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Southwest Pacific striped marlin population biology (Project 99)

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Executive summary

This paper describes work undertaken by CSIRO and Fish Ageing Services (FAS) to continue to assess age, growth and maturity estimates for Southwest Pacific striped marlin (WCPFC Project 99). The aim of the work was to evaluate the suitability of striped marlin otoliths for providing estimates of age and growth, and to evaluate the histological criteria used by Kopf et al. (2009; 2012) to determine maturity status (immature or mature) of females.

Otolith and ovary histology samples were obtained from Kopf et al. (2011; 2012) and additional samples were sourced from the WCPFC Tissue Bank. The majority of otoliths from Kopf et al. (2011) had been stored in glycerine and many were either missing or unreadable, which reduced the number of otoliths available for analysis. The available otoliths (n=61) were prepared and the number of opaque zones, which are assumed to form annually, were counted. A direct comparison of age estimates obtained from otoliths in this study and dorsal fin spines from Kopf et al. (2011) of the same fish indicated biases, with otoliths giving a smaller age estimate for young fish compared to spines (ages 1-2), and a progressively higher age estimate for fish > age 4 compared to spines. Although the number of otoliths analysed was small, our results indicate longevity to be at least ~15 years for males and 11 years for females, compared to a maximum age of ~8 and 7 years (males and females respectively) from spines (Kopf et al. 2011).

The growth curves and parameters obtained from ‘observed’ length at age data from otoliths or spines were very similar. These curves are quite different to the ‘back-calculation 1’ curve used in the 2012 and 2019 regional stock assessments (Davies et al. 2012; Ducharme-Barth et al. 2019b). We recommend using the observed spine-based growth parameters from Kopf et al. (2011) or the preliminary otolith-based growth parameters obtained in this study, in preference to the back-calculated spine-based growth parameters from Kopf et al. (2011), since there are inherent biases in back-calculation methods. We also recommend that additional otoliths (and spines of small fish) are collected from striped marlin across the southwest Pacific to provide further age information and to improve the data used to estimate decimal age from otoliths. Direct validation of the accuracy of the ageing method used (for spines or otoliths) is required to confirm the age

estimates. Consideration should be given to bomb radiocarbon (^{14}C) dating to validate the annual periodicity of the bands being count.

Ovary histology samples obtained from Kopf et al. (2012) were read using standard classification criteria for large pelagic tuna species. We found that methodological differences did not exist between Kopf et al. (2012) and the current study. The maturity status of only three of the 150 females classified differed between the two datasets. However, differences were detected in the shape of the maturity ogive, which was primarily due to the different classification of one female as immature in the current study and mature in Kopf et al. (2012). This highlights the need for larger sample sizes of young/small fish to accurately estimate the proportion that are mature at length/age and therefore we recommend additional sampling of length classes around and below the estimated $L_{50.}$

The maturity ogive in Kopf et al. (2012) is noticeably different to the current study, not due to differences in maturity classification, but due to the data in Kopf et al. (2012) being binned into 15 cm length classes prior to model fitting, and also to a different regression relationship being used. We recommend that the maturity ogive from the current study using the Kopf et al. (2012) data be used for future assessments of striped marlin in the WCPO until new ovary samples can be collected and included in the analysis.

Background

Accurate life history parameters are required for robust stock assessments and to develop management advice. Age, growth and maturity parameters were estimated for southwest Pacific striped marlin in the late 2000s by Kopf et al. (2011; 2012). Age was estimated using counts of assumed annuli in sectioned dorsal fin spines validated by marginal increment analysis, and daily increments counts on otoliths. Growth was estimated using observed and back-calculated length-at-age estimates, and the ‘back-calculation 1’ growth model has been input to striped marlin regional stock assessments since 2012 (Davies et al. 2012). A maturity ogive was developed from histological analysis of ovary samples collected at around the same time (Kopf et al. 2012) and was also input to regional stock assessments in 2012 (Davies et al. 2012).

In 2019, an assessment of 17 striped marlin otoliths indicated that they may live longer than previously estimated using spines (Farley et al. 2019). A (very) preliminary von Bertalanffy growth model was fit to the otolith annual age data and otolith daily age data from Kopf et al. (2011), for use as an alternative growth hypothesis in the 2019 stock assessment (Ducharme-Barth et al. 2019a). The stock status estimates had a high degree of uncertainty that was attributed to uncertainty in biological information, including growth parameters, and it was recommended that additional work on age and growth be prioritized to reduce the uncertainty in future assessments (Ducharme-Barth et al. 2019b).

The 2019 stock assessment for striped marlin also used an updated maturity ogive, which was a product of the sex ratio at length and the proportions of females mature-at-length from Kopf et al. (2012) (Ducharme-Barth et al. 2019a, b). The maturity ogive shifted the spawning potential to older individuals relative to the ogive used in the 2012 assessment. Some concerns were raised at SC15 that the change may result from a mis-identification of mature post-spawning individuals as immature, which would shift the maturity ogive towards larger fish.

In 2019, SC15 recommended research activities to improve estimates of life history parameters including growth and maturity studies in order to progress the assessment of southwest Pacific striped marlin. The WCPFC subsequently funded Project 99 to continue to evaluate the suitability of otoliths for providing estimates of age and growth, and to evaluate the histological criteria used to determine maturity status of females. This report describes the work undertaken in this project.

Age and growth

Annual age estimates - otoliths

Whole sagittal otoliths were obtained from Kopf et al. (2011) from fish caught in the southwest Pacific (Figure 1). Fish ranged in size from 99 to 269 cm LJFL (Figure 2) and were caught by both recreational (n=17) and longline (n=44) vessels. The otoliths were sent to Fish Ageing Services (Victoria) for preparation and reading. The majority of otoliths were stored in glycerine and many were either missing (possibly dissolved?) or unreadable, which substantially reduced the number of otoliths available for analysis. The otoliths were cleaned with alcohol and dried prior to preparation. A small number of additional otoliths were obtained from the WCPFC Tissue Bank.

Otoliths were prepared following the procedure described by Farley et al. (2016) for swordfish. In brief, the otoliths were ground down in a three-stage process to produce thin transverse sections approximately 200-250 µm in thickness. All otolith preparations were examined with transmitted light. Even though striped marlin otoliths are very small and difficult to prepare, several sections showed clear opaque/translucent zones, similar to those observed in WCPO swordfish otoliths (Farley et al. 2016). An image analysis system was used to count and measure the distance of each manually-marked opaque zone from the primordium to the edge, and to capture an annotated image from each sample aged. Opaque zones at the terminal edge of the otolith were counted only if some translucent material was evident after the opaque zone, signifying the completion of the opaque zone. Otoliths prepared and read in 2019 (Farley et al. 2019) were re-read for consistency in interpretation and included in the analysis. Only one reading was made of each otolith so the precision of age estimates was not estimated. Annual age estimates (counts of opaque zones) were obtained for 61 fish.

Comparison of ages (zone counts) in otoliths and spines

Fin spine age estimates were obtained from Kopf et al. (2011). Since 27% of spines had an area of vascularisation near the core, where increments are obscured, Kopf et al. (2011) estimated the total age of these fish based on the counts of observed (narrow) translucent zones after the vascularised area plus an estimate of the number of increments (translucent zones) 'lost' due to vascularisation following Hill et al. (1989).

An age bias plot (Figure 3) and a modified age bias plot (Figure 4) (Ogle et al. 2020) compare zone counts from otoliths and spines sampled from the same fish (n=52). Although the sample size is low, differences in counts between structures occurred in both young and older fish. In young fish ≤age 2, spines counts were higher on average than otolith counts ($p<0.017$, paired t-test on otolith age 2 fish). See examples in Appendix 1 where the counts between structures were the same and were different. Further work is needed on a larger sample of otoliths and spines from small/young fish to investigate the differences further and to determine which is accurate.

In for fish > age 4, spine counts were lower on average than otolith counts (paired t-tests, $p<0.05$ in all otolith age classes ≥5 years). See examples in Appendix 2. The bias in larger/older fish may be because the increments are deposited so close together on the margin of spines as the fish gets older that readers cannot differentiate/resolve them.

