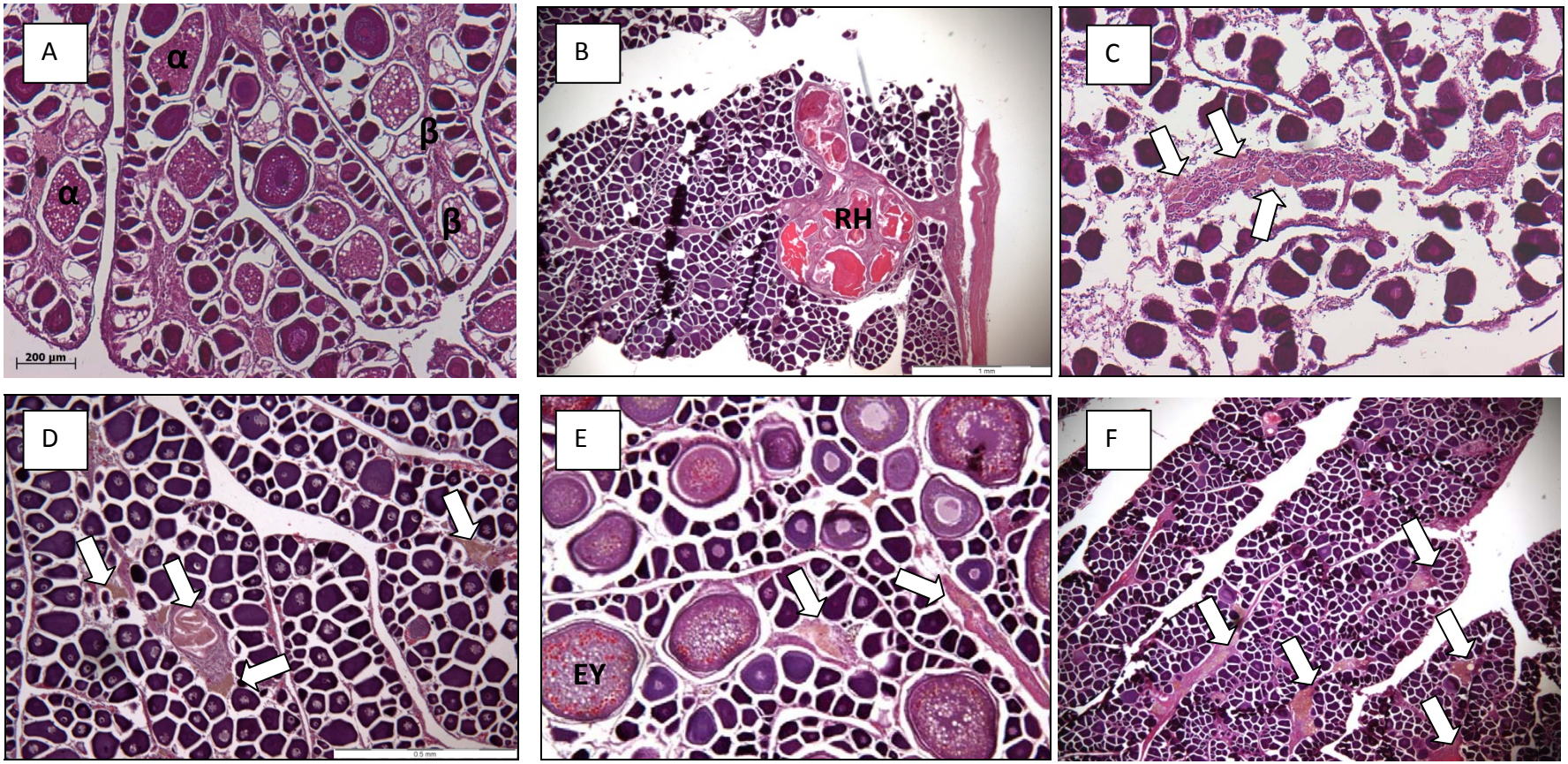


Table 6. Histological classification criteria for albacore. MAGO = most advanced group of oocytes, POF = postovulatory follicle.

Class	Maturity status	Activity	Development class	MAGO and POF stage	α and β atresia of yolked oocytes	Maturity markers[1]
1	Immature	Inactive	Immature	Unyolked, no POFs	Absent	None
2	Immature	Inactive	Developing	Early yolked, no POFs	Absent	None
3	Mature	Active	Spawning capable	Advanced yolked, no POFs	<50% α atresia, β atresia may be present	May be present
4	Mature	Active	Spawning	Migratory nucleus or hydrated and/or POF's	<50% α atresia, β atresia may be present	May be present
5	Mature	Inactive	Regressing - potentially reproductive	Advanced yolked, no POFs	>50% α atresia, β atresia present	May be present
6a	Mature	Inactive	Regressed 1	Unyolked or early yolked, no POFs	100% α atresia, β atresia may be present	May be present
6b	Mature	Inactive	Regressed 2	Unyolked or early yolked, no POFs	No α atresia, β atresia present	May be present
7	Mature	Inactive	Regenerating	Unyolked or early yolked, no POFs	Absent	Present

[1] gamma and delta stages of atresia (brown bodies) and /or residual hydrated oocytes.

6.5.4 Spawning frequency and batch fecundity

Spawning frequency of females was estimated by the postovulatory follicle method of Hunter and Macewicz (1985a). This method uses the incidence of mature females with postovulatory follicles less than 24 hours old to define the fraction of the population spawning per day (spawning fraction) which is then converted into spawning frequency (inverse of spawning fraction). The daily cycle of oocyte maturation, spawning time, and POF degeneration rate were examined using ovaries obtained from 71 females sampled immediately after death in the Cook Islands and American Samoa. The time of death was compared to the MAGO present in the ovary and the age assigned to POFs.

Batch fecundity was estimated by the gravimetric method (Hunter *et al.*, 1985) for females with late stage migratory nucleus or hydrated oocytes. For each fish, a core subsample of between 0.05-0.09 g was taken from the middle region of each ovary lobe, weighed to the nearest 0.01 mg, and fixed in 10% buffered formalin. Each subsample was teased apart and the number of migratory nucleus or hydrated oocytes was counted under a Wild M5a stereomicroscope. The number of oocytes per weight of the subsample was raised to the weight of the ovary lobe to give an estimate of batch fecundity for the lobe. Estimates for the two lobes were summed to give a batch fecundity estimate for the fish.

6.6 Spatial variation in maturity

6.6.1 Data collection

The development class and maturity status of 1496 females was obtained from the reproduction component of the project. As already shown, ovaries were sampled from a broad geographic area in the southwest Pacific, with almost the full latitudinal range of the species sampled west of 175˚E (see Figure 1). Estimates of annual age were obtained for 951females sampled in 2009 and 2010 (Table 7) which included all females ≥ 70 cm *FL* sampled in Australia.

Table 7. Number of female albacore with maturity status and decimal age obtained by region in the South Pacific. High seas 1 refers to the waters between the Australian and New Caledonian Exclusive Economic Zones, High seas 2 refers to the waters south of the Pitcairn Islands.

Region	Maturity status	Age estimate
American Samoa	159	65
Australia	605	451
Cook Islands	55	39
Fiji	19	15
French Polynesia	164	101
High seas 1	55	51
High seas 2	3	3
New Caledonia	102	84
New Zealand	264	89
Tonga	70	53
Total	1496	951

6.6.2 Maturity analysis

We used an information theoretic, multi-model inference approach to compare alternative models of the relationships between maturity state and the potential covariates (*FL*, age, latitude and longitude). We evaluated the relative support for each model using Akaike's Information Criteria for small sample sizes (AIC_c: Burnham and Anderson, 2002) using the methods given in Section 6.4 above (see equation 6). We examined variation in length- and age-at-maturity with latitude and longitude using generalized linear mixed models, with the lme4 package (Bates *et al.,* 2011) in R version 2.13.2 (R Development Core Team, 2011). The maturity state was treated as a binomial response variable with logit link function, and modelled as a function of individual covariates age and *FL*, and the spatial covariates latitude and longitude. These continuous covariates were modelled as linear variables or as cubic splines with nodes at quantiles of the data, with AIC_c used to estimate the most appropriate number of degrees of freedom. Fishing set was modelled as a random effect term, because multiple individual fish were often sampled at the same time from a single location and, therefore, not all samples were independent. The generalised model used to predict the probability of an individual being mature (p) was:

$$p(Mature_{i,w}) = logit\ (f(C_i) + g(latitude_i) + h(longitude_i) + X_w + error_i)$$

where *f()*, *g()* and *h()* are cubic splines with *l*, *m* and *n* degrees of freedom, C_i is the fork length or age of each individual, and X_w is a random effect associated with set *w*.
We compared the relative explanatory power of *FL* and age as predictors of maturity by taking the subset of data for which ages had been estimated and comparing model fits using AIC_c.

6.6.3 Maturity ogive for the ETBF

The Spawner Per Recruit (SPR) reference points in the decision rule of the harvest strategy for albacore in the ETBF currently assume a single maturity ogive for females. Given the spatial differences observed in life history stages with latitude for albacore, a single representative maturity ogive cannot be obtained by simply fitting a model to all of the maturity data because sampling was not proportional to female abundance at all latitudes. To estimate a single maturity ogive for the ETBF, we first fitted a logistic model to the maturity data for the ETBF including an effect for latitude, where latitude was divided into discrete levels. Specifically, we treated maturity state as a binomial response variable ('mature' or 'immature') and modelled it as a function of fork length (FL) and latitude using a logit link function. The model was fit in R using the glm function, as follows:

> glm(Maturity = ='Maturity'~FL*Latitude -1, family = binomial(link='logit'), data=maturity.dat)

This model is similar to the one described in the previous section (above), except that longitude is not included because it was not found to be significant (for the ETBF region, or more broadly for the wider southwest Pacific region – see Results 7.5 below). Furthermore, latitude was included as a factor with 3 levels, instead of as a cubic spline, so that the proportion of mature females could be predicted in discrete regions for which we have estimates of abundance (see below for details).

Using this model, we predicted the proportion of females of length *l* that are mature in each latitudinal area *a*, denoted by $P(mature \mid l, a)$. Then, to estimate the proportion of

females of length *l* that are mature across all areas, $P(mature|l)$, we calculated a weighted average of the area-specific predicted proportions mature, where the weights are the estimated proportions of female abundance by length in each latitudinal area ($P(a|l)$). That is:

$$P(mature|l) = \sum_{a=1}^{3} P(mature|l,a) * P(a|l)$$

where

$$P(a|l) = \frac{N_f(a,l)}{\sum_{a=1}^{3} N_f(a,l)}.$$

$N_f(a,l)$ is the number of females of length *l* in area *a*. We estimate $N_f(a,l)$ as follows:

$$N_f(a,l) = N(a) * p(l|a) * p(f|l,a),$$

where $N(a)$ is number of fish (male and female) in latitudinal area a, $p(l|a)$ is the proportion of fish in area a of length l, and $p(f|l,a)$ is the proportion of fish of length l in area a that are female.

For the results presented in this report, $N(a)$ was obtained using estimates of the relative number of fish by area from standardised CPUE (Campbell, 2011); noting that only relative abundance estimates are necessary since the weights are proportions scaled to sum to 1. The area definitions used in the CPUE standardisation for albacore are shown in Figure 6. For the purpose of estimating a single maturity ogive for the ETBF, we combined CPUE areas within the same latitudinal bands since we have no evidence of longitudinal differences in maturity and also because some of the CPUE areas have small sample sizes. This resulted in 3 latitudinal areas (Figure 6):

1. Lat area 1 = CPUE areas 1 and 2;
2. Lat area 2 = CPUE areas 3, 4 and 5;
3. Lat area 3 = CPUE areas 6 and 7.

Ideally, $p(l \mid a)$ would be estimated using length samples from the catch within each area, assuming the samples are representative of the population, or else taking into account selectivity. This information was not readily available, as size sampling of albacore has only recently been initiated in the ETBF, so for illustrative purposes we used the length distribution from all fish sampled in the ETBF for this study (males and females combined). We used 5cm length classes (46-50cm, 51-55cm, etc.) to obtain adequate sample sizes within each length class and latitudinal area. Finally, we estimated the proportion of females within each length class and latitudinal area, $p(f \mid l, a)$, from the same sample data, assuming that the sex ratio at length in our sample is representative of the population.

Lastly, we calculated the variance of the predicted proportion of mature females by length for the ETBF using:

$$Var\left\{\hat{P}\left(mature \mid l\right)\right\} = Var\left\{\sum_{a=1}^{3} \hat{P}\left(mature \mid l, a\right) * \hat{P}\left(a \mid l\right)\right\}$$

For simplicity, we assume that $\hat{P}\left(a \mid l\right)$ is known accurately, in which case the above reduces to

$$Var\left\{\hat{P}\left(mature \mid l\right)\right\} = \sum_{a=1}^{3} \left\{\hat{P}\left(a \mid l\right)\right\}^2 Var\left\{\hat{P}\left(mature \mid l, a\right)\right\}.$$

where the variance of $\hat{P}\left(mature \mid l, a\right)$ can be obtained using predict.glm in R. To account for uncertainty in $\hat{P}\left(a \mid l\right)$ would require having estimates of uncertainty for the area-specific CPUE abundance estimates, the area-specific length distributions, and the area and length-specific sex ratio estimates. Variance formulas for the product of random variables would then be required.

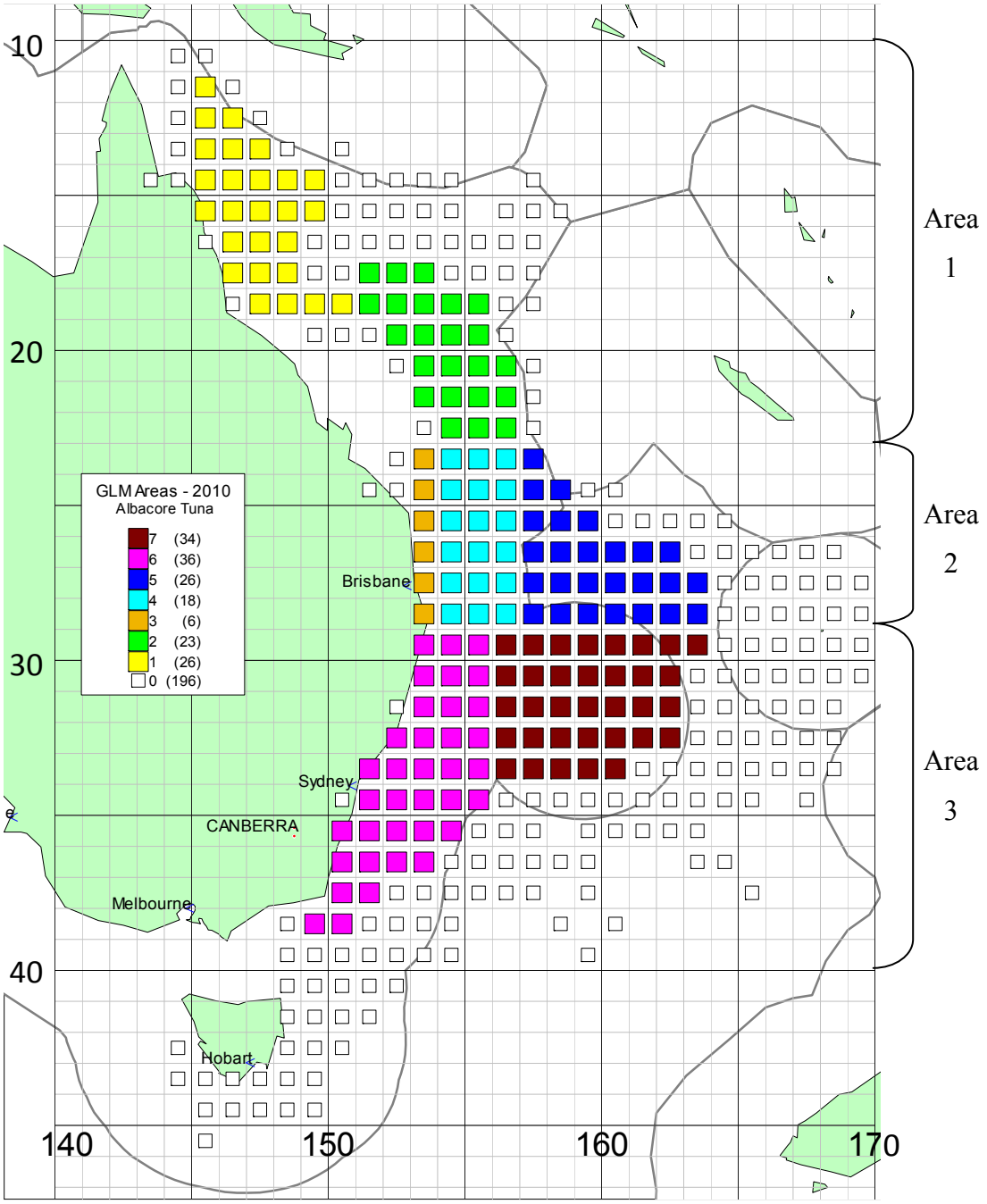


Figure 6. Map of ETBF indicating the designated areas used in the GLM analyses to standardize CPUE for albacore tuna by Campbell (2011). The number in brackets indicates the number of 1-degree squares associated with each area. Latitude areas 1 to 3 for statistical analysis of maturity are shown.

7. Results and discussion

7.1 Length-weight relationship

The relationship between *FL* and *W* did not differ significantly between male and female albacore in Australia ($F = 3.32$, df = 1, $P = 0.07$) or New Zealand ($F = 0.92$, df = 1, $P = 0.34$), or for sexes combined between Australia and New Zealand ($F = 3.90$, df = 1, $P = 0.05$), so data were pooled across sexes and regions (Figure 7). The estimated parameters of the *FL–W* relationship for all fish measured and for those caught in the ETBF are given in Table 8.

A comparison of published *FL-W* relationships from the South Pacific suggests the presence of geographic and/or temporal variation in the condition of albacore. Albacore sampled in the current study were heavier on average for length compared to previous studies (Table 8; Figure 8) and also appear to be in better condition than fish caught off the east coast of Australia by Japan in the late-1980s to early-1990s (Campbell, 2007). The overall lack of comprehensive studies on albacore length-weight relationships in the South Pacific, however, makes it difficult to determine if this increase in condition is a widespread trend occurring across the South Pacific, or a more localised phenomenon.

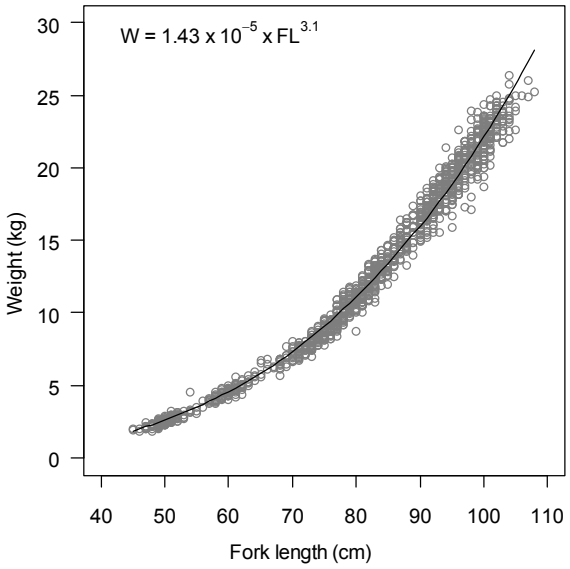


Figure 7. Weight-at-length data and fitted power curve for South Pacific albacore from Australian and New Zealand waters (n=1756).

Table 8. Regression coefficients for albacore length-weight (cm-kg) relationships in the South Pacific (sex combined). STCZ = Subtropical Convergence Zone, AS = American Samoa, LL = longline. * all fish with *FL* measured, not only those with *FL*-*W*.

#	Area	a^1	*b*	*n*	*FL* (cm)	Mean *FL*(cm)	Years	Gear	Source
1	Aus/NZ	1.43	3.10	1756	46-102	80.0	07-10	LL & troll	Current study
2	Aus	0.96	3.18	1273	56-108	88.2	07-10	ETBF LL	Current study
3	Aus	0.82	3.20	22530	50-120	83.1*	87-97	Jap. LL	Campbell (2007)
4	STCZ	2.74	2.94	39	59-92		82	Troll	Hallier & Gall (1983)
5	AS	8.84	2.68	887	78-108				Foreman (1980)
6	STCZ	3.14	2.90	1268	~47-96		88-89	Troll	Hampton *et al.*, 1989
7	NZ	4.41	2.86	31273	38-99*	63.7*	99-05	Troll	Griggs (2005)
8	NZ	3.61	2.81	3626	37-135*	79.8*	99-04	LL	Griggs (2005)

[1] $x10^{-5}$

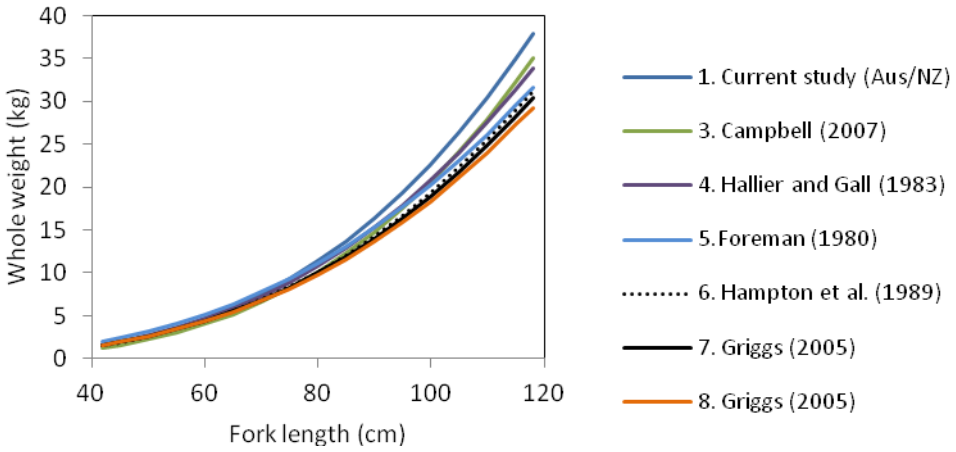


Figure 8. Length-weight relationships for albacore in the South Pacific from published studies (see Table 8).

Previous studies indicate that albacore caught in New Zealand and the STCZ are in relatively poor condition (compared to the current study), especially for fish > 80 cm. Although we sampled only 9 fish of this size in New Zealand/Tasmania (i.e. south of 38°S), they were also all in poor condition relative to the mean. Of these, three were female and they were post-spawning (classed as regressed or regenerating; see Section 7.4 below). The presence of post-spawning fish at high latitudes during the sampling months (summer to autumn for all studies) may explain the lower length to weight relationship reported at these latitudes. In addition, morphometrics may not be the best

indicator of fish condition and measuring fat content may be better proxy in future studies (e.g., Willis and Hobday, 2008).

7.2 Annual age determination and validation

7.2.1 Otolith reading and precision

The clarity of increments in albacore otoliths varied between individuals. Many otoliths contained increments that were distinct and regularly spaced while others were more difficult to interpret. Opaque growth zones were generally wide with alternating narrow translucent zones. The distal edge of the first opaque zone was often the most difficult to locate as it was less distinct than subsequent zones. Bumps along the medio-ventral ridge, however, were occasionally associated with the opaque zones assisting in their identification. Paired opaque zones were often visible at the edge of large otoliths and if joined at the margin they were counted as a single opaque zone (Gunn *et al.*, 2008). Having multiple sections prepared for most otoliths had the advantage of at least one being clear enough to interpret; often the section not including the primordium was easier to interpret.

A final increment count, ranging from 1 to 14 for both males and females, was assigned to 1969 otoliths and the remaining 151 (6.8%) otoliths were either considered unreadable or the MIR could not be measured. The IAPE between readings by OR1 was 4.77% indicating a reasonable level of precision given their 14 year range in estimated age. Overall, 74.3% of the otoliths were given a confidence score of 3 to 5 (45 were given a score of 5). The mean confidence was 2.86 ± 1.09 SD. A significant linear relationship was not found between count and mean confidence score ($P = 0.16$) suggesting that the variation in confidence cannot be explained by variation in age (~otolith size).

A comparison of counts by independent readers found that 53.9% were in agreement and 93.8% were within ± 1. However, counts by OR2 were slightly (but significantly) higher on average relative to OR1 (paired *t*-test; d.f. = 195, $P < 0.001$) (Figure 9a). The classification of the otolith edge was also compared between readers and found to be

different for 33.5% of otoliths. In the majority (92.1%) of these cases, OR2 classified the edge as narrow (an opaque zone had recently finished forming) while OR1 classified the edge as wide (an opaque zone had not recently finished forming). These differences in edge classification are likely to have contributed to the bias in counts if, for example, OR2 counted an additional opaque zone near the otolith edge (i.e. count +1 and a narrow MI) while OR1 did not (i.e. count and a wide MI). To determine if this was the case, 1 was subtracted from OR2's counts when the edge was classified as narrow by OR2 and wide by OR1. Conversely, 1 was added to OR2's counts when the classification difference was reversed. The resulting comparison of counts showed that 92.1% were within ± 1, the age bias was not longer evident (paired *t*-test, $P > 0.05$) (Figure 9b) and the overall IAPE was only slightly higher than the intra-reader IAPE at 6.82%.

7.2.2 Fin spine reading and precision

In the cross sections of fin spines, the clarity of growth increments varied between fish and of the 234 examined, 12 were considered unreadable and not given a final count. The IAPE between readings by OR3 was 5.12%. Only 36.8% of the spines were given a confidence score of 3 or 4 (none were given a score of 5). The mean confidence score was 2.34 ± 0.90 SD. Unlike otoliths, a significant linear (negative) relationship was found between count and mean confidence score ($P < 0.01$) suggesting that spines became more difficult to interpret with increasing age.

In small spines, the core was not obscured by vascularisation and resorption (see Figure 3). In the very smallest spines, up to two zones were apparent and if present we counted as one increment following Body (2010). The mean diameter of the first three opaque zones and the mean diameter of the spine are given in Table 9. In spines with obscured cores, these measurements were used to estimate the number of opaque zones potentially missing due to resorption before the first complete observed opaque zone. The first opaque/translucent zone in the core of spine sections was obscured to some degree due to vascularisation and resorption in 54% of fish aged 3. This percentage increased with age to 100% in sections with 6 zones or more, and in many of these sections the second and third increments were also considered to be obscured.

