



Size, maturity and age composition of mako sharks observed in New Zealand tuna longline fisheries

New Zealand Fisheries Assessment Report 2016/22

M. P. Francis

ISSN 1179-5352 (online)

ISBN 978-1-77665-237-2 (online)

April 2016



Requests for further copies should be directed to:

Publications Logistics Officer
Ministry for Primary Industries
PO Box 2526
WELLINGTON 6140

Email: brand@mpi.govt.nz
Telephone: 0800 00 83 33
Facsimile: 04-894 0300

This publication is also available on the Ministry for Primary Industries websites at:
<http://www.mpi.govt.nz/news-resources/publications.aspx>
<http://fs.fish.govt.nz> go to Document library/Research reports

© Crown Copyright - Ministry for Primary Industries

TABLE OF CONTENTS

EXECUTIVE SUMMARY	1
1. INTRODUCTION	2
2. METHODS	3
2.1 Collecting biological data	3
2.2 Analysis of observer data	3
2.3 Age, growth and age frequency of catch	4
3. RESULTS	7
3.1 Observer sampling	7
3.2 Maturity	8
3.3 Age, growth and age frequency of catch	9
4. DISCUSSION	10
5. MANAGEMENT IMPLICATIONS	12
6. ACKNOWLEDGMENTS	13
7. REFERENCES	14
8. TABLES	16
9. FIGURES	18
APPENDIX 1	31
APPENDIX 2	34

EXECUTIVE SUMMARY

Francis, M.P. (2016). Size, maturity and age composition of mako sharks observed in New Zealand tuna longline fisheries.

New Zealand Fisheries Assessment Report 2016/22. 34 p.

Pelagic sharks are routinely taken as bycatch in New Zealand's surface longline (SLL) fisheries, and to a lesser extent in midwater trawl fisheries. The mako shark (*Isurus oxyrinchus*) is the second most-caught pelagic shark (after blue shark), with estimated catches of about 50–100 tonnes per year between fishing years 2004 and 2014, and a current Total Allowable Commercial Catch of 200 tonnes. Due to their migratory nature, management is done on a regional basis with New Zealand being responsible for monitoring its fisheries and providing these data to regional fisheries management organisations. This study assesses the catch composition of mako sharks taken by SLL in New Zealand waters using data and samples collected by observers. Data were stratified by fleet (chartered Japanese or New Zealand domestic vessels) and region (North region = Fisheries Management Areas 1, 2, 8 and 9, and Southwest region = FMAs 5 and 7). Length-frequency distributions were scaled up to estimate the size composition of the commercial catch for the fishing years 2007 to 2015. Maturity and reproductive status were assessed from observer data collected between 2011 and 2015. Vertebrae were sectioned, and growth bands counted to estimate the age of a subsample of sharks. An ageing protocol was developed and growth curves were fitted to the length-at-age data. A scaled age-frequency distribution of the catch was generated by applying an age-length key to the scaled length-frequency distributions (by sex). The proportions of mature animals in the catch were estimated by applying the median length at maturity to the scaled length-frequency distributions (by sex).

Observer sampling of length data was compromised by their inability to measure every shark caught, and evidence that unmeasured, discarded sharks may have a different size composition from measured, discarded sharks. The proportion of makos discarded or released alive under Schedule 6 of the Fisheries Act continued to increase, reaching 94% of the catch in 2015. In the North region, the proportion of makos measured dropped to 10% in 2015, and observer coverage was low. High observer coverage of the Japanese charter fleet resulted in about 46% of makos being measured in 2015 in the Southwest region, but this was a big decline from previous years. The decline in percentages of mako sharks measured results from the implementation of a shark finning ban at the beginning of the 2015 fishing year, and that makes it difficult to assess recent patterns of size composition, sex ratio, maturity composition, and age composition.

The SLL mako catch was dominated by juveniles, with most sharks being shorter than 200 cm fork length, and an estimated 89% of males and 99.5% of females being immature; however, these proportions may have been over-estimated if significant numbers of large mature adults were being discarded unmeasured. The 0+ age class constituted about one-quarter of the catch, and most of the catch was less than 6 years old. Mature females are not considered vulnerable to the New Zealand SLL fishery, although they may be taken by other fleets in international waters. There is an urgent need to validate mako ageing to determine whether one or two band pairs per year are deposited on their vertebrae. Such validation could be achieved by injection of oxytetracycline into tagged and released sharks to mark their vertebral centra with a time stamp. Assuming that one band pair per year is deposited, males and females grow at similar rates up to about 16 years, beyond which there were few aged sharks. Nevertheless, length at maturity differed between the two sexes, so their estimated ages at maturity also differed: about 9–10 years for males and 20–21 years for females.

Uncertainties and gaps in our knowledge of the biological parameters and catch composition of mako sharks require that management is cautious, and that efforts are made to fill the gaps through appropriate research. In particular, a quantitative stock assessment is required to pull together New Zealand and overseas data into a coherent model in order to estimate the status of the stock.

1. INTRODUCTION

Pelagic sharks are routinely taken as bycatch in New Zealand's tuna longline fisheries, and to a lesser extent midwater trawl fisheries (Clarke et al. 2013; Francis 2013; Griggs & Baird 2013). The shortfin mako shark (*Isurus oxyrinchus*) is the second ranked pelagic shark (after blue shark), with estimated commercial catches of about 70–100 tonnes per year between 2003–04 and 2012–13, declining to under 50 t in 2013–14, and a current Total Allowable Commercial Catch of 200 tonnes (Ministry for Primary Industries 2015). Highly migratory species (HMS), including makos, are managed by Regional Fisheries Management Organisations (RFMOs). The important RFMO for New Zealand makos is the Western and Central Pacific Fisheries Commission (WCPFC). As a member of WCPFC, New Zealand has numerous obligations, including the provision of specific data and submission of annual reports describing the fisheries and research activities. Within New Zealand fisheries waters, New Zealand implements the objectives of the WCPFC's conservation and management measures via catch limits for the main HMS shark species.

Due to their HMS nature, assessments for these stocks are done on a regional basis with New Zealand being responsible for monitoring its fisheries and providing these data to WCPFC. In addition to the requirement for assessments, quantitative data on elasmobranch catches are also useful for monitoring the New Zealand component of these stocks, particularly as New Zealand fishes the extremes of the range for most HMS. The National Plan Of Action – Sharks (Ministry for Primary Industries 2013) additionally requires that New Zealand fills some of the current data gaps in information on its shark fisheries.

Historically, most biological information for HMS species has been collected by observers at sea in the tuna longline fishery (Francis & Duffy 2005; Francis 2013, 2015). The low levels of domestic observer coverage result in low quantities of data being collected, and the need for multi-year sampling to answer key questions. Low observer coverage rates greatly reduce our ability to quantitatively monitor the components of the stock that migrate through or reside in New Zealand waters. Under a recent Ministry for Primary Industries research project (HMS2010-03), Francis (2013) characterised the fisheries for mako sharks (and also blue and porbeagle sharks), documented observer collections of vertebral samples and data on maturity and fin weights, analysed time series of length-frequency, maturity and sex ratio data from tuna longline catches, and made recommendations for improved data and sample collection. This study extends and builds on the previous project by ageing mako shark vertebrae collected by observers in 2011–15, establishing a reference library of vertebral sections, estimating the length and age composition of tuna longline catches, and updating previous analyses of maturity composition and sex ratio. The results will be used as inputs to future stock assessments being undertaken by WCPFC.

The objectives of this study were:

1. To analyse the sex, maturity state, length and age structure of the commercial catch and review conversion factor data from mako sharks
2. To age vertebrae collected by fishery observers
3. To develop an ageing library from the material used in this study

Results from an analysis of mako shark conversion factor data (part of objective 1) were reported elsewhere (Francis 2014) and are not included here.

2. METHODS

2.1 Collecting biological data

A set of instructions was prepared for observers on sampling pelagic shark length, sex, maturity, vertebrae and fin weight (Appendix 1). Vertebrae were inventoried and archived in a freezer, and maturity and fin data were punched. From 2014, observers were also asked to record the presence or absence of spermatophores in the ampulla epididymis (seminal vesicle) of males (Pratt & Tanaka 1994). Spermatophore occurrence is a useful complement to clasper development when determining the maturity status of male makos (Francis & Duffy 2005). Other observer data were punched and loaded using routine processes into the *COD* database managed by NIWA for the Ministry for Primary Industries (MPI).

2.2 Analysis of observer data

The analyses in this report were based on data and specimens collected by observers. Most data and all specimens came from surface longline (SLL) vessels targeting tunas. A total of 349 SLL observer trips made between April 1993 and September 2015 were included. Five of those trips (1.4%) were omitted from analyses because of known species identification problems, or data quality issues. Observer data were stratified into fleets (chartered Japanese or New Zealand domestic vessels) and regions because previous studies have identified spatial variation in pelagic shark length-frequency distributions (Francis et al. 2001; Francis 2013, 2015). The North region comprised Fisheries Management Areas (FMAs) 1, 2, 8 and 9, and the Southwest region comprised FMAs 5 and 7. Fork length (FL) was adopted as the measurement standard in this study. Hereafter, all references to years are for fishing years (1 October to 30 September) and each year is labelled after the second of the pair of calendar years (e.g. the 2012–13 fishing year is labelled as 2013).

When large numbers of sharks (particularly blue sharks) are caught on SLL sets, observers may not be able to record data from individual fish. In these cases, observers ‘tally’ (count) the sharks but do not measure and sex them or record other data such as the time of landing, fate, or processing method. Tallies are not an important issue for makos: between 1993 and 2015, only 0.2% of 6926 observed makos were tallied. However, many makos that were individually recorded (51.0% of 6910 sharks) were not measured.