Daily age estimates

Daily age estimates from otoliths were obtained from Kopf et al. (2011) for use in this study. The otoliths used for daily ageing were predominantly caught by longline fisheries in Australian (n=8) and Fiji (n=20) (Figure 1). Fish ranged in length from 99-214 cm LJFL (Figure 2). The otoliths were prepared using the same method as in the current study for annual ageing, although the sections were ground to ~50 µm thickness. No daily age estimates were made by FAS as part of the current study.

Figure 5 shows the relationship between daily age and LJFL. Fish were aged up to 868 days (2.3 years). Measurements on the otolith from the primordium to the edge of the ventral lobe were also obtained. Figure 6 shows the relationship between the measured distances and daily age for fish aged ~0.3 to 0.6 years. The distance from the primordium to the otolith edge ranged from ~0.3 to 0.5 µm, which is similar to the range measured from the primordium to the first opaque increment in the annual sections

Decimal (fractional) age

Following Farley et al. (2020), decimal age was calculated from the annual otolith counts made by FAS using three steps:

Step 1: Use the relationship between daily age and primordium to edge measurements (Figure 6) to estimate the age of each fish when the first opaque zone was completed in the transverse section. The relationship is uncertain and would be improved by additional data, but we currently don’t need to extrapolate outside of it. The distance from the primordium to when the first opaque zone was completed ranged between 0.29 and 0.48 mm.

Step 2: Calculate the number of complete annual increments in the otolith. A complete annual increment is one opaque zone + one translucent zone, which represents one year of growth, and is calculated as the total count of opaque zones minus 1 (the first opaque zone is accounted for in step 1).

Step 3: Estimate the time elapsed after the last counted opaque zone was deposited and when the fish was caught. This was calculated using the size of the marginal increment as a proportion of the mean size of the complete annulus for that age group (Figure 7).

Adding together the output from all three steps gives a decimal age estimate for each fish. Ageing additional otoliths would improve the relationship between daily age and otolith size, as well as the estimation of the mean increment width values.

Growth analysis

A von Bertalanffy (VB) growth model was fit to the otolith age and length data for males and females separately, as well as to the combined data. Note that the data includes the daily age estimates from Kopf et al. (2011) and the decimal age estimates derived from annual counts in the current study. The VB model has the form:

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

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. We used maximum likelihood estimation assuming a Gaussian error structure with mean 0 and variance σ^2.

Figure 8 shows the observed length at age estimated for striped marlin by sex, with a VB growth model fit to the data. The daily age estimates align relatively well with the decimal annual age estimates, even though for other large pelagic species, including swordfish (Farley et al. 2016), we do not recommend using daily age data for fish >1 year in growth models. The decimal ageing relied on daily age data to estimate the age when the first opaque zone was completed (step 1 above), however, the fish were estimated to be only ~0.5 years old at the time, so it does not explain the 'alignment' of annual and daily length at age estimates in older fish.

Although the number of otoliths analysed was small, our results indicate longevity to be at least ~15 years for males and 11 years for females. The estimated growth curves are slightly different for males and females, but both indicate very fast growth in the first year of life. Two 'outliers' in the data set are the two youngest males that are relatively large for their age, which may be evidence of size selective fishing for fast-growing young fish (the larger members of a year class become vulnerable to the fishery first). Kopf et al. (2011) noted that the use of direct length at age observations from striped marlin spines may result in a biased growth curve if there is size selectivity by the fishing gear and they recommended using back-calculated length-at-age estimates as opposed to observed length-at-age estimates. Back-calculating growth involves estimating fish length at previous ages (prior to capture) using increment measurement data for each otolith or spine. However, back-calculating length at age can also result in biased growth curves (Kopf et al. 2011, Campana 1990), and in fact size-selective fishing is one cause of the bias. In particular, if the fast-growing fish in the younger year classes have higher mortality than the slow-growing fish, then the slow-growing fish become overrepresented in older samples, leading to smaller back-calculated length at age estimates in earlier years (this is one cause of Lee's Phenomenon; Ricker 1975). This may be the reason that the back-calculated growth curves using spines by Kopf et al. (2011) resulted in lower length at age compared to growth curves estimated using the observed length and age data. Kopf et al. (2009) advocated using a back-calculated growth model to avoid fishery size selectivity, but Kopf et al. (2011) noted there was no way to determine which was more biologically accurate. And, as just discussed, if size-selectivity exists in the fishery, then it affects not only the observed length and age data (biasing the samples towards larger fish in the younger year classes), but also the back-calculated data (biasing the samples towards slower-growing older fish with smaller lengths at younger age classes).

Figure 9 compares the VB growth curve estimated in the current study (based on otoliths) with the four VB curves estimated by Kopf et al. (2011) based on fin spines (one using only observed length and age data, and three using back-calculated length and age data derived from different methods). For both sexes, the VB curves estimated using only observed length at age data for otoliths and spines were similar. This is because the largest bias in age estimates between structures was detected from age 4 years onwards, when the fish are already reaching their individual asymptotic length. These curves were also more like the ‘back-calculation 3’ growth curve using spines but were quite different to the ‘back-calculation 1’ curve used in the 2012 and 2019 regional stock assessments (Davies et al. 2012; Ducharme-Barth et al. 2019b).

The estimate of L_∞ obtained in the current study (244 cm LJFL sexes combined) is higher than estimated by Fitchett (2019) for striped marlin off Hawaii (182 cm EFL, ~211 cm LJFL[1]), but it is slightly lower to L_∞ estimated by Sun et al. (2011) off Taiwan (263 cm LJFL).

Reproduction and maturity

Histological analysis

Histological sections of striped marlin ovaries were obtained for 150 of the samples used in Kopf et al. (2012) for fish caught in the southwest Pacific (Figure 10). Fish ranged in size from 126 to 269 cm LJFL and were caught by both recreational (n=59) and longline (n=91) vessels (Figure 11). Gonad weight data was available for 140 of the females.

The histological sections were read using standardised terminology and classification criteria for large pelagic tuna species (Brown-Peterson et al. 2011; Schaefer 2001; Farley et al. 2017). The most advanced group of oocytes (MAGO) was staged into one of 6 classes: primary growth, cortical alveolar, primary, secondary or tertiary vitellogenic, migratory nucleus or hydrated. Each ovary was also scored according to the presence or absence of postovulatory follicles (POFs), tertiary vitellogenic oocytes undergoing alpha (α) or beta (β) atresia and maturity markers. The maturity markers used were well defined muscle bundles, numerous “brown bodies”, a thick ovary wall, and residual hydrated oocytes, which are considered signs of prior reproductive activity. Residual hydrated oocytes occurred in the ovary lumen as single or ‘clumps’ or as unovulated oocytes within the connective tissue of the ovary. Residual hydrated oocytes are relatively common in regressing or regenerating swordfish and striped marlin. Females were classified into reproductive phases and subphases depending on the MAGO, POFs, atresia and maturity markers present in the ovary using criteria similar to that developed for broadbill swordfish (Farley et al. 2016), and the maturity status of each female was determined from this classification (Table 2).

Of the ovaries examined, 23 were classed as immature and 127 as mature. The number of immature and mature females was consistent with the results of Kopf et al. (2012); only three of the 150 ovaries examined were classified differently. When comparing the specific reproductive phases, only an additional ~20 differed, but these differences did not affect the mature/immature classification.

As expected, the spatial and seasonal spawning pattern observed is consistent with that reported in Kopf et al. (2012). Spawning capable and actively spawning females were predominantly caught off Australia’s east coast (~18-32°S) between October to January (austral spring and early summer), but their relative abundance was highest in November and December (Figure 12). One

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[1] Length conversions from Williams and Smith (2018). EFL = eye fork length.

spawning female was caught in Fiji. Regressing females were most abundant in January and February as females completed spawning. Regenerating females gradually increased in relative abundance from December.

A comparison of ovary weight at length by reproductive phase suggests that the classification scheme used in the current study is appropriate (Figure 13). The smallest female classed as mature was 211 cm LJFL (regenerating) and the smallest fish classed as actively spawning was 220 cm LJFL. The largest immature female was 235 cm. Based on the ovary weight to length data, length at maturity appears to be in around of 220 cm LJFL (Figure 13).

