SCIENTIFIC COMMITTEE
ELEVENTH REGULAR SESSION

Pohnpei, Federated States of Micronesia
5-13 August 2015

Project 71 Progress Report
South Pacific swordfish biology: age, growth and maturity

Jessica Farley and Naomi Clear[1]

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[1] CSIRO Oceans and Atmosphere Flagship

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WCPFC Project 71

Jessica Farley and Naomi Clear

CSIRO Oceans and Atmosphere Flagship

Australian Government
Australian Fisheries Management Authority

Western and Central Pacific Fisheries Commission

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Executive summary

At the 9th session of the Western and Central Pacific Fisheries Commission Scientific Committee, concern was expressed regarding biological aspects of the 2013 South Pacific Swordfish stock assessment. The stock assessment had a high degree of uncertainty that was attributed to uncertainty in the accuracy of growth and maturity parameters. The Scientific Committee recommended that additional work on age, growth and age validation be undertaken, and agreed to financially support an AFMA/CSIRO project "Determination of Swordfish growth and maturity relevant to the southwest Pacific stock".

The aim of the project is to determine the degree to which differences in swordfish growth and maturity parameters obtained in previous Australian and Hawaiian studies are methodological or due to spatial variation in life-history, and to develop standardised protocols for interpreting spines, otoliths and ovaries to re-estimate growth and maturity parameters for swordfish in the southwest Pacific. The project is on schedule and due for completion in 2016. The main findings to date are:

1. Methodological differences did exist between the ageing studies of DeMartini et al. (2007) in Hawaii and Young and Drake (2004) in Australia, which could account for the different growth rate estimates obtained by these studies. However, no major methodological differences exist between the Hawaiian and the **current** methods used by CSIRO to age Australian swordfish using spines. In addition, no major methodological differences exist between the Hawaiian and those used by CSIRO (and Fish Ageing Services) to age swordfish using otoliths.

   A preliminary comparison of age estimates based on otoliths and spines from Australian swordfish indicates bias for both males and females. Spine-based counts were similar on average to otolith-based counts for the youngest age classes. However, a difference was evident in age classes >4 years for males and >7 years for females, where otolith counts were higher on average than spine counts. Maximum age estimates from spines and otoliths were 14 and 21 respectively. Age verification work will be undertaken before final growth parameters are estimated.

2. Methodological differences did exist between the maturity studies of DeMartini et al. (2000) in Hawaii and Young and Drake (2002) in Australia, which could account for the different maturity ogive estimates obtained by these studies. Methodological differences still exist between the Hawaiian and **current** methods used by CSIRO to differentiate immature from mature-regenerating females. However, these differences are necessary because the Australian ovary material was frozen before being fixed, resulting in poorer quality histological sections. It was agreed that the histological classification system used by CSIRO was appropriate and was successfully identifying mature and immature female swordfish.

   A preliminary estimate of L_{50} for female swordfish in Australia is 154.1 cm orbital fork length. This is higher than estimated by DeMartini et al. (2000) (143.7 cm) in Hawaii, but substantially lower than obtained by Young and Drake (2002) (181.0 cm) in Australia.

1   Background

Broadbill swordfish are a large pelagic species distributed between ~50°N and 50°S in all the major oceans. In the Pacific, there is genetic evidence of three independent populations (north, southwest and southeast) with no mixing across the equator in the western Pacific (Reeb et al. 2000). Recent tagging work suggests there may be structure within the southwest population as fish tagged off eastern Australia showed little propensity to move far to the east remaining instead within the western half of the Coral and Tasman Seas (Evans et al. 2014). This 'Australian population' may range from the east coast to approximately 165°E.

In the mid-to-late 1990s, the swordfish fishery expanded off eastern Australia and New Zealand and concerns were raised about the sustainability of catches since catch rates and the size of fish caught were both declining. There was an urgent need to determine the status of the stock and develop a stock assessment. Unfortunately, life-history parameters for input to stock assessments of swordfish were not available at the time. In response, CSIRO undertook two studies in the early 2000s to estimate key parameters such as length-at-age, longevity, sex ratio, maturity, spawning frequency and fecundity (FRDC projects 1999/108, 2001/014). The reproductive work was published (see Young et al. 2003) but the age, growth and maturity work were not because some of the methods and results were called into question by the NOAA/PIFSC Honolulu Fisheries Laboratory, which had been doing similar work (DeMartini et al. 2000; 2007). As a consequence of these methodological uncertainties, the alternative growth and maturity parameters were both admitted into southwest Pacific stock assessments as equally likely alternative hypotheses (Kolody et al. 2008; Davies et al. 2013).

The different biological assumptions, however, have important implications for the stock status advice (Davies et al. 2013). Using the Australian growth curve, the assessment indicated that "overfishing was occurring but that the stock was not in an overfished state" while the Hawaiian curve indicated "that no overfishing was occurring and that the stock was not in an overfished state" (Davies et al. 2013).

In 2013, WCPFC SC acknowledged the inconsistencies in the Australian and Hawaii growth schedules and recommended that "additional work on age, growth and age validation be undertaken" as a high propriety project (Anon. 2013). In response to this, and a call for research by the AFMA Research Committee (ARC) in Australia, CSIRO submitted an ARC proposal to re-examine swordfish age, growth and maturity in the southwest Pacific. The WCPFC Secretariat supported this proposal financially and suggested an expansion of the research in collaboration with the NOAA/PIFSC Honolulu Fisheries Laboratory, to include Hawaiian swordfish data in the study to meet the needs of the WCPFC.

This paper presents the project objectives and progress to date.

2   Project objectives

1. Evaluate the use of otoliths to estimate the annual age of swordfish in the southwest Pacific.

2. Re-examine ageing methodology of Young and Drake (2004) and confirm age estimates obtained for a representative sample of fin ray sections.

3. Re-examine the ovary histology from Young & Drake (2002) and use new methods to estimate the maturity status of females.

4. Undertake a range of verification and/or indirect validation methods to determine the accuracy of age and maturity interpretations from fin spines, otoliths and ovaries.

5. Examine the effect of the different growth curves and maturity ogives on population models and make recommendations for future assessment and harvest strategy evaluation activities.

6. Collaborate with NOAA PIFSC scientists (Hawaii) to resolve possible methodological differences in direct age and maturity estimation.

3   Progress

3.1   Collaboration meeting, NOAA PIFSC, Hawaii

Meetings were held with Dr. Edward DeMartini and Dr. Robert Humphries at the NOAA Pacific Islands Fisheries Science Center (PIFSC) in Honolulu in January 2015. The purpose was to undertake direct collaborative work to resolve possible methodological differences in estimates of age and maturity of swordfish in the southwest Pacific and Hawaiian regions. The specific objectives were to:

- Compare spine, otolith and ovary histology interpretation methods between laboratories.
- Examine the spine inter-laboratory calibration study data.
- Undertake cross-readings of a sub-set of spines, otoliths and ovary histology.
- Discuss age validation methods.