Observer length-frequency distributions were scaled up to estimate the size composition of the commercial catch using NIWA’s catch-at-length-and-age program CALA v2.0-2015-01-28 (rev. 371) (Francis, R.I.C.C. et al. 2014). Measured sharks were aggregated into four strata (Charter North, Charter South, Domestic North and Domestic South) and scaled up to the fishing year catch by SLL using the proportion of hooks observed in each stratum. Annual length-frequency distributions were then further scaled to the total catch for the years 2007–2015 using the ratio of the number of hooks set by the entire fleet in each year to the number of hooks set in 2008 (the year with the lowest fishing effort in the time series). Years before 2007 were not included because they had low observer coverage in the important Domestic North fishery (maximum 4.7% coverage but usually less than 3% and sometimes zero) (Griggs & Baird 2013). Coefficients of variation (CVs) for each length class, and mean weighted CVs (MWCVs) across all length classes, were estimated by bootstrap re-sampling (N=1000 samples) with replacement at the stratum level. No re-sampling was done at the year level.

Maturity and reproductive status were assessed from observer data collected between 2011 and 2015. Maturity was scored on a 3-stage elasmobranch scale (immature, maturing and mature; see Appendix 1). Three additional stages (4–6) were used to classify mature females into reproductive stages (gravid I and II, post-partum). Immature and maturing sharks (classes 1 and 2) were combined as ‘immature’ and mature sharks (classes 3–6) were combined as ‘mature’. Maturity ogives were fitted to the proportions of sharks that were recorded as mature after grouping them into 5-cm length classes.

Logistic regressions (binomial error structure with a logit link function) were fitted to the data using the GLM function in R statistical software (R Development Core Team 2008).

2.3 Age, growth and age frequency of catch

The following description of methods used for ageing mako shark in this study is also proposed as an age determination protocol for future ageing of this species. It follows the format and content of the Ministry of Fisheries document 'Guidelines for the development of fish age determination protocols' (Ministry of Fisheries Science Group 2011).

Vertebrae preparation

A block of 3–4 vertebrae was removed from beneath the first dorsal fin of each shark, trimmed of neural and haemal arches, muscle and connective tissue, and then frozen. Sex was recorded and FL was measured in a straight line from the tip of the snout to the fork in the tail, rounded down to the centimetre below actual length. All vertebrae available at the time of preparation (N=132) were selected for sectioning. The vertebral blocks were defrosted, the largest visible vertebra was dissected, and it was physically trimmed of connective tissue and residual neural and haemal arches.

Vertebrae were sectioned with a Struers Secotom-10 diamond blade saw. Vertebrae were briefly bleached (about 15 min), air dried overnight, and glued to small wooden blocks with epoxy resin. The wooden blocks were then placed in the saw's chuck for sectioning. Vertebrae were sectioned in the frontal plane (Wilson et al. 1987) by making two cuts with a single diamond-edged blade to produce a section about 0.6 mm thick. This produced 'bowtie' sections (Figure 1), although these frequently broke into two pieces at the focus. No grinding, polishing or staining was performed. Sections were stored in 70% isopropyl alcohol until they were aged. This preparation technique is the same as that used in a previous age and growth study of New Zealand makos (Bishop et al. 2006).

In studies of shark age and growth, vertebral radius is typically measured between the focus of the 'bowtie' section and the vertebral margin along the corpus calcareum (Natanson et al. 2002). In this study, the half-bowtie sections were frequently broken near the focus, rendering measurement of the vertebral radii impossible. Instead, we measured centrum length (CL) as the maximum distance between the outer edges of the corpus calcareum in the antero-posterior direction (Figure 1D).

Vertebrae interpretation

Sections were drained and read wet using a Leica MZ12 stereomicroscope at 12.5× magnification. Illumination was by reflected white light (two fibre optic sources arranged at approximately 45° from the horizontal on either side of the specimen) against a black background.

Shark species often display a 'birth band', which is a prominent contrasting band in the centrum deposited about or soon after birth. Identification of this band is important in order to determine where subsequent band counts should begin. The birth band in makos was defined as the first prominent translucent (dark under reflected light) band (Figure 1). It was sometimes accompanied by a slight change in the angle of the centrum face (the outer edge of the corpus calcareum). CL at the outer edge of the birth band averaged 4.44 mm (range 3.52–5.44 mm, N = 132), compared with the mean CL for 0+ mako sharks of 5.09 mm (N=16), confirming the identification of the birth band. In the present study, if the location of the birth band was uncertain, the point at which CL was approximately 4.5 mm, measured with an ocular micrometer, was used to assist with its identification. However, this distance measure was not used as a primary criterion, as the location of the birth band varies naturally among sharks (through variation in size or time of birth), and with the position along the vertebral column from which vertebrae were collected (vertebral size varies with position (Bishop et al. 2006)).

Parturition in New Zealand makos peaks in late winter and spring, and the theoretical birthday has been defined as 1 October (Duffy & Francis 2001; Bishop et al. 2006). The four smallest mako sharks aged

in the present study (71–79 cm FL) all had one translucent band in their centra; two sharks captured in October and January had no opaque material deposited outside the birth band, whereas two sharks captured in February and June had narrow and wide opaque bands respectively deposited outside the birth band. This suggests that the birth bands, and presumably also subsequent translucent bands, are deposited during spring, and opaque bands are deposited in summer–autumn.

Counts were made of translucent bands beyond the birth band on high resolution photo-micrographs (Figure 1). Distinct bands usually traversed the corpus calcareum (the highly calcified outer surface of the centrum) and the intermedialia (the more porous, triangular wedge between the corpora calcarea). Indistinct bands could often not be traced across both structures, but the full width of the section was examined where possible. In larger sharks, band pairs (one translucent and one opaque band) near the margin became much narrower and difficult to resolve. Increased magnification and adjustment of lighting angle was sometimes necessary to visualise and count these finer bands. In porbeagle sharks, Francis et al. (2007) showed using radiocarbon dating that at least some of these narrow bands become unresolvable beyond an age of about 20 years, leading to substantial age underestimation of older sharks. Because this age under-estimation may also occur in makos, and because few old makos were present in the commercial catch, we grouped all sharks aged 16 and older as a ‘16-plus’ group when estimating the scaled age-frequency distribution.

Ageing procedures

Two readers counted vertebral bands: Reader 1 (Silver Bishop, MPI) and Reader 2 (Malcolm Francis, NIWA). Reader 1, who was experienced in reading mako vertebrae (Bishop et al. 2006), carried out a single count of all 132 sections. Reader 2, who was experienced with ageing other shark species but not makos, carried out an initial ‘familiarisation’ read of all 132 sections while knowing the age estimates assigned by Reader 1. In future, this step should use sections assigned to the ageing library, and should cover a range of ages from 0+ to old sharks. Reader 2 then made two further ‘blind’ counts of all vertebrae; i.e. without knowing the previous age estimates of either reader, or the length or sex of the shark.

Caution is required when ageing mako sharks caught in October–January, when a translucent band is in the process of being formed at the margin of the vertebra. For example, 1+ sharks sampled in November could have (a) one translucent band followed by a wide opaque band at the margin, (b) one translucent band followed by one opaque band and an incomplete translucent margin, or (c) two translucent bands with no opaque material at the margin. To ensure that sharks are correctly assigned to age classes during October–January, sections with a wide opaque margin or incomplete translucent margin should have their translucent band counts incremented by one.

The final age estimate for each section was taken as the translucent band count of Reader 1 corrected for the time of year of capture by adding the elapsed time between the theoretical birthdate (1 October) and the capture date. The age interpretation used in this study is the same as that used previously for mako sharks in New Zealand (Bishop et al. 2006), and it assumes that mako sharks deposit one band pair per year (1 bpy) on their vertebrae. However, validation studies carried out elsewhere draw conflicting conclusions about whether one or two band pairs are deposited per year, and New Zealand length-frequency modes are more consistent with 2 bpy (see Results and Discussion for further details).

Estimation of ageing precision

Within-reader and between-reader age-estimation bias and precision were explored with NIWA R package *AgeCompare* for (a) readings 2 and 3 of Reader 2, and (b) the first and third readings of Readers 1 and 2 respectively. *AgeCompare* produces a plot comparing the two readings, a frequency distribution of the age differences, an age-bias plot (Campana et al. 1995), and plots of the average percent error (APE) and the mean coefficient of variation (CV) (Campana et al. 1995; Campana 2001). CV is numerically $\sqrt{2}$ (= 1.414) times greater than APE.

Estimation of growth

Growth curves were fitted to the length-at-age data using the R package *FSA* (version 0.1.7) which fits non-linear curves using the R package *nlstools*. Following Bishop et al. (2006), the growth model suite developed by Schnute (1981) and extended by Quinn & Deriso (1999) was applied. The generalised model (Case 1) has four parameters: L_1 and L_2 which are the estimated lengths at two selected reference ages τ_1 and τ_2 , and κ and γ which determine the shape of the curve. Case 1 reduces to four sub-models (Cases 2–5) depending on whether the parameters κ and γ are zero, one, or another value. The von Bertalanffy, Gompertz, Richards, Logistic and a number of other growth models are special cases of the generalised Schnute model, depending on the values of the parameters κ and γ (Schnute 1981). Reference ages τ_1 and τ_2 were set at 1 and 10 years respectively.