Maturity at length

Logistic regression curves were fit to the maturity data from the current study and to the maturity data from Kopf et al. (2012) for the same samples (n=150):

$$P(\text{maturity} \mid L) = (\exp(a+bL)) / (1+\exp(a+bL))$$

where P is the estimated proportion of mature individuals at fork length L, and a and b are parameters that define the shape and position of the fitted curve. The predicted length at 50% maturity (L_{50}) was calculated as: $L_{50} = -a/b$. L_{50} was estimated to be 214 cm LJFL using data from the current study, and 212 cm using data from Kopf et al. (2012). This corresponds to an age of ~2 years based on the otolith growth curve. The maturity status (immature or mature) only differed for three samples between the two datasets, yet the maturity ogive is visibly different (Figure 14). The Kopf et al. (2012) data indicates a greater proportion of fish are mature in the length classes around and below L_{50}. However, if the maturity status of the smallest of the three fish (119 cm) was changed from mature to immature, the two ogives are almost identical. This highlights the sensitivity of estimating maturity schedules using small sample sizes, particularly for lengths around L_{50}. Figure 11 shows that in the current study there were very few females sampled <210 cm LJFL.

A maturity ogive estimated using all the maturity data from Kopf et al. (2012) (n=184) was almost identical to the ogive based on the subset of 150 ovaries (Figure 15). However, the shape of ogive was different to that reported in Kopf et al. (2012). The difference was due to Kopf et al. (2012) binning the data into 15 cm length classes prior to model fitting, and also using a different regression relationship (one that allows the expected proportion mature to exceed 1).

The estimate of L_{50} obtained for females in the current study (214 cm LJFL or ~184 cm EFL[1]) is higher than estimated by Humphreys and Brodziak (2019) for striped marlin off Hawaii (160 cm EFL), but it is similar to L_{50} estimated by Chang et al. (2018) off Taiwan (181 cm EFL).

Summary and recommendations

Age and growth

Numerous studies have indicated that age estimates from otoliths are likely to be more reliable because spines are subject to bone remodelling and resorption. A direct comparison of age estimates obtained from otoliths and spines of the same fish in the current study indicated bias, with otoliths giving a slightly smaller age estimate for young fish (ages 1-2) and a progressively higher age estimate for fish > age 4. The use of otolith age estimates significantly extends longevity estimates for the species. Although only a small number of otoliths were analysed, the maximum age was 15 years for males and 11 years for females, compared to a maximum age of ~8 and 7 years (males and females) from spines (Kopf et al. 2011).

The growth curves obtained using 'observed' age and length data from otoliths here and spines from Kopf et al. (2011) were very similar. We recommend using growth parameters obtained from either study in preference to the back-calculated spine-based growth parameters from Kopf et al. (2011) currently used in the stock assessment, since there are inherent biases in back-calculation methods. We also recommend that additional otoliths (and spines of small fish) are collected from striped marlin across the southwest Pacific to provide further age information, and to improve the data used to estimate decimal age from otoliths (i.e., the relationship between daily age and otolith size and the estimates of mean increment width by age class). Direct validation of the accuracy of the ageing method used (for spines or otoliths) is required to confirm the age and growth estimates. Consideration should be given to bomb radiocarbon (^{14}C) dating to validate the annual periodicity of the bands being count.

Reproduction and Maturity

We found that methodological differences did not exist between Kopf et al. (2012) and the current study to determine the maturity status (immature or mature) of striped marlin. Only three samples differed between the two datasets (n=150). However, differences were detected in the shape of the maturity ogive, which was primarily due to the classification of one female as immature in the current study and mature by Kopf et al (2012). This highlights the need and importance of adeqsuate sample size to accurately estimate the proportion mature at length/age and we recommend additional sampling to improve the maturity analysis, particularly for length classes around and below the estimated $L_{50.}$

We also found the shape of the maturity ogive in Kopf et al. (2012), which is currently used in the recent stock assessment (Ducharme-Barth et al. 2019b) is different to the current study due to the data being binned into 15 cm length classes and a logistic regression being fitted to the binned data rather than individual fish data. We recommend that the maturity ogive from the current study using the Kopf et al (2012) data be used for future assessments of striped marlin in the WCPO until new ovary samples can be collected and included in the analysis.

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Tables and figures

Table 1. Parameter estimates from fitting a von Bertalanffy (VB) growth model to the striped marlin otolith derived age and length data for males (M) and females (F), and males and females combined (M+F).

Sex	n	L_∞	k	t_0	σ
M	45	237.46	0.87	-0.42	13.14
F	40	248.90	0.86	-0.35	9.10
M+F	85	244.75	0.84	-0.40	11.96

Table 2 Number of females by histological classification. MAGO = most advanced group of oocytes, POF = postovulatory follicle. Maturity markers include well defined muscle bundles, numerous "brown bodies", a thick ovary wall, and residual hydrated oocytes.

Maturity status	Phase	Sub-phase	MAGO and POF stage	Atresia (α or β) of Vtg3 oocytes	Atresia of CA, Vtg1 or Vtg2 oocytes	Maturity markers	Total
Immature	Immature		Oogonia or PG, no POFs	Absent	Absent	Absent	22
Immature	Developing (1st time)	Early	CA, no POFs	Absent	May be present	Absent	1
		Late	Vtg1 or Vtg2, no POFs	Absent	May be present	Absent	0
Mature	Spawning capable	Non-spawning	Vtg3, no POFs	May be present (0-50% of Vtg3)	May be present	Possible	8
		Actively spawning	MN or Hyd or POFs	May be present (0-50% of Vtg3)	May be present	Possible	16
Mature	Regressing		PG, CA, Vtg oocytes, no POFs	50-100% of Vtg3	May be present	Possible	9
Mature	Regenerating		PG, no POFs	Absent	May be present	Present	70
Mature	Developing (repeat)	Early	CA, no POFs	Absent	May be present	Present	8
		Late	Vtg1 or Vtg2, no POFs	Absent	May be present	Present	16

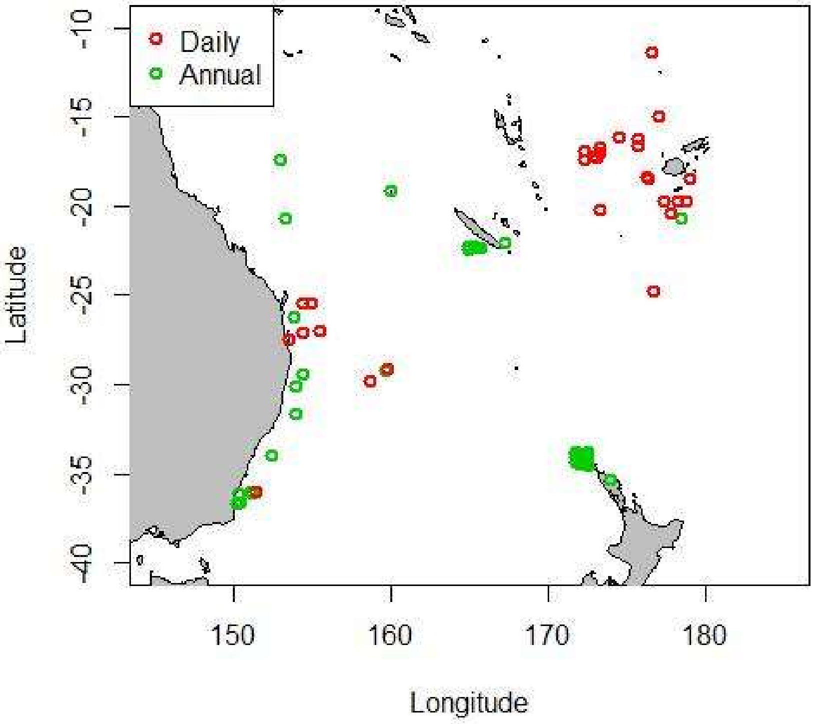


Figure 1. Map showing the locations of fish from which otoliths analysed in the project were sampled. Otoliths shown in green were prepared for annual ageing and those shown in red were prepared for daily ageing. Longitude is shown in degrees east. Points near New Zealand have been jittered slightly to give a better indication of sample size since the majority were collected at the same location.