Prior to the meeting, digital images of 100 sectioned swordfish anal spines were provided to CSIRO from an age calibration exercise undertaken in the early 2000s (DeMartini et al. 2007). In that study, the precision and bias of age estimates among five laboratories were examined – the National Marine Fisheries Service, Honolulu; the Centro de Investiga-cion Cientifica y de Educacion Superior de Ensenada, Mexico; the Instituto de Fomento Pesquero, Chile; the National Research Institute of Far Seas Fisheries, Japan; and the National Taiwan University. The coefficient of variation (CV) (Campana et al. 1995) among and between readers was around 10-15% and was considered "adequately precise" (DeMartini et al. 2007). The analysis, however, showed that one laboratory was underestimating age and it was recommended that these data be removed from our analysis (DeMartini, pers comm).

The spines were read by two CSIRO readers to determine if the reading methods used (see section 3.2 below) are consistent with other laboratories in the region. All readings were undertaken without knowledge of the size of fish or date of capture. The CV between CSIRO readers was 12.4%. The CV between CSIRO and the median count obtained by the four Pacific laboratories (DeMartini et al. 2007) was 13.71% (CSIRO 1) and 13.33% (CSIRO 2). The plots in Figure 1 suggest no or very little bias in the counts and the results indicate good overall precision and consistency in readings between CSIRO and other laboratories in the Pacific.

During the meeting at NOAA PIFSC it was concluded that:

1. No major methodological differences exist between the Hawaiian and current methods used by CSIRO to age swordfish using spines. However, examination of images of individual spines highlighted potential areas of disagreement, especially in assigning the first increment and at the spine margin. Additional counts of daily growth increments out to one year will aid the identification of first increment in spines.

2. Methodological differences did exist between the ageing studies of DeMartini et al. (2002) and Young and Drake (2002), which could account for the different growth rate estimates obtained by these studies.

3. No major methodological differences exist between the Hawaiian and current methods used by CSIRO (and Fish Ageing Services) to age swordfish using otoliths (see section 3.3 below).
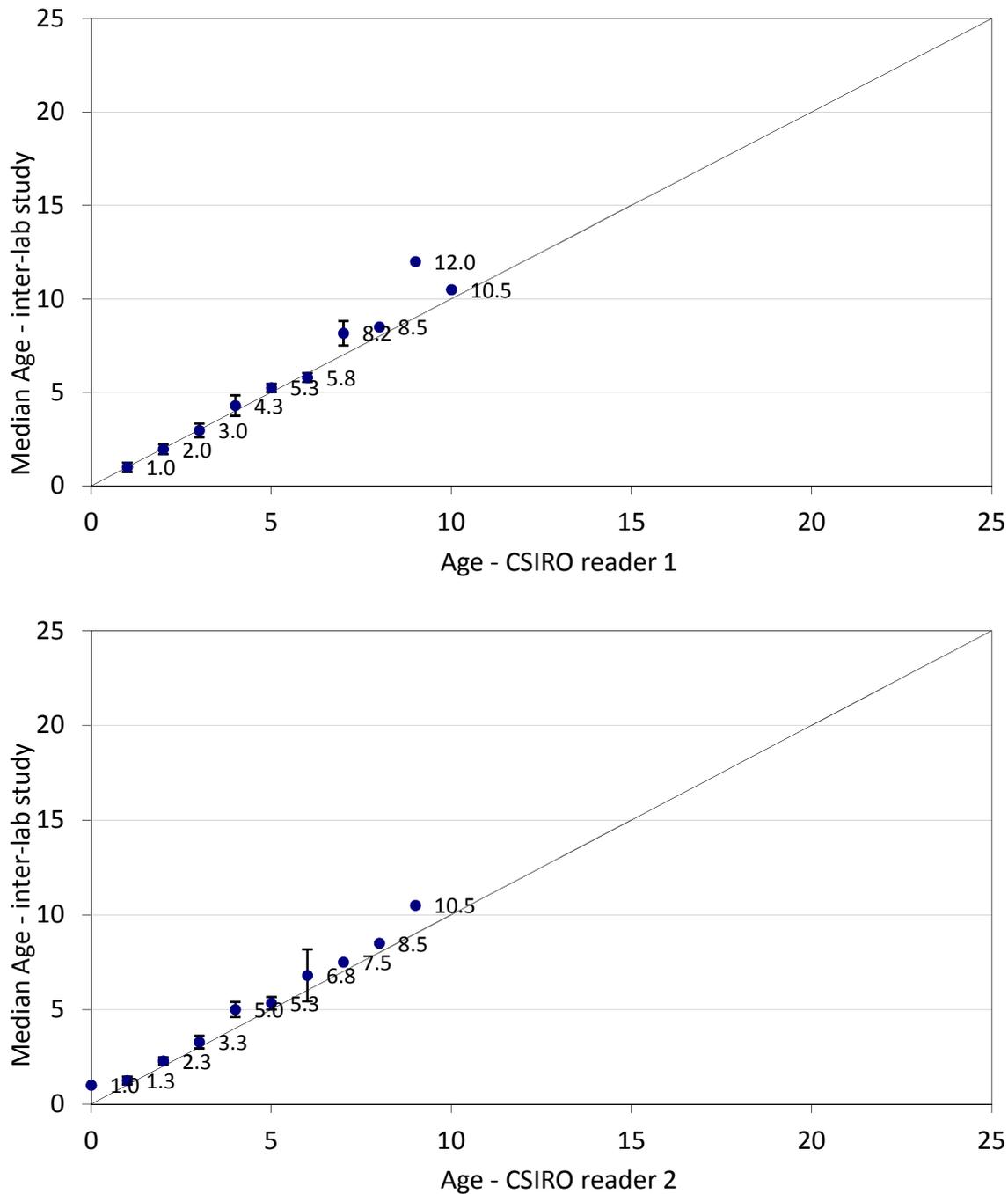
Figure 1. Age bias plots for comparisons of counts of translucent zones in spines by CSIRO 1 (top) and CSIRO 2 (bottom) and the median age obtained by 4 labs in an inter-laboratory study (DeMartini et al. 2007).

During the meeting at NOAA, ovary histology classification schemes used by CSIRO and Hawaii were also discussed and compared. It was concluded that methodological differences do exist between the Hawaiian and current methods used by CSIRO to differentiate immature from mature-regenerating females. However, these differences were necessary because the Australian ovary material was frozen before being fixed, resulting in poorer quality histological sections. It was agreed that the histological classification system used by CSIRO was appropriate and was

successfully identifying mature and immature females. For tissue that has been frozen, the Australian classification of "maturity" uses muscle bundles, late-stage atresia and melano-macrophage centres for females caught during non-spawning months.

3.2 Re-evaluation of Australian spines

Of the swordfish sampled by Young and Drake (2004) in the southwest Pacific, 310 were selected for age estimation in the current project. Fish were selected based on the presence of both the anal fin spine (already prepared for ageing) and whole sagittal otolith in the collection. Of these, fish were then selected based on length, sex and month of capture to obtain as many fish as possible from the full size range by sex and across all months of capture.

Multiple cross-sections of each fin spine were prepared by Young and Drake (2004). We selected the d/2 section for reading as this is most commonly used in ageing studies of swordfish. Occasionally another section was used if d/2 was unreadable or not present (e.g., D or 3/4D).

Each section was examined using a stereo-microscope under reflected light. A digital image of the section was captured and a calibrated scale was put onto each image. The images were enhanced using Photoshop Elements. All interpretations and measurements were done using the digital images.