Initially, the five cases of the Schnute growth model were fitted to the vertebral data for both sexes combined, and for each reader separately:

Case 1, where $\kappa \neq 0$ and $\gamma \neq 0$:

$$L_t = \left(L_1^\gamma + (L_2^\gamma - L_1^\gamma) \frac{1 - e^{-\kappa(t-\tau_1)}}{1 - e^{-\kappa(\tau_2-\tau_1)}} \right)^{\frac{1}{\gamma}}$$

Case 2, where $\kappa \neq 0$ and $\gamma = 0$:

$$L_t = L_1 e^{\left(\ln \left(\frac{L_2}{L_1} \right) \frac{1 - e^{-\kappa(t-\tau_1)}}{1 - e^{-\kappa(\tau_2-\tau_1)}} \right)}$$

Case 3, where $\kappa = 0$ and $\gamma \neq 0$:

$$L_t = \left(L_1^\gamma + (L_2^\gamma - L_1^\gamma) \frac{t - \tau_1}{\tau_2 - \tau_1} \right)^{\frac{1}{\gamma}}$$

Case 4, where $\kappa = 0$ and $\gamma = 0$:

$$L_t = L_1 e^{\left(\ln \left(\frac{L_2}{L_1} \right) \frac{t - \tau_1}{\tau_2 - \tau_1} \right)}$$

Case 5, where $\kappa \neq 0$ and $\gamma = 1$:

$$L_t = \left(L_1 + (L_2 - L_1) \frac{1 - e^{-\kappa(t-\tau_1)}}{1 - e^{-\kappa(\tau_2-\tau_1)}} \right)$$

Each Case was fitted by non-linear least squares, which for a normal error model is equivalent to maximising the log-likelihood (Manning & Sutton 2004):

$$LL = -\frac{n}{2} [\ln(2\pi\sigma^2) + 1]$$

where $\sigma^2 = \frac{RSS}{n}$, RSS is the residual sum of squares from the least squares fit, and n is the sample size. The best fitting case was determined using Akaike's (1973) Information Criterion (AIC):

$$AIC = -2\ln(LL) + 2p$$

where p equals the number of parameters fitted in the model (including σ^2).

In the second step, the best fitting Schnute case (Case 1) was fitted to the same dataset using separate parameters for the two sexes, and the resulting fit was compared with the combined-sexes model using the AIC .

Reference collection

The recommended size for a reference collection for a species of medium longevity is 500 vertebral sections, with 200 being randomly drawn for reading prior to ageing a new sample. The present study aged only 132 mako vertebral sections, so all sections have been placed in the reference collection, and the collection will be augmented by new sections following any future studies. The reference sections and band counts will be archived in the NIWA *Age* database.

The precision for reading shark vertebrae in other studies is typically low, with CVs usually exceeding 10% (Campana 2001).

Scaled age composition

The length-at-age data for Reader 1 were used as an age-length-key (ALK) to convert the scaled observer length-frequency distributions by sex to scaled age-frequency distributions. The procedure was carried out in CALA (Francis, R.I.C.C. et al. 2014) (see Section 2.2 for more details). CVs for each age class, and MWCVs across all age classes, were estimated by bootstrap re-sampling of the length-frequency distributions within strata, and bootstrap resampling of the data in the ALK with replacement (N = 1000 samples).

3. RESULTS

3.1 Observer sampling

All sets from all of the chartered Japanese SLL vessels were observed and sampled in 2011–15 (Table 1. Appendix 2). However, few domestic trips and only 3–7% of the domestic sets were observed, and even smaller proportions were sampled for vertebrae, maturity data or fin weights on domestic trips.

Data and samples were collected from 54 observer trips, 50 of them aboard SLL vessels and four aboard trawlers (Appendix 2). Most vertebrae and data came from SLL vessels operating in FMAs 1, 2, 5 and 7 during April–August. A total of 146 mako sharks were sampled for vertebrae, 188 for maturity, and 82 for fin weights. Only 13 male makos were sampled for spermatophores, all of them on one trip. Comparison of the length-frequency distributions of makos sampled for vertebrae and maturity with the distributions for all makos measured by observers over the same period showed that samples were generally representative of the sharks measured (Figures 2–3).

Observers on SLL vessels were not always able to measure every shark, and this may introduce biases into the recorded length-frequency distributions. Potential biases include:

1. Observers may not be able to measure all the sharks that are caught because of other priorities, or because they may not observe an entire haul if it continues beyond the end of a 12-hour day.
2. Some sharks may be cut or shaken off the line alongside the boat, and not brought aboard; others are lost during hauling. This issue may be more important on smaller domestic vessels which are less able to bring large sharks aboard, particularly in bad weather. These sharks are not usually measured or sexed.
3. Discarded sharks are often not measured. There are two issues here. First, fishers may selectively discard or release particular size classes; e.g. small sharks have less-valuable fins than large sharks and (up until October 2014 when shark finning was banned) may have been preferentially released. Second, if released sharks are large and lively, they may be difficult and dangerous to measure, leading to biased sample selection.

No data are available from which to assess the magnitude of the first two biases listed above, but only about half of the individually-recorded makos were measured in 2011–15. Anecdotal information from observers confirms that those issues exist, and that size-related biases are likely (L. Griggs, NIWA,

pers. comm.). There is no way to determine whether discarded sharks differ in length composition from retained sharks. Changes in fisher behaviour might be expected to have occurred at the time of the introduction of the sharks to the QMS (October 2004) and when shark finning was banned (October 2014).

The proportion of mako sharks discarded on observed SLL vessels has increased steadily from less than 20% in the mid 1990s to 94% in 2015, the highest value ever recorded (Figure 4). In the North region, the proportion of mako sharks measured by observers varied greatly among years up to 2006, but since then it has declined steadily from 52–57% in 2007–09 to only 10% in 2015 (Figure 5). In the Southwest region, the proportion measured was relatively stable between 1997 and 2014, averaging 81%, but declined steeply to 46% in 2015. The big changes in proportions discarded and measured in 2015 reflect the introduction of a ban on shark finning at the beginning of the fishing year.

The proportion of males in the observed catch showed no clear temporal trends (Figure 6). The proportion of males in the North region was generally higher in the first half of the time series than in the second half, although the relationship was weak, and the value for 2014 was relatively high (61.9%). Too few sharks were sexed in 2015 to estimate the proportion of males. Overall, there were equal numbers of males and females in the North (50% males), but four times more males than females in the Southwest (81% males).

Scaled length-frequency distributions for the whole SLL fishery for the period 2007–2015 are shown in Figure 7. Both sexes had several strong modes of sharks smaller than 175 cm (see also Section 3.3). MWCVs were moderate (0.26–0.28), although sample sizes were high. Most makos of both sexes were shorter than 250 cm. For 2007–2015, the ratio of males to females in the scaled catch was 1.26:1 (55.8% males).

3.2 Maturity

Both male and female makos showed a clear progression in median lengths across maturity classes 1–3 (Figure 8). Males showed good representation of both immature (classes 1 or 2) and mature (class 3) individuals, although the two smallest sharks recorded as mature (109 and 112 cm respectively) were likely to have been errors as they are well below the length at maturity (Figure 8). Most females were immature, with only two mature females recorded; however one of the latter was erroneous as it was too small to be mature (182 cm).

For males, a well-defined logistic growth curve was fitted after removal of the two small outliers (Figure 8). The estimated logistic parameters were $\beta_0 = -17.08 \pm 3.45$ (SE) and $\beta_1 = 0.089 \pm 0.018$. The estimated median length at maturity was 192.0 cm (95% confidence limits 184.9–199.1 cm). Only one of the observer trips recorded the presence or absence of spermatophores in males, and the sample size was only 13. Five sharks of lengths 161–176 cm had no spermatophores whereas eight sharks of lengths 200–210 cm had spermatophores. Although there is a big gap between the length ranges of males with and without spermatophores, the results are consistent with the estimated length at maturity of 192 cm. Only one mature female was sampled (after removal of a small outlier), so it was not possible to fit a logistic curve or estimate the length at maturity (Figure 8).

Francis & Duffy (2005) estimated the median length at maturity of male New Zealand makos as 180–185 cm. They used SLL observer data and data collected by scientists at recreational fishing competitions, and had much larger sample sizes than in the present study (236 clasper length measurements, 163 spermatophore determinations, and 52 sharks staged by scientists). Their estimate (midpoint 182.5 cm) was therefore adopted in preference to the observer based estimate of 192 cm from the present study. The Francis & Duffy (2005) estimate of median length at maturity of female makos of 280 cm was also used. These lengths at maturity were applied to the relevant (unscaled) length-frequency distributions to estimate the percentages of sharks that were mature in the 1993–2015 observer time series (Figure 9). Mature male makos made up 17% overall of the sharks measured in the North region, but the percentage fluctuated markedly among years and there appeared to be a step down

between 2001 and 2005. The Southwest region had a much higher percentage of mature males (64% overall). Few mature females were observed: over the whole time series, estimated percentages mature were 2% in both North and Southwest regions. Based on the scaled length-frequency distributions for 2007–2015 (Figure 7), the percentages of mature makos in the entire New Zealand SLL catch were estimated to be 10.7% for males and 0.5% for females.