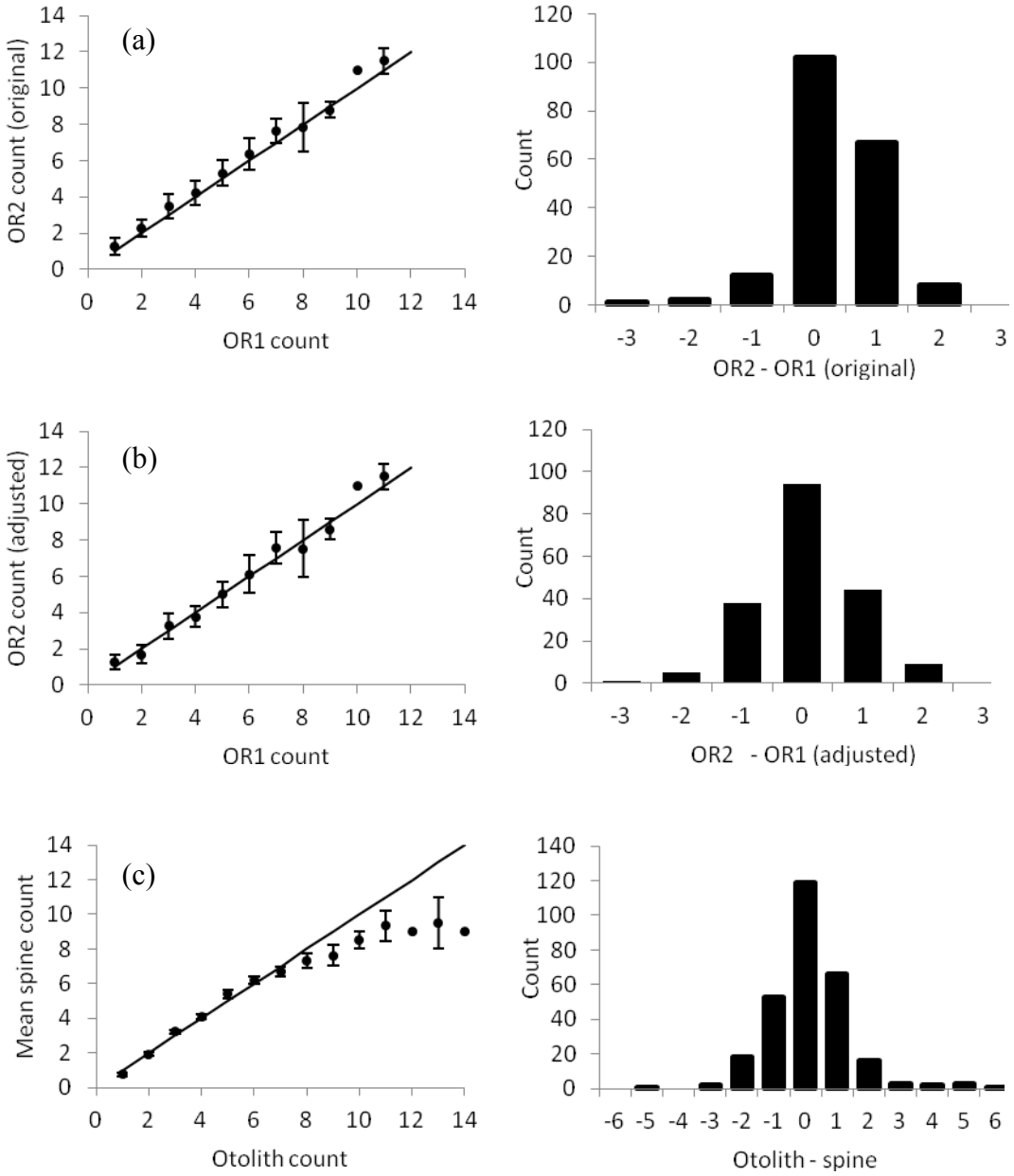


Figure 9. Age bias (left) and age difference (right) plots for comparisons of (a) counts by OR1 and OR2 (unadjusted, n=192), (b) counts by OR1 and OR2 (adjusted, n=191), and (c) counts from otolith and spines (n=292). Error bars are SE.

Table 9. Mean diameter (mm) of the spine and the first three opaque zones used to "assign an age" to the first observed translucent band in sections with the core obscured. Measurements shown in bold were used to estimate the number of opaque zones potentially missing due to resorption before the first complete observed opaque zone.

	Opaque zone count		
	1	2	3
Mean diameter	**2.33**	2.47	2.45
n	**17**	28	26
Mean diameter		**3.14**	3.12
n		**28**	48
Mean diameter			**3.71**
n			**48**
Mean spine diameter	2.93	3.64	4.12
n	17	28	48

7.2.3 Comparison of structures

A direct comparison of counts from otoliths and spines could be made for 205 fish. The age estimate from spines agreed with the estimate from otoliths in 42.0% of cases and 84.9% were within ±1 of each other. To increase the sample size for the comparison of structures, opaque zone counts for otoliths and spines were obtained for 79 albacore sampled in Australia by Farley and Clear (2008) as the otolith readers were the same as for the current study. The overall IAPE for counts between otoliths and spines was 11.8%. The age bias plot that shows there was minimal difference in counts between the two structures up to age seven (Figure 9c). A bias is apparent for age classes older than seven years where otolith-based age estimates were generally higher than spine-based age estimates.

7.2.4 Age validation

Location of the first annual increment

Counts of assumed daily increments were obtained for 16 of the 18 otoliths examined for microincrement analysis and ranged from 185 to 552 days (mean ± S.D. = 392 ± 81). Measurement from the first inflection point to the 365th microincrement (Y1) was obtained for the 15 otoliths with counts > 365 and for one additional otolith for which a final count could not be resolved. The position of Y1 on the otolith occurred after the first opaque zone in 100% of sister otoliths. The average distance from the first inflection point to the outer edge of the first opaque zone was 660 µm, to the 356th increment (Y1) was 759 µm, and to the otolith edge was 944 µm. This confirms that the first opaque zone is being successfully identified in sectioned otoliths as it occurred prior to the first birthday in these fish.

Counts of assumed daily increments were obtained for 47 of the subsequent 50 otoliths from juvenile fish examined and ranged from 258 to 445 days (mean ± S.D. = 352 ± 41). Of these, an opaque zone was visible in 41; the other sections were too thin to clearly locate the opaque zones. Similar to the above, the average distance from the first inflection point to the outer edge of the first opaque zone was 668 µm, and to the edge of the otolith was 926 µm again supporting the conclusion that the first opaque zone is being successfully identified in these fish.

Direct validation

Examination of the otoliths from the two recaptured OTC-injected fish supports the hypothesis of annual formation of growth zones in albacore. For both recaptured fish, an OTC mark was clearly visible in the otolith when viewed under ultraviolet light (Figure 10). Fish no.1 was injected with OTC on 28 February 2009 and recaptured 16 February 2010 and fish no.2 was injected with OTC on 10 May 2010 and recaptured 28 March 2011. The OTC marks in the otoliths of both fish were adjacent to the distal edge of the second last opaque zone suggesting that opaque zones are deposited over summer. The amount of otolith growth in the 11-12 months subsequent to the OTC injection is consistent with expected otolith growth if opaque zones are deposited

annually, since a thin translucent zone is present after the OTC mark and an additional opaque zone is almost complete at the edge of both otoliths. The final opaque zone counts for the two injected fish were two and four with MIRs of 81.3% and 66.7% respectively. The high MIRs indicate that the 3rd and 5th opaque zones were forming at the otolith margin when the fish were recaptured.

Examination of the spines of the two OTC injected fish was more ambiguous. An OTC mark is present on the fin spine of fish no.1 but not of fish no. 2 (Figure 11). It was noted that here was a lot of background fluorescence associated with the spines so it is possibly that the apparent OTC mark for fish no. 1 may be background fluorescence.

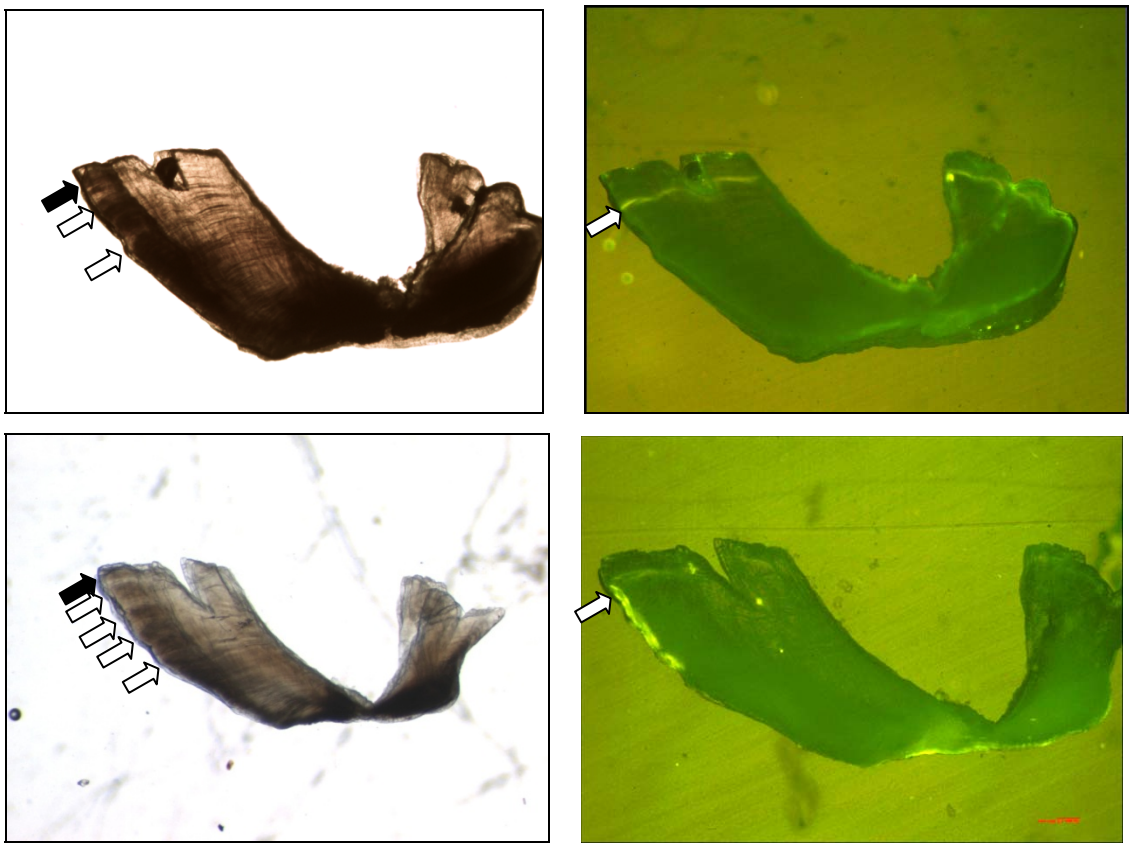


Figure 10. Transverse section of albacore otoliths injected with oxytetracycline (OTC). Fish no.1 (top) and Fish no.2 (bottom). Left: Location of the distal edges of the opaque zones (white arrow) counted under transmitted light with a partially completed opaque zone at the margin (dark arrow). Right: The OTC mark visible under ultraviolet light (white arrow).

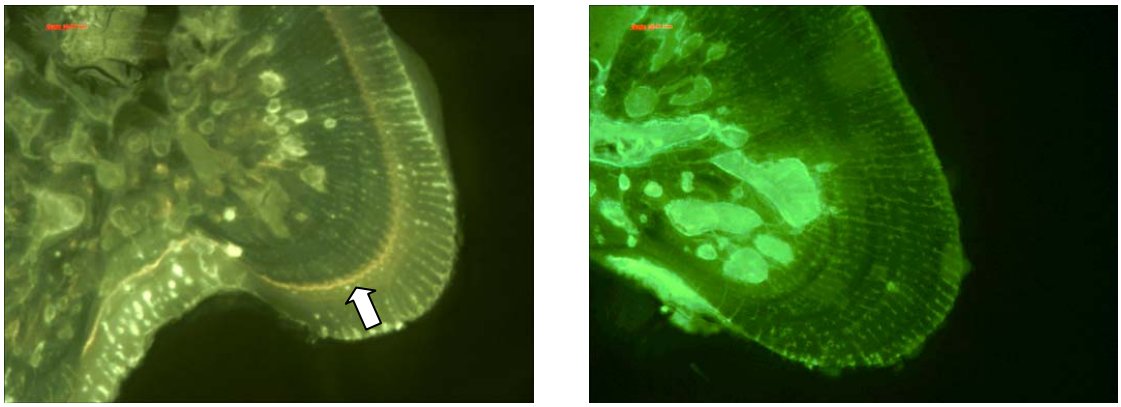


Figure 11. Transverse section of albacore fin spines injected with oxytetracycline (OTC). Left: Fish no.1 with possible location of the OTC mark visible under ultraviolet light (white arrow). Right: Fish no.2, no OTC mark visible.

Indirect validation

Analysis of variance indicated no significant differences in monthly MIR between age classes four, five and six years (Table 10). However, there was a significant year × month interaction indicating that monthly MIR varied between years. This result is most likely due to lower MIRs in June, July and August in 2010 compared to 2009 (Figure 12). To compare the pattern of monthly MIR between regions, it was necessary to pool data across years as there were only 3 months of data for 2009 in the eastern region.Age classes were also pooled for each region based on the inference that MIR did not differ significantly among age classes other than ages four to six years. Analysis of variance for these pooled data indicated that MIR differed significantly between the western and eastern regions for at least some months (region × month interaction) for all age classes combined (Table 11). However, pairwise comparisons, using the Bonferroni adjusted significance value of 0.007 (0.05/7), revealed no significant differences in the monthly MIR between regions. This result is most likely due to slightly higher MIRs in February and lower MIRs in June in the eastern region compared to the western region (Figure 13). For all other months when data were available, the MIRs were similar between the western and eastern regions. MIR data were available for all months in the western region where there was a strong seasonal cycle in MIR indicating that one opaque zone forms per year, between April and September. During these months, the MIR changes from being very large (opaque zone almost fully formed) to very small (new translucent

zone forming). Figure 14 demonstrates of the monthly cycle of the marginal increment in albacore otoliths.

Table 10. Analysis of variance comparing MIRs between 2009 and 2010 and among the four, five & six-year age classes in the western region.

	Df	Sum Sq	RSS	*F*	*P*
Year	1	587	152134	1.75	0.19
Age	2	1661	153208	2.48	0.09
Month	9	10314	161861	3.42	<0.001
Year*Age	2	1876	153422	2.80	0.06
Year*Month	8	6141	157688	2.29	0.02
Age*Month	16	5729	157276	1.07	0.38
Year*Age*Month	14	5224	156771	1.11	0.34

Table 11. Analysis of variance comparing MIRs between the western and eastern regions.

	Df	Sum Sq	RSS	*F*	*P*
Region	1	1649	543124	3.85	0.05
Month	6	13230	554705	5.15	<0.001
Region*Month	6	7500	548975	2.92	0.008

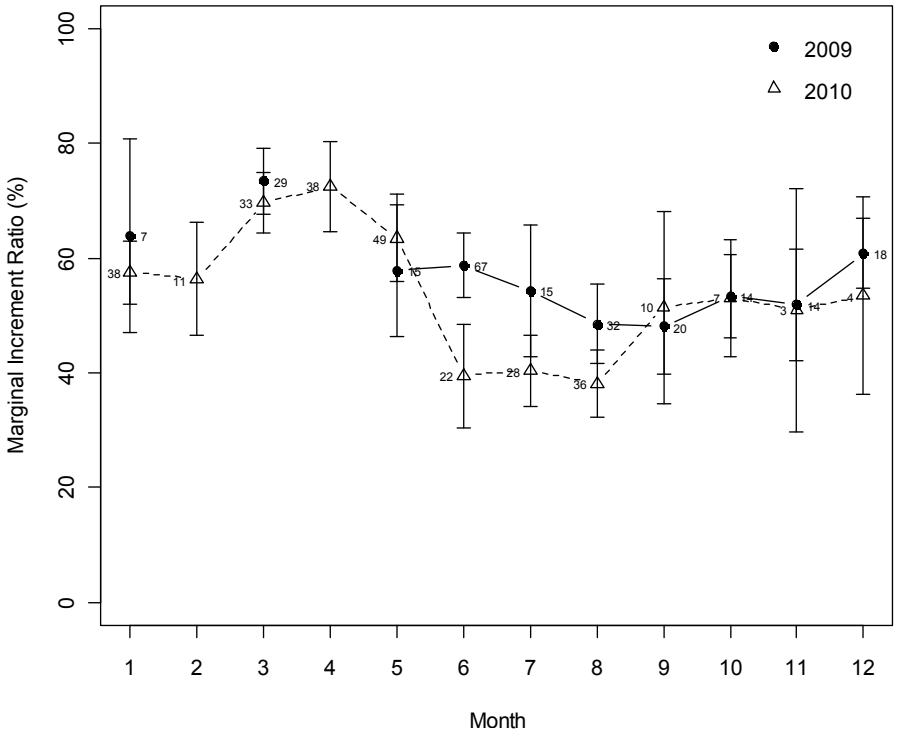


Figure 12. Mean monthly marginal increment ratio (MIR +/- 95% CI) for 2009 and 2010 in the western region. Data were pooled across age classes 4-6 years.

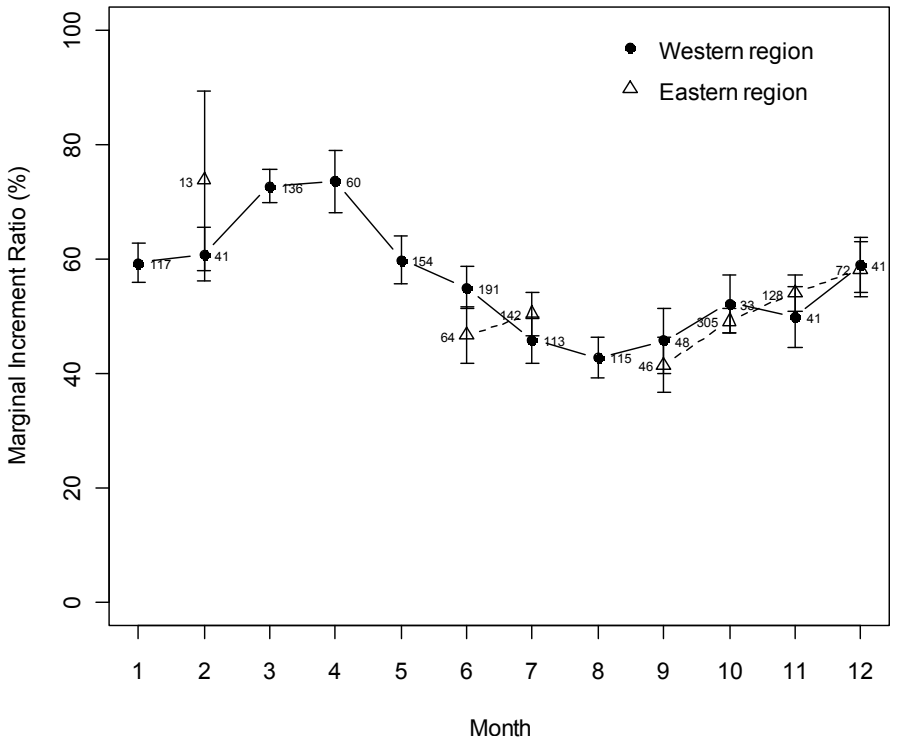


Figure 13. Mean monthly marginal increment ratio (MIR +/- 95% CI) for the western and eastern regions. Data were pooled across years and age classes.

Caught: May
Edge: Wide opaque zone almost complete.
MIR: 85.2

Caught: July
Edge: Translucent zone.
MIR: 41.7

Caught: August
Edge: Narrow opaque zone
MIR: 49.2

Caught: December
Edge: Medium opaque zone
MIR: 61.1

Figure 14. Sectioned otoliths from four albacore demonstrating the annual cycle in opaque zone formation. The white arrows indicate distal edge of opaque zones counted, and the white arrows indicate if an additional opaque zone was forming at the otolith edge (not counted). A wide MIR is shown in otolith sampled in May (85.2) and a narrow MIR is shown in otolith sampled in July (41.7). The MIR then increased from July to December.

7.2.5 Decimal age

A decimal age was calculated for each fish using the count of opaque zones, an assumed birth date, the MIR, and date of capture. A birth date of December 1 was assigned based on the middle of the spawning season for albacore in the South Pacific (Otsu and Hansen, 1962; and see Section 7.4 below). It was then assumed that fish caught in December to March (classified pre-increment fish) had not yet completed an opaque zone since their last birthday while fish caught in September to November (classified post-increment) had completed an opaque zone. Given the variability in MIR for fish caught between April and August (i.e. the period when opaque increments are completed) (Figure 15), it was not known whether a fish with a MIR in the order of 40-70% was still completing an opaque zone (in which case it should be classified as pre-increment) or had already completed the opaque zone and had started on the next increment (in which case it should be classified as post-increment). To assign these fish into their probable age class, we specified an MIR value for each of these five uncertain months above which otoliths were classified as pre-increment, and below which they were classified as post-increment. The MIR values used were based on calculating the mean MIR - 2 standard deviations (SD) for December to March and the mean MIR + 2SD for September to November, and then fitting a regression line through these points (Figure 15). Then, an otolith from a fish caught in April to August was classified as pre-increment if its MIR value was above the regression line, and as post-increment if its MIR value was below the line.

The decimal age for albacore was calculated using the following algorithms following Eveson *et al.*, (2004):
For fish classified as pre-increment: $a = n + r/365$
For fish classified as post-increment: $a = n\text{-}1 + r/365$
Where a is the decimal age, n the count, and r the day of capture (expressed as number of days since the assumed birth day of 1 December).

The maximum age obtained was 14.3 years. The relationship between otolith weight and estimated age was curvilinear (Figure 16) with an R^2 value of 0.83 (cubic

polynomial fit). The high coefficient of determination indicates that the majority of fish are being assigned into their correct age classes.

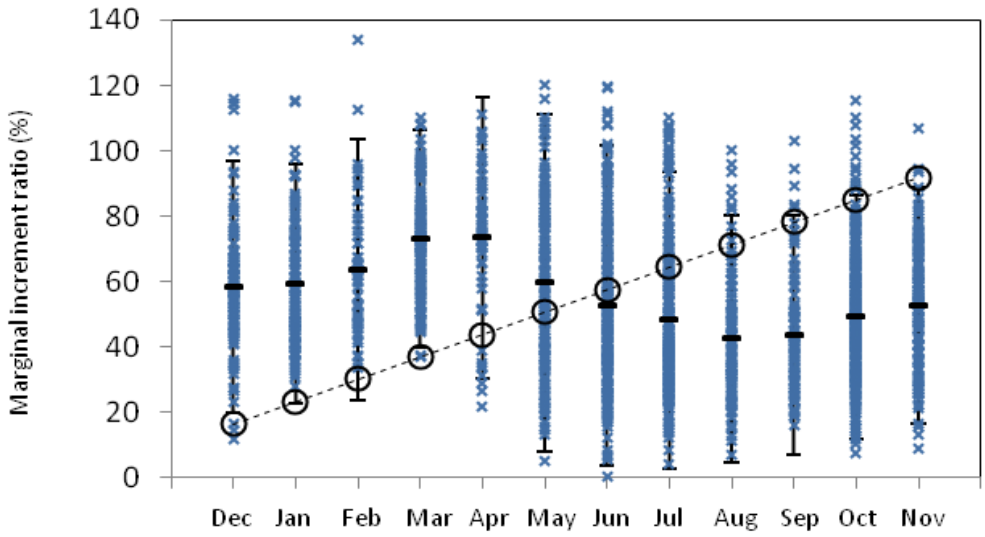


Figure 15. Marginal increment ratio (MIR) values by month for albacore (x). Mean monthly MIR values (●) +/-2 standard deviations (SD) are shown. Regression line is derived through the values of -2 SD of the mean MIR for December to March and +2 SD of the mean MIR for September to November (-----). The MIR values used to separate pre-and post increment otoliths for April to August are the fitted values from the regression line for these months (o).

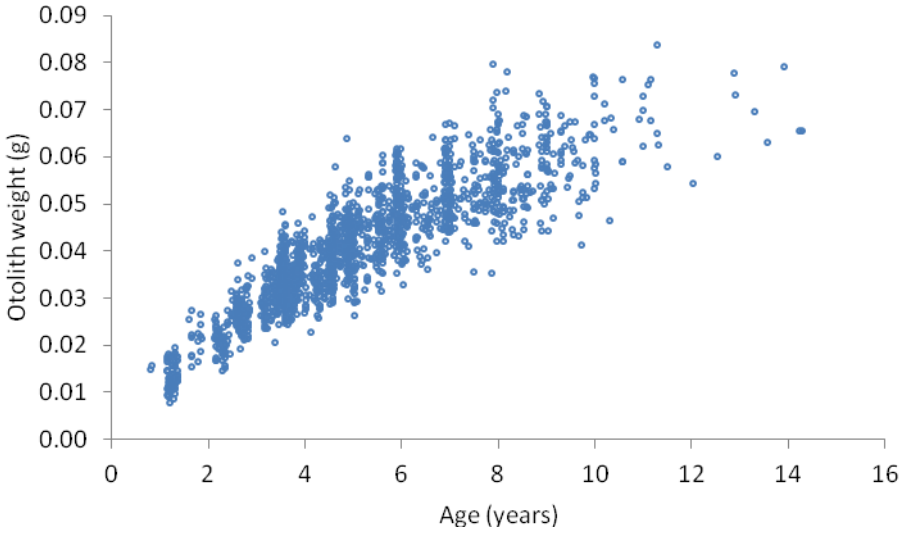


Figure 16. Relationship between otolith weight and decimal age for albacore.

7.2.6 Discussion

Validated annual age estimates using sectioned otoliths have been obtained for many fish species including tunas (Clear *et al.*, 2000; Farley *et al.*, 2006; Gunn *et al.*, 2008; Neilson and Campana, 2008; Green *et al*., 2009; Griffiths *et al.,* 2009; Clear and Leroy, in prep) and the results of the current validation work also support the use of sectioned otoliths as a structure to age albacore. Otoliths provide accurate age estimates and are considered unmatched by any other calcified structure because their growth is continuous and they are not subject to resorption or vascularisation (Secor *et al.*, 1995; Campana and Thorrold, 2001).