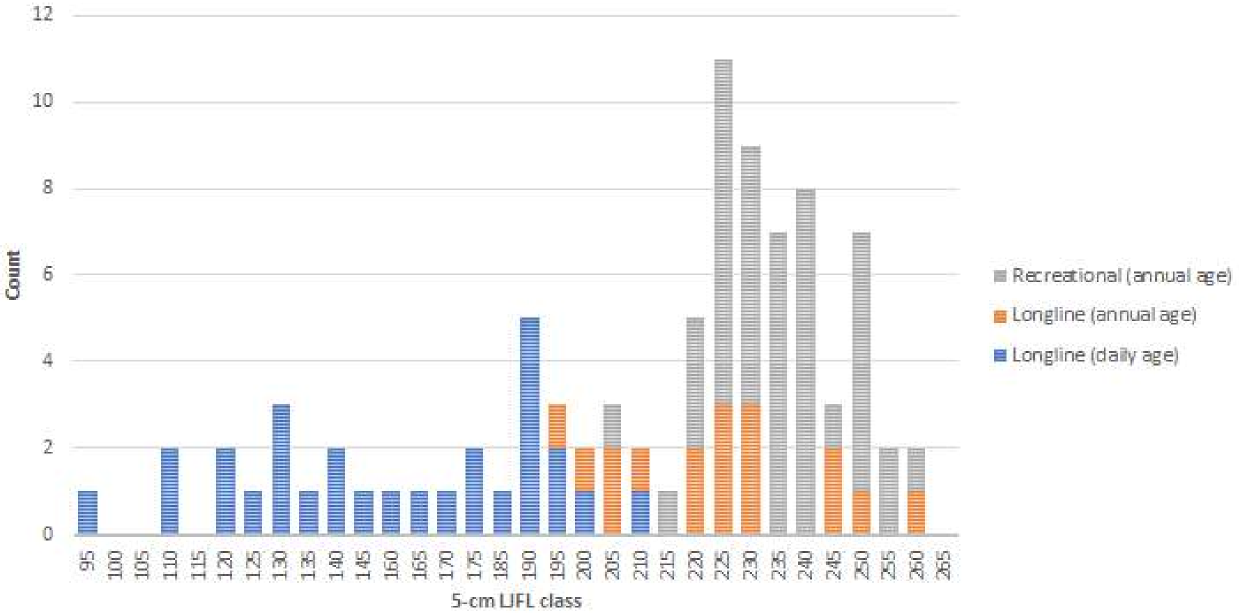


Figure 2. Length frequency of striped marlin with otolith analysed (annual and daily) and caught by recreational and longline vessels in the southwest Pacific Ocean. The lower boundary length value of the bin is shown.

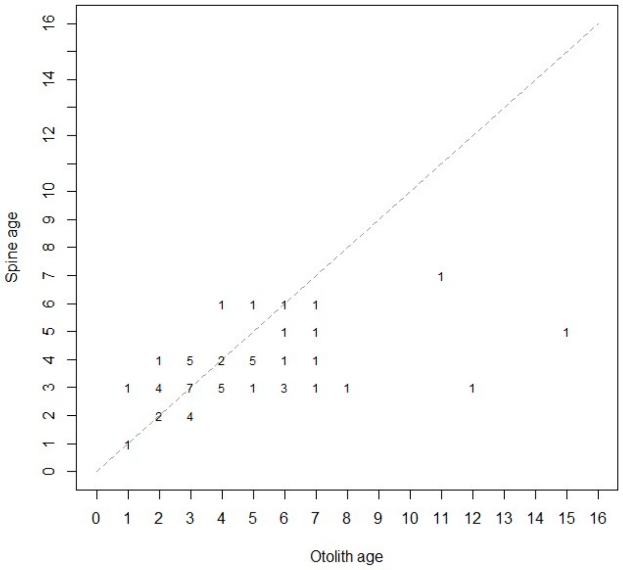


Figure 3. Number of fish with each otolith and spine age estimate combination. The dashed grey line represents age estimates that agree.

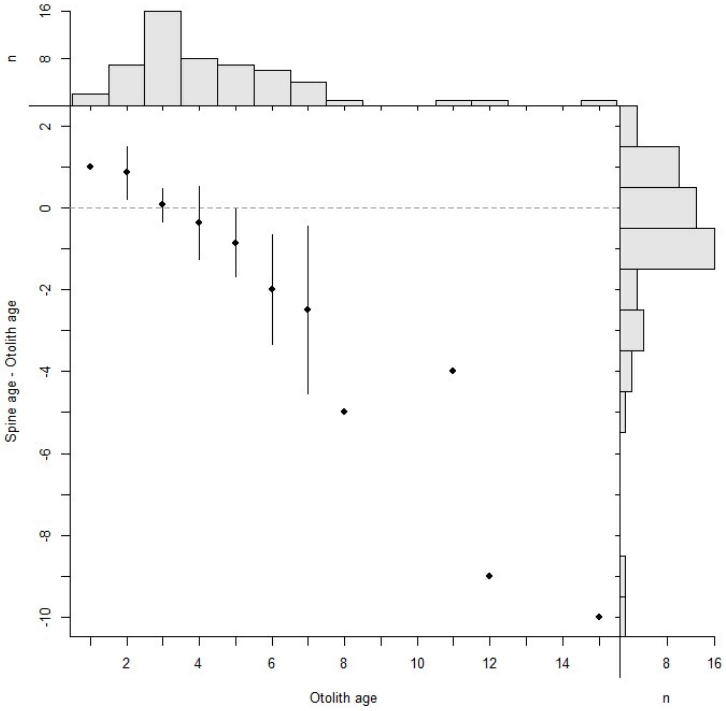


Figure 4. Modified age bias plots showing the difference in ages (zone counts) between otoliths and spines from the same fish. Points are mean age difference and vertical lines are 95% confidence intervals; note that CI's are only drawn for sample sizes > 2.

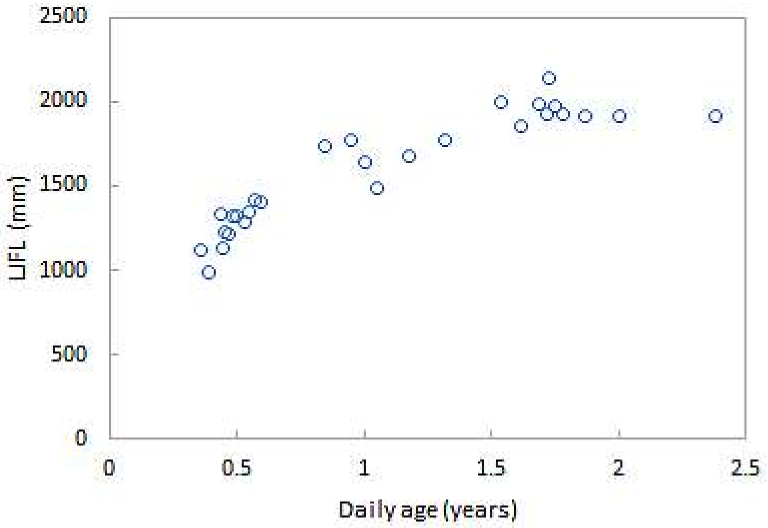


Figure 5. Relationship between fish length (LJFL) and daily ages from sectioned otoliths. Data from Kopf et al (2011). (N = 28).