3.3 Age, growth and age frequency of catch

There was a linear relationship between CL and FL (Figure 10):

$$CL = -0.413 + 0.0623 FL \quad (N = 132, R^2 = 0.92).$$

Vertebrae were difficult to read, particularly when counting the narrow increments near the margin of the vertebrae from old sharks, and in interpreting the banding pattern near band pairs 2–7. A between-reader comparison of reading 1 of Reader 1 and reading 3 of Reader 2 is shown in Figure 10 and an analysis of the differences in Figure 11. Readings were highly variable between readers, with an overall CV of 18.2% and APE of 12.9%, and absolute differences (Reader 1 minus Reader 2) ranging from –8 years to 6 years (mean –0.42) (Figure 11). Readings of 74% of the vertebrae agreed within ± 2 years. Reader 2 showed a marginally significant tendency to count more bands than Reader 1 (paired t-test, $P = 0.044$) (Figure 11A, B), but there was no clear systematic pattern, with the slope of the age-bias regression not significantly different from 1 (slope = 1.057, $P = 0.801$; Figure 11C). The within-reader variability of Reader 2 was lower than the between-reader variability (CV=11.3% and APE=8.0%; absolute differences ranged from –4 years to 4 years; 86% agreement within ± 2 years) and no bias was evident. However, Reader 1 had achieved even lower within-reader variability in a previous study on New Zealand mako sharks (CV=7.5% and APE=5.3% (Bishop et al. 2006)), so the age estimates derived from Reader 1's band counts were selected as the 'best' ages for further analysis.

The Schnute family of growth curves was fitted to the combined-sexes age estimates of Reader 1 (Figure 12). The Case 1 growth model best fitted the data (AIC = 1112.8, next lowest AIC for Case 3 = 1127.7). Case 1 was the only curve that adequately captured the rapid increase in length of sharks less than 2 years old. Fitting the Case 1 model to the data with separate growth parameters for males and females indicated that the two sexes had significantly different growth rates (Figure 12, AIC = 1109.9). However, most sharks were less than 16 years old, and there were too few older sharks ($N = 6$) to adequately define the shape of the upper ends of the fitted growth curves, resulting in curves that did not show any sign of reaching asymptotes. Removal of six sharks older than 16 years from the dataset and refitting Case 1 models revealed that the combined-sexes and separate-sexes models were practically identical (AIC = 1048.1 and 1048.2 respectively), indicating that the difference between the sexes in the full dataset was being driven by the few older sharks. Although the Case 1 separate-sexes model is the best fit to the available data, it should only be used for interpreting growth patterns up to an age of 16 years. The parameters and 95% confidence limits of this model are shown in Table 2.

Assuming annual deposition of band pairs, male and female makos grow very rapidly during their first 1–2 years, reaching predicted lengths of 119 cm and 111 cm respectively by the age of 2 years (but see the Discussion (Section 4) for different growth hypotheses based on various vertebral band deposition rates). This means that they nearly double their birth length of about 61 cm (Bishop et al. 2006) in 2 years. Thereafter, growth slows substantially and becomes essentially linear up to an age of at least 16 years. The data and fitted curves suggested that males were larger at a given age than females over the age range 3–8 years (Figure 12), but this may be an artefact of the small sample sizes, particularly for females.

Ages at maturity were estimated by applying the sex-specific Case 1 growth models to the estimated median lengths at maturity provided by Francis & Duffy (2005): 180–185 cm for males and 275–285 cm for females. The estimated ages at maturity were 9.2–10.0 years for males and 20.2–21.1 years for females (although the female ages are uncertain because they were predicted for lengths that are beyond the range of most of the data).

Scaled age-frequency distributions of the makos observed in the commercial fishery were generated assuming a 1 bpy deposition rate (Figure 7). The distributions were dominated by juveniles less than 1 year old (27% of the males and 25% of the females). Most males were less than 6 years old, and most females were less than 4 years old. However MWCVs were high (0.44–0.50) because of the small sample size of aged makos, and consequently a poorly-defined age-length key.

4. DISCUSSION

This study provides an updated and extended analysis of the composition of the catch of mako sharks in the New Zealand tuna longline fishery. The previous analysis (Francis 2013) was updated by three years to include the 2015 fishing year, and extended by generating scaled length-frequency distributions of the total SLL catch for 2007–2015, ageing a subsample of sharks from their vertebrae and fitting new growth curves, and estimating the scaled age-frequency composition of the catch. The present study therefore provides improved information on mako shark catch composition in the SLL fishery, which accounts for most of the New Zealand mako shark catch (92–95% by weight in 2008–2011 (Francis 2013)).

The quality of the data on which these analyses were based is limited in a number of respects. Observer sampling of length data was compromised by their inability to measure every shark caught, and evidence that unmeasured, discarded sharks may have a different size composition from measured, discarded sharks (Francis 2013). The proportion of observed makos discarded or released alive under Schedule 6 of the Fisheries Act continues to increase, reaching 94% of the SLL catch in 2015. This peak resulted from the introduction of a ban on shark finning at the beginning of the 2015 fishing year. The issue is most acute in the North region, where the proportion of makos measured dropped to 10% in 2015, and observer coverage was low (average 5.8% of hooks observed for the most recent five years 2011–15 for domestic vessels in North region). High observer coverage of the Japanese charter fleet in Southwest region (average 79.9% of hooks in 2011–15) means the situation is much better there, but even there the number measured has dropped to 46% in 2015. The decline in numbers of mako sharks measured by observers makes it difficult to assess recent patterns of size composition, sex ratio, maturity composition and age composition. The analyses presented here must therefore be interpreted cautiously.

Scaled length-frequency distributions for 2007–2015 showed that the commercial SLL mako catch was dominated by immature juveniles, a high proportion of them being under 200 cm long (compared with a maximum known length greater than 400 cm). The scaled distributions differ from previous unscaled distributions (Francis 2013) in having a higher proportion of sharks shorter than 200 cm. This change reflects the increased weight given to the North region catch, particularly by domestic vessels, in the scaled distributions. Only 10.7% of males and 0.5% of females were considered mature in catches measured during 2007–15, but these proportions may have been under-estimated if significant numbers of large mature adults were being discarded unmeasured. That scenario is plausible for males because a higher proportion of mature males was recorded by observers when discard rates were low and the proportion of sharks measured was high during the late 1990s and early 2000s (Figures 4, 5 and 9; Francis 2013 Appendices 6 and 7). However, it is not plausible for females, which have always been rare in the observer data. Mature females are not considered vulnerable to the New Zealand SLL fishery, although they may be taken by other fleets in international waters.

Mako sharks are born at a length of about 61 cm FL. Parturition peaks in late winter and spring, and the theoretical birthday has been defined as 1 October (Duffy & Francis 2001; Bishop et al. 2006). Most of the makos aged in this study were sampled in April–July, so they were mainly 0.5–0.75 years past their birthday. The age-frequency distribution of the catch of both sexes was dominated by juveniles (males mainly less than 6 years old and females less than 4 years old), and few sharks were more than 14 years old. However, older sharks may have been caught in greater numbers than indicated and discarded unsampled.

The age estimates derived in the present study are unvalidated, because validation would require resources well beyond those available in this project. Considerable debate exists among researchers worldwide about whether one or two opaque/translucent band pairs are deposited annually in shortfin mako shark vertebrae (called the 1 bpy and 2 bpy hypotheses). A number of recent studies in the North Pacific and North Atlantic oceans have addressed this issue, leading to a much better informed debate, but there is still no overall consensus. In the northwest Atlantic Ocean, bomb radiocarbon dating and oxytetracycline (OTC) injected and tagged sharks have provided compelling confirmation of the 1 bpy hypothesis, and this has been corroborated by growth rate estimates derived from length-frequency modal analysis and from tagged and recaptured sharks (Campana et al. 2002; Ardizzone et al. 2006; Natanson et al. 2006). Other studies off western Mexico and in the western and central North Pacific have supported 1 bpy using marginal increment and marginal state analysis (Ribot-Carballal et al. 2005; Semba et al. 2009). Conversely, OTC-injected mako sharks off California unequivocally deposited two bpy for at least the first five years of life, a conclusion also corroborated by growth rate estimates from length-frequency modal analysis and tagged and recaptured sharks from the same region (Wells et al. 2013). The conflict between these two conclusions (i.e. annual versus biannual deposition of vertebral bands) is currently unresolved, but may reflect regional variation caused by (a) an ontogenetic change (i.e. deposition is biannual in young sharks and switches to annual in older sharks), or (b) the seasonal migration pattern of Californian sharks and how that relates to oceanographic conditions (i.e. deposition rates in California are twice those in other populations that have been examined).

The band deposition rate of New Zealand mako sharks is unknown. Growth curves based on three hypotheses (1 bpy, 2 bpy, and 2 bpy switching to 1 bpy after five years) applied to the New Zealand band counts are shown in Figure 13. The growth curves based on the 2 bpy hypothesis show much faster growth rates and half the longevity of curves based on the 1 bpy hypothesis. Curves based on the switching hypothesis follow the 2 bpy curves up to 5 years of age and thereafter parallel the 1 bpy curves.

Aggregated, unscaled, observer length-frequency distributions for both sexes combined from 1993–2015 for the months April–July (when most sharks were sampled) showed five clear modes (Figure 14). If these modes represent sequential age classes, they are clearly more consistent with a 2 bpy hypothesis than a 1 bpy hypothesis (Figure 13). Nevertheless, until an age validation study is carried out on New Zealand makos, age estimation remains highly uncertain. In this study it is conservatively assumed that the 1 bpy hypothesis is correct for New Zealand makos, as this hypothesis has been confirmed in the vast majority of other shark species. However, an ageing validation study is urgently required because productivity estimates of mako sharks depend strongly on the correct interpretation of age: for example, the estimated ages at 200 cm FL are about 6 years and 12 years for the 2 bpy and 1 bpy hypotheses respectively.