Otoliths in albacore have clear growth increments that provided reproducible counts with a good level of precision. To assess inter-reader precision it was necessary to account for the edge classification assigned by each reader to their count. The resulting precision between readers was reasonable (IAPE of 6.82%) given the limited training provided to OR2. For some otoliths, the differences in edge classifications between readers suggested that OR1 delayed counting an opaque zone near the otolith margin until a clear wider translucent zone followed it, while OR2 counted the opaque zone at the edge when a narrower translucent zone was evident. These differences may be the result of using different microscopes and light sources which have different refractive effects on the otolith edge or OR1 simply being more cautious when interpreting the edge given that single opaque zones can appear as pairs. The algorithm developed to calculate decimal age for albacore takes into account the otolith edge interpretation (i.e., the MIR) by the reader.

Counts of (assumed) daily increments were consistent with the first opaque zone being successfully identified in sectioned otoliths and that this increment is deposited before the first birthday. This indirect validation method has been used in both tropical and temperate species but is best limited to fish in their first year of life (see review in Arneri *et al.*, 1998; Morales-Nin and Panfili, 2002). However, to use the method successfully, the periodicity of the microincrements counted must first be validated (Morales-Nin and Panfili, 2002). The only validation of daily increments for albacore is

from a tetracycline mark-recapture study in the North Pacific where a rate of 0.954 increments per day was found from the analysis of whole otoliths (Laurs *et al.*, 1985). Despite the limited validation in the South Pacific, the age estimates obtained are similar to those obtained for juvenile albacore in other studies in the region (Leroy & Lehodey, 2004; Kerandel *et al.*, 2006), and the size of estimated age 1 fish is consistent with the first mode observed in length-frequency data for the New Zealand troll fishery (Griggs, 2005).

Examining otoliths from two OTC-injected fish verified the annual periodicity of the third and fifth opaque zones in those fish. The dates of OTC injection and subsequent recapture both coincided with the distal edge of consecutive opaque zones in each fish suggesting that these zones are completed in late summer to early winter. This timing is consistent with the MIR analysis which showed sinusoidal patterns consistent with an annual cycle of increment formation (Campana, 2001). The opaque zones formed consistently during the austral summer and were completed between April and August (MIR changes from highest to lowest). Otolith marginal increment analysis for other tunas in the southern hemisphere suggests a synchronicity to increment formation. In southern bluefin tuna, the marginal increment peaked in May and was lowest in August (Gunn *et al.*, 2008) while in longtail tuna the incidence of otoliths with a narrow translucent margin was highest in May to October (Griffiths *et al.*, 2009). The annual cycle of increment formation was less clear in bigeye tuna, which may be due to the greater difficulty in interpretation of bigeye otoliths, the high variability between individuals and/or less marked migration resulting in a less marked seasonal pattern in increment formation (Farley *et al.*, 2006). It is important, however, given the low number and restricted age range, that OTC-injected fish continue to be released and recaptured to provide a basis for more comprehensive validation and accurate estimation of decimal age.

Dorsal fin spines have been the preferred structure for ageing albacore primarily due to their ease of sampling (Davies *et al.*, 2008a; Boyd, 2010). Our study confirmed that spines from albacore in the South Pacific also have growth increments that provided reproducible counts with a good level of precision. Otoliths and spines also provided similar counts for fish up to age seven. Beyond this age, however, estimates based on

spines appear to negatively biased and the size of this bias is sufficient to be important for estimates of population parameters and stock assessments.

Different physiological pathways determine growth in otoliths and spines. Otoliths are composed of metabolic inert calcium aragonite (Sweeting *et al*., 2004) while spines are vascularised, skeletal material and, as such, are subject to resorption (Drew *et al.*, 2006; Boyd, 2010). This resorption can result in the core area of the spines being obscured and hence the inner increments, deposited when the fish was young, may not be observed (or counted). This process is common but the extent and timing of vascularisation and absorption varies among individuals. Therefore the number of obscured increments must be estimated for each section based on direct measurements.

The agreement of counts in otoliths and spines up to age seven indicates that the loss of early growth zones in spines due to vascularisation does not result in substantial bias prior to this age. However, it is unclear whether the underestimation of counts in spines after this age was due to vascularised inner zones not being accounted for in older fish, increments in spines not forming annually throughout life, or whether some increments were not being counted at the edge of the spines due to crowding of opaque and translucent zones. Vascularisation of the core and crowding of increments have been suggested as limiting factors in the use of spines to age large albacore accurately (Boyd, 2010). It was difficult to verify the annual periodicity of opaque zones in spines since the OTC marks were either faint or absent in the two fish examined. Faint marks in spines and clear marks in the matching otoliths may be due to the difference in the composition and matrix of the two structures or that the composition of spines makes the fluorescence mark more susceptible to UV exposure. Ortiz de Zarate *et al.* (1996) reported that even a few minutes of exposure during examination decreased the intensity of the mark in spines and several short exposures made the mark disappear completely. In the southern bluefin tuna, strontium-marks were obvious in otoliths but not in vertebrae (Clear *et al*., 2000).

As noted, otoliths are immune from the resorption, are generally easier and more consistently interpretable and appear to be a more reliable structure for accurately estimating the age of large albacore. This is consistent with results for southern bluefin

and Atlantic bluefin tuna where otoliths were also found to be the best structure for estimating age over their full life span (Gunn *et al.*, 2008; Rodríguez-Marín, 2007). For southern bluefin tuna, spines were useful only up to age four, while vertebrae underestimated age compared to otoliths after age 10 years. This latter age was also the limit recommended for spines and vertebrae for Atlantic bluefin tuna, after which age estimates were underestimated relative to otoliths. The longest period at liberty reported for a tagged albacore is 11 years (Langley and Hampton, 2005), although this fish is likely to have been between 12 and 15 years old as the tagging program was releasing fish aged one to four years. This longevity estimate is consistent with the current study, as the oldest age estimated was 14.

Bias in age estimation leads to bias in other age related population parameters such as growth and mortality. In particular, underestimation of age leads to overestimation of growth and natural mortality, which in turn leads to biases in age-based stock assessments that are likely to result in overfishing (Campana, 2001). Currently, the majority of stock assessments for tropical tuna fisheries are length based and use length-frequency decomposition methods and mark-recapture data to estimate age-based population parameters from commercial catch data (e.g., Hoyle, 2011). The results from this study, together with those for bigeye (Farley *et al.,* 2006), longtail (Griffiths *et al.*, 2009) and southern bluefin tuna (Gunn *et al.*, 2008) demonstrate that it is possible to obtain accurate and reliable direct age data from routine aging of otoliths for tropical tuna. The ageing algorithm developed for albacore allows the decimal age of fish across their entire lifespan to be estimated. These age estimates will provide greater precision for determining age-based metrics such as growth and reproductive parameters and should significantly improve the accuracy of models fits to catch-at-length data which is the main data input to most tuna stock assessments.

7.3 Spatial variation in growth

7.3.1 Growth modelling

None of the five candidate growth models was unambiguously the best model for albacore growth as indicated by ΔAIC_c values <3 and Akaikes weights between 0.15 and 0.53 for the three best-fitting growth models (Table 12). The logistic model was found to be the best approximating model among all candidate models ($w = 0.53$), although there was substantial support also for the Richards model ($\Delta AIC_c = 1.63$, $w = 0.24$). There was less support for the Schnute-Richards and Gompertz models (ΔAIC_c values > 2) and the VBGM was least supported among the set of candidate models with a $\Delta AIC_c > 10$ and weight of evidence of 0.

Separate sex-specific growth models were strongly supported by the data with a difference of 331.61 between the AIC_c from the best fit of the logistic model to all data ($AIC_c = 11807.77$) and the sum of the AIC_cs from the fit of the same model to female and male data ($AIC_c = 5746.90 + 5729.26 = 11476.16$) (Table 12). The fitted logistic growth curves for females and males were very similar up until age 4 years, after which the length-at-age for males was on average greater than that for females (Figure 17). The predicted mean asymptotic length (L_∞) from the best-fit models was 8.37 cm greater for males than for females (Table 12).

Table 12. Parameter estimates (± standard error) from five candidate growth models fitted to length-at-age data for South Pacific albacore. Parameter estimates also given for the logistic model fitted separately to female and male length-at-age data. The small-sample bias-corrected form of Akaike's information criterion AIC_c are provided for each model fit, and Akaike differences Δ_i, and Akaike weights w_i are given for the fit of the five candidate models to all data. Note that the parameters *k* and *t* are defined differently in each model (see text for definitions), such that values are not comparable across models.

Sex	Model	L_∞	*k*	*t*	*p*	δ	γ	*v*	AIC_c	ΔAIC_c	*w*
All	VBGM	104.52	0.40	-0.49					11831.67	23.89	0
		(0.44)	(0.01)	(0.05)							
	Gompertz	103.09	0.50	0.47					11811.54	3.77	0.08
		(0.37)	(0.01)	(0.03)							
	Logistic	102.09	0.61	1.12					11807.77	0.00	0.53
		(0.33)	(0.01)	(0.03)							
	Richards	102.30	0.58	0.98	1.32				11809.40	1.63	0.24
		(0.49)	(0.04)	(0.24)	(0.68)						
	Schnute-Richards	101.52	0.05			-0.97	3.54	2.07	11810.25	2.48	0.15
		(0.60)	(0.08)			(0.08)	(2.65)	(0.76)			
Female	Logistic	96.97	0.69	0.99					5746.90		
		(0.37)	(0.02)	(0.03)							
Male	Logistic	105.34	0.59	1.25					5729.26		
		(0.44)	(0.02)	(0.04)							

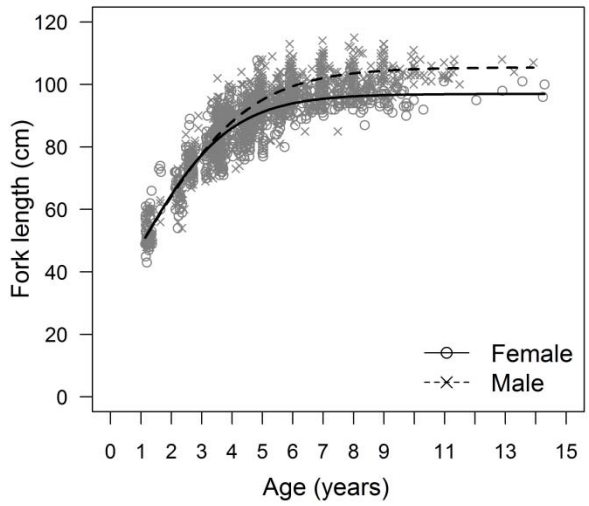


Figure 17. Length-at-age data and logistic growth models for female and male South Pacific albacore. Parameters of the models are presented in Table 12.

The LME and GLM models revealed that the residual length-at-age from the logistic growth models for females and males varied significantly with longitude (Table 13). The relationship between residual length-at-age and longitude was described best by a cubic spline with 3 degrees of freedom for both females and males, as indicated by the lowest AIC_c values for these models (Table 13). However, there was also substantial support ($\Delta AIC_c = 0.93$, $w = 0.39$) for a cubic spline model with 2 degrees of freedom for females. There was a strong relationship between the residuals and longitude for both males and females, with residual length-at-age predicted to be consistently greater at more easterly longitudes than at westerly longitudes (Figure 18). The results from the GLM and LME models were nearly identical (Figure 18) indicating a negligible effect from the non-independent samples, which were not considered in subsequent analyses. Very similar results were obtained from an analysis of a subset of the length-at-age data from latitudes north of 25°S, suggesting that the observed longitudinal patterns in the residuals were not affected significantly by latitude. Similarly, adding a latitude term to the regression did not improve model fit.

The inclusion of additional parameters for longitude in the growth models was strongly supported by both female and male length-at-age data (Table 14). A growth model with non-linear variation in k and linear variation in L_∞ was best supported ($w = 0.44$) by the

data for females, although there was also substantial support ($\Delta AIC_c = 0.80$, $w = 0.30$) for a growth model with non-linear variation in k and L_∞ (Table 14). For males, there was unequivocal support for a growth model with non-linear variation in k and L_∞ with a weight of evidence of 0.82. In all cases, growth models predicted that k and L_∞ were larger at more easterly longitudes than at westerly longitudes for both females and males (Figure 19), similar to the trends in fork length residuals (Figure 18). However, predicted values of L_∞ peaked at around 190° E for males, and the lowest values of k were predicted at approximately 155° E for females and 165° E for males (Figure 19). The predicted magnitude of variation in k across longitudes was similar for females and males (approx. 55%), but the predicted magnitude of longitudinal variation in L_∞ was greater for males (9%) than for females (3%) (Figure 19). Predicted growth curves in the west (150° E), central (185° E) and east (220° E) regions of the South Pacific demonstrate the magnitude of variation in growth of albacore that could be expected across the longitudinal range of this study (Table 15, Figure 20). These growth curves show the small variation in L_∞ and larger variation in k for female albacore, with higher k values in the east than in the central and west regions. For males, these growth curves demonstrate the variation in L_∞ and k, with lower L_∞ and k values in the west region than in the central and east regions.

Table 13. Parameter estimates from the linear mixed effects (LME) and generalized linear models (GLM) fitted to the fork length residuals from the logistic growth models fitted to female and male South Pacific albacore length-at-age data. R is the residual fork length, α_{lon} is the effect of longitude (*lon*), β_{set} is the random effect of fishing set, and ε is the error term.

Sex	Model type	Longitudinal effect	Model	AICc	ΔAICc	*w*
Female	LME	None	$R = \beta_{set} + \varepsilon$	5677.34	75.93	0
		Linear	$R = \alpha_{lon} + \beta_{set} + \varepsilon$	5616.06	14.65	0
		Cubic spline (df = 2)	$R = spline_2(lon) + \beta_{set} + \varepsilon$	5602.34	0.93	0.39
		Cubic spline (df = 3)	$R = spline_3(lon) + \beta_{set} + \varepsilon$	5601.41	0	0.61
	GLM	Linear	$R = \alpha_{lon} + \beta_{set} + \varepsilon$	5627.45	4.01	0.07
		Cubic spline (df = 2)	$R = spline_2(lon) + \beta_{set} + \varepsilon$	5623.44	0	0.51
		Cubic spline (df = 3)	$R = spline_3(lon) + \beta_{set} + \varepsilon$	5623.83	0.39	0.42
Male	LME	None	$R = \beta_{set} + \varepsilon$	5667.88	129.33	0
		Linear	$R = \alpha_{lon} + \beta_{set} + \varepsilon$	5562.72	24.17	0
		Cubic spline (df = 2)	$R = spline_2(lon) + \beta_{set} + \varepsilon$	5547.01	11.48	0
		Cubic spline (df = 3)	$R = spline_3(lon) + \beta_{set} + \varepsilon$	5535.06	0	1.00
	GLM	Linear	$R = \alpha_{lon} + \beta_{set} + \varepsilon$	5561.54	10.87	0
		Cubic spline (df = 2)	$R = spline_2(lon) + \beta_{set} + \varepsilon$	5559.78	9.12	0.01
		Cubic spline (df = 3)	$R = spline_3(lon) + \beta_{set} + \varepsilon$	5550.67	0	0.99

Table 14. Summary of growth models used to examine longitudinal variation in growth parameters *k* and L_∞ of female and male South Pacific albacore. L_∞ and *k* from the logistic model ($L_t = L_\infty(1+e^{-k(t-t_0)})^{-1}$) were modelled as linear or non-linear functions of longitude (*l*) where f_1 and f_2 are functions of the growth parameters and α_1 and α_2 describe the relationship between L_∞ and *l*, and β_1 and β_2 describe the relationship between *k* and *l*. The number of estimated model parameters (plus one for variance) (*K*), small-sample bias-corrected form of Akaike's information criterion AIC_c, Akaike differences Δ_i, and Akaike weights w_i are also given for each model fit.

Longitude functions			Female			Male		
f_1	f_2	*K*	AIC_c	ΔAIC_c	*w*	AICc	ΔAIC	*w*
L_∞	k	4	5746.90	140.76	0	5729.26	224.51	0
$L_\infty + \alpha_1 l$	k	5	5618.36	12.22	0	5532.11	27.36	0
$L_\infty + \alpha_1 l + \alpha_2 l^2$	k	6	5618.49	12.35	0	5519.44	14.69	0
L_∞	$k + \beta_1 l$	4	5623.76	17.61	0	5522.68	17.93	0
L_∞	$k + \beta_1 l + \beta_2 l^2$	5	5608.20	2.06	0.16	5524.52	19.76	0
$L_\infty + \alpha_1 l$	$k + \beta_1 l$	6	5611.47	5.32	0.03	5516.91	12.16	0
$L_\infty + \alpha_1 l + \alpha_2 l^2$	$k + \beta_1 l$	7	5609.80	3.65	0.07	5507.89	3.14	0.17
$L_\infty + \alpha_1 l$	$k + \beta_1 l + \beta_2 l^2$	7	5606.14	0	0.44	5513.20	8.45	0.01
$L_\infty + \alpha_1 l + \alpha_2 l^2$	$k + \beta_1 l + \beta_2 l^2$	8	5606.94	0.80	0.30	5504.75	0	0.82

Table 15. Predicted growth model parameter estimates in the west (150° E), central (185° E) and east (220° E) South Pacific Ocean based on predicted longitudinal trends in the growth parameters L_∞ and *k* for female and male South Pacific albacore. Common values of the growth parameter t_0 were used across regions for males and females.

Sex	Region	L_∞ (cm)	*k*	t_0 (years)
Female	West	95.49	0.67	0.92
	Central	96.59	0.73	0.92
	East	97.69	0.94	0.92
Male	West	100.30	0.56	1.06
	Central	106.23	0.57	1.06
	East	102.93	0.81	1.06

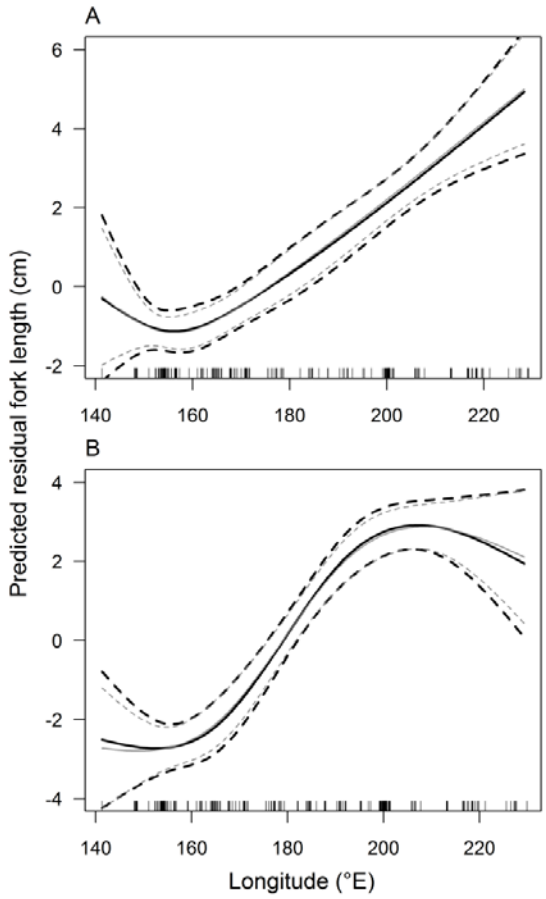


Figure 18. Predicted longitudinal trends in residual fork lengths from the logistic growth models for female (A) and male (B) South Pacific albacore. Dashed lines represent 2 standard deviations from the mean. Predictions from LMEs (dark lines) and GLMs (light lines) are shown.

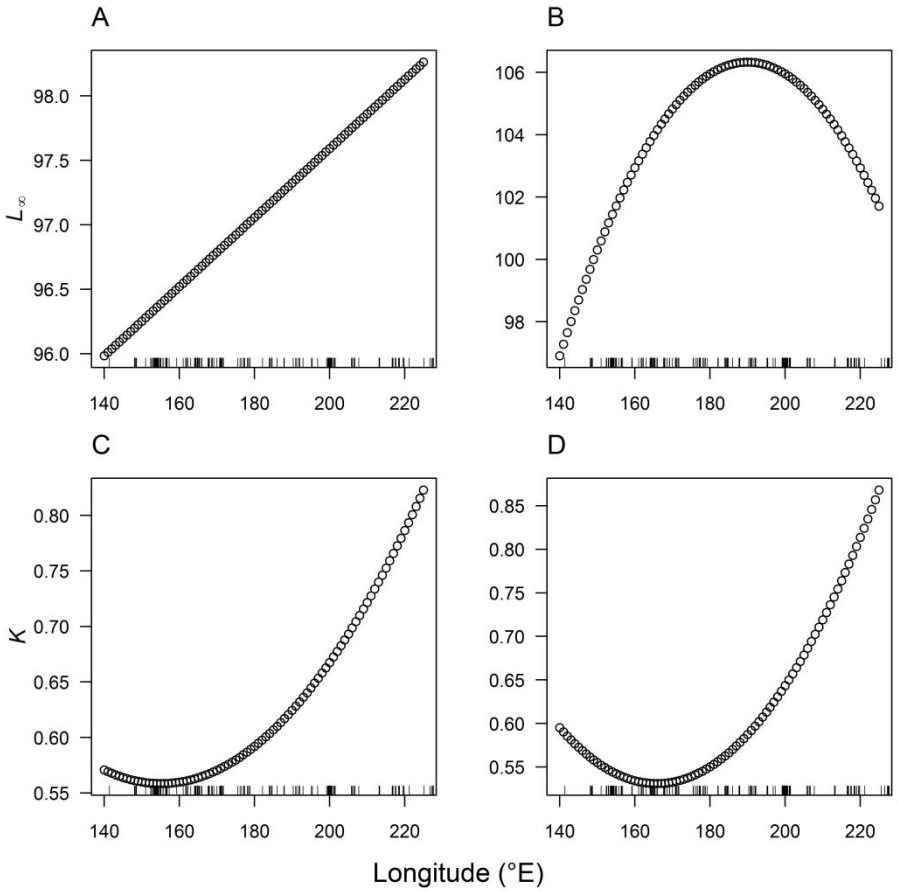


Figure 19. Predicted longitudinal trends in growth model parameters L_∞ and k based on the logistic growth model for female (A and C) and male (B and D) South Pacific albacore (see Table 14 for model details).

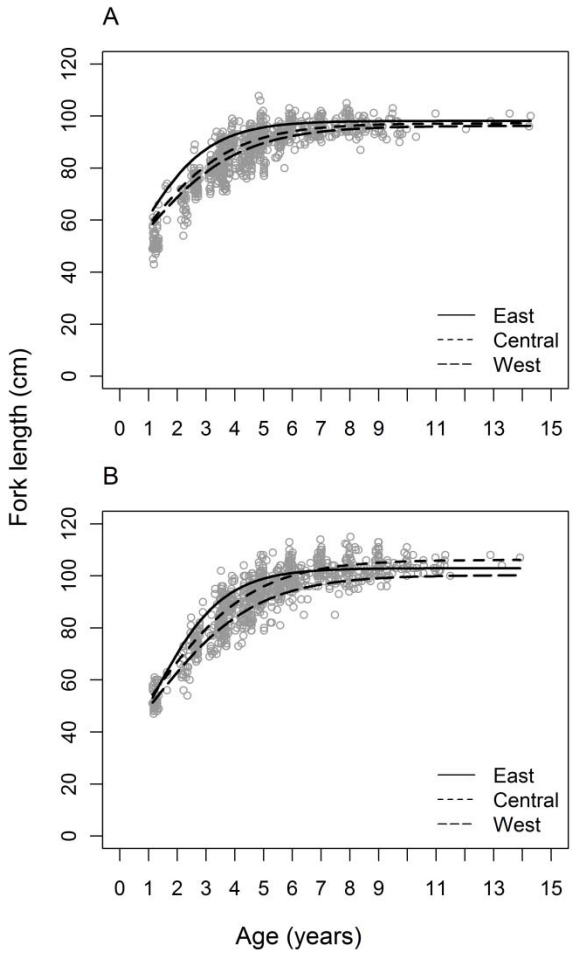


Figure 20. Predicted growth curves in the west (150° E), central (185° E) and east (220° E) South Pacific Ocean based on predicted longitudinal trends in L_∞ and k for female (A) and male (B) South Pacific albacore.

7.3.2 Discussion

We found evidence for significant variation in growth of albacore between females and males and across 90° of longitude in the South Pacific Ocean. Growth varied more between sexes than with longitude, with males growing to an average maximum size nearly 10% greater than females. The magnitude of longitudinal variation in length-at-age was similar for females and males, with fish approximately 6 cm longer on average at eastern longitudes than at western longitudes. However, longitudinal variation in average maximum size was more pronounced for males than for females, with the greatest difference in average maximum size being 2% and 6% for females and males, respectively. The magnitude of spatial variation observed for South Pacific albacore

was comparable to that observed for other demersal marine species at similar spatial scales (e.g. Meekan *et al*., 2001; Robertson *et al*., 2005; Trip *et al*., 2008), suggesting that the forces structuring local adaptation in growth can operate at similar spatial scales for demersal and highly mobile pelagic species.

Spatial variation in growth of fishes may be a consequence of variation in environmental factors, genetics, or a combination of both (Conover *et al*., 2006). Separating the effects of phenotypic and genotypic variation is difficult and 'common garden' experiments are usually employed to control environmental variables so that the environmental and genetic components of phenotypic variation are revealed (Conover *et al*., 2006). Such experiments are possible for small sedentary species, but impractical for large highly mobile pelagic species such as tuna. It will be difficult, therefore, to assess the relative contribution of environmental and genetic variation to the observed spatial variation in growth of albacore.

Growth in fishes often varies spatially in association with environmental gradients in abiotic or biotic factors, such as temperature and food availability (Weatherley & Gill, 1987). Water temperature is an important influence on growth in many fish populations, but the relationship usually varies among species and depends on the temperature range considered (Yamahira & Conover, 2002). Often, fish populations with a broad latitudinal range grow faster and reach larger maximum sizes at higher latitudes, where water temperatures are cooler (Boehlert and Kappenman, 1980; Parrish *et al*., 1985; Conover and Present, 1990; Conover *et al*., 1997; Yamahira and Conover, 2002; Conover *et al*., 2006). However, this pattern generally applies to demersal species or to those with limited movement for which individuals remain in a similar environment. The effects of temperature on the growth of pelagic species, such as albacore, are less clear due to their highly migratory behaviour and their ability to thermoregulate. Albacore experience water temperatures ranging from at least 8 to 30°C during their seasonal migrations and their vertical movements in the water column (Domokos *et al*., 2007; Childers *et al*., 2011), although adults in the South Pacific appear to prefer a temperature range between 20 and 25°C (Domokos *et al*., 2007). The available habitat for albacore within this temperature range varies significantly with longitude across the South Pacific, as the depth of the thermocline is significantly shallower east of 180°E

than in the west (Picaut *et al*., 1996). It is unclear how the reduction in available habitat at preferred temperatures may affect growth of albacore, but it may act to concentrate prey species in a narrower depth range and reduce the energy required by albacore to forage.