A preliminary reading of each image was made by CSIRO without reference to the size of fish or capture date. The location of all translucent growth zones was marked on each image using the criteria of Ehrhardt et al. (1996) and Quelle et al. (2014). Translucent zones at the terminal edge were only marked and counted if opaque material was evident after the translucent zone. The outer edge of each complete translucent zone was measured and the edge type was assigned as opaque or translucent. Each reading was assigned a confidence score of 0-5 (poor-good). Figure 2 shows an example of a sectioned spine with presumed annual translucent zones indicated. The spines often contained 'split' translucent zones which were difficult to interpret, and some spines also had vascularised cores area making age estimation for large individuals difficult. Estimates of the number of translucent zone missing due to vascularisation (if present) were determined based on (i) the mean (and 1SD) of translucent zones in spines where vascularisation did not obscure the first translucent zones, and (ii) the distribution pattern of the visible translucent zones to infer the number missing.

A second "blind" reading of all spines was made after discussing spine reading protocols with scientists at the NOAA PIFSC (see section 3.1 above). A final count ("age estimate") was obtained based on a final reading with knowledge of the previous two readings. The edge type (opaque or translucent) and width (narrow, intermediate or wide) was noted for each spine. Age estimates were obtained for 263 spines and the remaining 47 were unreadable. Of the 263 spines that were readable, 126 were assessed to have between one to three missing zones due to vascularisation of the core. The maximum ages obtained were 10 and 14 for males and females respectively.

A comparison of age estimates obtained from spines by CSIRO and age estimates from Young and Drake (2004) indicates a systematic difference between the two readers (Fig. 3). Counts by Young and Drake (2004) were higher on average than CSIRO over the age range examined.
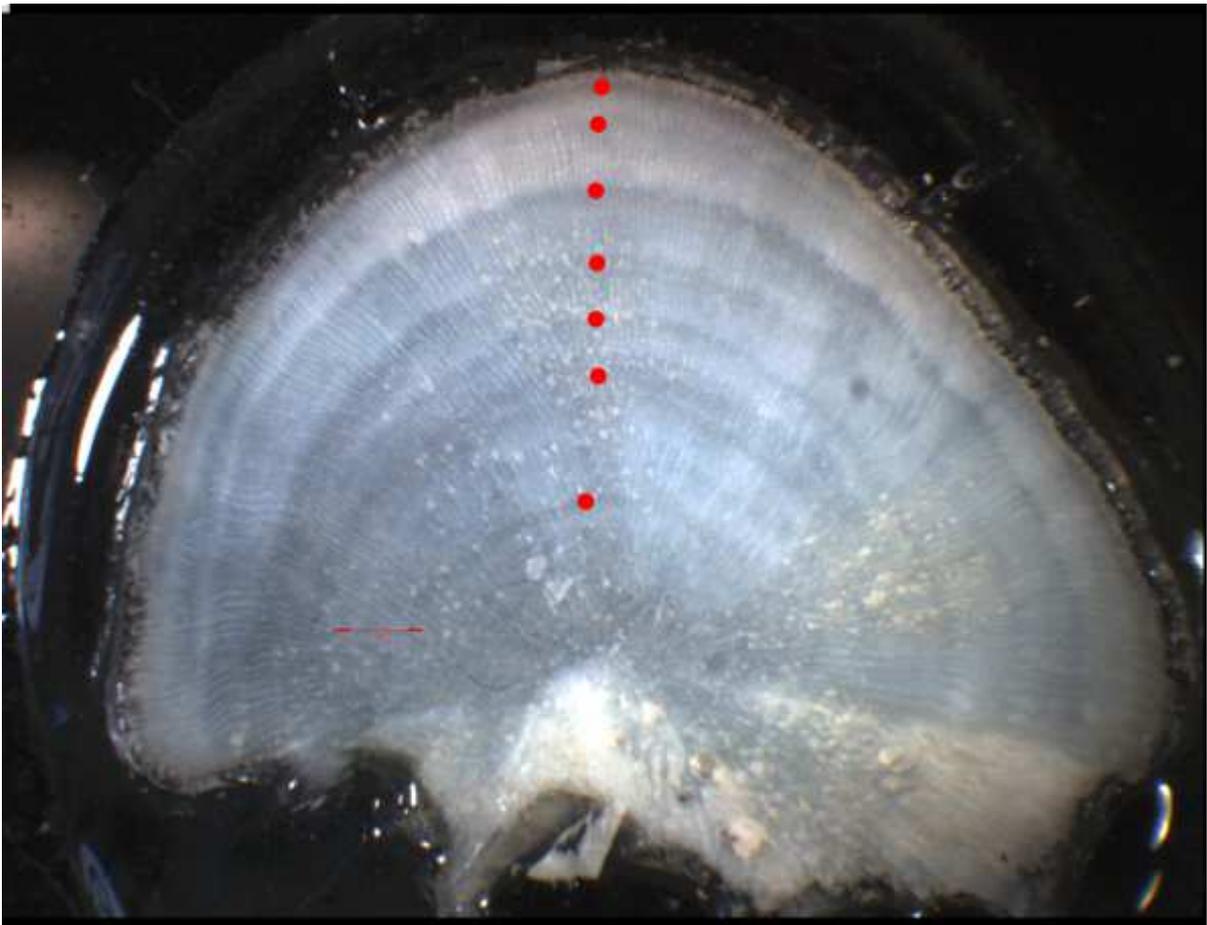
Figure 2. Swordfish 1589 (male, 175 cm OFL) anal fin spine prepared for annual ageing with the outer edge of translucent zones indicated by red dots.
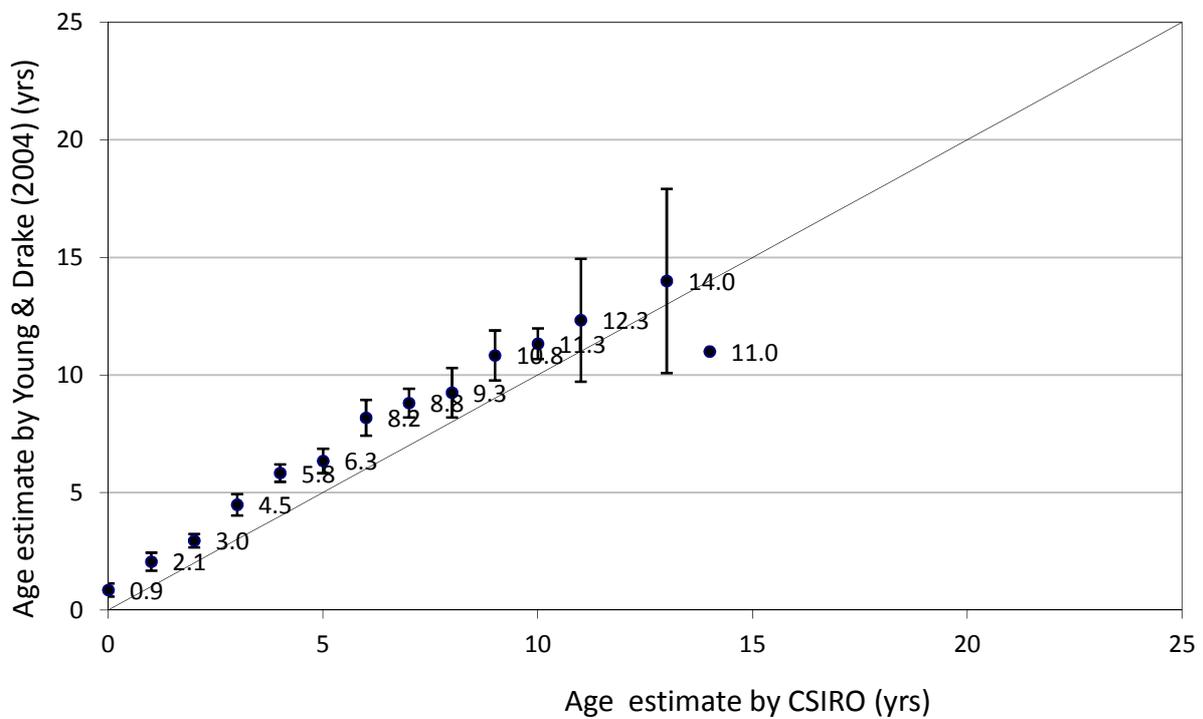
Figure 3. Age bias plots for comparisons of counts of translucent zones in spines by CSIRO and Young and Drake (2004).