For both sexes, the fitted growth curves from the present study lie beneath those reported by Bishop et al. (2006) in an earlier study of New Zealand makos (Figure 15). The difference between studies was greatest for females, perhaps reflecting the small sample size of females in the present study. The paucity of mako sharks older than 16 years in the present study prevents comparison with older sharks in the earlier study, which had larger sample sizes (145 males and 111 females). Until the ageing of New Zealand makos has been validated, there seems little point in comparing the New Zealand growth curves with those from other parts of the world (see Cerna & Licandeo 2009 for the southeast Pacific off Chile; and Clarke et al. 2015 for a review of multiple North Pacific studies), because any differences are as likely to reflect different growth hypotheses as different growth rates.

Most mako sharks caught by the tuna longline fishery since 2007 (and also earlier) were juveniles. Both sexes were mostly shorter than 200 cm FL, with an estimated 89% of males and 99.5% of females immature. Similarly, most makos were young sharks, with the 0+ age class constituting about one-quarter of the catch, and most of the catch being less than 6 years old. Under a 2 bpy hypothesis, the proportions of 0+ sharks would have been considerably higher than one-quarter, and most of the catch would have been less than 3 years old. However, the increased discarding, and potential size-related

discarding, of mako sharks in recent years may have biased these estimates towards smaller and younger sharks.

Both the present and previous studies have found that males and females have significantly different growth curves. However, the growth differences appeared only after about 16 years, beyond which there were few aged sharks in either study. Thus the question of whether the sexes grow at different rates remains open. For practical purposes this is not important because juveniles under 6 years old dominated the SLL catch, and growth rates of the two sexes up to 6 years were practically identical. Nevertheless, length at maturity differed markedly between the two sexes, so their estimated ages at maturity also differed: about 9–10 years for males and 20–21 years for females. These are similar to the previous estimates of 7–9 and 19–21 years respectively (Bishop et al. 2006).

5. MANAGEMENT IMPLICATIONS

For the first time, this study provides scaled length-frequency and age-frequency estimates of the mako shark catch composition in the SLL fishery, which accounts for most of the New Zealand catch. Subject to caveats about the representativeness of the observer sampling, the scaled distributions show that the catch is dominated by juveniles less than 6 years old, with older juveniles and some mature males up to about 14 years comprising most of the rest of the catch. Few mature sharks are caught, especially mature females which make up a negligible part of the catch. The New Zealand mako shark fishery is therefore mainly a juvenile fishery that provides an apparent refuge for mature breeding females. Only one pregnant female mako shark has been reported from New Zealand (Duffy & Francis 2001). The whereabouts of mature females is unknown, although tagging indicates that there is considerable movement between New Zealand and the tropical islands to the north of New Zealand, and to a lesser extent to eastern Australia (Holdsworth & Saul 2014), and that larger makos travel further than smaller makos (M. Francis, unpublished data). It is also possible that mature females are caught by SLL vessels working in international waters beyond New Zealand's EEZ, and efforts should be made to determine the catch composition of such vessels.

Fisheries on juvenile sharks can be sustainable if enough juveniles grow through the 'gauntlet' age range to replenish adults dying from natural causes (Simpfendorfer 1999). Currently, SLL fishing effort in New Zealand waters is near its lowest point in over 30 years: about 2.5 million hooks are set per year compared with over 25 million hooks in the early 1980s (Ministry for Primary Industries 2015). A range of indicators suggest that the population size of makos has either been stable or increased since 2005 (Francis, M.P. et al. 2014). Nevertheless, caution is required because:

- ageing has not been validated, so a conservative approach has been adopted here by assuming 1 bpy is deposited on vertebrae
- female makos mature at a high age of about 20 years
- makos have a high longevity of about 30 years (Bishop et al. 2006)
- makos have a low fecundity averaging 12.5 pups per litter (range 4–25) (Mollet et al. 2000)
- the period of the reproductive cycle is unsure but may be three years (Mollet et al. 2000); if so, the annual production of young would be about 4 young per year
- stock structure is uncertain, but Southwest Pacific shortfin mako sharks are genetically distinct from those in the Southeast Pacific and the North Pacific. This stock separation is supported by tagging studies that show regular movement around the Southwest Pacific but only one known movement of a Southwest Pacific shark to the North Pacific, and none to the Southeast Pacific (Holdsworth & Saul 2014; Clarke et al. 2015)
- there are no historical and current mako catch histories outside the New Zealand EEZ
- there is no information on the survival rate of sharks released alive under Schedule 6

These uncertainties in addition to low biological productivity require that management is cautious, and that efforts are made to fill the knowledge gaps through appropriate research. In particular, a quantitative stock assessment is required to pull together New Zealand and overseas data into a coherent model in order to estimate the status of the stock. The revised or new estimates of growth rate, age at maturity,

and length-frequency and age-frequency of the SLL catch provided here will be important contributions to that process.

6. ACKNOWLEDGMENTS

Special thanks go to the MPI observers for collecting the data and specimens used in this study. Warrick Lyon organised and inventoried the observer biological data and vertebral specimens, and punched the data. Lynda Griggs extracted and summarised observer data from the *COD* database and Caoimhghin ÓMaolagáin prepared the vertebral sections for ageing. Silver Bishop (MPI) was one of the age readers for the mako shark vertebrae. Reyn Naylor reviewed the draft manuscript. This work was completed under MPI project HMS201402.

7. REFERENCES

- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. *In*: Petrov, B.N.; Csaki, F. (eds). International symposium on information theory, edition, pp. 267–281, Akademiai Kiado, Budapest, Hungary.
- Ardizzone, D.; Cailliet, G.M.; Natanson, L.J.; Andrews, A.H.; Kerr, L.A.; Brown, T.A. (2006). Application of bomb radiocarbon chronologies to shortfin mako (*Isurus oxyrinchus*) age validation. *Environmental Biology of Fishes* 77: 355–366.
- Bishop, S.D.H.; Francis, M.P.; Duffy, C.; Montgomery, J.C. (2006). Age, growth, maturity, longevity and natural mortality of the shortfin mako (*Isurus oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research* 57: 143–154.
- 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.
- Campana, S.E.; Annand, M.C.; 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.; Natanson, L.J.; Myklevoll, S. (2002). Bomb dating and age determination of large pelagic sharks. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 450–455.
- Cerna, F.; Licandeo, R. (2009). Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. *Marine and Freshwater Research* 60: 394–403.
- Clarke, S.; Coelho, R.; Francis, M.; Kai, M.; Kohin, S.; Liu, K.-M.; Simpfendorfer, C.; Tovar-Avila, J.; Rigby, C.; Smart, J. (2015). Report of the Pacific Shark Life History Expert Panel Workshop, 28–30 April 2015. *Western Central Pacific Fisheries Commission Scientific Committee eleventh regular session WCPFC-SC11-2015/EB-IP-13*. 111 p.
- Clarke, S.C.; Francis, M.P.; Griggs, L.H. (2013). Review of shark meat markets, discard mortality and pelagic shark data availability, and a proposal for a shark indicator analysis. *New Zealand Fisheries Assessment Report* 2013/65. 74 p.
- Duffy, C.; Francis, M.P. (2001). Evidence of summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* 35: 319–324.
- Francis, M.P. (2013). Commercial catch composition of highly migratory elasmobranchs. *New Zealand Fisheries Assessment Report* 2013/68. 79 p.
- Francis, M.P. (2014). Estimation of fin ratios and dressed weight conversion factors for selected shark species. *New Zealand Fisheries Assessment Report* 2014/68. 31 p.
- Francis, M.P. (2015). Size, maturity and age composition of porbeagle sharks observed in New Zealand tuna longline fisheries. *New Zealand Fisheries Assessment Report* 2015/16. 30 p.
- Francis, M.P.; Campana, S.E.; Jones, C.M. (2007). Age under-estimation in New Zealand porbeagle sharks (*Lamna nasus*): is there an upper limit to ages that can be determined from shark vertebrae? *Marine and Freshwater Research* 58: 10–23.
- Francis, M.P.; Clarke, S.C.; Griggs, L.H.; Hoyle, S.D. (2014). Indicator based analysis of the status of New Zealand blue, mako and porbeagle sharks. *New Zealand Fisheries Assessment Report* 2014/69. 109 p.
- Francis, M.P.; Duffy, C. (2005). Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fishery Bulletin* 103: 489–500.
- Francis, M.P.; Griggs, L.H.; Baird, S.J. (2001). Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine and Freshwater Research* 52: 165–178.
- Francis, R.I.C.C.; Rasmussen, S.; Fu, D.; Dunn, A. (2014). CALA: Catch-at-length and -age user manual, CALA 2.0-2015-01-28 (rev. 371). Unpublished report, National Institute of Water and Atmospheric Research Ltd, Wellington. 92 p.
- Griggs, L.H.; Baird, S.J. (2013). Fish bycatch in New Zealand tuna longline fisheries 2006–07 to 2009–10. *New Zealand Fisheries Assessment Report* 2013/13. 73 p.
- Holdsworth, J.; Saul, P. (2014). New Zealand billfish and gamefish tagging, 2012–13. *New Zealand Fisheries Assessment Report* 2014/11. 26 p.