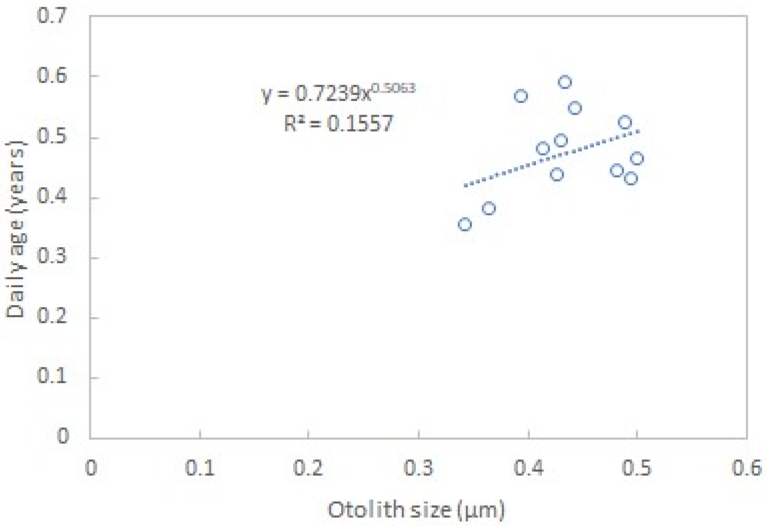


Figure 6. Relationship between daily age and primordium to otolith edge measurement distances with fitted power curve. Otolith size is the distance from the primordium to the edge on the ventral arm in sectioned otoliths (N = 12).

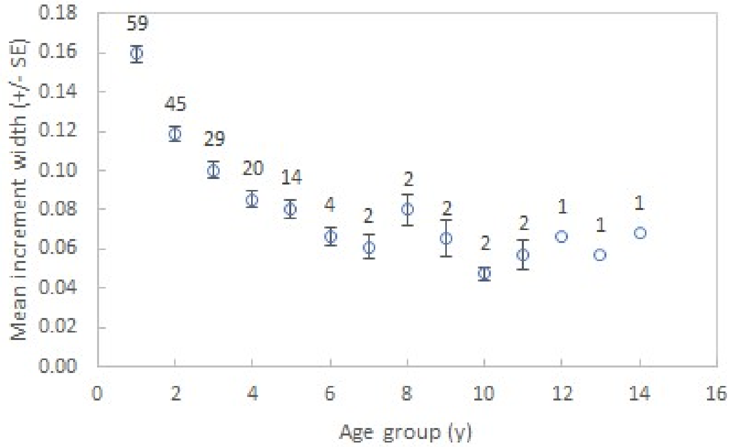


Figure 7. Mean (+/- SE) annual increment width in millimetres by age class for striped marlin. Numbers indicate sample sizes in each age group.

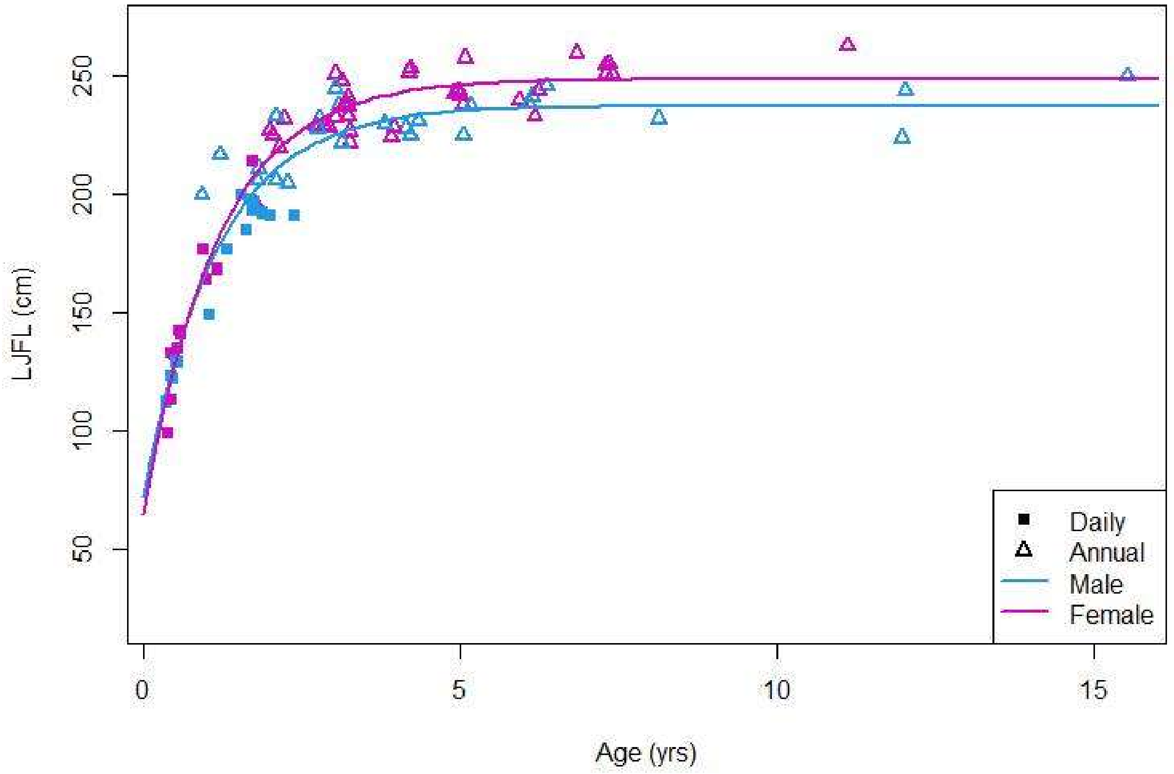


Figure 8. Von Bertalanffy (VB) growth curves fitted to length at age (daily and annual) from otoliths by sex (F = pink, M = blue). Length is LJFL in cm.

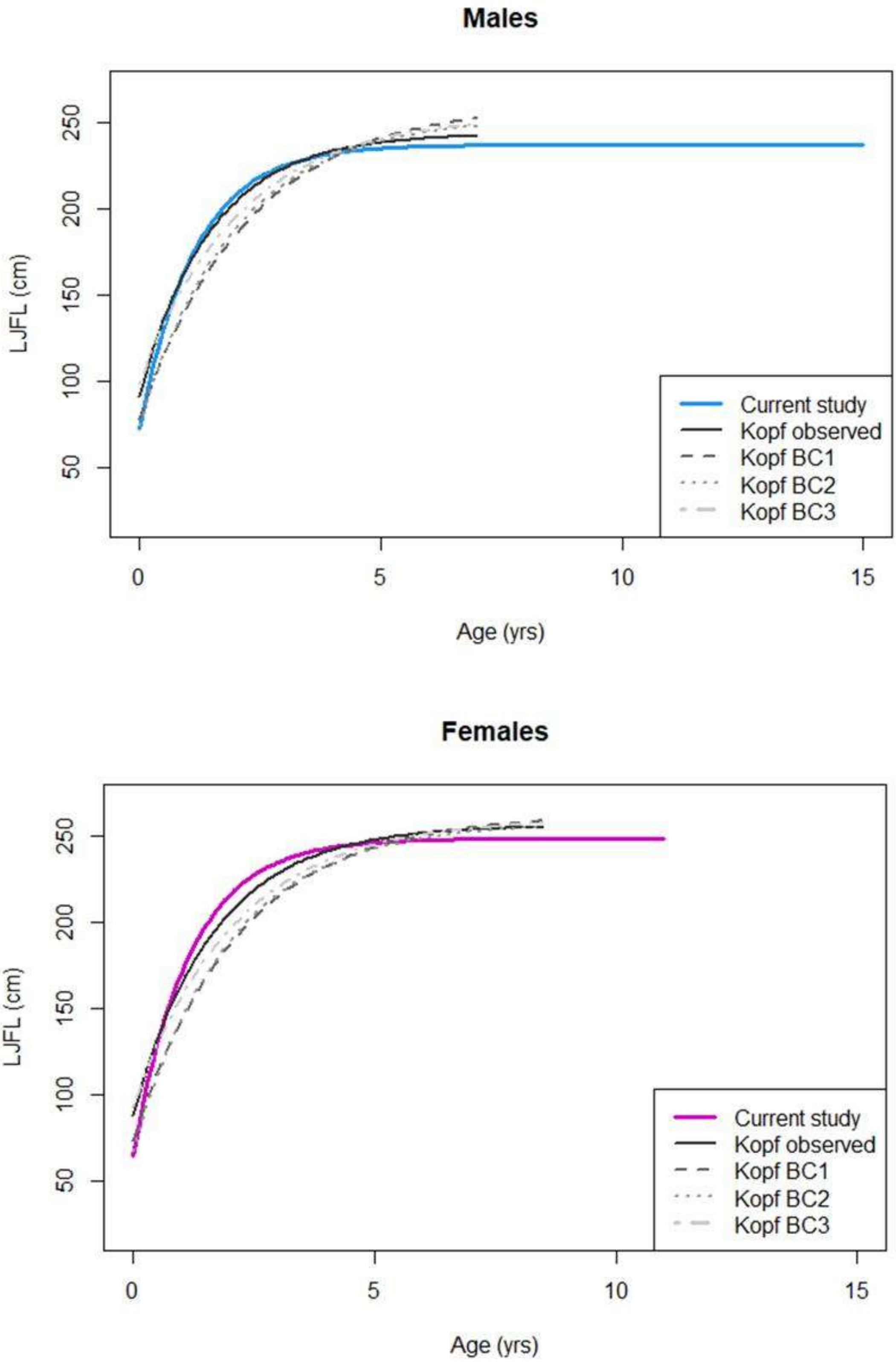


Figure 9. Comparison of sex-specific VB curves from current study with VB curves from Kopf et al. (2011); BC=back-calculated. The growth curves are truncated at the maximum age estimated by sex and ageing structure used.