3.3   Evaluation of Australian otoliths

Daily ageing

To determine the most appropriate method of otolith preparation for counting (assumed) daily growth increments, 11 sagittae were selected for trial preparation. Otoliths were selected from 7 small fish between 70 and 120 cm OFL and 4 larger fish between 137 and 230 cm OFL. All otoliths were prepared and read by Fish Ageing Services Pty Ltd.

The trial work showed that the preferred method for preparation was individual transverse sections of the sagittae. The otoliths were embedded on the edge of a slide in crystal bond, with the rostrum off the end of the slide. Using P800 Wet Dry, the rostrum was ground away to the primordia. The otolith was then placed in the middle of another slide with the ground surface facing down. Using P800 and then P1200, the otolith was ground down to the primordia. This continued until the primordia and (daily) increments were visible.

Preparations of the dorsal lobe (ground distally) often removed the primordia area while longitudinal sections were too difficult to align reliably and structure too fine to prepare. Some lapillus otoliths were prepared and they generally had good primordia and mid-section regions, but the outer edges had irregular growth and were deemed unlikely to be suitable for recording daily growth.

The transverse sections were examined at 640-1000x magnification. Daily growth increments were counted on the ventral lobe (Fig. 4). Measurements were taken from the primordium to the end of the clear portion of the otolith (measurement A) (Fig. 5). The distance between the primordia and the proximal edge of the otolith along the same path at measurement A was also measured (measurement B). Finally, the distance from the primordia to the distal inflection and the inflection to the proximal tip was measured (measurement C).

In the smaller fish (≤120 cm OFL), increments were generally clear for the first 150-170 which coincided with the first opaque area (assumed first opaque zone). After a count of 150-170, the structure was difficult to interpret and the pattern irregular. Total counts ranged from 164 in an 80 cm fish to 299 in a 108 cm fish (Fig. 6). A count could not be obtained for the 120 cm fish. In larger fish (≥137 cm OFL), counts appear to underestimate daily age although the first 150-170 increments consistently co-coincided with the first opaque area (zone).

The mean distance to the first opaque area (A) in small fish was 0.543 mm (+/- 0.024 SE) (n=7) and the distance to the proximal edge (B) ranged from 0.735 mm for the smallest sample that could be measured (108 cm OFL) to 0.960 mm for the largest sample (120 cm OFL) examined.
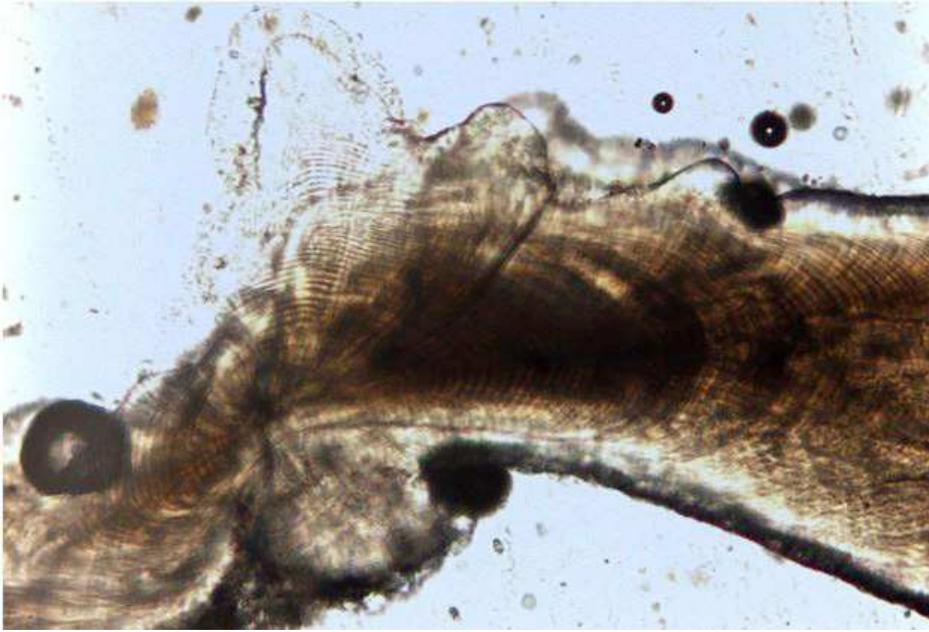
Figure 4. Example of assumed daily increments in a transverse sectioned sagittae otolith.
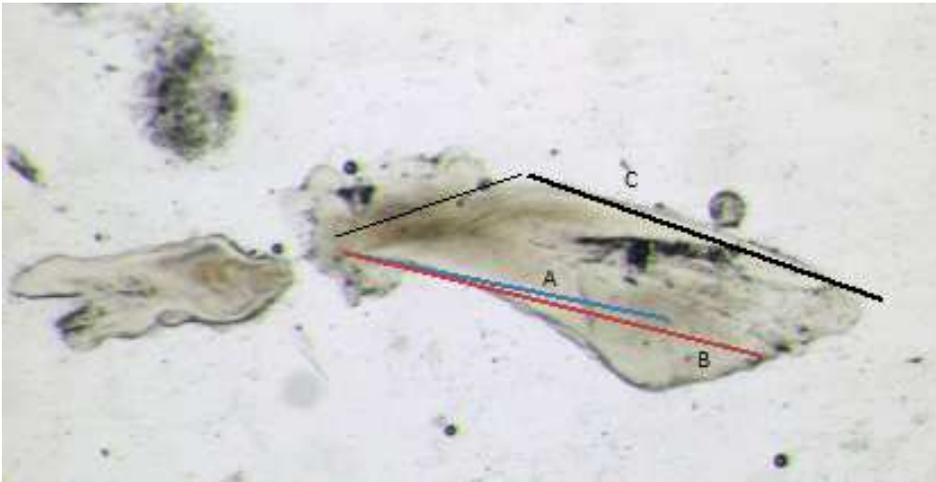
Figure 5. Transverse section of an otolith indicating the locations of measurements taken. Blue line measurement A, red line measurement B and black line measurement C.
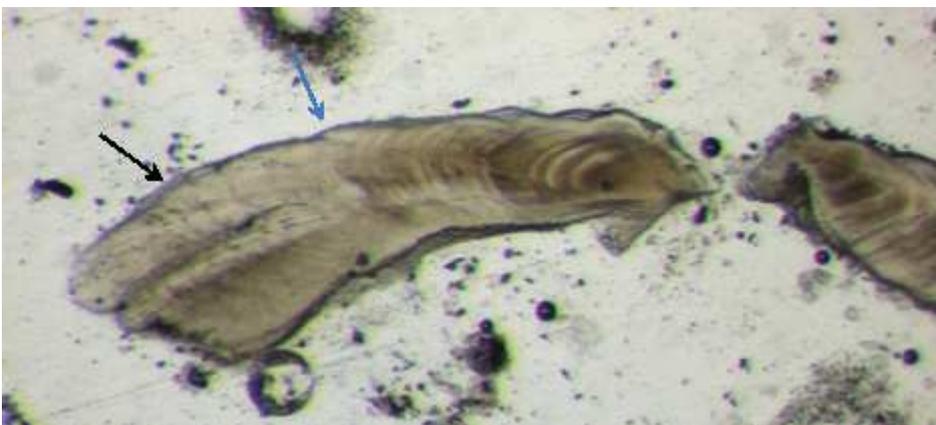
Figure 6. Transverse section of an otolith (108 cm OFL). Blue arrow indicates 100 increments and the black arrow indicates 150 increments. The total count was 299 increments.