- Manning, M.J.; Sutton, C.P. (2004). Age and growth of giant stargazer, *Kathetostoma giganteum*, from the west coast of the South Island (STA 7). *New Zealand Fisheries Assessment Report* 2004/17. 60 p.
- Ministry for Primary Industries. (2013). National plan of action for the conservation and management of sharks 2013. Ministry for Primary Industries, Wellington. 32 p.
- Ministry for Primary Industries. (2015). Fisheries Assessment Plenary: stock assessments and stock status, November 2015. Compiled by the Fisheries Science Group, Ministry for Primary Industries, Wellington, New Zealand. 535 p.
- Ministry of Fisheries Science Group (2011). Guidelines for the development of fish age determination protocols. Unpublished report available from <http://www.fish.govt.nz/en-nz/Publications/Research+and+Science+Information+Standard.htm>. Ministry of Fisheries, Wellington, New Zealand. 19 p.
- Mollet, H.F.; Cliff, G.; Pratt, H.L.; Stevens, J.D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin* 98: 299–318.
- Natanson, L.J.; Kohler, N.E.; Ardizzone, D.; Cailliet, G.M.; Wintner, S.P.; Mollet, H.F. (2006). Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. *Environmental Biology of Fishes* 77: 367–383.
- Natanson, L.J.; Mello, J.J.; Campana, S.E. (2002). Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin* 100: 266–278.
- Pratt, H.L.; Tanaka, S. (1994). Sperm storage in male elasmobranchs: a description and survey. *Journal of Morphology* 219: 297–308.
- Quinn, T.J.; Deriso, R.B. (1999). Quantitative fish dynamics. Oxford University Press, New York. 542 p.
- R Development Core Team. (2008). R: A language and environment for statistical computing. <http://www.R-project.org>. R Foundation for Statistical Computing, Vienna, Austria.
- Ribot-Carballal, M.C.; Galván Magaña, F.; Quiñónez-Velázquez. (2005). Age and growth of the shortfin mako shark, *Isurus oxyrinchus*, from the western coast of Baja California Sur, Mexico. *Fisheries Research* 76: 14–21.
- Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1128–1140.
- Semba, Y.; Nakano, H.; Aoki, I. (2009). Age and growth analysis of the shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific Ocean. *Environmental Biology of Fishes* 84: 377–391.
- Simpfendorfer, C.A. (1999). Demographic analysis of the dusky shark fishery in southwestern Australia. *American Fisheries Society Symposium* 23: 149–160.
- Wells, R.J.D.; Smith, S.E.; Kohin, S.; Freund, E.; Spear, N.; Ramon, D.A. (2013). Age validation of juvenile shortfin mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California. *Fishery Bulletin* 111: 147–160.
- Wilson, C.A.; Beamish, R.J.; Brothers, E.B.; Carlander, K.D.; Casselman, J.M.; Dean, J.M.; Jearld, A.; Prince, E.D.; Wild, A. (1987). Glossary. In: Summerfelt, R.C.; Hall, G.E. (eds). Age and growth of fish, edition, pp. 527-529, Iowa State University Press, Ames, USA.

8. TABLES

Table 1: Number of surface longline (SLL) vessels and sets, observer coverage, and number of vessels sampled for vertebrae, maturity data or fin weights during 2011–15.

Fishery	Fleet	Fishing year	No. of trips	No. of sets	Observed trips	Observed Sets	% sets observed	Trips sampled
SLL	Charter	2011	4	151	4	151	100.0	4
SLL	Charter	2012	4	164	4	164	100.0	4
SLL	Charter	2013	4	148	4	148	100.0	4
SLL	Charter	2014	4	186	4	186	100.0	4
SLL	Charter	2015	4	181	4	181	100.0	4
SLL	Domestic	2011	568	2736	14	172	6.3	3
SLL	Domestic	2012	560	2617	12	174	6.6	7
SLL	Domestic	2013	510	2497	9	85	3.4	6
SLL	Domestic	2014	430	2106	13	157	7.5	10
SLL	Domestic	2015	412	2043	13	123	6.0	4

Table 2: Schnute growth model. The best fit model was Case 1 with different parameters for the two sexes.

Formula :

$$FL \sim (L1[sex]^{gam} + (L2[sex]^{gam[sex]} - L1[sex]^{gam[sex]}) * (1 - \exp(-k[sex] * (age - tor1)))) / (1 - \exp(-k[sex] * (tor2 - tor1)))^{(1/gam[sex])}$$

Parameters :

	Estimate	Std. Error	t value	Pr(> t)	
gam male	5.15735	1.04657	4.928	2.60e-06	***
gam female	5.16614	1.03900	4.972	2.15e-06	***
k1 male	-0.12599	0.05933	-2.123	0.035709	*
k2 female	-0.20354	0.05451	-3.734	0.000286	***
L1 male	100.42510	4.53903	22.125	< 2e-16	***
L1 female	97.60837	4.85709	20.096	< 2e-16	***
L2 male	184.88020	2.06321	89.608	< 2e-16	***
L2 female	180.08810	2.95229	61.000	< 2e-16	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 15.62 on 124 degrees of freedom

Algorithm "port"

Confidence intervals for parameters

	2.5 %	97.5 %
gam male	3.1061181	7.208578800
gam female	3.1297415	7.202531321
k1 male	-0.2422841	-0.009696259
k2 female	-0.3103709	-0.096701710
L1 male	91.5287642	109.321428207
L1 female	88.0886444	107.128086355
L2 male	180.8363875	188.924015809
L2 female	174.3017264	185.874479416

9. FIGURES

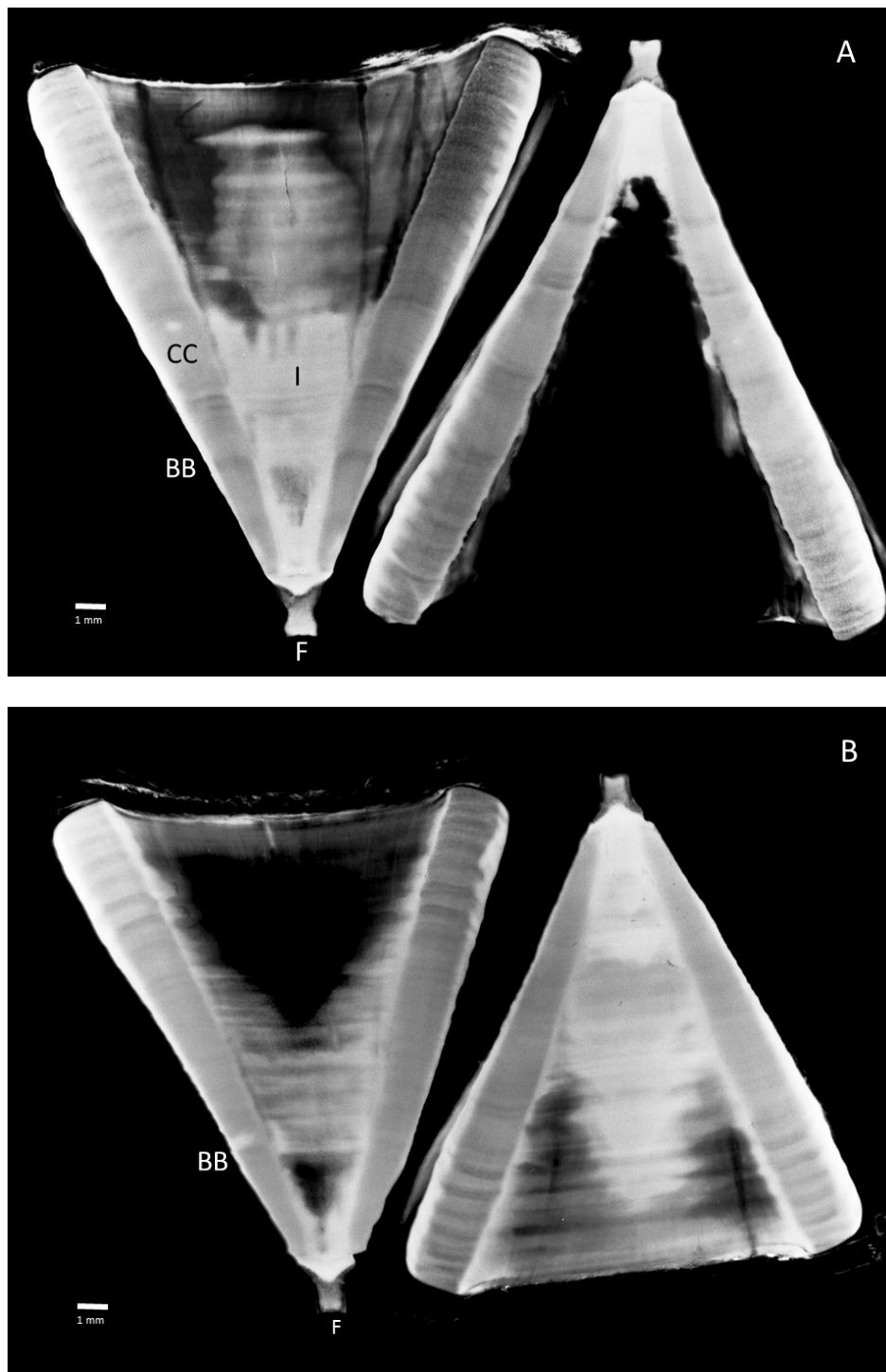


Figure 1: Half-bowtie thick sections of mako shark vertebral centra. A – 231 cm male aged 12.6 years (O314). B – 200 cm male aged 13.5 years (O397). BB, birth band; CC, corpus calcareum; I, intermedialia; F, focus. Scale bar = 1 mm.