Food availability is well known to have a direct effect on fish growth (Weatherley & Gill, 1987), with numerous studies demonstrating a clear positive correlation between availability of food and growth (Clifton, 1995; Jones, 1986; Kerrigan, 1994). Preliminary dietary studies of albacore in the South Pacific Ocean indicate that fish (e.g. Paralepidae and Myctophidae) are the dominant prey item, followed by squids and crustaceans (Allain, 2010). The distribution and abundance of these taxa in the South Pacific Ocean remains unknown, but it is generally considered that micronekton densities are higher at ocean fronts and eddies (Brandt, 1981; Sassa *et al*., 2002) where growth rates of predators are enhanced (Brandt, 1993). The density of albacore is typically greater in the vicinity of ocean fronts and boundaries in both the North (Laurs and Lynn, 1977; Laurs *et al*., 1977; Laurs *et al*., 1984; Fielder and Bernard, 1987) and South (Uda, 1973) Pacific Ocean. Kirby *et al*. (2000) developed a simulation model that predicted the aggregation behaviour of tunas, including albacore, at ocean fronts, based on water temperature and prey densities. The spatial and temporal distribution of ocean fronts and eddies in the western and central South Pacific Ocean is complex, with numerous areas of convergence and enhanced eddy activity (Qui and Chen, 2004). However, there is no evidence for increased fronts or eddy activity at the longitudes where the length-at-age of albacore was greatest. The longitudinal gradient in the depth of the thermocline is the most likely oceanographic feature affecting food availability and potentially growth rates for albacore.

The observed longitudinal variation in length-at-age could also be explained by spatial variation in the selectivity of fishing gear, or size-specific spatial variation in the availability of albacore due to size-specific migration. Higher selectivity for larger individuals at eastern longitudes than at western longitudes may result in a larger mean length-at-age in the east. However, similar longline gear is used throughout the fishery, so the effects of selectivity on length-at-age are likely to be minimal. Net migration of larger individuals from western to more easterly longitudes may also result in a larger

mean length-at-age in the east. However, there are no tagging data available to support or refute size-specific migration, so the contribution of size-specific movement to the observed variation in length-at-age is unknown. Nevertheless, the implications of the observed longitudinal variation in growth of albacore remain equally relevant whether they result from the migration of individuals or reflect genuine spatial differences in growth.

The growth trajectories for female and male South Pacific albacore were similar up until 4 years of age, after which the length-at-age for males was on average greater than that for females. The divergence in growth trajectories is most likely due to the onset of female maturity, which occurs at approximately 82 cm *FL* (see Section 7.5 below), and the subsequent additional energy required for ovarian development compared with spermatogenesis. Our results are consistent with other growth studies of albacore that have demonstrated significant differences in growth between females and males in the North Atlantic Ocean (Santiago and Arrizabalaga, 2005) and Mediterranean Sea (Megalofonou, 2000). However, our results contrast those from Labelle *et al*. (1993) who found no significant difference in growth between female and male South Pacific albacore using age estimates from increment counts in vertebrae. The use of vertebrae to estimate age has resulted in significant underestimates of age in other species, including other tunas (Gunn *et al*., 2008), suggesting that the growth curves estimated by Labelle *et al*. (1993) are likely negatively biased. Furthermore, their sample size of females (59) and males (70) was relatively low, potentially resulting in bias and imprecision in estimates of L_∞ and k and a low probability of detecting differences in growth between sexes.

Outputs from stock assessments for South Pacific albacore are highly sensitive to structural assumptions about growth and input estimates of growth parameters (Hoyle *et al*., 2008; Hoyle 2011). The current assessment model assumes a single growth curve for the entire South Pacific stock, which is estimated by fitting a VBGF model to length-frequency data (Hoyle 2011). Our results provide an opportunity to refine and improve the structure of the assessment model by assimilating into the model a better depiction of growth patterns for South Pacific albacore. Firstly, we demonstrated that the commonly used VBGF did not provide the optimal fit to albacore length-at-age data,

and we recommend that alternative growth models, including the logistic model, be examined in future stock assessments.

Secondly, our results strongly support the inclusion of separate growth curves for females and males. The length-at-age of females (>4 years) will be overestimated using a single growth curve for both sexes, potentially biasing other parameters estimated from the growth curve, such as maturity and spawning stock biomass and related management reference points. Thirdly, the significant longitudinal variation in growth observed contradicts the assumption of homogeneity in growth within the South Pacific albacore stock, and suggests that the use of a single growth curve for the entire stock may not be appropriate, even if sex-specific growth is accommodated.

This is the first study to examine explicitly the spatial variation in growth across an entire stock for any tuna species. We have demonstrated substantial differences in growth of albacore between sexes and across 90° of longitudinal in the South Pacific Ocean. The determinants of the longitudinal variation in growth of albacore remain unclear, but variation in oceanography, particularly the depth of the thermocline, may play a role in modifying growth of South Pacific albacore. Future development of assessment models for South Pacific albacore are likely to benefit from explicit consideration of sex-specific growth curves and, potentially, variation in growth within the stock. Such structural improvements are likely to provide more reliable estimates of biomass, fishing mortality and potential yields, and ultimately provide the foundation for more robust management decisions.

7.4 Reproductive dynamics

7.4.1 Size distribution and sex ratio

The size distribution of fish sampled differed among the three regions (Figure 21). In region A, fish ranged from 43 to 110 cm *FL*, while in regions B and C fish ranged from approximately 85 to 115 cm *FL.* The majority of small fish sampled in area A were caught south of 25˚S. When only fish caught between 10 and 25˚S were compared, the size range of fish sampled was similar (Figure 22), although the relative abundance of small females was still higher in region A; 14.5% were < 85 cm *FL* compared to only

1.1% and 0.6% in regions B and C (Figure 22). The relative abundance of large females sampled increased from west to east; only 2.2% of females in region A were ≥ 100 cm *FL* compared to 5.5% and 14.0% in regions B and C respectively.

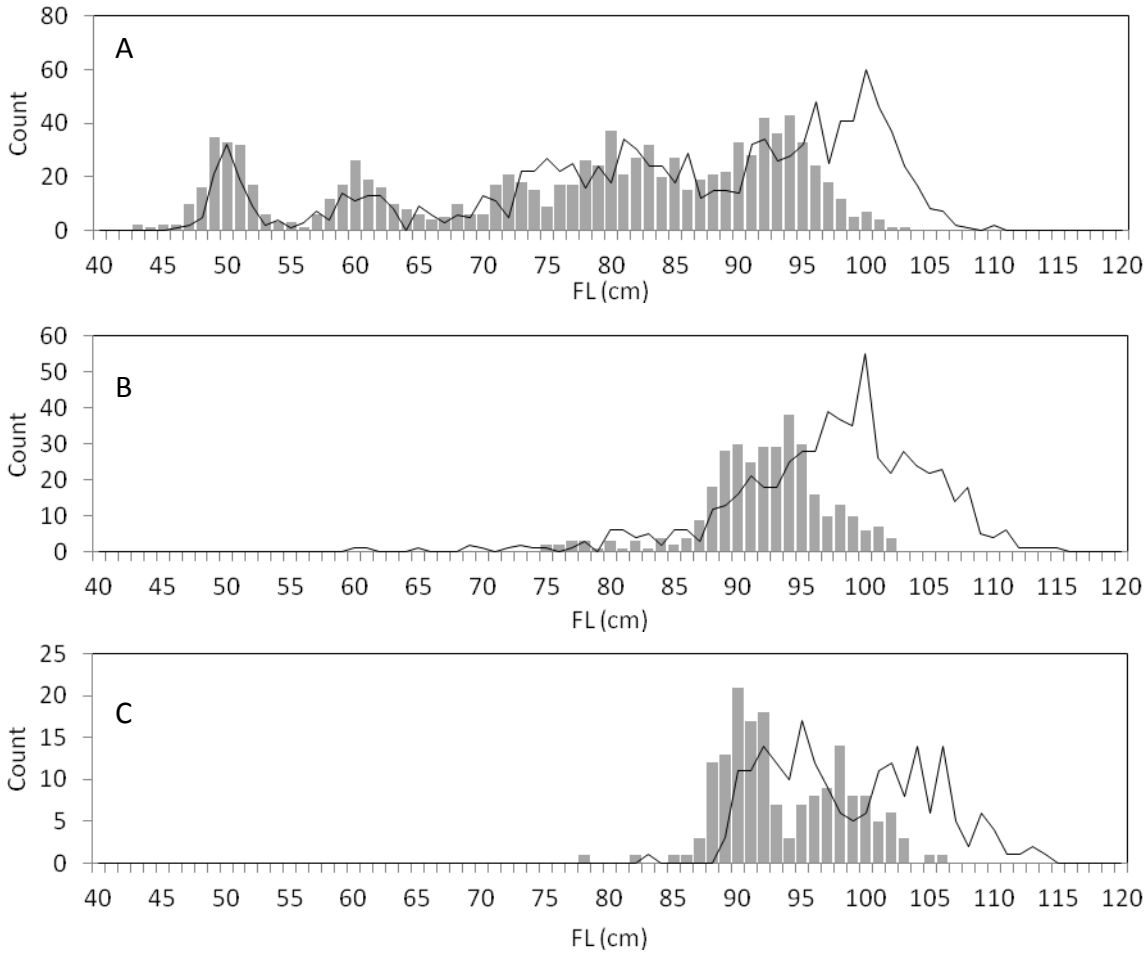


Figure 21. Length-frequency distribution of female (bar) and male (line) albacore sampled in the regions A, B, and C of the southwest Pacific Ocean.

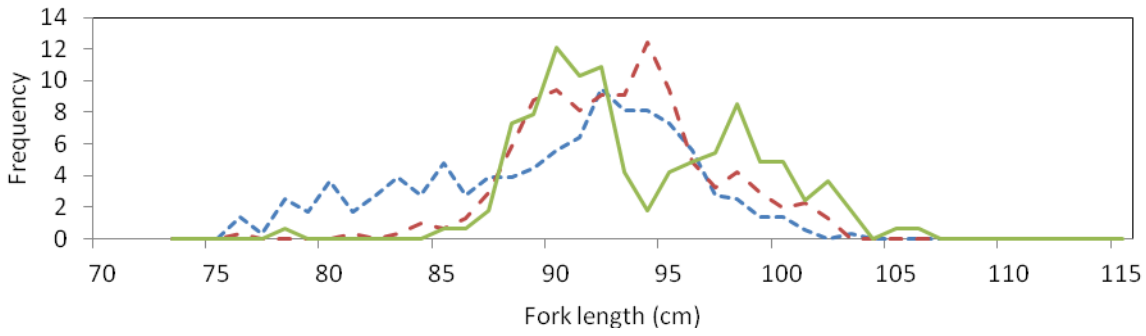


Figure 22. Length-frequency distributions of female albacore sampled in region A (green), B (red) and C (blue) between 10-25˚S.

Males dominated the sampling in all three regions, but the sex ratio varied by 5-cm *FL* class (Table 16). In general, females dominated length classes ≤ 90 cm *FL*, while males dominated length classes ≥ 95 cm *FL*. Chi-square tests indicated that in the small *FL* classes, where data were only available for region A, the sex ratio was significantly different from the expected 1:1 in the 45 cm, 50 cm and 60 cm *FL* classes (~60-70% females) (Table 16). Similarly, the sex ratio was significantly biased towards females in the 85 and/or 90 cm *FL* classes in all regions. If these two *FL* classes were combined, no significant differences were detected in the sex ratio among the three regions (43.7, 40.0, and 38.9% male respectively) ($\chi^2 = 1.85$, d.f. = 2, $P = 0.40$). The sex ratio then switched to be significantly male biased in the 95 cm, 100 cm and 110 cm classes in all regions apart from the 95 cm class in region C. The proportion male was almost identical in regions A and B at all *FL* classes ≥ 95 cm *FL*, and the sex ratios (*FL* separate or combined) were not significantly different between the two regions (78.9 and 80.7% male) (χ^2 tests, $P > 0.05$). The sex ratio in regions A and B combined for *FL* classes ≥ 95 cm was, however, significantly different from region C where the percent male was only 67.0 ($\chi^2 = 15.0$, d.f. = 1, $P < 0.01$).

Table 16. Sex ratio of albacore by region by 5-cm length class (lower value included). ‡ = $P < 0.05$ (females dominate), * = $P < 0.05$ (males dominate). Only shown where n > 5 for the length class.

5-cm FL	Region A			Region B			Region C		
(cm)	N	% male	X^2	N	% male	X^2	N	% male	X^2
45	94	30.9	13.8‡						
50	157	42.0	4.0‡						
55	68	42.6	1.5						
60	124	36.3	9.3‡						
65	60	48.3	0.1						
70	152	48.7	0.1						
75	206	55.3	2.4	16	31.3	2.3			
80	267	48.7	0.2	38	63.2	2.6			
85	193	46.1	1.2	104	39.4	4.7‡	33	9.09	22.1‡
90	317	42.3	7.6‡	264	40.2	10.2‡	124	46.8	0.5
95	278	67.3	33.2*	270	67.4	32.7*	95	51.6	1.0
100	197	93.4	148.4*	189	89.9	66.7*	74	70.3	12.2*
105	18	100.0	15.0*	83	100.0	83.0*	34	94.1	26.5*
110				14	100.0	14.0*	9	100.0	9.0*

7.4.2 Gonad development

Gonad weight was available for approximately half of the fish sampled. Based on these data, most fish < 85 cm *FL* showed little gonad development (Figure 23). Histological analysis indicated that females of this size were predominantly immature apart from a small number of fish between 74 and 85 cm *FL* which were mature and classed as either spawning capable, spawning, regressing or regenerating (Figure 24). The largest immature female was 94 cm *FL* while the smallest spawning female was 78 cm *FL*. All females with a *GI* > 1.7 were classed as mature and most were either spawning capable or spawning (Figure 24). A proportion of females with a *GI* < 1.7 were also mature (mostly regressing or regenerating) highlighting the importance of histological analysis of ovaries to assess maturity rather than relying solely on macroscopic or *GI* criteria.

Mean gonad index varied with longitude, being smallest in region A and largest in region C for fish with MAGOs of advanced yolked, migratory nucleus or hydrated oocytes (Figure 25a). A significant difference in mean *GI* was detected between all regions and MAGOs (unpaired t-tests, $P < 0.05$) apart from between regions B and C for ovaries with advance yolked or hydrated oocytes. The variation in *GI* may be related to oocyte size. A significant difference was detected in the diameter of advanced yolked oocytes between regions (unpaired t-tests, $P < 0.01$) with the smallest oocytes in region A (mean of 3.8 mm) and largest in region B and C (mean of 4.3 and 4.5 mm respectively) (Figure 25b). Significant differences were not detected in the size of migratory nucleus oocytes among regions.

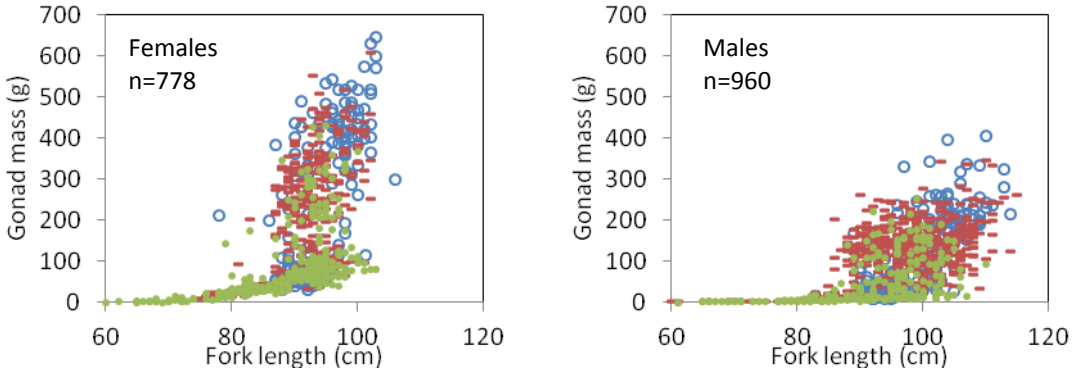


Figure 23. Relation between gonad weight and *FL* for albacore in region A (green), B (red) and C (blue).

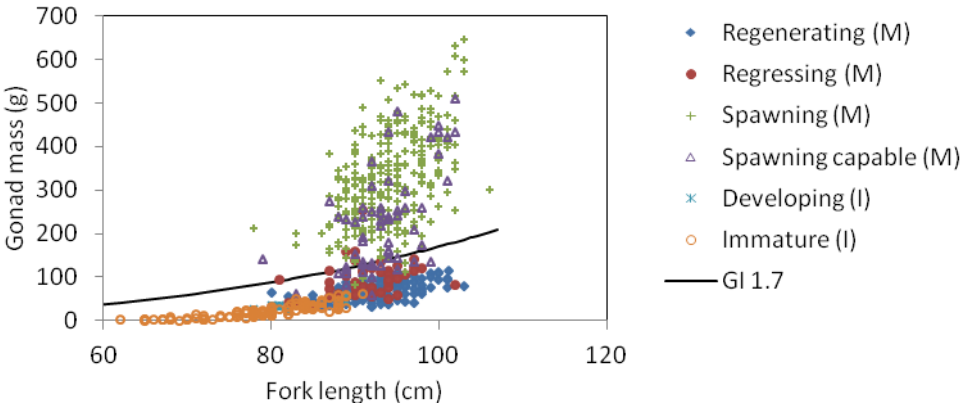


Figure 24. Relation between ovary weight and *FL* of albacore by reproductive state (regions combined). M = mature and I = immature. The regressing class includes classes 5, 6a and 6b (Table 6). The line represents a gonad index (GI) of 1.7 above which is assumed to indicate maturity by Ramon and Bailey (1996).

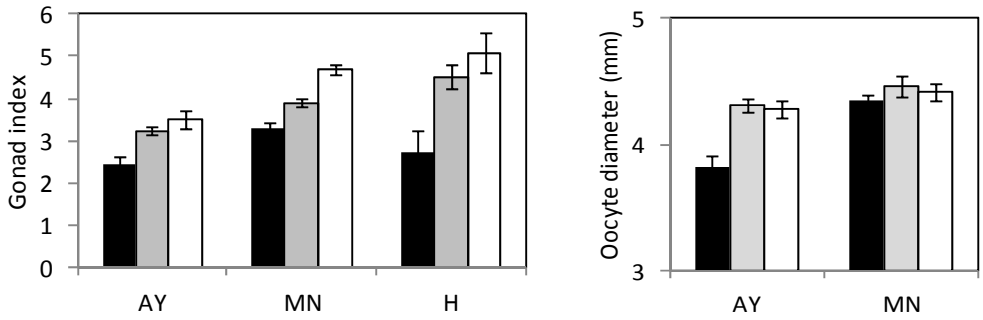


Figure 25. (a) Mean gonad index (n = 383) and (b) oocyte diameter (n = 154) for female albacore by MAGO stage for region A (black), region B (grey) and region C (white). AY = advanced yolked, MN = migratory nucleus and H = hydrated. Error bars are SE.

7.4.3 Spawning location and season

Active females were caught in a broad area between 10 and 25˚S (Figure 26). The seasonal patterns in mean monthly *GI* at these latitudes clearly suggest that fish spawn during the austral summer (Figure 27). For mature females, mean *GI* was highest (above 3%) between October and January in each region and then declined in February and March (Figure 27a). Mean *GI* peaked in November at 3.1, 4.0 and 5.1 in regions A, B and C respectively. Monthly patterns in mean *GI* for (all) males were similar to females, with the highest values in October to February (Figure 27b).

South of 25˚S, mean monthly *GI* was relatively constant and low throughout the year for both sexes (< 1.2 for mature females and < 0.3 for all males). All mature females sampled in this region were either regressing (n=11) or regenerating (n=85). Regressing females were sampled from October to April, while regenerating females were sampled in all months apart from January.

The seasonal pattern in frequency of development classes of mature females between 10-25˚S was consistent with the *GI* data (Figure 28). In region A, where the most comprehensive temporal sampling occurred, spawning and spawning capable females were present from August to April, although spawning activity peaked between October and March (Figure 28a). It is unknown whether significant levels of spawning also occur in September since no samples were obtained in this month. Regressing females were present in all months of the spawning season, while regenerating females increased in relative abundance after January and dominated the sampling from April to August.

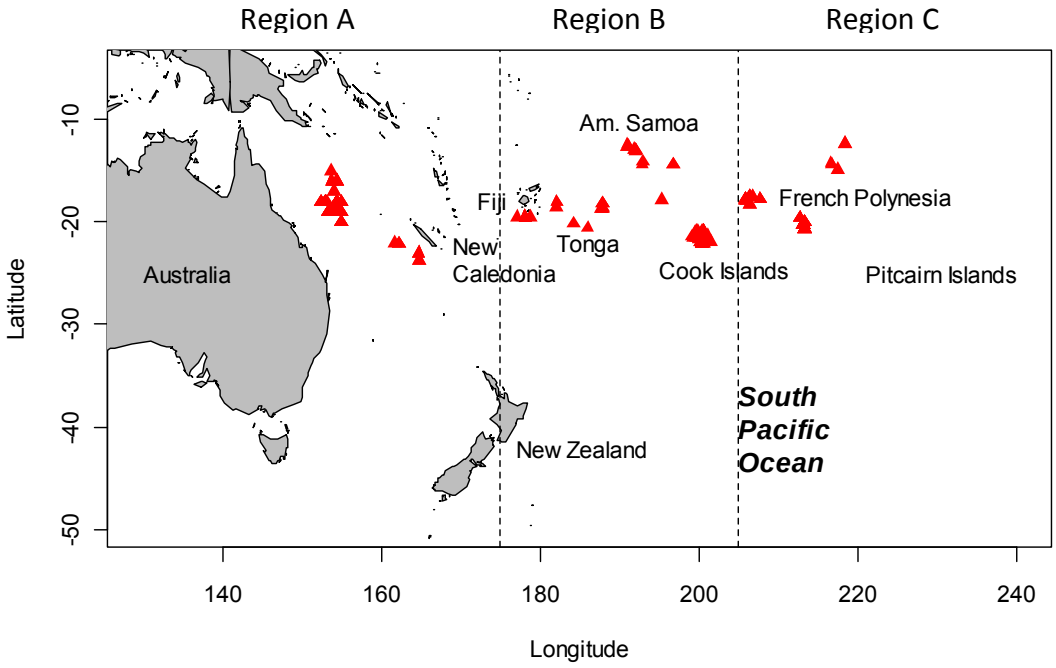


Figure 26. Sample locations of active (spawning and spawning capable) female albacore. Longitude is shown as degrees east. That is, 160˚W is shown as 200 (180-20) etc. Vertical lines indicate the division of the sampling area into region A (west of 175˚E), region B (175˚E to 155˚W) and Region C (east of 155˚W) for statistical analysis.

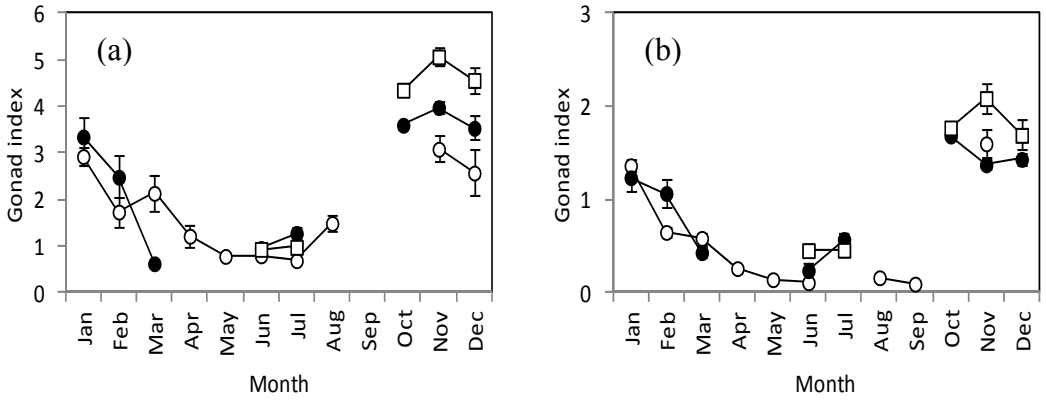


Figure 27. Mean monthly gonad index for (a) mature female (n=617) and (b) all male (n=895) albacore by region A (open circle), B (filled circle) and C (open square). Data were restricted to the spawning latitudes of 10-25˚S. Note that *GI* values are lower overall for males because the data used included both mature and immature fish. Error bars are SE.

The presence of regressing females throughout the spawning season suggests that individuals do not spawn for the entire period. The length of time that an individual spawns could not be determined but may be related to fish length. Of the mature females sampled in October to March in region A, the proportion in an active state (spawning capable and spawning) varied significantly with fish length ($\chi^2 = 18.63$, d.f. = 3, $P < 0.01$). Of females in the 95 cm *FL* class, 93.1% were active compared to only 33.3% in the 80 cm *FL* class (Figure 29a). The proportion of mature females in an active state did not vary significantly with age ($\chi^2 = 3.98$, d.f. = 6, $P = 0.55$), although the proportion active was lowest for females aged three and four years (Figure 29b). Despite the small sample size, when the data were examined by month the earliest an active female in the 80-89 cm *FL* class was sampled was October (Figure 29c), compared to August for females in the 90-98 cm *FL* class (Figure 29d). In addition, a greater proportion of fish in the 80-89 cm *FL* class were classed as regressing or regenerating in January to March (52.9%) compared to 90-99 cm females (8.0%). These results are consistent with small females having a shorter spawning season relative to large females.

Although sampling in regions B and C was restricted to a narrower range of months, the seasonal patterns in spawning activity were similar to region A with a few minor

exceptions: a small number of active females were sampled in June and July, no active females were sampled in March in region B, and fewer regressing females were sampled during the peak spawning season of October to January (Figure 28b; c).