Annual ageing

Otoliths from the 310 fish selected for ageing were weighed to the nearest 0.001 g. Otolith weight was compared to fish length to check that the capture data associated with each otolith was correct. No outlying data points were found in the data.

Fish Ageing Services Pty Ltd prepared one transverse section of all otoliths and made one reading. Initially, otolith measurements obtained from the daily ageing work (above) were compared to 'clear' prepared otoliths to help locate the first and subsequent opaque zones. Figures 8-10 show examples of sectioned otoliths with presumed annual opaque zones indicated. The number of opaque zones was counted in all sectioned otoliths under transmitted light without reference to the size of fish or capture date. In general, the first 3-4 zones were difficult to interpret but it is anticipated that additional daily ageing work will help refine the interpretation. After the 3rd pr 4th increment, the alternate opaque and translucent zones in the otoliths became distinct and regularly spaced (Fig. 10). The distance from the promordia to each opaque zone and to the otolith edge was measured. The otolith edge was classified as narrow, intermediate or wide, and each reading was assigned a confidence score of 0-5 (poor-good). A digital image was captured of each section and the opaque zones marked. The maximum ages obtained from otoliths were 17 and 21 for males and females respectively. These age estimates are similar to those obtained by Nishimoto et al. (2006) for otoliths from swordfish caught around Hawaii. In that study, the maximum age obtained from otoliths was 17 and 23 years for males and females respectively.

A preliminary comparison of age estimates based on otoliths and spines indicates bias for both males and female swordfish (Fig. 11). Spine-based counts were similar on average to otolith-based counts for the youngest age classes. However, a difference was evident in age classes >4 years for males and >7 years for females, where otolith counts were higher on average than spine counts (Fig. 11). (Note that our work suggests that the opaque zones counted in otoliths are equivalent to the translucent zones counted in spines.) The reason the age bias starts at different age classes is unknown, but may be related to higher growth rates of females relative to males. In both cases, the bias appears to occur after age at 50% maturity.

Although not presented here (due to preliminary nature of the data), ages estimates from otoliths and fin spines appear to produce significantly different growth curves. The 'otolith' growth curves indicate higher L_∞ and lower k parameters for both males and females compared to the 'spine' growth curves. Two CSIRO readers are currently reading all otoliths and will provide a final otolith-based age estimate for all fish. Precision and bias of estimates will be re-examined when these data are available. Marginal increment and edge type analysis will be used to examine the periodicity of increment formation as a method of indirect validation of the ageing methods.

Figure 8. Swordfish otolith prepared for annual ageing with two presumed annual opaque zones indicated by arrows. The blue arrow is at 0.550 mm and the green arrow at 0.750 mm from the primordium.
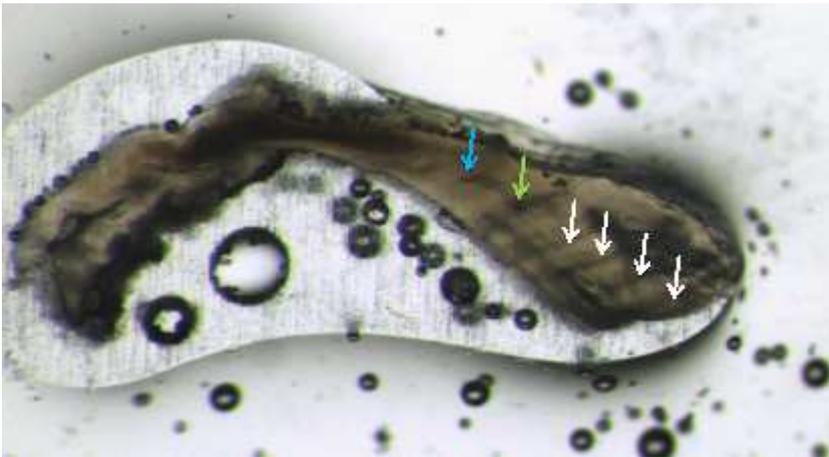
Figure 9. Swordfish 589 (161 cm OFL male) otolith prepared for annual ageing with presumed annual opaque zones indicated by arrows. The blue arrow is at 0.612 mm. The green and subsequent white arrows indicate the presumed 2nd to 6th opaque zones.