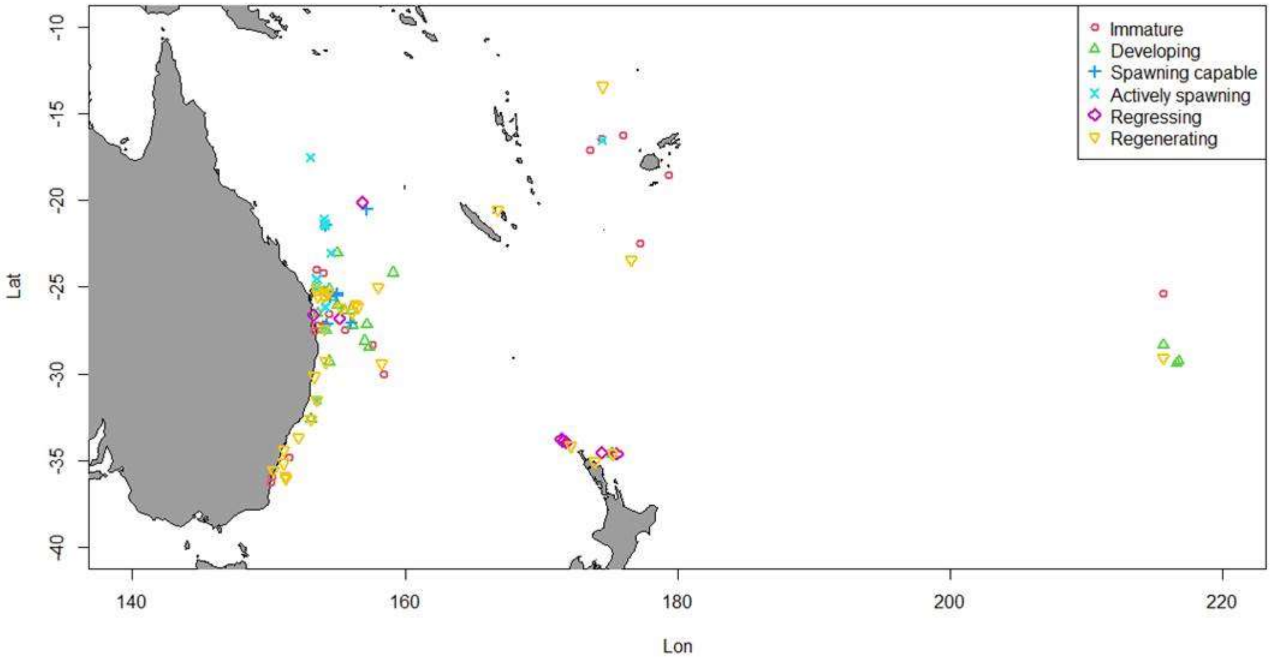


Figure 10. Map showing the sampling locations of fish with ovaries analysed in the project. Different colours and symbols represent different reproductive phases. Longitude is shown in degrees east.

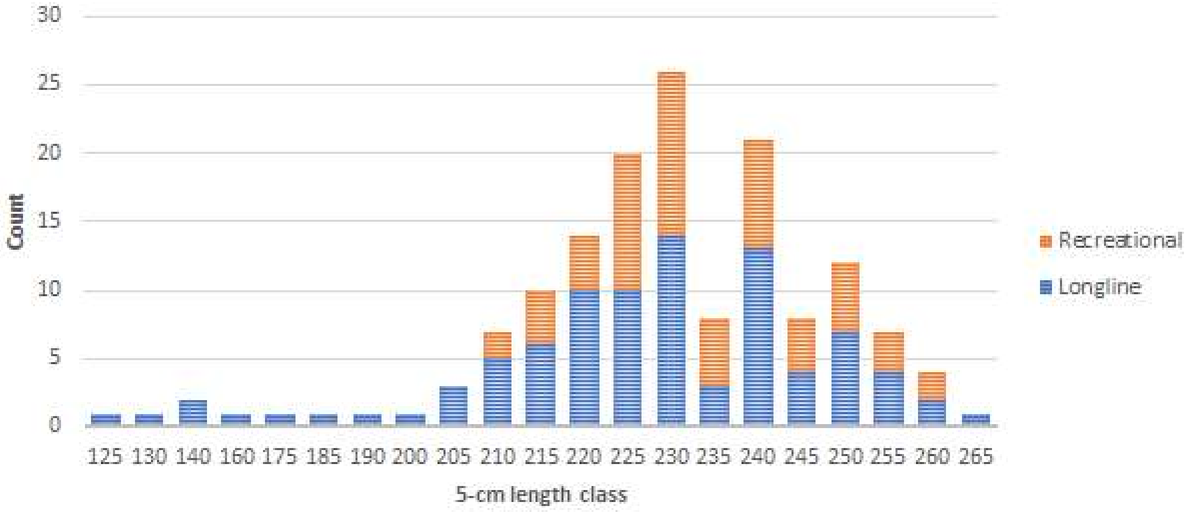


Figure 11. Length frequency of striped marlin with ovaries analysed and caught by recreational and longline vessels in the southwest Pacific Ocean. The lower boundary length value of the bin is shown.

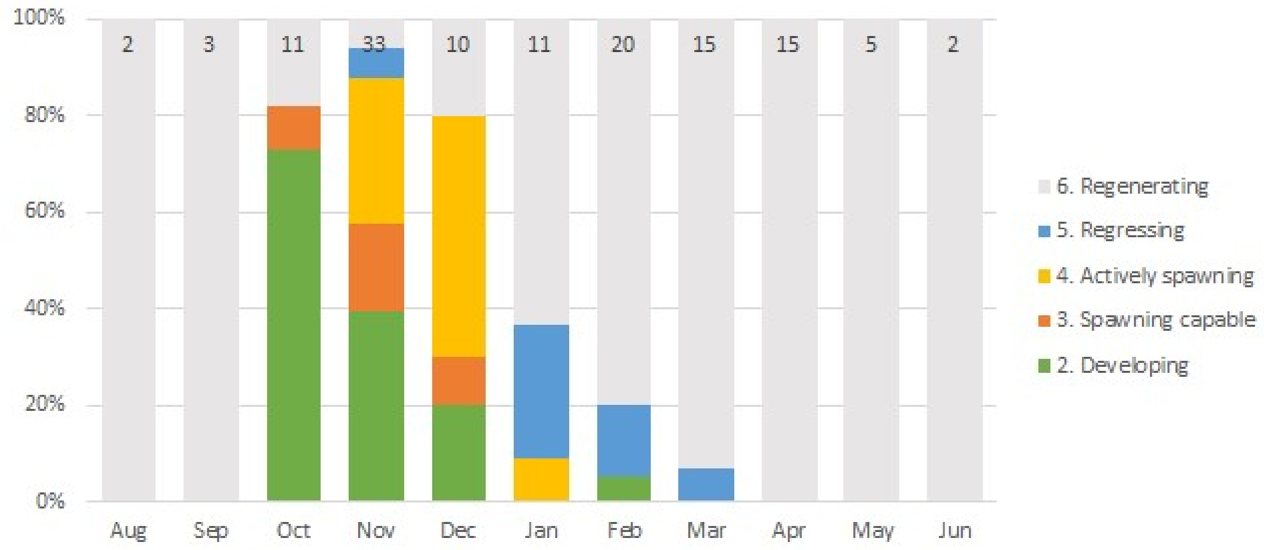


Figure 12. Proportion of mature female striped marlin by reproductive phases each month. Sample size per month is indicated at the top. Immature females are not included.