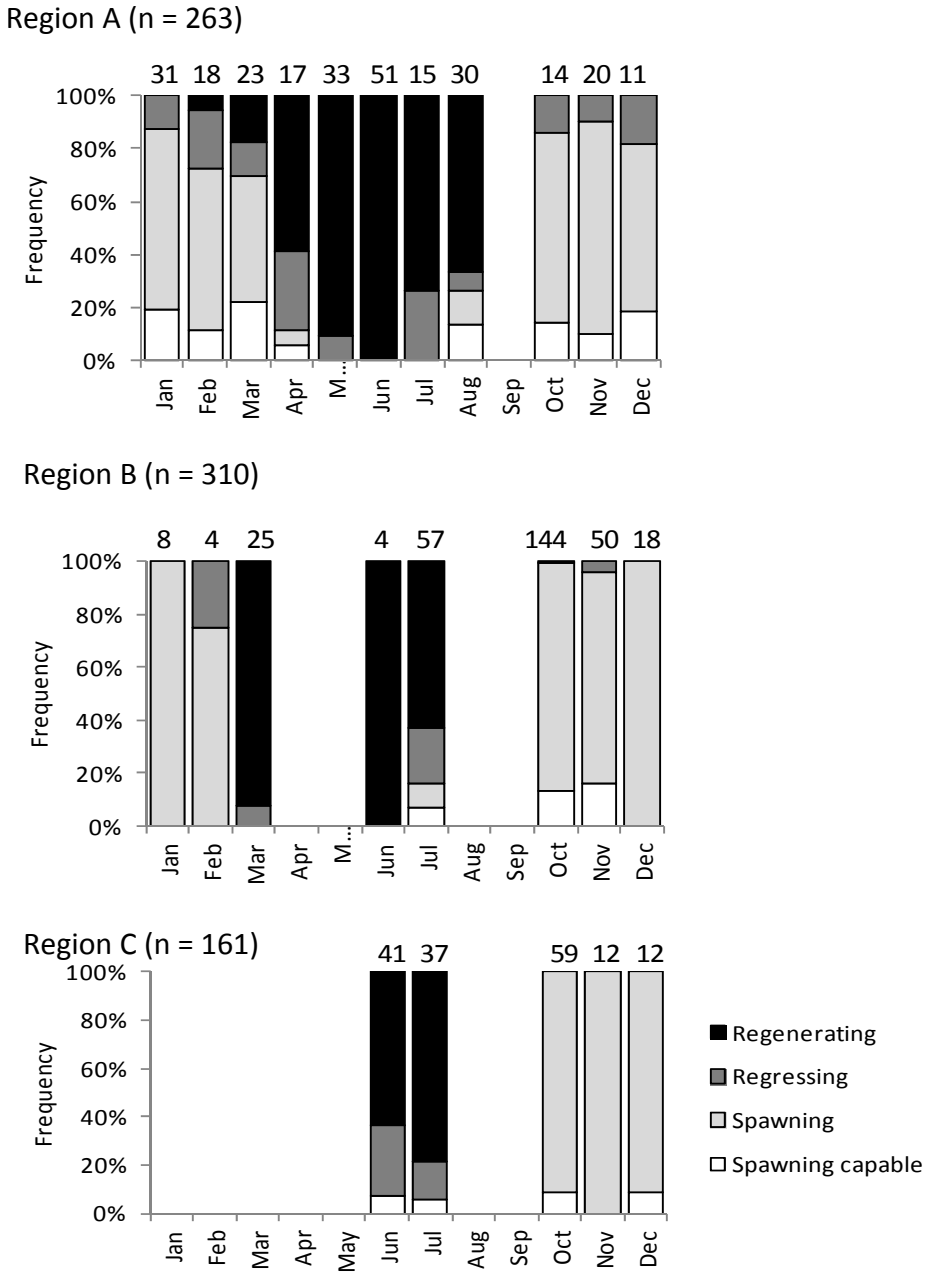


Figure 28. Percent frequency of development classes of mature female albacore by month and region. Data were restricted to the spawning latitudes of 10-25˚S. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top.

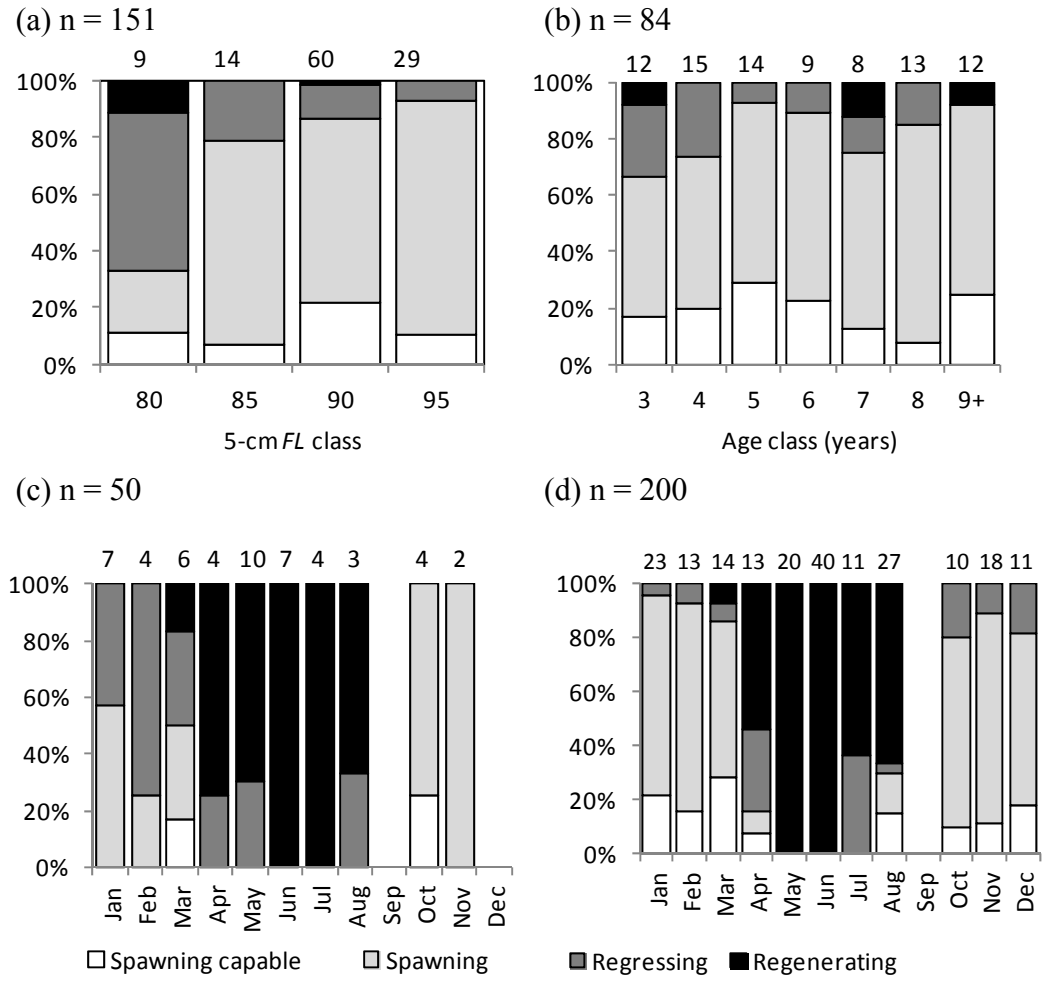


Figure 29. Percent frequency of development classes of mature female albacore in region A by (a) 5-cm *FL* class in October to March, (b) age class in October to March, (c) month for 80-89 cm fish, and (d) month for 90-99 cm fish. Data were restricted to the spawning latitudes of 10-25˚S. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top.

7.4.4 Time of spawning and POF degeneration

The majority of females sampled immediately after death were landed between 4 pm and midnight, although a few were also landed at other times (Figure 30). Of the females classed as spawning (n=58), advance yolked oocytes were apparent from 0551 until 1734 hrs (mean 1603 hrs), migratory nucleus oocytes from 1405 until 2325 hrs (mean 1933 hrs) and hydrated oocytes from 1812 until 0022 hrs (mean 2056 hrs) (Figure 30a). This suggests that spawning is synchronized in albacore and oocyte maturation is complete within 24 hours.

The ages assigned to POFs were consistent with a 24 hour cycle of degeneration in albacore. Only one fish had a stage 1 POF and this fish was sampled just after midnight (Figure 30b). The ovary also contained hydrated oocytes indicating that the fish was landed as it was about to spawn or that the fishing operation/sampling caused hydrated oocytes to be released. The absence of stage 1 POFs prior to midnight confirms that albacore spawn in the early hours of the morning. Although the sample size was low for the hours between 1am and 4 pm, POFs became progressively older during the day and all POFs assigned an age >12 hours were sampled after 2 pm (Figure 30b). No ovaries contained POFs of different ages.

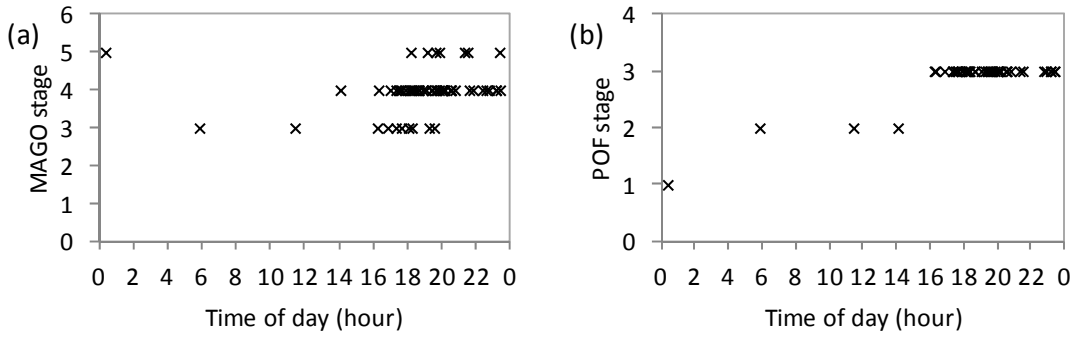


Figure 30. Relationship between time of death and (a) most advanced oocytes (MAGO) stage and (b) assigned postovulatory follicle (POF) age. Most advanced oocytes stages are: 3=Advanced yolked, 4=migratory nucleus, 5=hydrated. Postovulatory follicle stages are: 1 = new, 2 = <12hours, 3 = >12 hours.

7.4.5 Spawning frequency

Given the validation of a 24 hour cycle in POF degeneration in albacore, spawning frequency can be calculated using the postovulatory follicle method. Of the mature females sampled between 10 and 25˚S, the fraction with POFs was low in August and then increased to a relatively constant fraction from October to January before declining again by March or April (Table 17). In region A, the daily spawning fraction was 0.46 for the August to April spawning period, giving a mean spawning interval of 2.2 days. In the peak spawning months of October to March, spawning fraction did not vary significantly among months ($\chi^2 = 4.47$, d.f. = 5, $P = 0.48$) and when pooled over months,

the average spawning interval was 1.7 days (Table 17). The incidence of spawning varied significantly with fish size in region A (Table 18) but when the 80-cm *FL* class was removed from the analysis, no significant variation was detected among the remaining three *FL* classes ($\chi^2 = 1.94$, d.f. = 3, $P = 0.59$). The spawning fraction was only 0.18 for females in the 80 cm *FL* class (spawning interval of 5.5 days) compared to an average of 0.48 for the larger length classes combined (spawning interval of 2.1 days). Spawning fraction did not vary significantly with age class although a trend of increasing spawning frequency between ages 3 to 6 was evident (Table 18).

Spawning fraction did not differ significantly among the three regions when examined by month, apart from between regions B and C in November ($\chi^2 = 4.33$, d.f. = 1, $P = 0.04$). However, spawning fraction was often slightly higher in regions B and C, compared to region A (Table 17), which was probably driven by the low number of inactive females sampled east of 175˚E. When only active females were included in the analysis, spawning fraction was similar across months and regions and no significant differences were detected (Table 17) (χ^2 tests; $P > 0.05$). The spawning fraction was 0.77 in all three regions for the October to December period, which gives a mean spawning interval of 1.3 days during peak spawning. Significant differences were not detected in spawning fraction among length or age classes in regions B and C (separate or combined data; χ^2 tests; $P > 0.05$) (Table 18). Overall, the ovaries of 84.3% of active females contained evidence of recent or imminent spawning activity, and 46.5% contained evidence of two spawning events (postovulatory follicles and either migratory nucleus or hydrated oocytes) indicating that albacore is capable of spawning daily.

Table 17. Spawning fraction (SF) of all mature females and those classed as active by month and region. Data were restricted to the spawning latitudes of 10-25˚S. SS = spawning season (shown in grey).

	Region A				Region B				Region C			
Month	*n* mature	SF mature	*n* active	SF active	*n* mature	SF mature	*n* active	SF active	*N* mature	SF mature	*n* active	SF active
Jul	15	0.00			57	0.07	9	0.44	37	0.00	2	0.00
Aug	30	0.13	8	0.50								
Sep												
Oct	14	0.64	12	0.75	144	0.80	133	0.80	59	0.75	59	0.75
Nov	20	0.70	18	0.78	50	0.60	46	0.63	12	0.92	12	0.92
Dec	11	0.64	9	0.78	19	0.89	19	0.89	12	0.75	12	0.75
Jan	31	0.68	27	0.78	8	0.63	8	0.63				
Feb	18	0.50	13	0.69	4	0.50	3	0.67				
Mar	22	0.45	16	0.63	7	0.00						
Apr	17	0.06	2	0.50								
May	33	0.00										
Jun	49	0.00			4	0.00			41	0.00	3	0.00
SS	116	0.60	95	0.74	225	0.75	221	0.77	83	0.77	83	0.77

Table 18. Spawning fraction (n) of mature females by region, 5-cm *FL* class and age class for the months August to April. Only shown if n > 5. * = *P* < 0.05. Data were restricted to the spawning latitudes of 10-25˚S.

5-cm *FL* class	Region A	Region B	Region C	Age (yr)	Region A	Region B	Region C
80	0.18 (11)			3	0.29 (14)	0.76 (21)	
85	0.53 (19)	0.79 (34)		4	0.35 (26)	0.74 (39)	0.73 (15)
90	0.42 (89)	0.77 (111)	0.73 (15)	5	0.39 (18)	0.76 (17)	0.84 (19)
95	0.62 (39)	0.64 (59)	0.80 (40)	6	0.43 (14)	0.75 (24)	0.67 (12)
100		0.65 (17)	0.76 (21)	7	0.42 (12)	0.88 (8)	0.55 (11)
				8	0.72 (14)	0.67 (6)	
				9	0.54 (13)		
Total	0.46 (158)	0.72 (211)	0.78 (76)		0.43 (111)	0.76 (115)	0.72 (570
χ^2	8.25*	3.82	0.31	χ^2	7.30	0.92	3.24

7.4.6 Batch fecundity

Of the ovaries sampled whole, 71 contained hydrated oocytes (with no new POFs) or late stage migratory nucleus oocytes suitable for batch fecundity estimation. Batch fecundity ranged from 0.26 million oocytes for a 97 cm female sampled in Fiji to 2.83 million oocytes for a 98 cm female sampled in Tonga (mean ± S.D. = 1.20 ± 0.50). The relative batch fecundity ranged from 13.2 to 137.2 oocytes per gram of body weight (mean ± S.D. = 64.4 ± 24.7). Batch fecundity did not vary significantly among regions (ANCOVA using *FL* as the covariate, $P = 0.35$) so the data were combined. Although a significant, positive linear relationship was found between batch fecundity and *FL* ($F = 8.92$, $r^2 = 0.11$, $P < 0.01$) (Figure 31a), the low r^2 value suggests that *FL* only explains a small proportion of the variance in fecundity. Similarly, a significant negative linear relationship was found between relative batch fecundity and month during the spawning season ($F = 20.69$, $r^2 = 0.23$, $P < 0.01$) (Figure 31b) even when the high July data were removed ($F = 9.22$, $r^2 = 0.12$, $P < 0.01$). Again, the low r^2 value suggests month only has an indirect effect on fecundity. Batch fecundity did not vary significantly with age ($F = 0.15$, $r^2 = 0.004$, $P = 0.70$, n = 43).

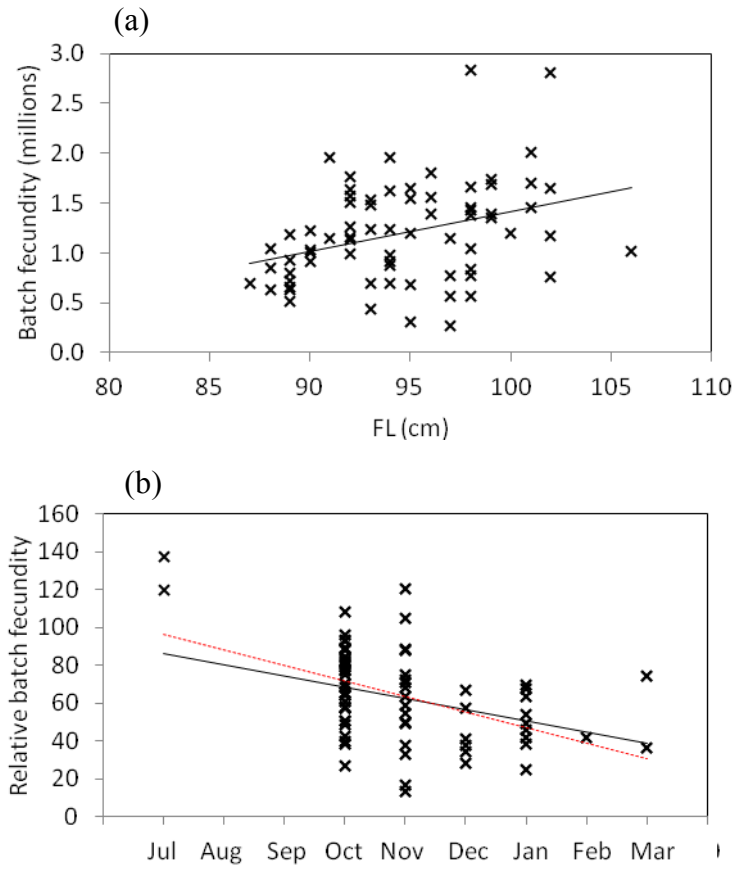


Figure 31. Relationship between (a) batch fecundity and *FL* and (b) relative batch fecundity (RBF) and spawning month of albacore (n=71). Regression lines shown in (b) are for all data (dotted line) and October to March (full line).

7.4.7 Discussion

The large biological sampling program undertaken across the southwest Pacific Ocean allowed us to provide high quality estimates of important reproductive parameters for albacore, and provide preliminary evidence for geographic variation in some of these. We found that although spawning activity appeared to be synchronized across the region (peaking between October and January), subtle regional differences in sex ratio, gonad development, spawning season and spawning frequency were detected which highlight the importance of ocean-scale sampling programs to examine the life-history parameters of species with broad geographic distributions.

Analysis of sex ratio indicated that males dominate length classes ≥ 95 cm *FL* west of 155˚W (regions A and B) and length classes ≥ 100 cm *FL* to the east (region C) (also see Section 7.3). A preponderance of males in larger size classes has been found in several tuna species including southern bluefin, Altantic bluefin, bigeye, yellowfin as well as albacore (Schaefer, 2001), and it has been suggested that this dominance could be due to sex related differences in availability, growth rates, or natural mortality (Everett and Punsly, 1994 *in* Harley and Maunder, 2003). Differences in natural mortality have generally been accepted as the most likely cause (Schaefer, 2001; Maunder and Watters, 2003) with higher mortality in females possibly due to greater costs associated with spawning (Schaefer, 1998). However, the current study suggests that differential growth rates between the sexes may also be a factor. We have shown that growth rates for males and female are significantly different with females reaching the same maximum age but at a smaller size than males (see Sections 7.2 and 7.3). In addition, the current work found a significant female bias in the length classes preceding those where there was a male bias. This accumulation of females is expected if sex-specific growth was responsible for the observed changes in sex ratio (Everett and Punsly, 1994 *in* Harley and Maunder, 2003). Length-at-age and L_∞ are also greater east of 155˚W for both males and females (Section 7.3) which may explain the switch to male dominance at a slightly larger size in that region. While ontogenetic shifts in availability or mortality cannot be unequivocally excluded, both these observations are consistent with female albacore diverting greater resources to reproduction than somatic growth following sexual maturity.

Spawning in albacore appears to be synchronised across the southwest Pacific Ocean between 10 and 25˚S. Although temporal sampling was limited to certain months of the year east of 175˚E, the peaks in *GI* and seasonal pattern of development of reproductive states were consistent across longitudes, with spawning activity occurring predominantly in spring and summer (October to March). Our results are similar to previous studies showing that spawning in the central South Pacific occurs between September/October and February/March, peaking in December (Otsu and Hansen, 1962; Ramon and Bailey, 1996). In the northeast Pacific Ocean, albacore also spawns over an extended spring/summer period (March to September) between 10- 20˚N (Chen *et al.*, 2010), although larval surveys suggest that some spawning also occurs during

winter and as far north as 30˚N (Nishikawa *et al.*, 1985). Although we found no evidence of year-round spawning in the South Pacific as suggested by Ueyanagi (1969), there was some evidence for a slightly earlier spawning season in regions B and C since a small number of active females were sampled in June and July, and no active females were sampled in March in region B. Additional sampling would be required to confirm spatiotemporal patterns of albacore spawning east of 175˚E.

The duration of spawning by individual albacore could not be determined, but the presence of post-spawning fish during all months of the spawning season in region A suggests that individuals may not spawn for the entire period. We found evidence to suggest that the duration of spawning is related to fish size, with smaller females having a shorter spawning season relative to larger females. The ratio of inactive to active mature females in the 80-85 cm *FL* class was 2:1 during the spawning season indicating that for these fish, the duration of the post-spawning phase was twice as long as the duration of the spawning phase in those months. By comparison, the ratio of inactive to active mature females in the 95-100 cm *FL* class was 0.07:1 indicating a significantly longer spawning period for large females. A shorter spawning season in smaller/younger fish has not been reported previously for tunas, but has been recognised in other pelagic species including jack mackerel and Pacific mackerel (Knaggs and Parrish, 1973; MacCall *et al.*, 1980). The low number of post-spawning females sampled in regions B and C during the peak spawning months may indicate that individuals spawn for a longer period (before becoming post-spawning) compared to those in region A, or that post-spawning females move quickly away from the spawning latitudes and were unavailable for sampling. It is unlikely that the lack of post-spawning females in these months is related to the slightly larger size of fish sampled in regions B and C, since large females were post-spawning in October to January in region A (see Figure 29d).

Like other tunas, albacore has asynchronous oocyte development and is considered to be a multiple spawner with indeterminate annual fecundity (Otsu & Uchida, 1959). Our results are consistent with albacore being nocturnal spawners with spawning activity synchronized during the early hours of the morning. Nocturnal spawning has been found in yellowfin, Altantic bluefin, and bigeye tuna and is common in many other fish

species (Schaefer, 2001; Gordoa *et al.*, 2009). After spawning, it is important to know the length of time that POFs remain visible in ovaries to estimate spawning frequency using the POF method (Hunter *et al.*, 1985a). The degeneration rate for POFs in skipjack and yellowfin tuna is 24 hours (Hunter *et al.*, 1996; Schaefer, 1989; McPherson, 1991). The current study has confirmed the albacore also has a 24 hour cycle for POF degeneration. Similar POF resorption rates for skipjack, yellowfin and albacore tuna is not surprising given that they spawn when surface temperatures are above 24°C (Schaefer, 2001) and water temperature is assumed to be the dominant factor determining POF resorption rates in fish (Fitzhugh and Hettler, 1995). However, albacore are believed to spawn at depths of ~100-200m where temperatures are cooler than at the surface (Chen *et al*., 2005). Since albacore are capable of regulating their body temperature (Carey *et al*., 1971), it may be internal temperature rather than water temperature that directly influences the rate of POF resorption in tuna.

Albacore is capable of spawning daily since the ovaries of nearly 50% of active females contained evidence of both recent (POFs) and imminent spawning (migratory nucleus or hydrated oocytes). However, we found that the fraction of females spawning varied to some extent by month, fish size and region. Lower spawning fractions at the start and end of a spawning season is expected as the proportion of fish spawning increases slowly and then declines at the end of the season. A low spawning fraction at the start of the spawning season was observed in southern bluefin tuna. In this case it was attributed to a delay in spawning by some females after they arrive on the spawning ground; this delay is thought to allow them to recover from their long migration from the southern oceans to the northeast Indian Ocean spawning area (Davis *et al.*, 2001). A low spawning fraction in small albacore is not surprising as many are probably becoming mature and adjusting to tropical waters for the first time and, as noted previously, have a shorter spawning season compared to larger females. A shorter season in small females may be a related to smaller energy reserves, and the need to balance their reproductive investment with somatic growth and future spawning success. Increasing spawning fraction with fish size has also been found in southern bluefin and yellowfin tunas (Schaefer, 1998; Davis *et al.*, 2001).

The mean spawning interval of 1.7 days for albacore in October to March in Region A is the same value found in a recent study in the North Pacific during peak spawning in April (Chen *et al*., 2010). The slightly higher spawning fraction values obtained in regions B and C again highlights that regional variation in spawning activity may exist across the southwest Pacific. However, the similarities in spawning fraction when only active females were examined during peak spawning months (0.77) suggests that the differences are driven by the absence of inactive females in region B and C, rather than differences in spawning dynamics.

The relationship between batch fecundity and albacore length was highly variable, although a significant relationship was detected when regions were combined. Variability in batch fecundity with length has been observed in several tuna species (Schaefer, 1987; Goldberg and Au, 1986; Schaefer, 1998; Nikaido *et al.*, 1991; Farley and Davis, 1998) and may be related to the stage in the spawning cycle when the fish were caught (Farley and Davis, 1998). This is supported by the negative relationship found between relative batch fecundity and spawning month; albacore appear to produce smaller batches as the season progresses. Although there have been no direct observations of this previously in tunas, a decrease in batch fecundity has been found in Atlantic mackerel as fish migrated north during the spawning season (Watson *et al.*, 1992). Our estimate of mean relative batch fecundity for albacore of 64 oocytes per gram of body weight is higher than in North Pacific albacore (50 oocytes per gram of body weight) (Chen *et al.*, 2010), but similar to yellowfin tuna in the eastern and western Pacific (62-68) (Schaefer, 1996; 1998; Sun *et al*., 2005), bigeye tuna in the western Pacific (60) (Sun *et al*., 2006) and southern bluefin tuna (57) (Farley and Davis, 1998). Lower mean relative batch fecundity was reported for bigeye tuna in the eastern and central Pacific Ocean (24-31) (Nikaido *et al.*, 1991 *in* Schaefer, 2001; Schaefer *et al.,* 2005).