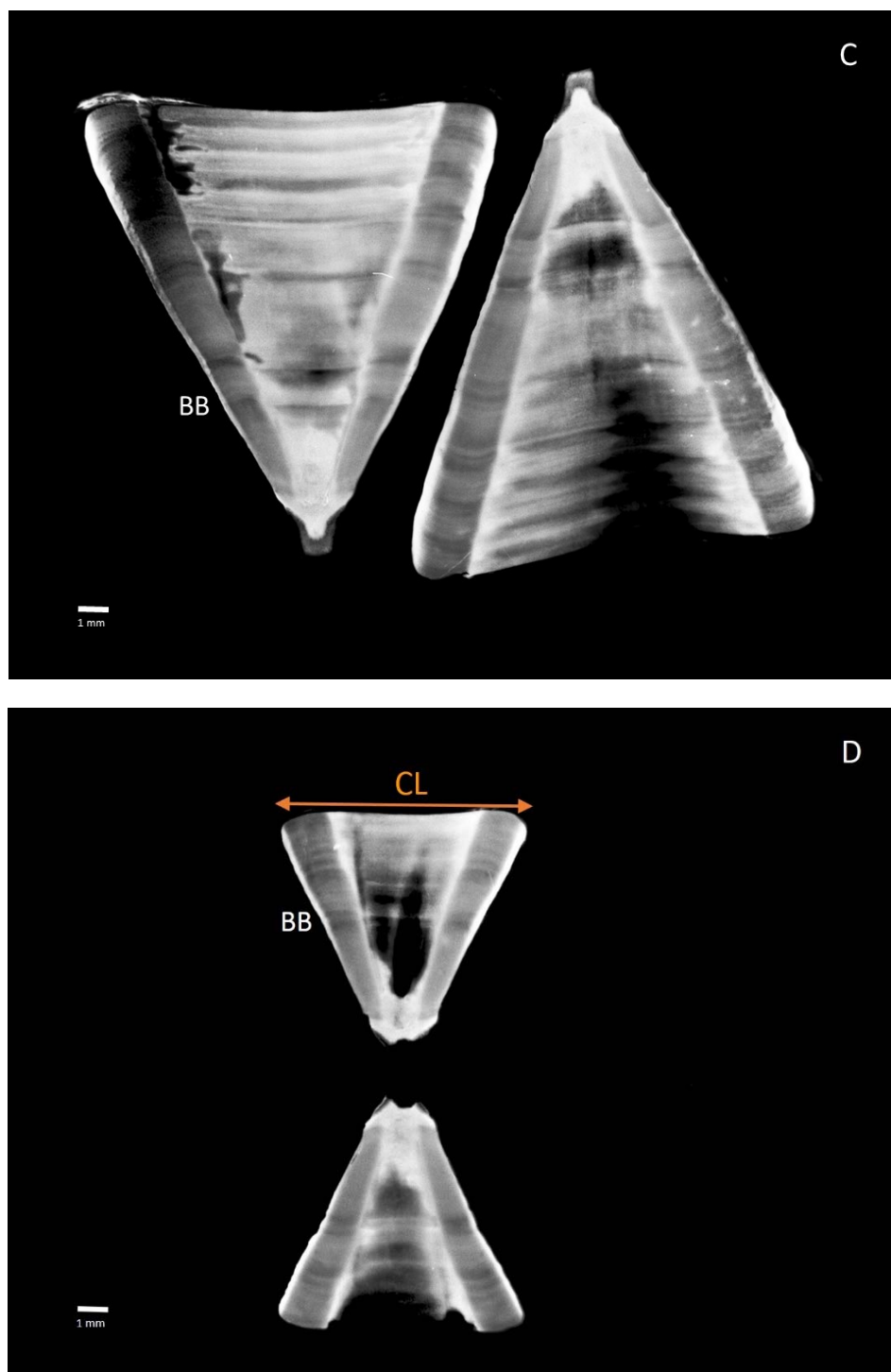


Figure 1 (continued): Half-bowtie thick sections of mako shark vertebral centra. C – 197 cm male aged 7.7 years (O306). D – 122 cm male aged 2.7 years (O335). CL, centrum length.

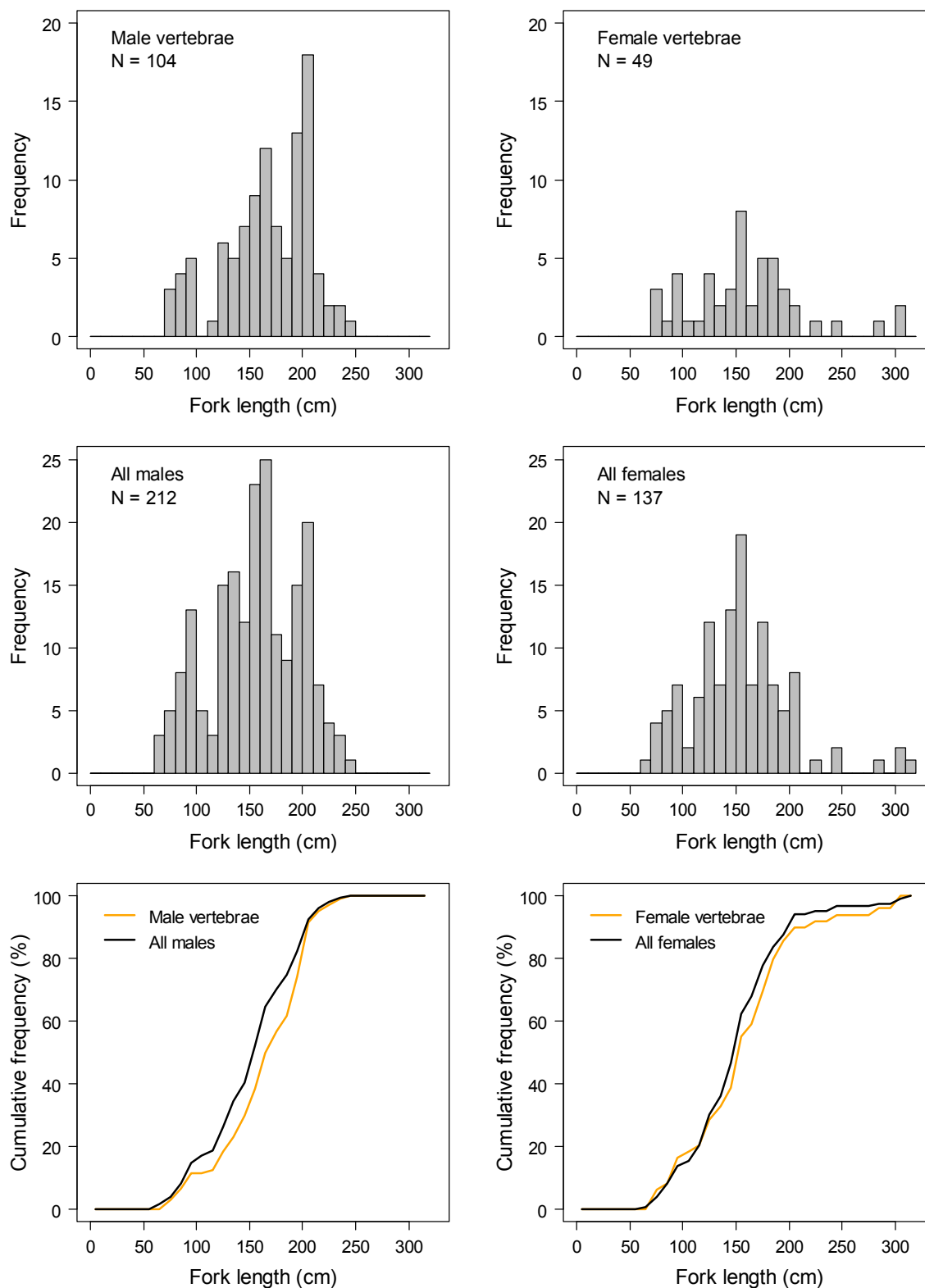


Figure 2: Length-frequency distributions of male and female mako sharks sampled in 2011–15 for vertebrae (top panels) compared with the distributions of all mako sharks measured during the same period (middle panels). The bottom panels show cumulative distribution curves for the data in the top and middle panels.