Figure 10. Swordfish 196 (257 cm OFL female) otolith prepared for annual ageing with presumed annual opaque zones indicated by crosses. The primordial and edge (E) are also marked with a cross.
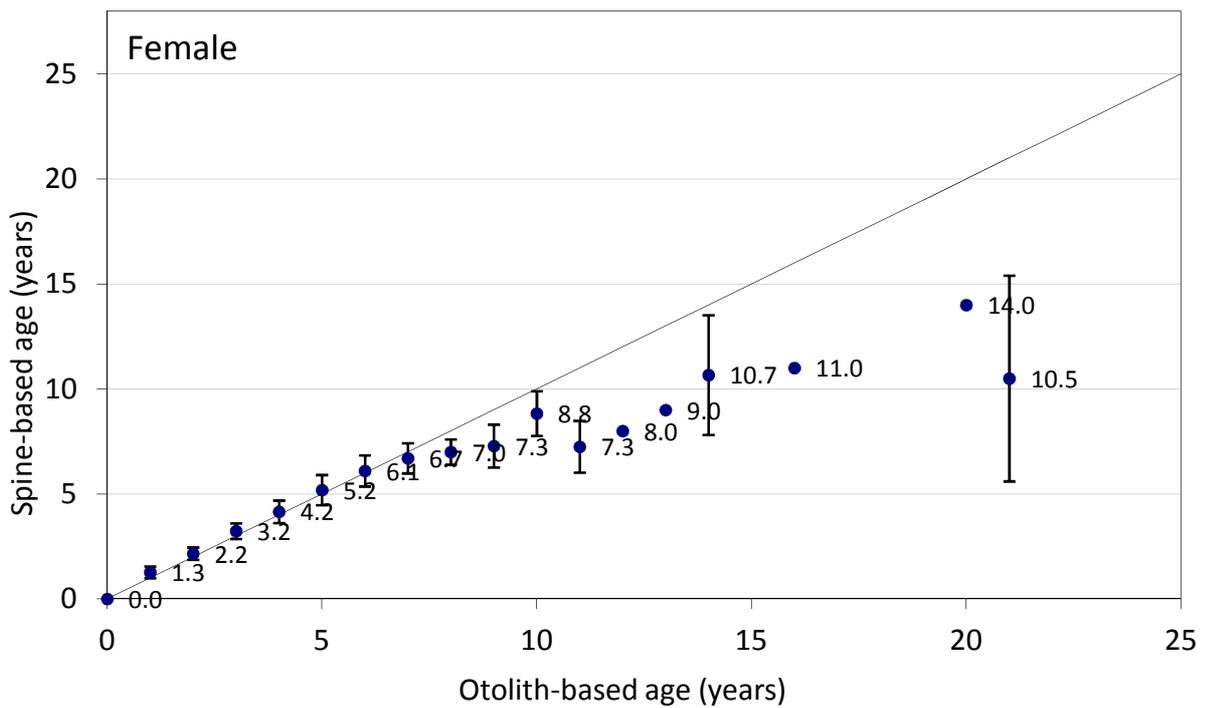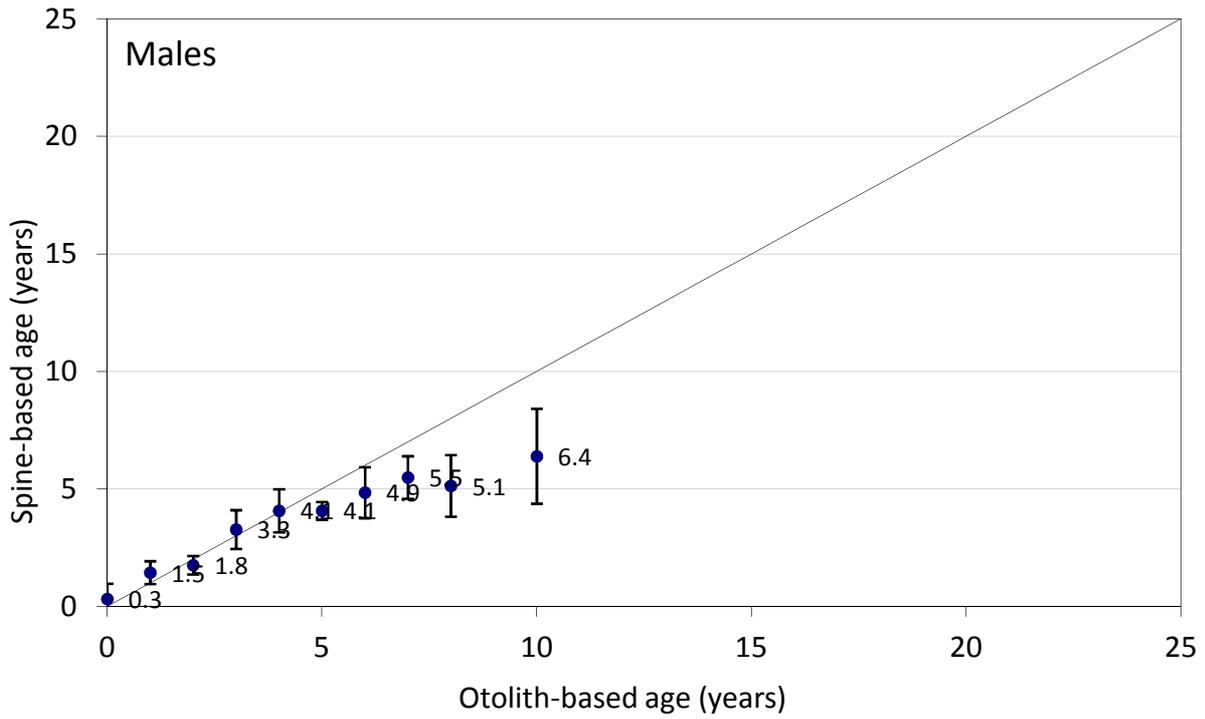
Figure 11. Age bias plots for comparisons of counts of opaque zones in otoliths by Fish Ageing Services (FAS) and translucent zones in spines by CSIRO for male and female swordfish.

3.4 Re-evaluation of Australian ovary histology

Young and Drake (2002) prepared standard histological sections (cut to 6 μm and stained with Harris' haematoxylin and eosin) of frozen- and fresh-fixed ovarian tissue for over 700 swordfish caught between 1998 and 2001. Of these, 688 were deemed suitable for re-analysis as the material was in good condition and of sufficient size for reading, and catch data were present (i.e., fish length, date and location). The fish were 55-300 cm orbital fork length (OFL) although the majority were 100-230 cm OFL. Gonad weight was obtained to the nearest 1 g for 659 fish and gonadosomatic index (GSI) was calculated following Hinton et al. (1997).

The histological sections were read and the ovaries classified using standardised terminology for classifying fish reproduction (Brown-Peterson et al. 2011) and criteria similar to that developed for other pelagic species including tunas (e.g. Farley et al. 2013). The most advanced group of oocytes (MAGO) was staged into one of 5 classes: unyolked (primary growth and cortical alveolar), early yolked (primary and secondary vitellogenic), advanced yolked (tertiary vitellogenic), migratory nucleus (germinal vesicle migration) or hydrated. Each ovary was also scored according to the presence or absence of postovulatory follicles (POFs) and by the level of alpha (α) and beta (β) stage atresia of advanced yolked oocytes present. Four levels of α stage atresia were recorded: <10% (minor atresia), 10-50% (moderate), >50% (major), 100% (complete). The β stage of atresia was recorded as being present or absent. Finally, maturity markers such as very late stages of atresia (gamma/delta), well defined muscle bundles, residual hydrated oocytes and melano-macrophage centres were recorded (Fig. 12-13). Maturity markers are considered to be signs of prior yolk development or reproductive activity, and have been used in many studies to identify mature-resting females during the non-spawning months (Kjesbu 2010; Brown-Peterson 2011).

All females were classified into reproductive phases and sub-phases depending on the MAGO, POFs, atresia and maturity markers present in the ovary (Table 1). The use of residual hydrated oocytes as a maturity marker was not found to be useful in swordfish as many small fish appeared to contain these structures but did not contain other maturity markers (Fig. 13). Small ("precocious?") fish with residual hydrated oocytes may have produced a small number of yolked oocytes which subsequently developed into hydrated oocytes, but the lack of other maturity markers indicated that these fish did not spawn and did not contribute to egg production. The ovaries of many large fish also contained residual hydrated oocytes either in the lamella or lumen (Fig. 12A). Only the presence of well defined muscle bundles, late stage atresia and/or melano-macrophage centres were used to identify mature-regenerating females.