We found evidence that *GI* in albacore varies with longitude in the South Pacific, being higher on average east of 175˚E compared to the west. It appears that this variation is due to a larger size of advanced yolked oocytes in the ovaries of fish in regions B and C, rather than the size of migratory nucleus oocytes or the number of hydrated oocytes

(batch fecundity). Although not assessed, it is also possible that the pool of unyolked oocytes may also be higher in the ovaries of females from regions B and C.

The current study significantly improves our understanding of the reproductive dynamics of albacore over a broad spatial range in the southwest Pacific Ocean, and provides estimates of reproductive parameters for use in future stock assessments. The current stock assessment model uses sex ratio, proportion mature, spawning frequency and fecundity to estimate relative reproductive output (Hoyle *et al*., 2008; Hoyle, 2011). Improvements in the assessment model would include accounting for the different spawning behaviour and reproductive output between the smallest and largest mature fish. Further temporal sampling is required to determine if reproductive output varies with longitude.

7.5 Spatial variation in maturity

7.5.1 Catch composition

In total, 684 of the females sampled were classified as immature (43-94 cm *FL*) and 812 as mature (74-109 cm *FL*). Importantly, 843 of the fish sampled were from the important transitional size range from 75 to 95 cm *FL*.

Immature females made up a small proportion of the females sampled north of 20˚S, while mature fish made up a small proportion of the females sampled south of 30˚S (Figure 32). In the area west of 175˚E (for which samples were collected across a wide range of latitudes), only 8.2% of the females sampled north of 20˚S were immature compared to 43.5% between 20-25˚S, 67.8% between 25-30˚S, and 96.2% south of 30˚S. Active females dominated the sampling between October and March north of 20˚S (Figure 33a). The relative abundance of females north of 20˚S classed as post-spawning (regressing and then regenerating) increased steadily from the middle of the spawning season (~ January) until June, while the abundance of immature females remained relatively low and constant (Figure 33a). To the south, between 20-25˚S, the relative abundance of regenerating females increased between March and August,

which is slightly later than observed to the north (Figure 33b). At 25-30˚S and below 30˚S, regenerating females increased in abundance even later, between May and September (Figure 33c,d). At the latitude bands south of 25˚S, the relative abundance of immature females declined during the post-spawning months (as regenerating fish increased) until August/September when the abundance of immature fish increased again prior to the following spawning season.

The percentage of females ≥ 70 cm *FL* with ovaries containing alpha and beta stage atresia was highest during the spawning season and lowest during the non-spawning period (Figure 34a). By comparison, the percentage of females with ovaries containing brown bodies and residual hydrated oocytes (maturity markers) was constant across months confirming that these structures persist in ovaries for a long time before being completely resorbed (Figure 34b).

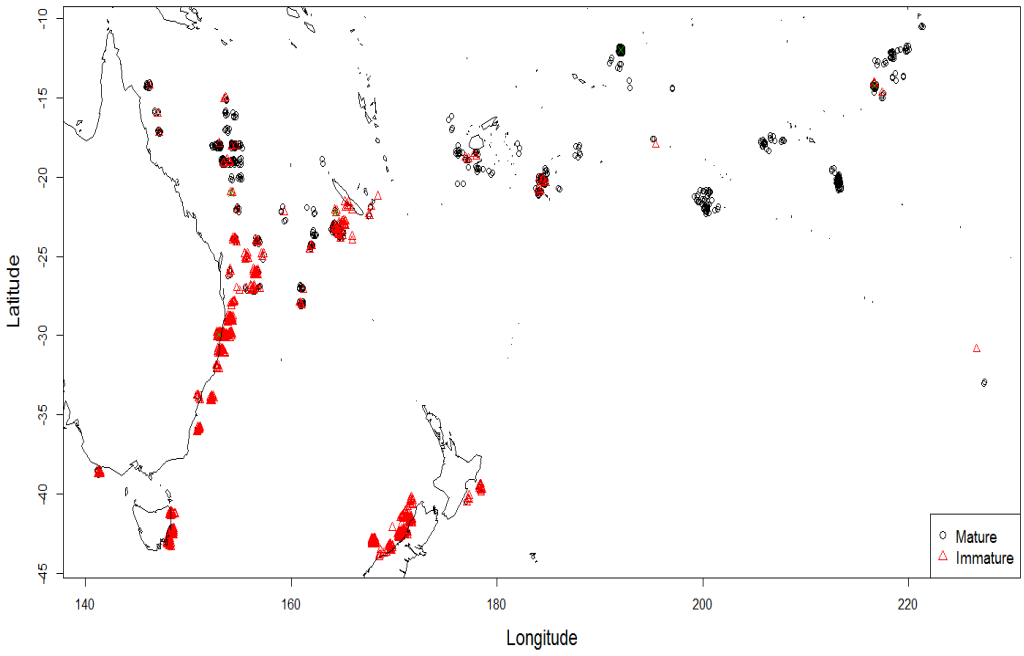


Figure 32. Sample locations of mature and immature female albacore.

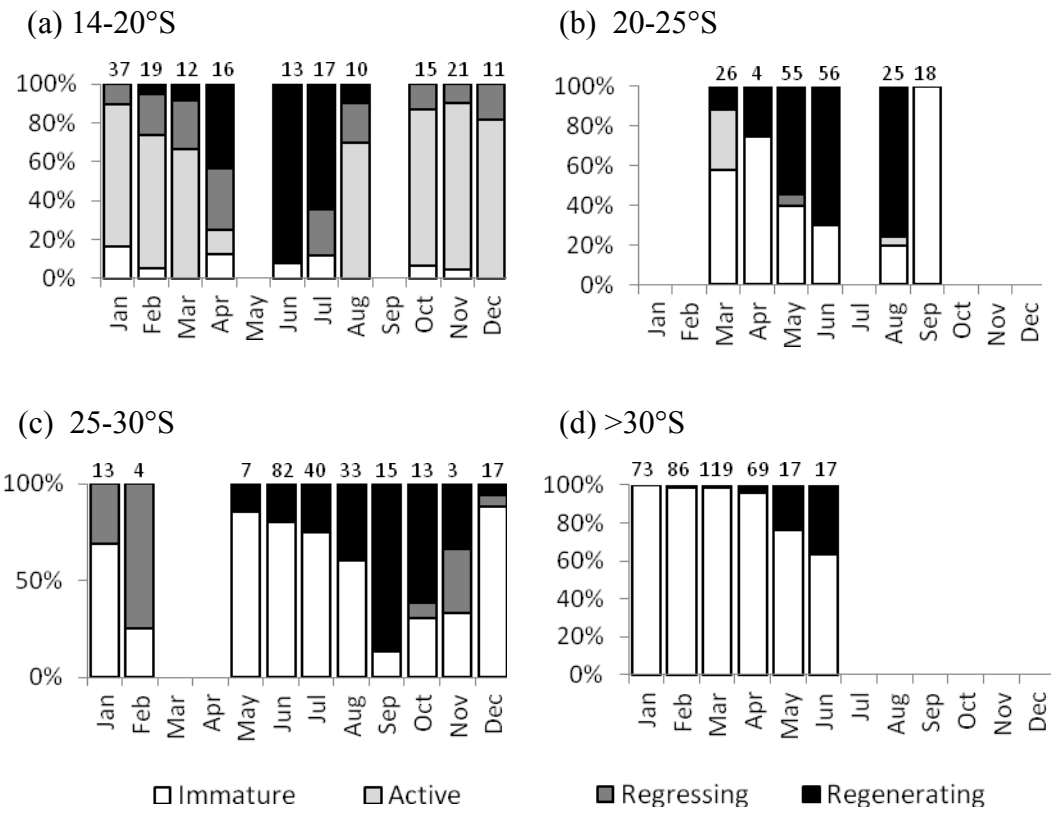


Figure 33. Percent frequency of development classes by month and latitude west of 175˚E. The regressing class includes classes 5, 6a and 6b (see Table 6). Sample size per month shown at top.

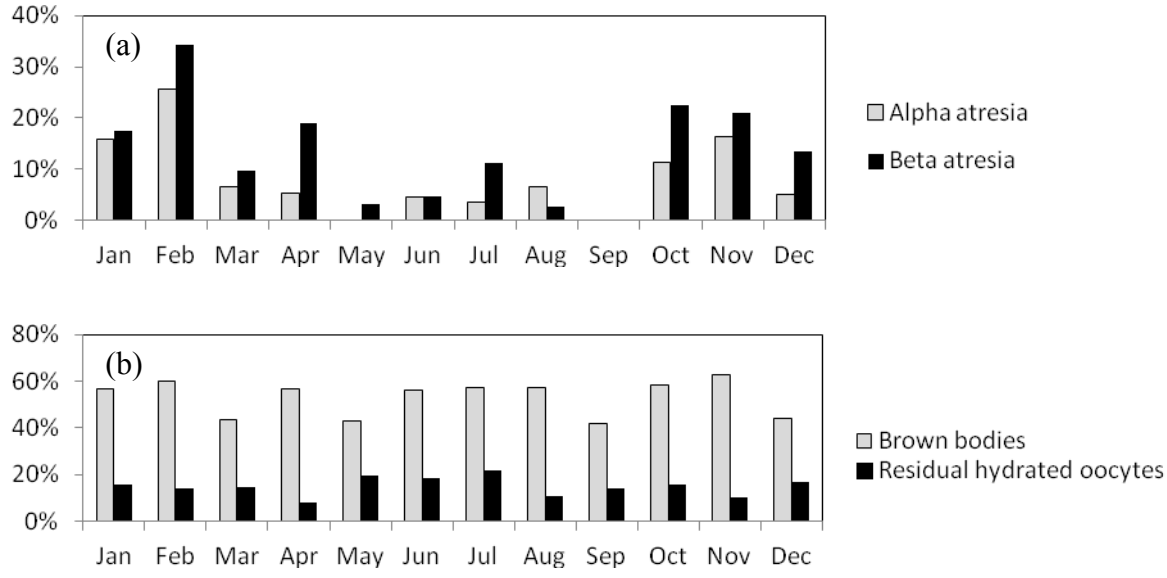


Figure 34. Percent of females ≥ 70 cm *FL* by month with (a) alpha or beta stage atresia and (b) brown bodies and residual hydrated oocytes.

7.5.2 Maturity analysis

Nine models describing the relationship between length at maturity and the spatial covariates of latitude and longitude had AIC_c weights greater than 1% (Table 19). Models that included a covariate for latitude, but not longitude, best described the relationship between length and maturity (Table 19). The four best approximating models, which included a cubic spline for latitude with 2, 3 or 4 degrees of freedom, had AIC_c values < 2 and AIC_c weights greater than 10% (Table 19). Based on the best approximating model (Model 9, Table 19), females at the northernmost latitude (10°S) were predicted to mature at significantly smaller lengths than females at all other latitudes (Figure 35). The predicted pattern in length at maturity was similar at latitudes 30°S and 40°S where the length at maturity was largest. The pattern in length at maturity was intermediate at 20°S. The estimated length at 50% maturity was approximately 88 cm *FL* between latitudes 45-25°S, and decreased significantly in the more northerly latitudes, reaching approximately 75 cm *FL* at 10°S (Figure 36).

Table 19. Comparison of all length-based models with AICc weights greater than 1%. The integers associated with the first three columns represent the number of degrees of freedom in the cubic spline used to define the relationship of the parameters length, latitude, and longitude with maturity. Where no df are given,df=0, the parameter was not included in the model.

Model	Length df	Latitude df	Longitude df	AIC_c	Δ AIC_c	Relative weight	AIC_c weights
1	2	2		354.975	5.223	0.073	2.0%
2	2	2		354.794	5.043	0.080	2.2%
3	5	2		354.036	4.284	0.117	3.3%
4	6	2	2	353.509	3.758	0.153	4.2%
5	3	2		352.053	2.302	0.316	8.8%
6	6	3		351.731	1.979	0.372	10.3%
7	4	2		350.498	0.746	0.689	19.1%
8	2	4		350.382	0.631	0.729	20.2%
9	6	2		349.752	0.000	1.000	27.8%

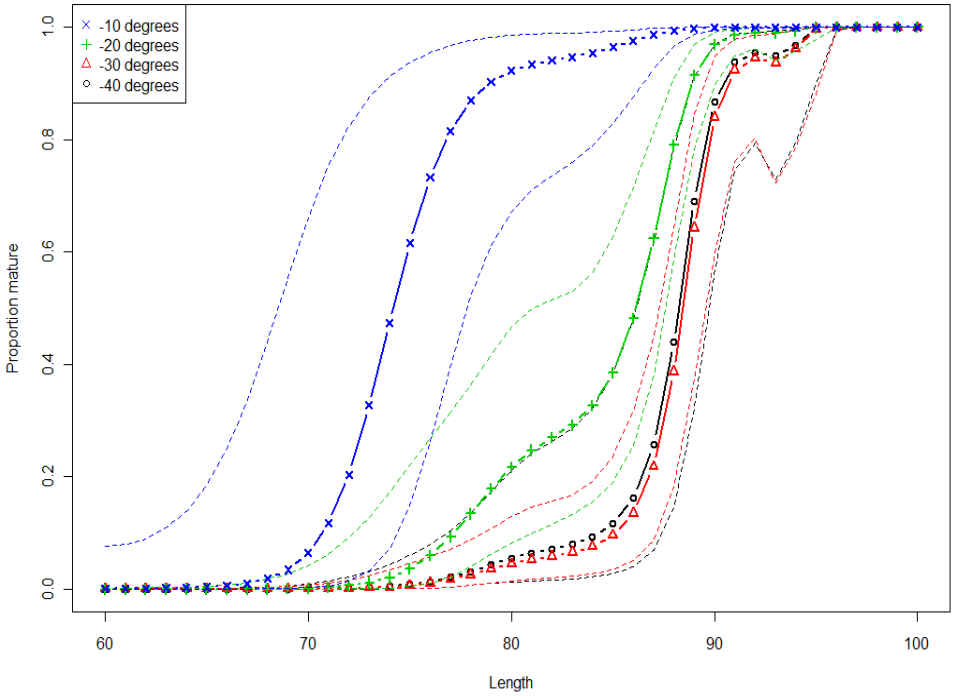


Figure 35. Predicted proportion of mature females by fork length at latitudes 10°S, 20°S, 30°S, and 40°S. Dashed lines represent 95% confidence intervals.

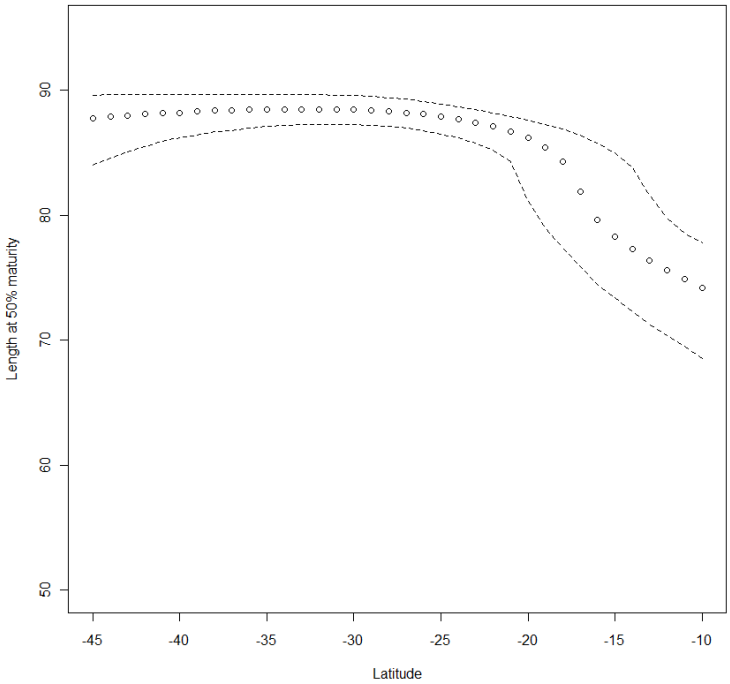


Figure 36. Predicted fork length at 50% maturity by latitude. Dashed lines represent 95% confidence intervals.

Thirteen models describing the relationship between age-at-maturity and the spatial covariates of latitude and longitude had AIC_c weights greater than 1% (Table 20). Similar to length at maturity, models that included a covariate for latitude, but not longitude, best described the relationship between age and maturity (Table 20). The two best approximating models, which included a cubic spline for latitude with 2 or 4 degrees of freedom, had AIC_c values < 2 and AIC_c weights greater than 10% (Table 20). Based on the best approximating model (Model 13, Table 20), females at the northernmost latitude (10°S) were predicted to mature at significantly smaller ages than females at all other latitudes (Figure 37). Again, the predicted pattern in age-at-maturity was similar at latitudes 30°S and 40°S where the age-at-maturity was largest. The pattern in length at maturity was intermediate at 20°S. The estimated age at 50% maturity was approximately age 5 between latitudes 45-30°S, and decreased to approximately age 2 at 10°S (Figure 38). Based on a comparison of the best approximating models for length and age, length is a better predictor of maturity than age (Table 21).

Table 20. Comparison of all age-based models with AICc weights greater than 1%. The integers associated with the first three columns represent the number of degrees of freedom in the cubic spline used to define the relationship of the parameters age, latitude, and longitude with maturity. Where df = 0, the parameter was modelled as a linear variable. Where no df are given, the parameter was not included in the model.

Model	Age df	Latitude df	Longitude df	AIC_c	Δ AIC_c	Relative weight	AIC_c weights
1	2	2	5	386.266	4.961	0.084	2.1%
2	1	2		386.055	4.750	0.093	2.4%
3	0	2		386.055	4.750	0.093	2.4%
4	2	2	2	385.960	4.654	0.098	2.5%
5	2	2		385.547	4.242	0.120	3.0%
6	2	2	1	384.950	3.644	0.162	4.1%
7	2	2	4	384.760	3.454	0.178	4.5%
8	5	2		384.352	3.046	0.218	5.5%
9	2	2	3	383.965	2.659	0.265	6.7%
10	6	3		383.384	2.078	0.354	9.0%
11	6	2	2	383.213	1.907	0.385	9.8%
12	2	4		382.353	1.047	0.592	15.0%
13	6	2		381.306	0.000	1.000	25.3%

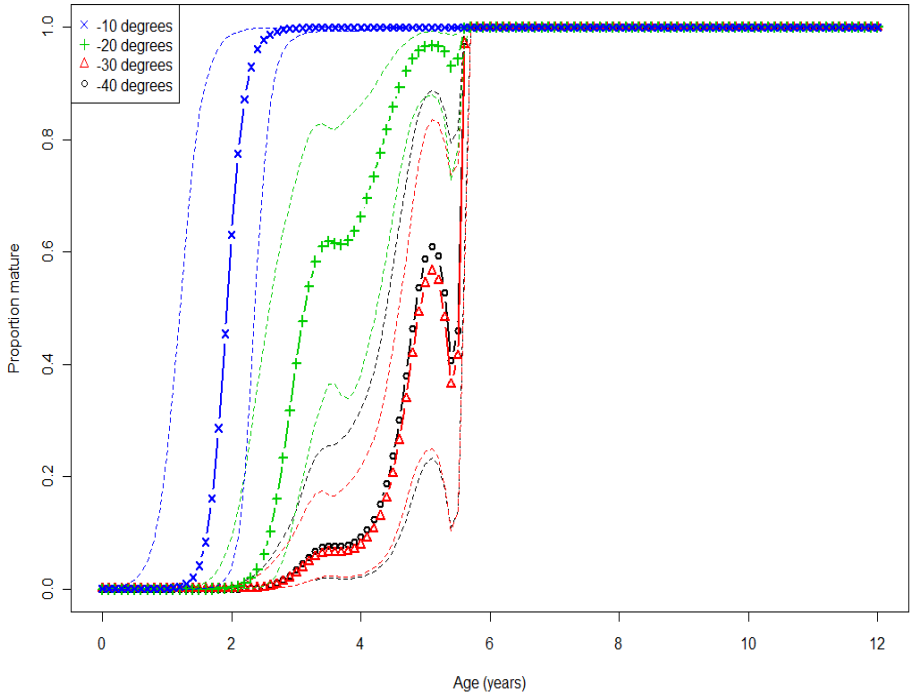


Figure 37. Predicted proportion of mature females by age at latitudes 10°S, 20°S, 30°S, and 40°S. Dashed lines represent 95% confidence intervals.

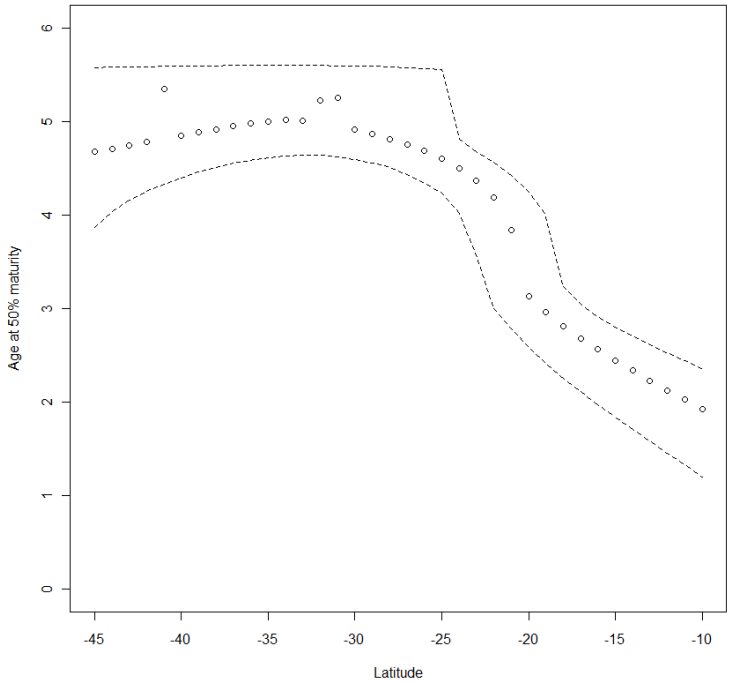


Figure 38. Predicted age at 50% maturity by latitude. Dashed lines represent 95% confidence intervals.

Table 21. Comparison of the best-fitting age-based model with the equivalent length-based model given the same dataset, using AICc. The integers associated with the column 2 represent the number of degrees of freedom in the cubic spline used to define the relationship between latitude and maturity.

Parameter ns(par,df=5)	Latitude df	AIC_c	Δ AIC_c	Relative weight	AIC_c weights
Age	2	381.306	107.505	4.52E-24	4.52E-24
Length	2	273.801	0.000	1.000	1.000

7.5.3 Maturity ogive for the ETBF

The estimated maturity ogives for the 3 latitudinal areas of the ETBF show that females in the northern-most area (lat area 1; < 23°S) are mature at smaller sizes than in the areas further south (Figure 39). This supports the results found in the previous section using samples collected from the whole South Pacific. Although the mean size at maturity for females in latitudinal area 2 is larger than for area 3, which is further south, the maturity curves for these two areas are not significantly different when confidence intervals are taken into account (Figure 39).

The weight assigned to the predicted proportion mature from each area (i.e., the proportion of females in each area) varied by length (Figure 40). As expected, small females (<85cm) are found in greater proportion furthest south (>29°S , lat area 3), whereas large females (>90cm) are found mostly north of 29°S (lat areas 1 and 2). The predicted proportion of mature females by length for the whole ETBF calculated using these weights is shown in Figure 40. The estimated length at 50% maturity for females in the ETBF is approximately 87 cm *FL*, and 100% mature at 95 cm *FL*. Using the predicted growth curve for females at 150˚E (Figure 20; Section 7.3), an 87 cm *FL* female would be 4.5 years old, and a 95 cm female would be age 7 years. The standard errors for the weighted maturity ogive (Figure 41) are underestimated because they do not contain any uncertainty in the weights, i.e., in the estimates of relative abundance, length distribution and sex ratio. If we had uncertainty estimates for these components, they could be incorporated into the estimated standard errors.

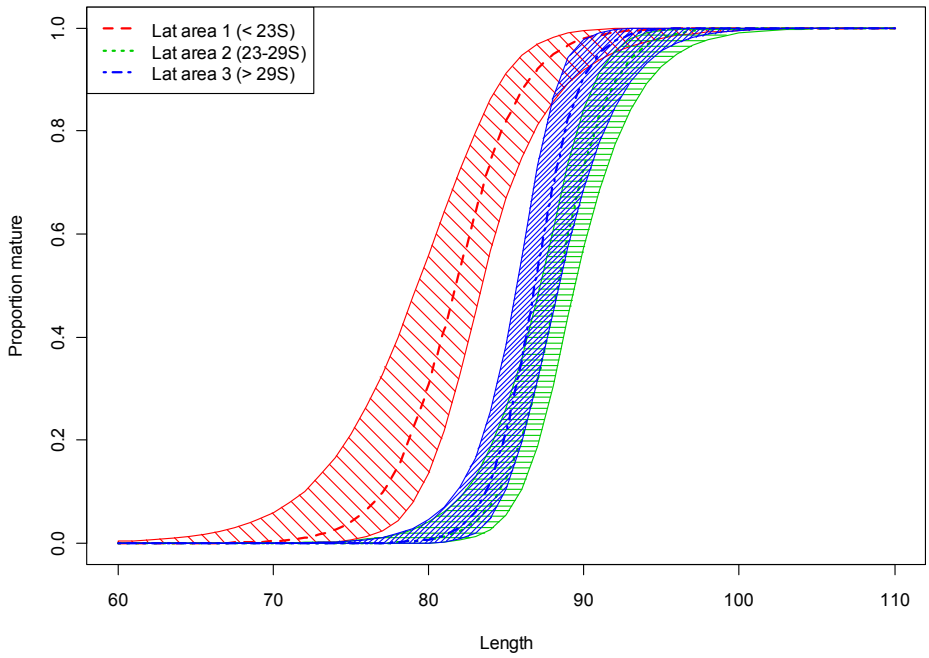


Figure 39. Predicted proportion of mature females by length in each latitudinal area of the ETBF. The shaded regions give approximate 95% confidence intervals.