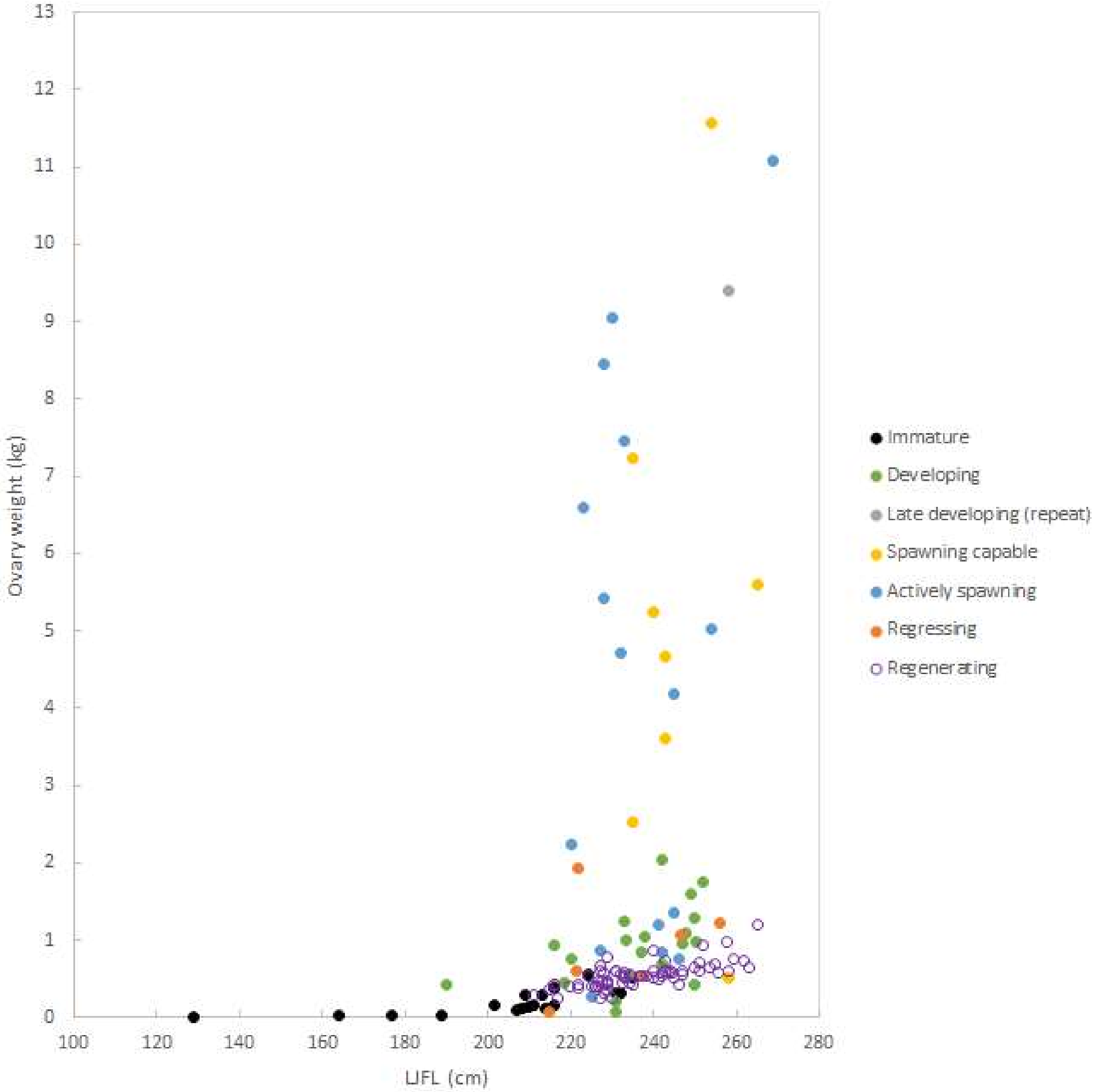


Figure 13. Observed ovary weight at orbital fork length (OFL) for female striped marlin (n=140).

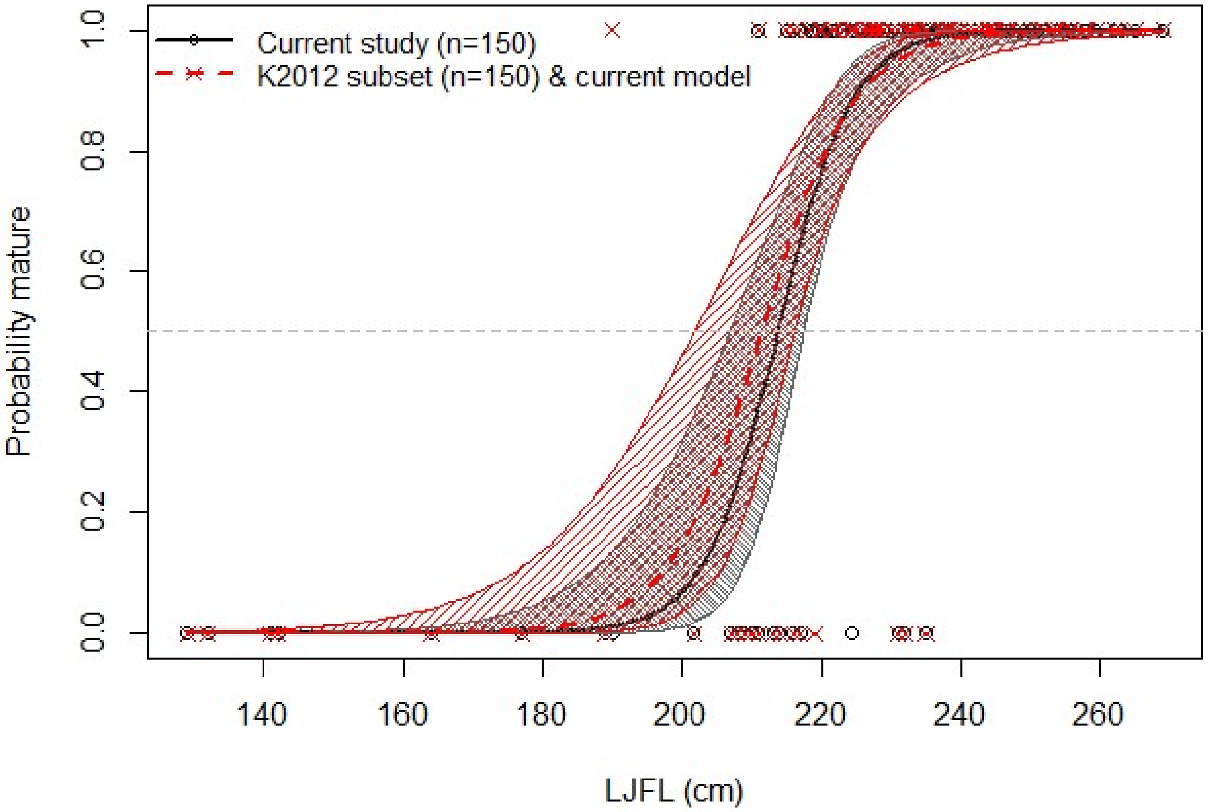


Figure 14. Logistic regression curves fitted to the maturity data from the current study (open black circles), and to the maturity data from Kopf et al. (2012) for the same samples (red crosses) (n=150). The shaded areas give approximate 95% confidence regions. L_{50} is estimated to be 213.8 cm using data from the current study, and 211.5 cm using data from Kopf et al. (2012).