The majority of females caught were classified as either immature (36.6%) or regenerating (44.5%), which is consistent with the results of Young et al. (2002). Young et al. (2002), however, did not distinguish between the two phases noting that after spawning, females absorb all their yolked eggs and appear histologically similar to immature females. Young and Drake (2002) limited their maturity analysis to the spawning months of September to March to reduce the likelihood that regenerating (mature-resting) females would be present. Our results indicate that regenerating females were observed in all months of the year, including the months of September to March (Fig. 14). Not differentiating between mature and immature females during the spawning season would explain the relatively high estimate of length at 50% maturity (L_{50}) obtained by Young and Drake (2002) compared to the Hawaiian study of DeMartini et al. (2000).

Figure 15 shows a preliminary maturity ogive for female Australian swordfish obtained from the current study. The estimate of L_{50} is 154.1 cm OFL. This is higher than estimated by DeMartini et al. (2000) (143.7 cm OFL) in Hawaii, but substantially lower than obtained by Young and Drake (2002) (181.0 cm OFL).
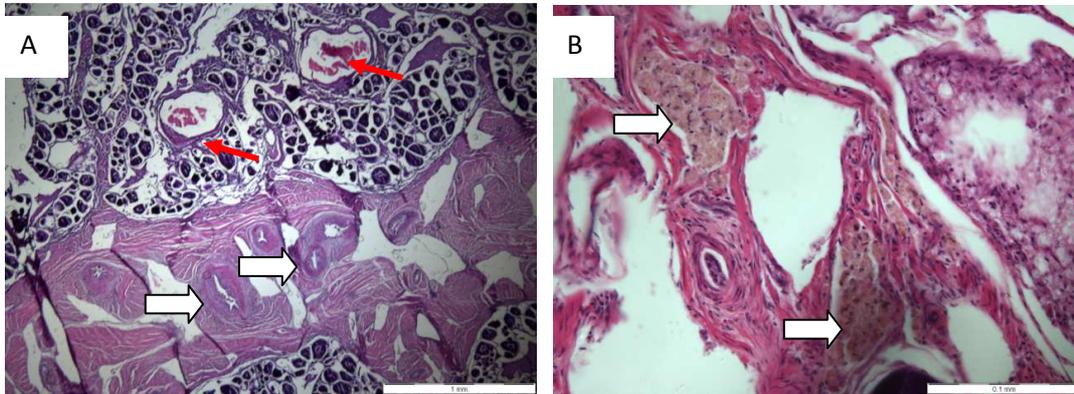
Figure 12. Histological sections of ovaries of mature females classed as regenerating based on the presence of maturity markers such as (A) well defined muscle bundles in a 226 cm fish and (B) melano-macrophage centres in a 240 cm OFL fish. White arrows indicate the maturity markers. Residual hydrated oocytes are also present in (A) (red arrows).
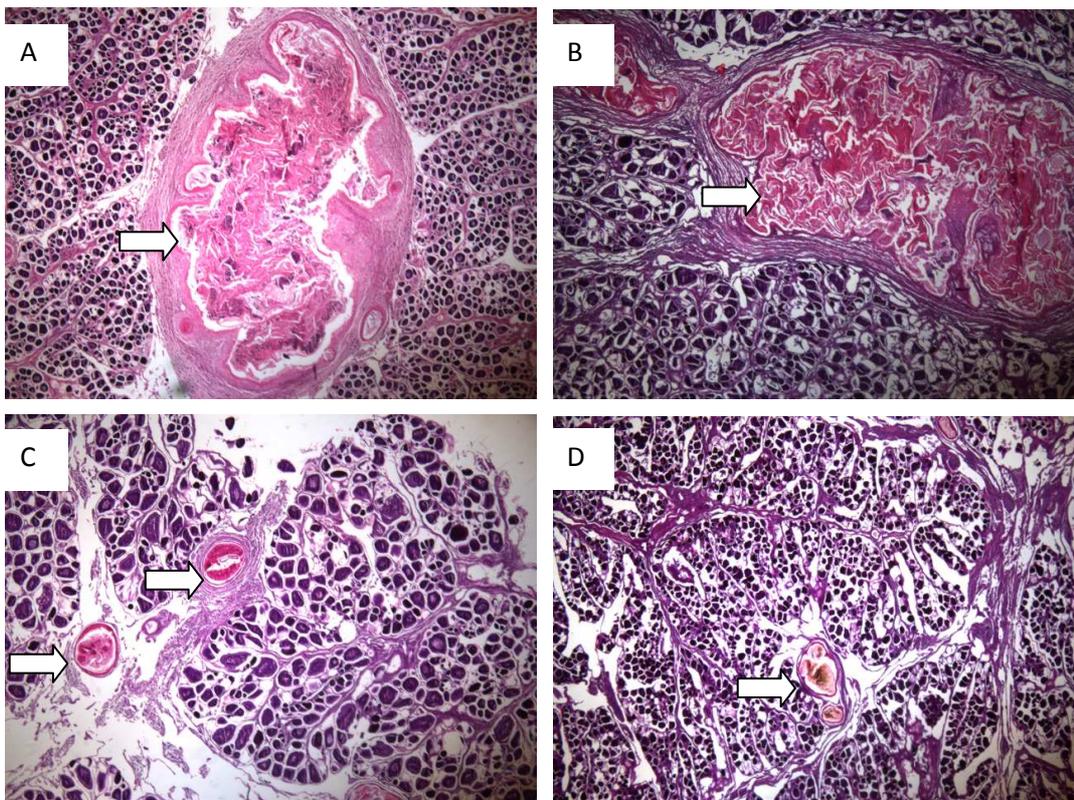
Figure 13. Examples of residual hydrated oocytes (RHO) (white arrows) in the ovaries of small swordfish. RHO's in the lumen of a (A) 97 cm and (B) 121 cm OFL fish. RHO's in the ovary tissue of a (C) 80 cm and (D) 98 cm OFL fish.

Table 1. Preliminary number of swordfish by histological classification

MATURITY STATUS	PHASE	SUB-PHASE	MAGO AND POF STAGE	ATRESIA OF ADVANCED YOLKED OOCYTES	MATURITY MARKERS	COUNT
Immature	Immature		Unyolked, no POFs	Absent	Absent	250
Immature	Developing		Early yolked, no POFs	Absent	Absent	6
Mature	Spawning capable	Non- spawning	Advanced yolked, no POFs	α and β atresia may be present	Possible	38
Mature	Spawning capable	Actively spawning	Migratory nucleus or hydrated and/or POF's	α and β atresia may be present	Possible	46
Mature	Regressing		Unyolked or early yolked, no POFs	All yolked oocytes are in the α or β stages of atresia	Possible	42
Mature	Regenerating		Unyolked or early yolked, no POFs	Absent	Present	306
Total						688