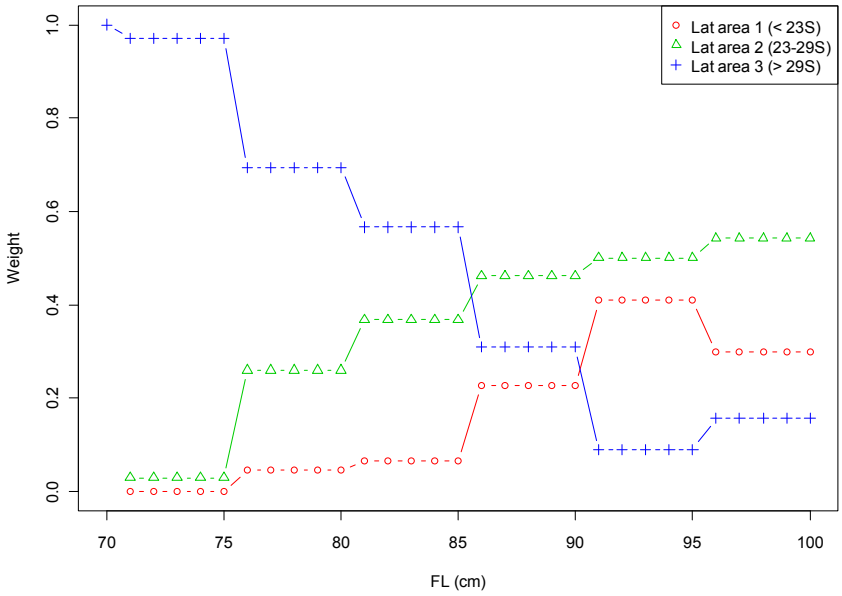


Figure 40. Weights given to the predicted proportion of mature females in each of the 3 latitudinal areas, where the weights are the estimated proportion of females in a given 5-cm length class found in each of the 3 areas.

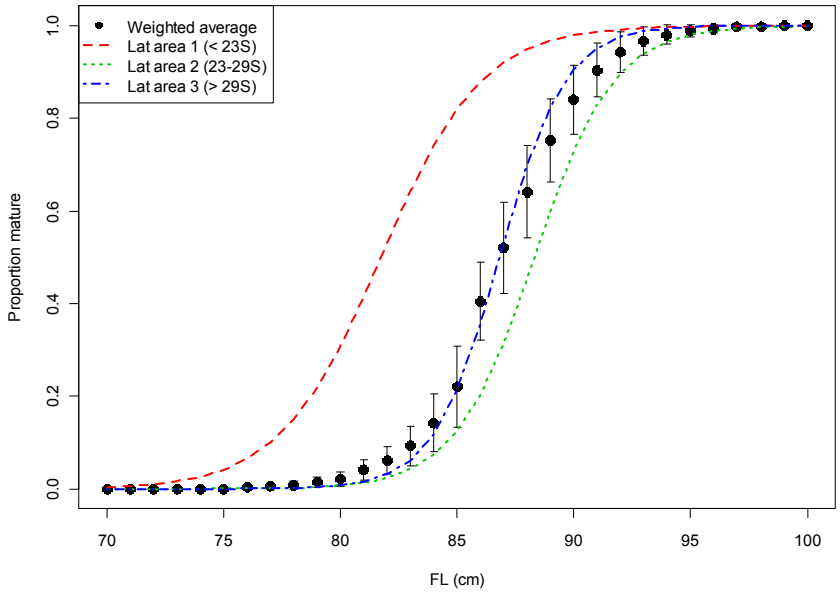


Figure 41. Results of proposed method to estimate a weighted maturity ogive for females in the ETBF region. Shown are: (i) the predicted proportion of mature females by length in each latitudinal area (as in Figure 39), and (ii) the predicted proportion of mature females by length +/- 2 standard errors across all areas (i.e., the weighted average of the area-specific curves). NOTE: the standard errors are underestimated because they do not include uncertainty in the weights (i.e., in the estimates of relative abundance of females by length in each area).

For comparison, we also calculated an "unweighted" maturity ogive for the ETBF by fitting a logistic model to the data with no consideration of latitudinal differences (Figure 42). The unweighted curve is representative of the sampled fish, but is not representative of the ETBF population since sampling was not proportional to female abundance at all latitudes. The weighted and unweighted curves lead to similar estimates of the length at 50% maturity (87cm and 86cm respectively). However, the predicted proportion mature differs substantially at some lengths; e.g., for 85cm females, the predicted proportion mature is 0.22 from the weighted (population) curve compared to 0.33 from the unweighted (sample) curve.

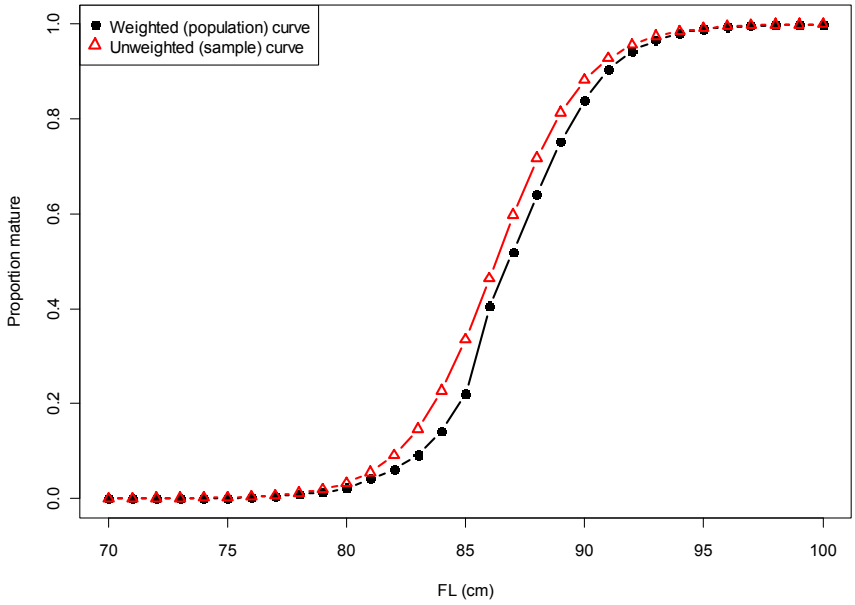


Figure 42. Comparison of the weighted maturity ogive, which should be representative of the female population for the whole ETBF, with the unweighted maturity ogive estimated directly from the sample data. The latter does not account for latitudinal differences in maturity and, therefore is not representative of the ETBF population because sampling was not done in proportion to abundance.

7.5.4 Discussion

The data in this study were collected using consistent histological criteria (see Table 6) to identify mature from immature females across all regions. The criteria used were precise enough to allow for mature but regenerating females to be distinguished from immature females well after the spawning season by the presence of maturity markers, such as encapsulated hydrated oocytes and/or brown bodies. Although brown bodies have been identified in bluefin tuna ovaries (called yellow pigment; Corriero *et al*., 2003; 2005), they have not been widely used to identify resting from immature females in other tuna species. Brown bodies are, however, used to identify resting females in other species (Saidapur, 1978; Crabtree *et al*., 1997; McDonough *et al*., 2005).

For many fish, mature and immature females can only be separated if sampled just prior to or during the spawning season because ovaries of resting females appear 'immature' after spawning when all POFs and yolked oocytes are resorbed (Hunter and Macewicz,

2003). The criteria used here to determine the maturity status of albacore, however, appear to be appropriate for females throughout the reproductive cycle. This conclusion is supported by three lines of evidence. Firstly, the proportion of females with maturity markers did not decline at any stage during the year, unlike the proportion with alpha or beta atresia, which declined after the spawning season. This demonstrates that the resoprtion of maturity markers is a slow and protracted process. Second, the size range that female's attained sexual maturity in our study was relatively narrow (74-94 cm *FL;* 20cm) and the largest female classified as immature was 94 cm *FL* which is the same as found in a recent study of North Pacific albacore (Chen *et al*., 2010). The absence of very large 'immature' females again suggests that the classification scheme is correctly identifying mature resting females.

Finally, the distribution and seasonal change in the relative abundance of development classes obtained is consistent with the assumed seasonal movement patterns of albacore in the South Pacific (see Background). The results clearly show that immature females make up a small proportion of the population in the spawning latitudes and become progressively more dominant to the south. The seasonal change in the relative abundance of mature regressing and regenerating females with latitude suggests a migration pattern where a proportion of post-spawning females migrate south after spawning, arriving at higher latitudes progressively later in the year. Their relative abundance at high latitudes then declines prior to the following spawning season as the regenerating females move north again to develop their gonads and spawn. This pattern of movement with latitude is consistent with the seasonal north-south migration observed in catch rate data in the ETBF (Campbell, 2011) and the broader western and central Pacific (Langley and Hampton, 2005).

Our results clearly demonstrate that the proportion mature-at-length for females varies with latitude in the southwest Pacific and that this variation can be attributed to different geographic distributions of mature and immature fish, rather than the presence of separate stocks with different maturity schedules. Mature females migrate to the spawning latitudes north of 20^{o}S during the spawning season, while immature fish of same length or age generally do not. Spatial variability in maturity-at-length/age clearly must be accounted for when obtaining a single population maturity schedule for the

Australian region and potentially other regions/oceans. The method proposed to obtain a single ogive by weighting the maturity-at-length data by an index of abundance within latitude bands is appropriate for albacore. Similar methods to account for spatial variation in maturity-at-length have been proposed previously (Murua, *et al*., 2003; ICES, 2008). The method proposed requires unbiased data on the size distribution of albacore for each of the three 3 latitudinal areas analysed, and assumes that the size distribution of the catch is representative of the population. The size data currently available for albacore caught in the ETBF is considered biased because much of the data are bulk weights (Farley and Dowling, 2009). Individual weight data are collected routinely by some processors on Australia's east coast, and the collection of additional individual weight data has recently been initiated in other processors (Farley and Dowling, 2009). However, these data are yet to be collated and were not available for inclusion in the current project.

Using the length data from the fish sampled during the project allowed us to obtain a preliminary estimate of the maturity ogive for albacore in the Australian region. The small difference between the weighted and unweighted ogives is due to the extensive sampling program undertaken in the ETBF as part of this project and minimal bias towards specific latitudes. The preliminary estimate of length at 50% maturity of 87 cm is within the range obtained in previous studies (Ueyanagi, 1957; Otsu and Uchida, 1959; Bard, 1981; Ramon and Bailey, 1996; Chen *et al*., 2010). However, the estimated age at 50% maturity of 4.5 years is slightly lower than age 5 that is currently used in the regional stock assessment. Similarly, the estimated age at 100% maturity of 7 years is lower than age 6 that is currently used in the assessment. The implications of these differences for current estimates of the state and the productivity of the stock will require an updated assessment.

8. Benefits

The project estimated a number of key biological parameters for albacore tuna in the ETBF and wider southwest Pacific Ocean including length-weight conversions, sex ratio statistics, validated age and growth estimates, reproductive parameters and maturity ogives. These parameters will benefit the 2012 regional stock assessment and should significantly increase the confidence in the current estimates of the state and productivity of albacore. The individual population parameters can also be used directly as indicators, or as the basis for calculating others, of the status of the stock over time. As such, the outputs of this project provide the biological basis for improved assessment of the status of the stock; improved management decisions; and ultimately the outlook of albacore fisheries in the southwest Pacific. This will have a widespread benefit for a number of fisheries active in the WCPO by providing an improved estimate of stock abundance and sustainable catch levels.

The project has also made significant contribution to the wider scientific community through the refinements or methods for albacore in direct ageing, growth analysis and reproductive biology, where comprehensive studies have previously been lacking. In doing so, it has demonstrated the value and importance of comprehensive, large-scale, collaborative sampling programs to provide robust estimates of important population parameters for these valuable fisheries. Importantly, it has also demonstrated that these programs can be run cost-effectively when done in collaboration with regional partners and the sectors of the regional fisheries (both recreational and commercial) that have an interest in the long-term sustainability of the resource. In the long-term, commercial fishers in the ETBF will benefit from this research because it will provide a valuable baseline for assessing the status of the albacore resource at an early stage of the development of the fishery that will be increasingly valuable in the future.

9. Further Developments

Presentations to the Tropical Tuna Research Assessment Group (RAG), the Tropical Tuna Management Advisory Committee (MAC), the WCPFC Scientific Committee

meeting, and international conferences will be important for disseminating the results of this collaborative project. The target audience will include fisheries managers (AFMA), CSIRO scientists, and SPC scientists ensuring that the results of the project are included appropriately in the stock assessment and ETBF harvest strategy. The results of this project will also be of significant interest to the wider scientific community given the lack of biological studies on albacore worldwide. The results will be published in the peer-reviewed literature to ensure wide dissemination to the scientific community.

The results of the project may be useful in refining the harvest strategy for albacore as part of the review process being undertaken by Tropical Tuna RAG and MAC in 2012-13. An improved understanding of biological parameters will result in a more reliable estimate of stock status, leading to more defensible MEY-based reference points. In turn, the size-based reference points used in the harvest strategy will be more reliable, as these are calculated by determining the size compositions corresponding to a desired level of stock status. It should be noted that updates to the harvest strategy will not take place in the short term, due to the current lack of a long time series of size data, but this is the case regardless of the current work, and when an update occurs, it will be with increased robustness given the outcomes of this project.

The 2012 South Pacific albacore stock assessment (currently in development) is being modified to take into account some aspects of growth variation in space and between sexes, with changes to the ogives for natural mortality and spawning potential at age, and separate models with eastern and western growth curves. Previous work suggests that such changes often have implications for stock status. The stock assessment software used to assess albacore stock status is currently being modified to more effectively include growth variation. These features, partly motivated by the results of this project, will be used in future stock assessments.

All data collected and analysed during the project is currently housed in a purpose-built MS Access database. The main data types are catch data (location, date, vessel), individual fish data (length, weight, sex, biological sample taken), as well as all measurements, age estimates, and histological data obtained during the project. Now that the project is complete, the data will be transferred into CSIRO's

ORACLE/ACCESS “Hardparts database”. The database schema will require some modification to accept new data types. The database is already structured around catch, individual, sample and age estimate data so these changes should be minimal. The data is maintained by the CMAR data centre and is backed up daily. The production database is located at the CSIRO Division of Marine and Atmospheric Research Hobart site and backups are kept offsite in Canberra.

There are additional areas of research currently underway or planned to be undertaken based on the South Pacific albacore sampling program:

1. Otolith microchemistry - potential information on stock structure across the South Pacific (SPC).
2. Blood chemistry - use samples collected as part of the current project to validate blood analysis to identify sex, maturity or possibly development stage (SPC/UTAS).
3. Stable isotope analysis of muscle tissue – potential to identify movement and migration behaviour of albacore (CSIRO).
4. Stomach content analysis – feeding habitats (CSIRO/UQ).

10. Planned Outcomes

The primary goal of the project was to continue the collection of biological samples from albacore caught in the ETBF and wider southwest Pacific, and to undertake the analysis of those samples in order to estimate important biological parameters for the assessment of the albacore stock and the refinement of the harvest strategy for albacore in the ETBF.

In the case of the harvest strategy for albacore in the ETBF, this project provides direct estimates of size at maturity and growth required to estimate the spawner per recruit relationship for albacore. The estimated spawner per recruit at 40% of unfished spawning biomass is used to determine the size-based target reference points in the harvest control rule in the ETBF Harvest strategy framework (Davies *et al*., 2008b;

Campbell, 2011). The results of this project provide the basis for ETBF specific estimates of this biological reference point.

Internationally, the project aimed to directly address stock assessment needs for one of the principal target species in the region. It therefore represents a direct contribution from Australia to the regional management arrangements and contributes to Australia's advocacy for the sustainable use of the resources. Three progress reports on the outcomes of the project, including Farley *et al.* 2011, have been submitted to and presented at the Scientific Committee of the WCPFC and the direct collaboration of SPC assessment staff (Simon Hoyle) through this project and the parallel SPC project has ensured direct communication of results through the progress of the project and direct uptake of final results of the project. An update of the South Pacific albacore assessment will be conducted in 2012, at the request of the Commission, and considered by the WCPFC SC at their August 2012 meeting. The close linkages with both the domestic and international aspects of the fishery and the strong and successful international collaboration with SPC and the PICT observer program have provided direct pathway for adoption of the projects research results and should significantly improve the research outcomes.

The project represents the most comprehensive study of albacore population biology to date, and as a result the outputs have significantly improved the understanding of several key biological parameters and albacore biology more generally. Internationally, in addition to the direct contributions to the harvest strategy and regional stock assessment, the systematic and extensive coverage of the project may indirectly influence the direction of future research and monitoring on other target species to investigate the degree to which spatial variation evident for albacore may be reflected in those species.

11. Conclusions

The project met its five key objectives. A successful large-scale biological sampling program was undertaken in the ETBF and across the southwest Pacific. International collaborations crucial to the success of this sampling program were consolidated and strengthen, and material was received from fish caught over a wide range of longitudes from 130°E to 130° W.

The study found that albacore caught in the ETBF are in better condition on average (greater weight for length) than albacore caught previously in the Australian region (1987-97) or in several other regions in the South Pacific. Unfortunately, comprehensive studies of albacore length-weight relationships have not been undertaken across the South Pacific and this should be a priority for future sampling programs.

A significant finding was that counts of growth zones in sectioned otoliths provide accurate estimates of age in albacore, and that the longevity of albacore is at least 14 years. Dorsal spines are commonly used to estimate the annual age of albacore, yet our results suggest that spine-based age estimates were generally lower than otolith-based estimates after age seven, possibly due to resorption at the core or poor increment clarity at the spine edge as spines grow. The ageing algorithm developed for albacore allowed us to estimate the decimal age of fish across their entire lifespan. These age estimates provided greater precision for determining age-based metrics such as growth and reproductive parameters, which are required for age-based stock assessments, and should significantly improve the fits of the models to catch at length data.. We recommend the use of validated annual counts of sectioned otoliths as the preferred method for providing age-based parameters for assessment and management advice for these important stocks.

This is the first study to explicitly examine the spatial variation in tuna growth across an entire stock. We demonstrated that significant variation in growth of albacore occurs between the sexes and across 90° of longitudinal in the South Pacific. The determinants of the longitudinal variation in growth of albacore remain unclear, but variation in

oceanography, particularly the depth of the thermocline, may play a role in determining growth of South Pacific albacore. Future development of assessment models for South Pacific albacore may benefit from explicit consideration of sex-specific growth curves and, if feasible, spatial variation in growth within the stock. Such structural improvements are likely to provide more reliable estimates of biomass, fishing mortality and potential yields.

Our study found that the different growth rates by males and females may be driving the observed bias in the sex ratio towards males in the largest length classes, rather than differences in natural mortality as previously assumed. We showed that females reach the same maximum age as males, but at a smaller size. Again, we recommend that these differences are taken into consideration in the stock assessment.

This study also significantly improved our understanding of the reproductive dynamics of albacore over a large part of their range in the south Pacific. We found that spawning is synchronised across the southwest Pacific between 10 and 25°S during the austral summer. We confirmed that albacore spawn during the early hours of the morning and that batch fecundity increases with *FL*. It was important to quantify the degeneration rates of POFs to ensure that estimates of spawning frequency were accurate. We confirmed that albacore are capable of spawning daily, but the fraction spawning per day is 0.77 during the peak spawning months. Our finding that the smallest mature fish are behaving differently to larger fish (i.e. their spawning season is shorter) is important and their reproductive output needs to be accounted for in the population models.

It was also important to develop a histological classification scheme for ovaries that was precise enough to allow for mature but regenerating females to be distinguished from immature females well after the spawning season. This finding allows for year-round sampling of albacore to determine maturity, rather than restricting the sampling program to the spawning months. Based on our classification scheme, we found that the proportion of females mature-at-length varied significantly with latitude in the Australian region, and that this variation was due to different geographic distributions of mature and immature fish during the year. A method was proposed to account for this latitudinal variation, and the weighted maturity ogive obtained showed that the age at

50% maturity for albacore is age 4.5, and 100% maturity is at age 7. These estimates are younger than current used in the harvest strategy or stock assessment for albacore.

Overall, we have provided considerable new information on the population biology of albacore in the South Pacific, which will enable scientists to significantly improve the regional stock assessment for albacore scheduled for 2012 and refine the harvest strategy for albacore in the ETBF.

12. References

Allain, V. (2010). Trophic structure of the pelagic ecosystems of the western and central Pacific Ocean. Information paper EB-IP-10, 6th Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 10-19 August 2010, Nukualofa, Tonga.

Anon. (2002). A manual for age determination of southern bluefin *Thunnus maccoyii*. Otolith sampling, preparation and interpretation. The direct age estimation workshop of the CCSBT, 11-14 June 2002, Queenscliff, Australia, 39 pp. Available at: http://www.ccsbt.org/site/reports_past_meetings.php.

Anon. (2005). Report of the first regular session of the Scientific Committee of the Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean, Noumea, New Caledonia, 8-19 August, 2005.

Anon. (2006). Tunas and billfishes in the eastern Pacific Ocean in 2005. Fishery Status Report No. 4, Inter-American Tropical Tuna Commission, La Jolla, California.

Anon. (2011). Report of the 2011 ICCAT South Atlantic and Mediterranean albacore stock assessment sessions. July 25-29, 2011, Madrid, Spain. Available at: http://www.iccat.org/Documents/Meetings/Docs/2011_ALB_ASSESS_EN.pdf.

Arneri, E., Mosegaard, H., Wright, P.J. and Morales-Nin, B. (1998). Microstructural validation of annual increments. In The present status of otolith research and applications (Wright, P.J., ed.), pp. 54-59. EFAN Report 1-98.

Bates, D., Maechler, M. and Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.R-project.org/package=lme4.

Beamish, R.J. and Fournier, D.A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 982–983. doi: 10.1139/f81-132.

Begg, G.A. and Cadrin, S.X. (2009). Stock identification. In Fish Reproductive Biology, Implications for Assessment and Management (Jakabsen, T., Fogarty, M.J., Megrey, B.A. and Mosksness, E., eds), pp. 230-292. West Sussex, United Kingdon: Wiley-Blackwell.

Boehlert, G.W. and Kappenman, R.F. (1980). Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. *Marine Ecology Progress Series* 3, 1–10.

Boyd, J. (2010). The age and growth of albacore tuna (*Thunnus alalunga*) of the north east Atlantic Ocean as inferred from the Irish pelagic trawl fishery of 2002. *ICCAT, Collect Volume of Scientific Papers* 65, 1268-1281.

Brandt, S.B. (1981). Effects of warm-core eddy on fish distributions in the Tasman Sea off East Australia. *Marine Ecology Progress Series* 6, 19–33.

Brandt, S.B. (1993). The effect of thermal fronts on fish growth: a bioenergetics evaluation of food and temperature. *Estuaries* 16, 142–159.

Burnham, K.P. and Anderson, D.R. (2002). Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd edition. New York: Springer. 488 p.

Campana, S.E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59, 197-242. doi: 10.1006/jfbi.2001.1668.

Campana, S.E., Annand, M.C., and McMillan, J.I. (1995). Graphical and Statistical Methods for Determining the Consistency of Age Determinations. Transactions of the American Fisheries Society 124, 131-138.

Campana, S.E. and Thorrold, S.R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fish and Aquatic Sciences* 58, 30-38.

Campbell, R. (2007). Summary of Catch, Effort and Size Data and Fishery Indicators Pertaining to Albacore Tuna in the ETBF and the SW Pacific. Background paper presented to the ETBF Resource Assessment Group meeting, 18-19 July, Sydney, Australia.

Campbell, R. (2011). Implementation of the ETBF harvest strategy and calculation of recommended biological commercial catches for swordfish and striped marlin in 2012. Working Paper to Tropical Tuna RAG, Brisbane, August 2011.

Campbell, R., Prince, J., Davies, C., Kolody, D., Dowling, N., Ward, P. and McLoughlin, K. (2007). Development of an Empirical-Indicator based Harvest Strategy for the Australian Eastern Tuna and Billfish Fishery. Working paper ME

SWG/WP-4, 3rd Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 13-24 August, Honolulu, United States of America.

Carey, F.G., Teal, J.M., Kanwisher, J.W. and Lawson, K.D. (1971). Warm-bodied fish. *American Zoologist* 11, 137-145.

Chen, K.-S., Crone, P.R. and His, C.-C. (2010). Reproductive biology of albacore *Thunnus alalunga*. Journal *of Fish Biology* 77, 19-136.

Chen, I.-C., Lee, P.-F. and Tzeng, W.-N. (2005). Distribution of albacore (*Thunnus alalunga*) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography* 14, 71 80.

Chen, Y. and Paloheimo, J.E. (1994). Estimating fish length and age at 50% maturity using a logistic type model. *Aquatic Science* 56, 206-219.

Childers, J., Snyder, S. and Kohin, S. (2011). Migration and behavior of juvenile North Pacific albacore (*Thunnus alalunga*). *Fisheries Oceanography* 20, 157–173.

Clear, N.P., Gunn, J.S. and Rees, A.J. (2000). Direct validation of annual increments in the otoliths of juvenile southern bluefin tuna, *Thunnus maccoyii*, by means of a large scale mark recapture experiment with strontium chloride. *Fishery Bulletin* 98, 25–40.

Clear, N. and Leroy, B. (In prep). Direct validation of annual increments in otoliths of bigeye tuna, *Thunnus obesus*, from the eastern Australian region.

Clifton, K.E. (1995). Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. *Marine Ecology Progress Series* 116, 39–46.

Conover, D.O., Brown, J.J. and Ehtisham , A. (1997). Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 2401–2409.

Conover, D.O., Clarke, L.M., Munch S.B. and Wagner G.N. (2006). Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. *Journal of Fish Biology* 69, 21–47.

Conover, D.O. and Present, T.M.C. (1990). Countergradient variation in growth rate: compensation for the length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83, 316–324.

Corriero, A., Desantis, S., Deflorio, M., Acone, F., Bridges, C. R., De la Serna, J. M., Megalofonou, P. and De Metrio, G. (2003). Histological investigation on the

ovarian cycle of the bluefin tuna in the western and central Mediterranean. *Journal of Fish Biology* 63, 108-119.

Corriero, A., Karakulak, S., Santamaria, N., Deflorio, M., Spedicato, D., Addis, P., Cirillo, F., Fenech-Farrugia, A., Vassallo-Aguis, R., de la Serna, J.M., Oray, Y., Cau, A., Megalofonou, P. and Metrio, G.D. (2005). Size and age at sexual maturity of female bluefin tuna (*Thunnus thynnus*, L. 1758) from the Mediterranean Sea. *Journal of Applied Ichthyology* 21, 483–486.

Crabtree, R.E., Snodgrass, D. and Harnden, C.W. (1997). Maturation and reproductive seasonality in bonefish, *Albula vulpes*, from the waters of the Florida Keys. *Fishery Bulletin* 95, 456-465.