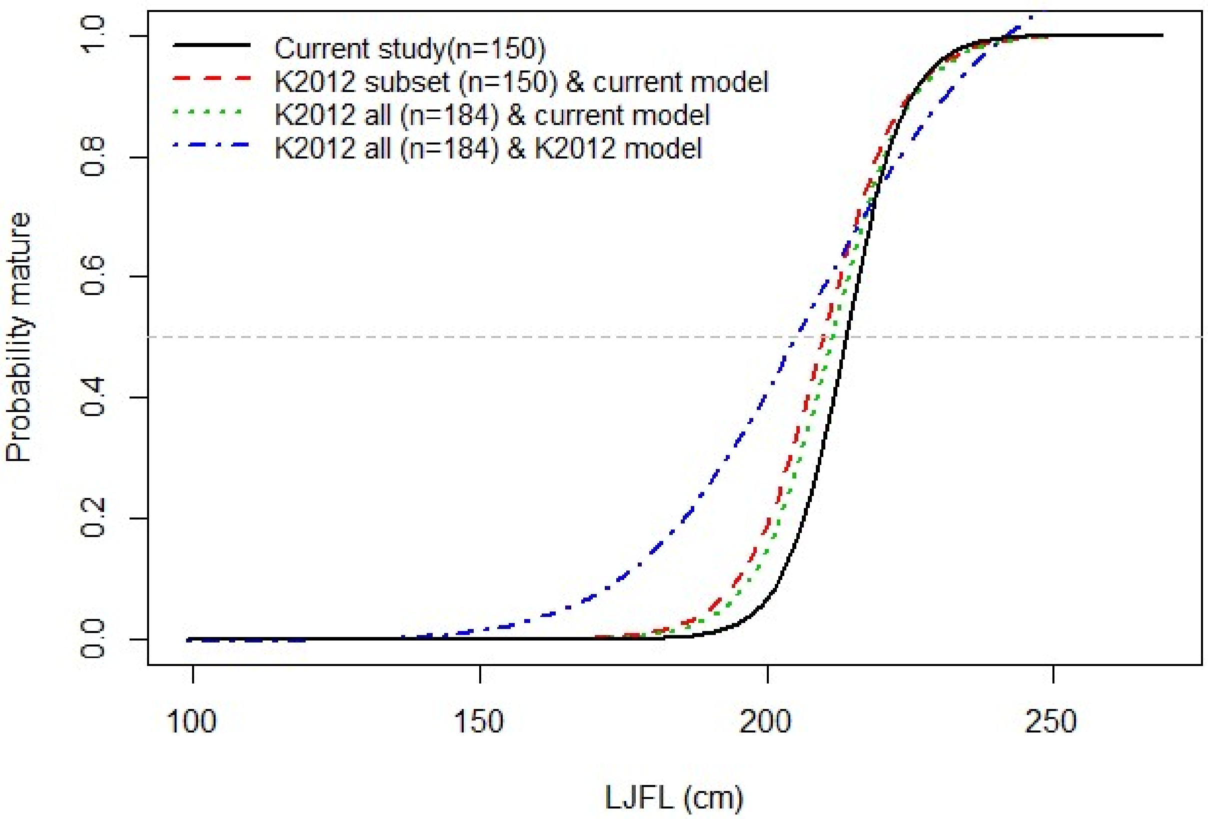
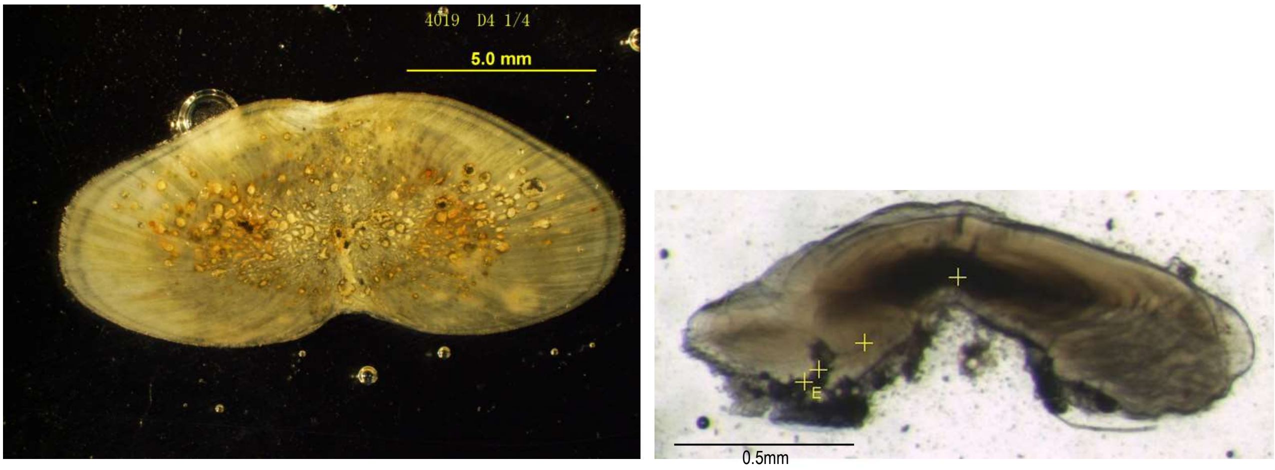


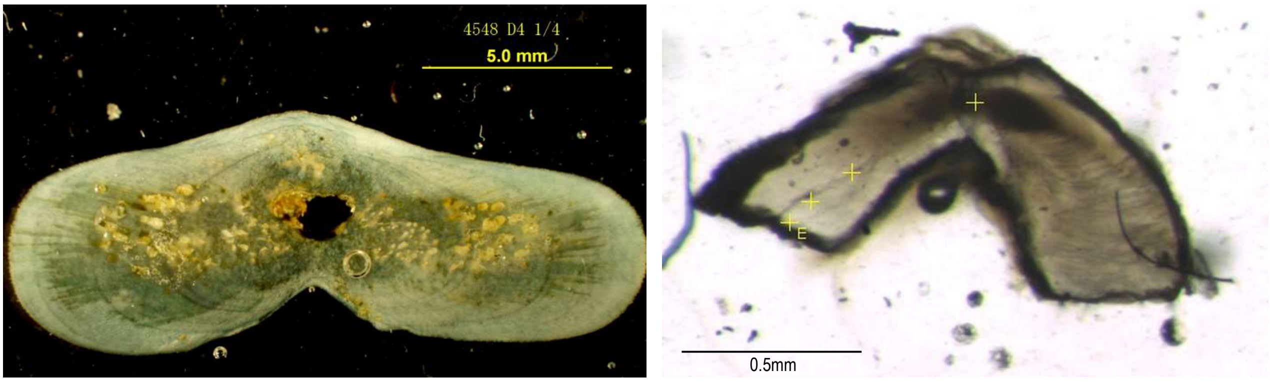
Figure 15. Logistic regression curves fitted to the maturity data from the current study (black line), the maturity data from Kopf et al. (2012) for the same samples (red line), data from Kopf et al. (2012) for all fish (green line). Also shown is the maturity-at-length ogive from Kopf et al. (2012) which used a different regression relationship fitted to data binned into 15 cm length classes (blue line).

Appendix 1.

Examples of sectioned spines and otoliths from small/young fish with the same (#4019) and different (#4548) increments (zone) counts.



Fish 4019. Sectioned spine aged 2 years (top) and sectioned otolith aged 2 years (bottom). + = annual growth zones counted in the otolith. Male, 206 cm LJFL.



Fish 4548. Sectioned spine aged 3 years (top) and sectioned otolith aged 2 years (bottom). + = annual growth zones counted in the otolith. Female, 220 cm LJFL.

Appendix 2.

Examples of sectioned spines and otoliths from large/old fish with different increment (zone) counts. Counts from otoliths are higher compared to spines.

Fish #3421. Sectioned spine aged 5 years (top) and sectioned otolith aged 15 years (bottom). + = annual growth zones counted in the otolith. Male, 250 cm LJFL.

Fish #4040 Sectioned spine aged 5 years (top) and sectioned otolith aged 7years (bottom). + = annual growth zones counted in the otolith. Male, 251 cm LJFL.