MAGO = most advanced group of oocytes, POF = postovulatory follicle. Maturity markers include gamma and delta stages of atresia and well defined muscle bundles.
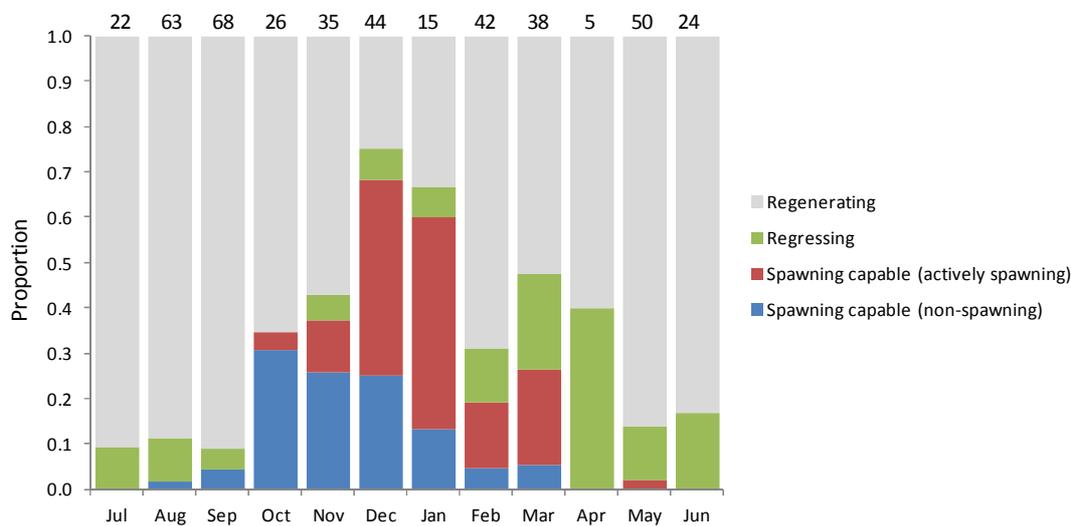
Figure 14. Proportion of mature female swordfish by reproductive phases sampled by month. The sample size per month is shown at the top of each bar.
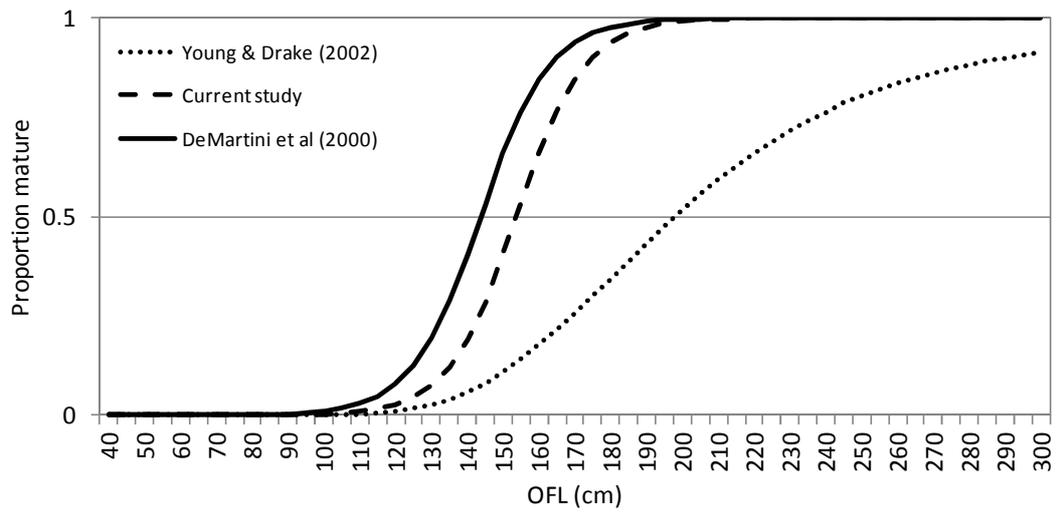
Figure 15. Proportion of females mature by length estimated by Young and Drake (2002), DeMartini et al. (2000) and the current study (preliminary estimate).

4 Discussion/future work

Higher maximum age estimates from otoliths compared to spines from the same fish have been reported in several species including tunas and billfish (e.g., Atlantic bluefin tuna, Rodríguez-Marín et al. 2007; South Pacific albacore tuna, Farley et al. 2013; Atlantic sailfish, Prince et al. 1986). In each case, otoliths were the preferred structure to estimate age across the full size range. Otoliths are considered to be the more accurate structure to age fish (Campana et al. 1995) and validated annual age estimates using otoliths have been obtained for Atlantic sailfish (Prince et al. 1985) as well as Atlantic bluefin, southern bluefin, bigeye, albacore, and longtail tunas (Clear et al. 2000; Farley et al. 2006; 2013; Neilson & Campana 2008; Griffiths et al. 2009; Shimose et al. 2009).

There are several potential causes of the different counts obtained from Australian swordfish spines and otoliths. The difference could be due to the difficulty of estimating the number of translucent zones missing in spines due to vascularisation of the core. Spines are subject to resorption, re-working and vascularisation, while otoliths are not (Secor et al. 1995; Campana and Thorrold 2001). However, the maximum vascularisation observed in spines only obscured the first three translucent zones, and is therefore unlikely to be the main source of error contributing the age bias between structures from large/old fish.

The difference in age estimates may be due to readers not being able to distinguish the more closely-spaced increments near the margin of spines compared to otoliths. It is also plausible that more increments are being deposited in otoliths, or fewer increments in spines, each year after a certain age. Alternatively, the material in spines could be re-worked after a certain age, and the zones observed are no longer annuli. Figure 16 shows an example of the sectioned otolith and spine from the same swordfish; the otolith shows clear zones while the spine is unreadable.

The results presented here are preliminary and further readings of hardparts, analysis and investigations will be undertaken, including indirect age validation, before growth parameters are estimated. Once finalised, the effect the different growth curves and maturity ogives on population models for South Pacific swordfish will be examined.
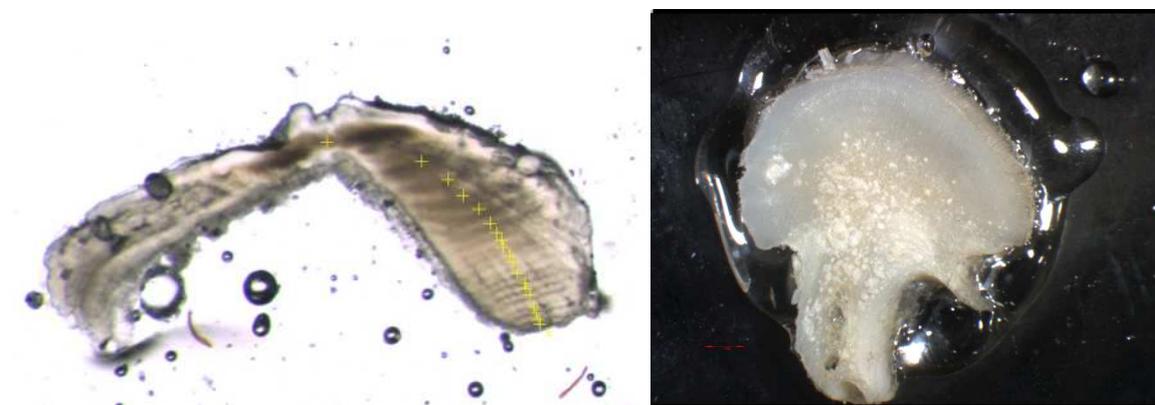
Fig. 16. Swordfish 207 (177 cm OFL male) sectioned otolith with presumed annual opaque zones indicated by crosses (top) and sectioned spine which was unreadable possibly due to vascularisation, reworking or material and/or the increments are too close to interpret (bottom).

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