Davies, C.A., Brophy, D., Megalofonou, P., Gosling, E., Griffin, N., Leroy, B. and Clear, N. (2008a). Age estimation in calcified calcareous structures; preliminary findings of an inter-laboratory comparison. *ICCAT, Collective Volume of Scientific Papers* 62, 899-910.

Davies, C., Campbell, R., Prince, J., Dowling, N., Kolody, D., Basson, M., McLoughlin, K., Ward, P., Freeman, I., and Bodsworth, A. (2008b). Development and preliminary testing of the harvest strategy framework for the Western Tuna and Billfish Fishery. Report to Australian Fisheries Management Authority, Canberra, 56pp.

Davis, T., Farley, J., Bravington, M. and Andamari, R. (2001). Size at first maturity and recruitment into egg production of southern bluefin tuna. Final report for FRDC project 1999/106.

Davis, T., Farley, J. and Gunn, J. (2001). Size and Age at 50% Maturity in SBT: An integrated view from published information and new data from the spawning ground. Working paper 0108/16, CCSBT Scientific Meeting, 28-31 August, Tokyo, Japan.

Domokos, R., Seki, M.P., Polovina, J.J. and Hawn, D.R. (2007). Oceanographic investigation of the American Samoa albacore (*Thunnus alalunga*) habitat and longline fishing grounds. *Fisheries Oceanography* 16, 555–572.

Drew, K., Die, D.J., Arocha, F. (2006). Understanding vascularisation in fin spines of white marlin (*Tetrapturus albidus*). *Bulletin of Marine Science* 79, 847-852.

Everett, E. and R. Punsly. (1994). Sex ratios of yellowfin tuna in the eastern Pacific Ocean. Unpublished analysis, IATTC. (Cited in Harley and Maunder, 2003).

Eveson, J. P., Laslett, G. M., & Polacheck, T. (2004). An integrated model for growth incorporating tag–recapture, length–frequency, and direct aging data. *Canadian Journal of Fisheries and Aquatic Sciences* 61, 292-306.

FAO. (2001). Research implications of adopting the precautionary approach to management of tuna fisheries. *FAO Fisheries Circular* C963, Rome.

Farley, J. and Clear, N. (2008). Preliminary study of age, growth, and spawning activity of albacore in australia's Eastern Tuna and Billfish Fishery. Working paper BI-IP-1, 4th Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 11-22 August, Port Morseby, Papua New Guinea.

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. Final report for FRDC project 2000/100. CSIRO Marine and Atmospheric Research. GPO Box 1538, Hobart, Tasmania 7000 Australia.

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 and Freshwater Research* 57, 713 724. doi:10.1071/MF05255.

Farley, J.H. and Davis, T.L.O. (1998). Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*. *Fishery Bulletin* 96, 223-236.

Farley, J. and Dowling, N. (2009). Industry based size-monitoring and data collection program for albacore tuna in the ETBF. Final report for FRDC Tactical Research Fund Project 2008/075.

Farley, J., Williams, A., Davies, C. and Nicol, S. (2011). Regional study of South Pacific albacore population biology: year 3 – biological sampling and analysis. Working paper SA-WP-05, 7th Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 9-17 August, Pohnpei, Federated States of Micronesia.

Fielder, P. and Bernard, H. (1987). Tuna aggregation and feeding near fronts observed in satellite imagery. *Continental Shelf Research* 7, 871-881.

Foreman, T.J. (1980). Synopsis of biological data on the albacore tuna, *Thunnus alalunga* (Bonnaterre, 1788), in the Pacific Ocean. I-ATTC Special Report 2, 17–70.

Fournier, D.A., Hampton, J., Sibert, J.R. (1998). MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2105-2116.

Fitzhugh, G.R. and W.F. Hettler. (1995). Temperature influence on postovulatory follicle degeneration in Atlantic menhaden, *Brevoortia tryannus*. *Fishery Bulletin* 93, 568-572.

Goldberg, S.R. and Au, D.W.K. (1986). The spawning of skipjack tuna from southeastern Brazil as determined from histological examinations of ovaries. In Proceedings of the ICCAT Conference on the International Skipjack Year Program (Symons, P.E.K., Miyake, P.M. and Sakagawa, G.T., Eds.), pp. 277-284, ICCAT, Madrid, Spain.

Gompertz, B. (1825). On the nature of the function expressive of the law of human mortality and on a new mode of determining the value of life contingencies. Philosophical *Transactions of the Royal Society of London* 115, 515–585.

Gordoa, A., Olivar, M.P., Arevola, R., Viñas, J., Molí, B. and Illas, X. (2009). Determination of Atlantic bluefin (*Thunnus thynnus*) spawning time within a transport cage in the western Mediterranean. *ICES Journal of Marine Science* 66, 2205–2210. doi:10.1093/icesjms/fsp211.

Green, B.S., Mapstone, B.D., Carlos, G. and Begg, G.A. (2009). Tropical fish otoliths: Information for assessment, management and ecology. Book series: Reviews: Methods and Technologies in Fish Biology and Fisheries. Springer, Netherlands.

Griffiths, S. P., Fry, G. C., Manson, F. J. and Lou, D. C. (2009). Age and growth of longtail tuna (*Thunnus tonggol*) in tropical and temperate waters of the central Indo-Pacific. *ICES Journal of Marine Science* 67, 125-134. doi: 10.1093/icesjms/fsp223.

Griggs, L. (2005). Catch monitoring of the New Zealand albacore troll fishery. Working paper SAIP-1, 1st Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 8–19 August, Noumea, New Caledonia.

Gulland, J.A. (1988). Fish Population Dynamics: the Implications for Management, 2nd edition. New York, NY: John Wiley and Sons.

Gunn, J.S., Clear, N.P., Carter, T.I., Rees, A.J., Stanley, C.A., Farley, J.H. and Kalish, J.M. (2008). Age and growth in southern bluefin tuna, *Thunnus maccoyii*

(Castelnau): direct estimation from otoliths, scales and vertebrae. *Fisheries Research*, 92, 207–220. doi:10.1016/j.fishres.2008.01.018.

Gust, N., Choat, J.H. and Ackerman, J.L. (2002). Demographic plasticity in tropical reef fishes. *Marine Biology* 140, 1039–1051.

Haddon, M. (2001). *Modelling and Quantitative Methods in Fisheries*. London: Chapman & Hall.

Hallier, J.-P., and Gall, J.-Y. L. (1983). A surface albacore survey in the central and western Pacific Ocean. SPC Fisheries Newsletter No. 24 January, March 1983.

Hampton, J. (1999). The convention area. Working paper MHLC-2, 12th meeting of the Standing Committee on tuna and billfish. 16–23 June, Papeete, Tahiti, French Polynesia.

Hampton, J. (2002). Stock assessment of albacore tuna in the South Pacific Ocean. Working paper ALB-1, 15th meeting of the Standing Committee on tuna and Billfish, 22-27 July, Honolulu, Hawaii, USA.

Hampton, J., Murray, T. and Sharples, P. (1989). South Pacific albacore observer program 1988-1989. Tuna and Billfish Assessment Programme Technical Report No. 22, pp 22.

Harley, S. and Maunder, M. (2003). A simple model for age-structured natural mortality based on changes in sex ratios. Inter-American Tropical Tuna Commission, IATTC, 4th Meeting of the Scientific Working Group, La Jolla, USA, May 19-21 2003.

Hilborn, R. and Walters, C.J. (1992). Quan*titative fisheries stock assessment: choice, dynamics and uncertainty*. New York, NY: Chapman and Hall.

Hill, K.T., Cailliet, G.M. and Radtke, R.L. (1989). A comparative analysis of growth zones in four calcified structures of Pacific blue marlin, *Makaira nigricans*. *Fishery Bulletin*, 87, 829−843.

Hillary, R.M. (2008). Risk assessment of Indian Ocean albacore stock status using an age-structured production model. Indian Ocean Tuna Commission Working Party on Temperate Tunas, Bangkok, Thailand, 1 November 208. IOTC-2008-WPTe-09. Available at http://www.iotc.org/files/proceedings/2008/wptmt/IOTC-2008-WPTe-09.pdf.

Hoyle, S. (2011). Stock assessment of albacore tuna in the South Pacific Ocean. Working paper SA-WP-06, 7th Scientific Committee meeting of the Western and

Central Pacific Fisheries Commission, 9-17 August, Pohnpei, Federated States of Micronesia.

Hoyle, S., Langley, A. and Hampton, J. (2008). Stock assessment of albacore tuna in the South Pacific Ocean. Working paper SA-WP-8, 4th Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 11-22 August, Port Moresby, Papua New Guinea.

Hunter, J.R. and Macewicz, B.J. (1980). Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. *California Cooperative Oceanic Fisheries Investigations Reports* 21, 139-149.

Hunter, J.R. and Macewicz, B.J. (1985a). Measurement of spawning frequency in multiple spawning fishes. In R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., *NOAA Technical Report NMFS* 36, 79-94.

Hunter, J.R. and Macewicz, B.J. (1985b). Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. *Fishery Bulletin* 83,119-136.

Hunter, J. and B. Macewicz. (2003). Improving the accuracy and precision of reproductive information used in fisheries. *In* Workhop on modern approaches to assess maturity and fecundity.

Hunter, J. R., and B. J. Macewicz. (2003). Improving the accuracy and precision of reproductive information used in fisheries. *In:* Report of the working group on Modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids. Bergen, Norway 4-7 September 2001. Kjesbu, O. S., J. R. Hunter and P. R. Witthames, editors. Fisken og Havet. Nr. 12-2003, pp. 57-68.

Hunter, J.R., Macewicz, B.J. and Sibert, R.J. (1986). The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the south Pacific. *Fishery Bulletin* 84, 895-903.

Hunter, J.R., Lo, N.C.H. and Leong, R.J.H. (1985). Batch fecundity in multiple spawning fishes In R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., *NOAA Technical Report NMFS* 36, 67-77.

ICCAT (2010). Report of the 2009 ICCAT Albacore Stock Assessment Session, Madrid, Spain, July 13 to 18, 2009. *ICCAT, Collect Volume of Scientific Papers* 65, 1113-1253.

ICCAT (2011). Report of the 2011 ICCAT South Atlantic and Mediterranean albacore stock assessment sessions. July 25-29, 2011, Madrid, Spain. Available at: http://www.iccat.org/Documents/Meetings/Docs/2011_ALB_ASSESS_EN.pdf.

ICES (2008). Report of the workshop on maturity ogive estimation for stock assessment (WKMOG), 3-6 June 2008, Lisbon, Portugal. ICES CM2008/ACOM:33. 72 pp

ISC (2010). Report of the ISC – Albacore Working Group Workshop. October 12-19, 2010, Southwest Fisheries Science Centre, La Jolla, USA. Available at: http://afrf.org/albwg3.pdf.

ISSF (2011). Status of the world fisheries for tuna: Management of tuna stocks and fisheries, 2011. ISSF Technical Report 2011-05. International Seafood Sustainability Foundation, McLean, Virginia, USA. 19 p.

Itano, D. (2000). The reproductive biology of yellowfin tuna (*Thunnus albacares*) in Hawaiian waters and the western tropical Pacific Ocean: Project summary. SOEST 00-01, JIMAR Contribution 00-328. Available at: http://www.soest.hawaii.edu/pfrp/biology/itano/itano_yft.pdf.

Itoh, T., Shina, Y., Tsuji, S., Endo, F. and Tezuka, N. (2000). Otolith daily increment formation in laboratory reared larval and juvenile bluefin tuna *Thunnus thynnus*. *Fisheries Science* 66, 834-839. doi: 10.1046/j.1444-2906.2000.00135.x

Jenkins, G.P. and Davis, T.L.O. (1990). Age, growth rate, and growth trajectory determined from otolith microstructure of southern bluefin tuna *Thunnus maccoyii* larvae. *Marine Ecology Progress Series* 63, 93-104. doi:10.3354/meps063093.

Jones, G.P. (1986). Food availability affects growth in a coral reef fish. *Oecologia* 70, 136–139.

Jones, J.B. (1991). Movements of albacore tuna (*Thunnus alalunga*) in the South Pacific: evidence from parasites. *Marine Biology* 111, 1-9.

Katsanevakis, S. and Maravelias, C.D. (2008). Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. *Fish and Fisheries* 9, 178–187.

Kerandel, J-A., Leroy, B. and Kirby, D.S. (2006). Age and growth of albacore by otolith analysis. SPC Oceanic Fisheries Programme Internal Report, Secretariat of the Pacific Community, Noumea, November 2006.

Kerrigan, B.A. (1994). Post-settlement growth and body condition in relation to food availability in a juvenile tropical reef fish. *Marine Ecology Progress Series* 111, 7–15.

Knaggs, E.H. and Parrish, R.H. (1973). Maturation and growth of Pacific mackerel Scomber japonicus Houttuyn. California Department of Fish Game, Marine Resource Technical Report 3, 19p.

Kolody, D.S., Preece, A.L., Davies, C.R., Hartog, J.R. and dowling, N.A. (2010). Integrated evaluation of management strategies for tropical multi-species long-line fisheries. Final report for FRDC project 2007/017.

Kritzer, J.P. and Sale, P.F. (2006). *Marine metapopulations*. New York: Academic Press. 576 p.

Labelle, M. and Hampton, J. (2003). Stock assessment of albacore tuna in the south Pacific Ocean. Working paper ALB-1, 16th meeting of the Standing Committee on tuna and billfish. 9–16 July 2003, Mooloolaba, Queensland, Australia.

Labelle, M., Hampton, J., Bailey, K., Murray, T., Fournier, D.A. and Sibert, J.R. (1993). Determination of age and growth of south Pacific albacore (*Thunnus alalunga*) using three methodologies. *Fishery Bulletin* 91, 649-663.

Langley, A. (2004). An examination of the influence of recent oceanographic conditions on the catch rate of albacore in the main domestic longline fisheries. Working Paper SA-4, 17th Meeting of the Standing Committee on Tuna and Billfish. Majuro, Marshall Islands. 9-18 August 2004, Majuro, Marshall Islands.

Langley, A. and Hampton, J. (2005). Stock assessment of albacore tuna in the South Pacific Ocean. Working paper WP-3, 1st Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 8–19 August, Noumea, New Caledonia.

Laurs, R.M. and Lynn, R.J. (1977). Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: distribution, relative abundance, and association with Transition Zone waters. *Fishery Bulletin* 75, 795-822.

Laurs, R. M., Yuen, H. S. H. and Johnson, J. H. (1977). Small-scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. *Fishery Bulletin* 75, 347-355.

Laurs, R.M. and Wetherall, J.A. (1981). Growth rates of north Pacific albacore, *Thunnus alalunga*, based on tag returns. *Fishery Bulletin* 79, 293–302.

Laurs, R.M., Fielder, P.C. and Montgomery, D.R. (1984). Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep Sea Research* 31, 1085–1099.

Laurs, R.M., Nishimoto, R. and Wetherall, J.A. (1985). Frequency of increment formation on sagittae of North Pacific albacore (*Thunnus alalunga*). *Canadian Journal of Fisheries and Aquatic Sciences* 42, 1552–1555. doi:10.1139/cjfas-42-9-1552.

Le Cren, E.D. (1951). The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* 20, 201-219.

Lee, L.K. and Yeh, S.Y. (2007). Age and growth of South Atlantic albacore – a revision after the revelation of otolith daily ring counts. *ICCAT, Collective Volume of Scientific Papers* 60, 443–456.

Leroy, B. and Lehodey, P. (2004). Note on the growth of the South Pacific albacore. Working Paper INF-BIO-2, 17th meeting of the Standing Committee on tuna and billfish, 8-18 August, Majuro, Republic of Marshall Islands.

MacCall, A.D., Frey, H. W., Huppert, D.D., Knaggs, E.H., McMillan, J.A. and Stauffer, G.D. (1980). Biology and economics of the fishery for Jack Mackerel in the northeastern Pacific. *NOAA Technical Memorandum NMFS* SWFC-4.

Majkowski, J. (2007). Global fishery resources of tuna and tuna-like species. *FAO Fisheries Technical Paper* 483, 1-54.

Maunder, M.N. and Watters, G.M. (2003). A-scalia: an age-structured statistical catch-at-length analysis for assessing tuna stocks in the eastern Pacific Ocean. *Inter-American Tropical Tuna Commission Bulletin* 22, 435-582.

McDonough, C.J., Roumillat, W.A. and Wenner, C.A. (2005). Sexual differentiation and gonad development in striped mullet (*Mugil cephalus* L.) from South Carolina estuaries. *Fishery Bulletin* 103, 601-619.

McPherson, G.R. (1991). Reproductive biology of yellowfin tuna in the eastern Australian fishing zone, with special reference to the North-western Coral Sea. *Australian Journal of Marine and Freshwater Research* 42, 465-477.

Meekan, M.G., Ackerman J .L. and Wellington, G.M. (2001). Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology Progress Series* 212, 223–232.

Megalofonou, P. (2000). Age and growth of Mediterranean albacore. *Journal of fish biology* 57, 700-715.

Morales-Nin, B. and Panfili, J. (2002). Validation and verification methods. B. indirect validation. In *Manual of fish sclerochronology* (Panfili, J., de Pontual, H., Troadec, H. and Wrigth, P.J., eds), pp. 135-137. Brest, France: Ifremer-IRD.

Murray, T. (1994). A review of the biology and fisheries for albacore, *Thunnus alalunga*, in the South Pacific Ocean. In: Shomura, R.S., J. Majkowski and S. Lan*GI* (eds.). Interactions of Pacific tuna fisheries. Proceedings of the First FAO Expert Consultation on Interactions of Pacific Tuna Fisheries, 3-11 December 1991, Noumea, New Caledonia. Vol. 2: Papers on biology and fisheries. *FAO Fisheries Technical Paper* 336, 188-206.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P. R., Thorsen, A. and Junquera, S. (2003). Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fishery Science* 33, 33-54

Neilson, J.D. and Campana, S.E. (2008). A validated description of age and growth of western Atlantic bluefin tuna (*Thunnus thynnus*). *Canadian Journal of Fisheries and Aquatic Sciences* 65, 1523-1527. doi:10.1139/F08-127.

Nikaido, H., Miyabe, N. and Ueyanagi, S. (1991). Spawning time and frequency of bigeye tuna, *Thunnus obesus*. *Bulletin of the National Research Institute of Far Seas Fisheries* 28, 47-73.

Nishikawa, Y., Honma, M., Ueyanagi, S. and Kikawa, S. (1985). Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. *Far Seas Fisheries Research Laboratory S Ser.* 12, 1 99.

Ortiz De Zarate, V., Megalofonou, P., De Metrio, G. & Rodriguez-Cabello, C. (1996). Preliminary age validation results from tagged-recaptured fluorochrome label albacore in northeast Atlantic. *ICCAT, Collective Volume of Scientific Papers* 43, 331–338.

Otitz de Zárate, V., Quelle, P. and Luque, P.L. (2011). Albacore (*Thunnus alalunga*) stock structure in the Mediterranean Sea. *ICCAT, Collective Volume of Scientific Papers* 66, 1872-1881.

Otsu, T. and Hansen, R. (1962). Sexual maturity and spawning of albacore in the central South Pacific Ocean. *Fishery Bulletin* 62, 151-161.

Otsu, T. and Uchida, R.N. (1959). Sexual maturity and spawning of albacore in the Pacific Ocean. *Fishery Bulletin* 148, 287-305.

Parrish, R.H., Mallicoate, D.L. and Mais, K.F. (1985). Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. *Fishery Bulletin* 83, 483–496.

Pauly, D. (1979). Gill Size and Temperature as Governing Factors in Fish Growth: A Generalization of von Bertalanffy's Growth Formula. Berichte aus dem Instiute fuer Meereskunde 63, Kiel University, Kiel, Germany.

Picaut, J., Ioualalen, M., Menkes, C., Delcroix, T.and McPhaden, M.J. (1996). Mechanism of the Zonal Displacements of the Pacific Warm Pool: Implications for ENSO. *Science* 274, 1486–1489.

Pitcher, C.R. (1992). Growth of juvenile coral reef damselfish: spatial and temporal variability, and the effect of population density. *Australian Journal of Marine and Freshwater Research* 43, 1129–1149.

Punt, A.E. (2003). The performance of a size-structured stock assessment method in the face of spatial heterogeneity in growth. *Fisheries Research* 65, 391–409.

Qiu, B. and Chen, S. (2004). Seasonal modulations in the eddy field of the South Pacific Ocean. *Journal of Physical Oceanography* 34; 1515–1527.

Quinn, T.J. and Deriso, R.B. (1999). *Quantitative Fish Dynamics*. New York: Oxford University Press. 542 p.

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ramon, D. and Bailey, K. (1996). Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean. *Fishery Bulletin* 94, 725-733.

Ravaglia, M.A. and Maggese, M.C. (1995). Melano-macrophages Centres in the gonads of the swamp eel *Synbranchus marmoratus* Bloch, (Pisces, Synbranchidae):

histological and histochemical characterization. *Journal of Fish Disease* 18, 117-125.

Richards, F.J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany* 10, 290–300.

Ricker ,W.E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin 191, *Fisheries Research Board of Canada*. 382 p.

Robertson, D.R., Ackerman, J.L., Choat, J.H., Posada, J.M. and Pitt, J. (2005). Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series* 295, 229–244.

Rodríguez-Marín, E., Clear, N., Cort, J.L., Megalofonou, P., Neilson, J.D., Neves dos Santos, M., Olafsdottir, D., Rodriguez-Cabello, C., Ruiz, M. and Valeiras, J. (2007). Report of the 2006 ICCAT workshop for bluefin tuna direct ageing. *ICCAT, Collective Volume of Scientific Papers* 60, 1349-1392.

Saidapur, S.K. (1978). Follecular atresia in the ovaries of nonmammalian vertebrates. *International Review of Cytology* 54, 225-244.

Santiago, J. and Arrizabalaga, H. (2005). An integrated growth study for north Atlantic albacore (*Thunnus alalunga* Bonn. 1788). *ICES Journal of Marine Science* 62,740-749.

Sassa, C., Kawaguchi, K., Kinoshita, T. and Watanabe, C. (2002). Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. *Fisheries Oceanography* 11, 193–204.

Schaefer, K.M. (1987). Reproductive biology of black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. *Inter-American Tropical Tuna Commission Bulletin* 19, 169-260.

Schaefer, K.M. (1996). Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. *Fishery Bulletin* 94, 98-112.

Schaefer, K.M. (1998). Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-American Tropical Tuna Commission Bulletin* 21, 201-272.

Schaefer, K.M. (2001). Reproductive biology of tunas. In Tuna: physiology, ecology and evolution. Volume 19, *Fish Physiology*. (Eds B. A. Block and D. E. Stevens.) pp 225-269. Academic Press: New York, USA.

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.

Schmitt, C.C. and St-Pierre, G. (1997). Evaluation of two methods to determine maturity in Pacific halibut. IPHC Tech. Rep. 35. International Pacific Halibut Commission, Seattle,Washington. Available at www.iphc.washington.edu/halcom/pubs/techrep/tech0035.pdf.

Schnute, J.T. and Richards, L.J. (1990). A unified approach to the analysis of fish growth, maturity, and survivorship data. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 24–40.

Secor, D.H., Dean, J.M. and Campana, S.E. (Editors). (1995). *Recent developments in fish otolith research*. University of South Carolina Press, Columbia, S.C.

Sun, C-L, Wang, W-R., Yeh, S. (2005). Reproductive biology of yellowfin tuna in the central and western Pacific Ocean. Working paper BI WP-1, 1st Scientific Committee meeting of the Western and Central Pacific Fisheries Commission, 8-19 August, Noumea, New Caledonia.

Sweeting, R,M., Beamish, R.J. and Neville, C.M. (2004). Crystalline otoliths in teleosts: Comparisons between hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia. *Reviews in Fish Biology and Fisheries* 14, 361-369.

Takagi, M., Okamura, T., Chow, S. and Taniguchi, N. (2001). Preliminary study of albacore (*Thunnus alalunga*) stock differentiation inferred from microsatellite DNA analysis. *Fishery Bulletin* 99, 697-701.

Trip, E.L., Choat, J.H., Wilson, D.T.and Robertson, D.R. (2008). Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Marine Ecology Progress Series* 373, 97–109.

Uda, M. (1973). Pulsative fluctuation of oceanic fronts in association with the tuna fishing grounds and fisheries. *Journal of the Faculty of Marine Science and Technology, Tokai University* 7, 245-265.

Ueyanagi, S. (1957). Spawning of the albacore in the Western Pacific. *Report Nankai Regional Fisheries Research Laboratory* 6,113-124.

Ueyanagi, S. (1969). Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning area of albacore,

Thunnus alalunga. *Bulletin of the Far Seas Fisheries Research Laboratory* 2, 177-219.

von Bertalanffy, L. von (1938). A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology* 10, 181–213.

Watson, J.J., Priede, I.G., Witthames, P.R. and Owori-Wadune, A. (1992). Batch fecundity of Atlantic mackerel, *Scomber scombrus* L. *Journal of Fish Biology* 40, 591-598.

Weatherley, A.H. and Gill, H.S. (1987). *Biology of Fish Growth*. New York, NY: Academic Press.

Willis, J. and Hobday, A.J. (2008). Application of bioelectrical impedance analysis as a method for estimating composition and metabolic condition of southern bluefin tuna (*Thunnus maccoyii*) during conventional tagging. *Fisheries Research* 93, 64-71.

Woodhams, J, Stobutzki, I, Vieira, S, Curtotti, R and Begg GA (eds) (2011). Fishery status reports 2010: status of fish stocks and fisheries managed by the Australian Government, Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra.

Wootton, R.J. (1990). *Ecology of teleost fishes*. London: Chapman & Hall.

Yamahira, K. and Conover, D.O. (2002). Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* 83, 1252–1262.

13. Appendix A – Intellectual Property

None arising

14. Appendix B – Project staff

CSIRO Staff

Jessica Farley

Campbell Davies

Naomi Clear

Paige Eveson

Thor Carter

Tonya van de Velde

Mitch Zischke

SPC collaborators

Ashley Williams

Simon Nicol

Simon Hoyle

Contact Us

Phone: 1300 363 400
+61 3 9545 2176

Email: enquiries@csiro.au

Web: www.csiro.au

Your CSIRO

Australia is founding its future on science and innovation. Its national science agency, CSIRO, is a powerhouse of ideas, technologies and skills for building prosperity, growth, health and sustainability. It serves governments, industries, business and communities across the nation.