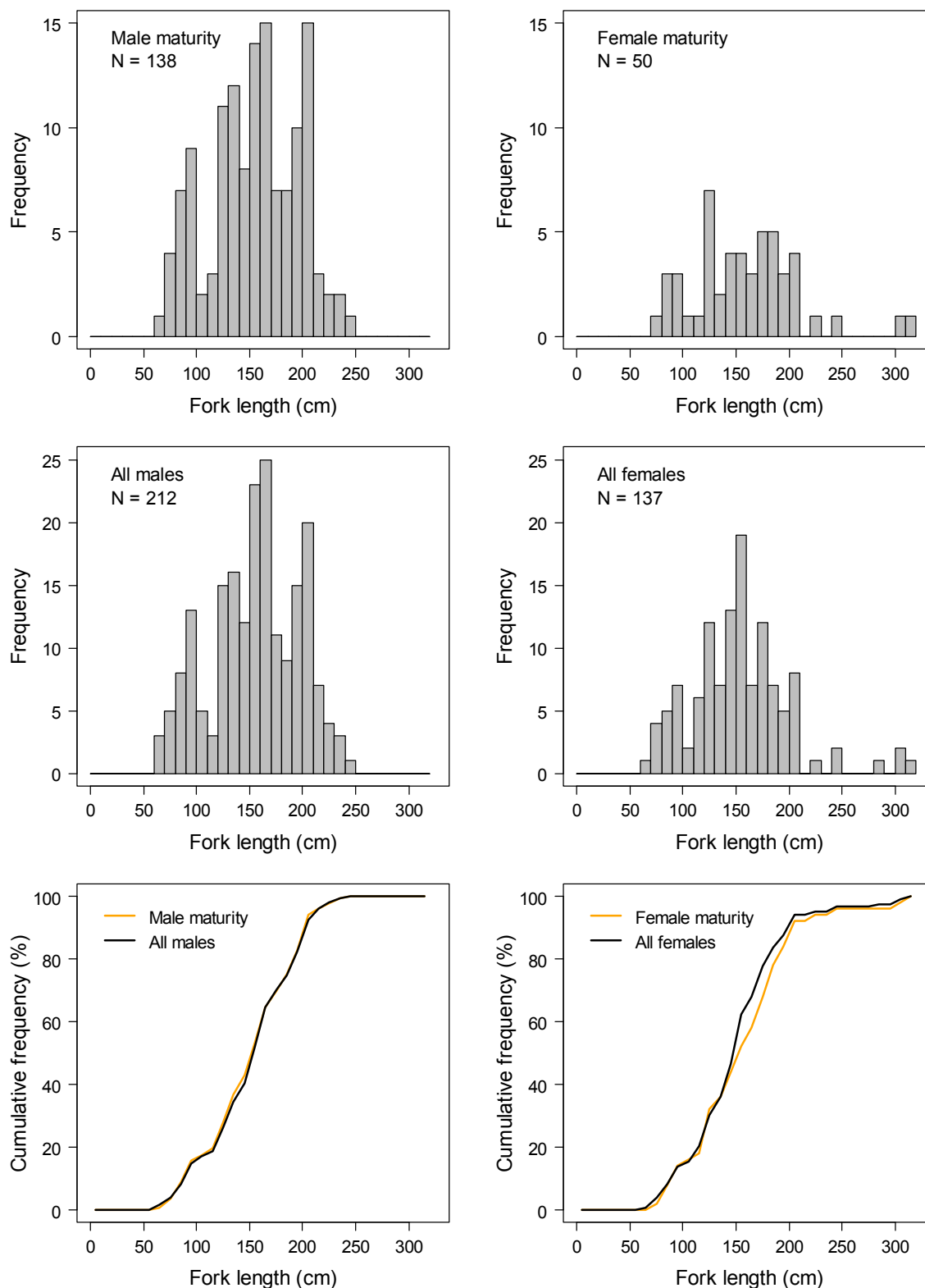


Figure 3: Length-frequency distributions of male and female mako sharks sampled in 2011–15 for maturity (top panels) compared with the distributions of all mako sharks measured during the same period (middle panels). The bottom panels show cumulative distribution curves for the data in the top and middle panels.

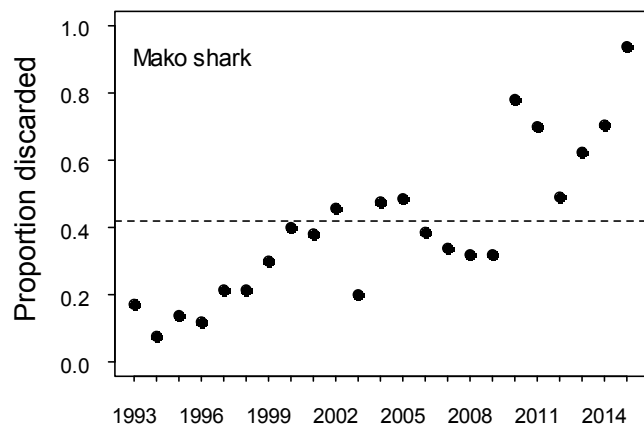


Figure 4: Proportion of mako sharks discarded from surface longline vessels, 1993–2015. The horizontal dashed line indicates the overall discard rate for the whole time series.

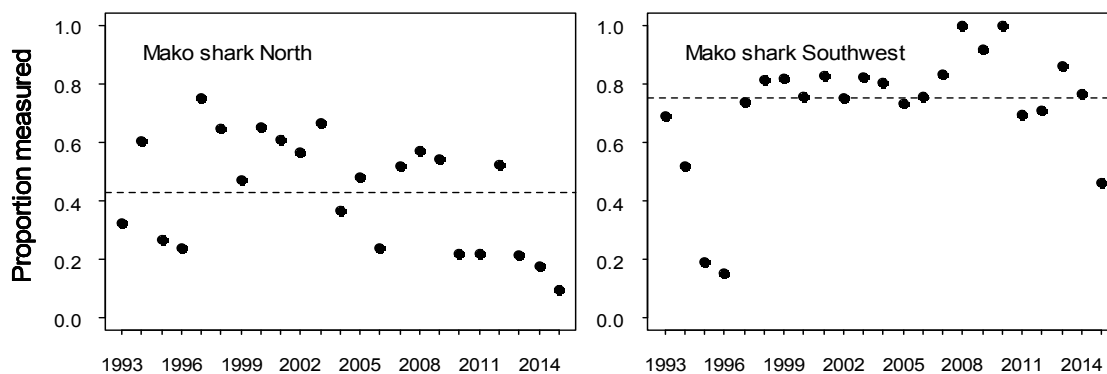


Figure 5: Proportion of mako sharks measured from surface longline vessels in North and Southwest regions, 1993–2015. The horizontal dashed lines indicate the proportion measured for the whole time series.

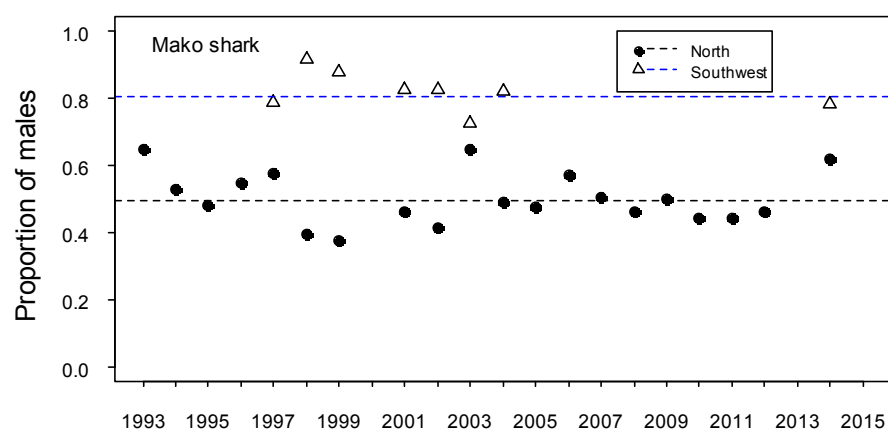


Figure 6: Proportion of male mako sharks by region from surface longlines, 1993–2015. The horizontal dashed lines indicate the proportions of males for the whole time series in each region. Only sample sizes greater than 50 are shown.

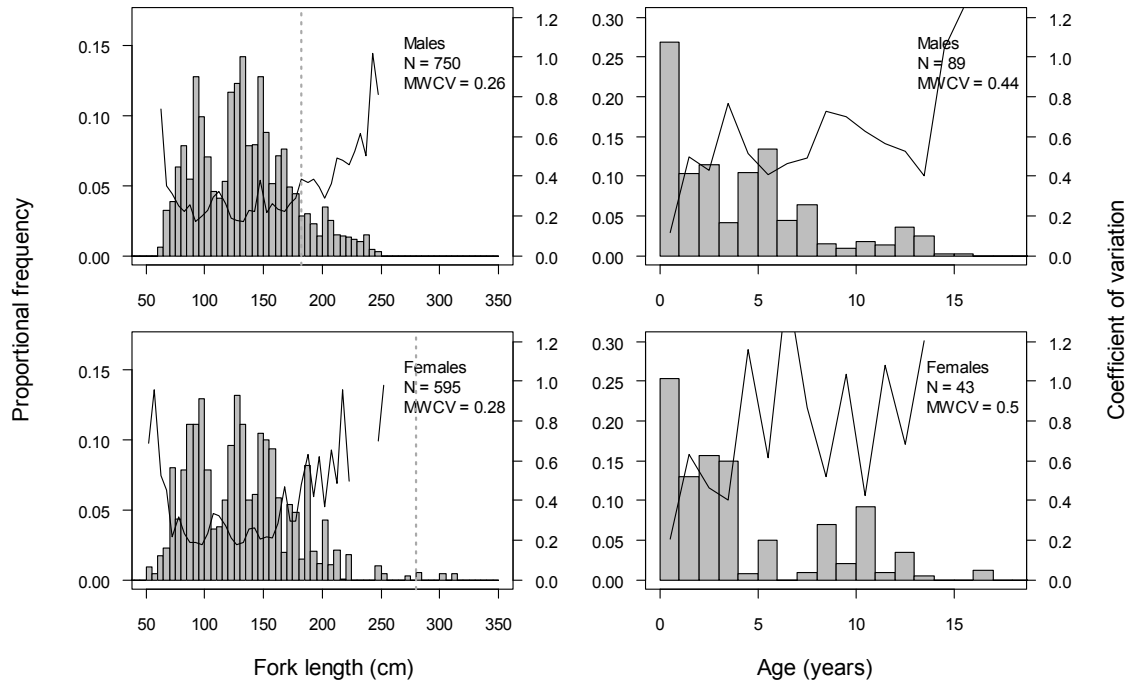


Figure 7: Mako shark scaled length-frequency (left) and age-frequency (right) distributions by sex with bootstrapped coefficients of variation (CV, solid lines) and mean weighted CVs (MWCV) for the whole SLL fishery, 2007–2015. Sample sizes for length distributions are the number of sharks measured, and for age distributions are the number of sharks aged and used for the age-length key.

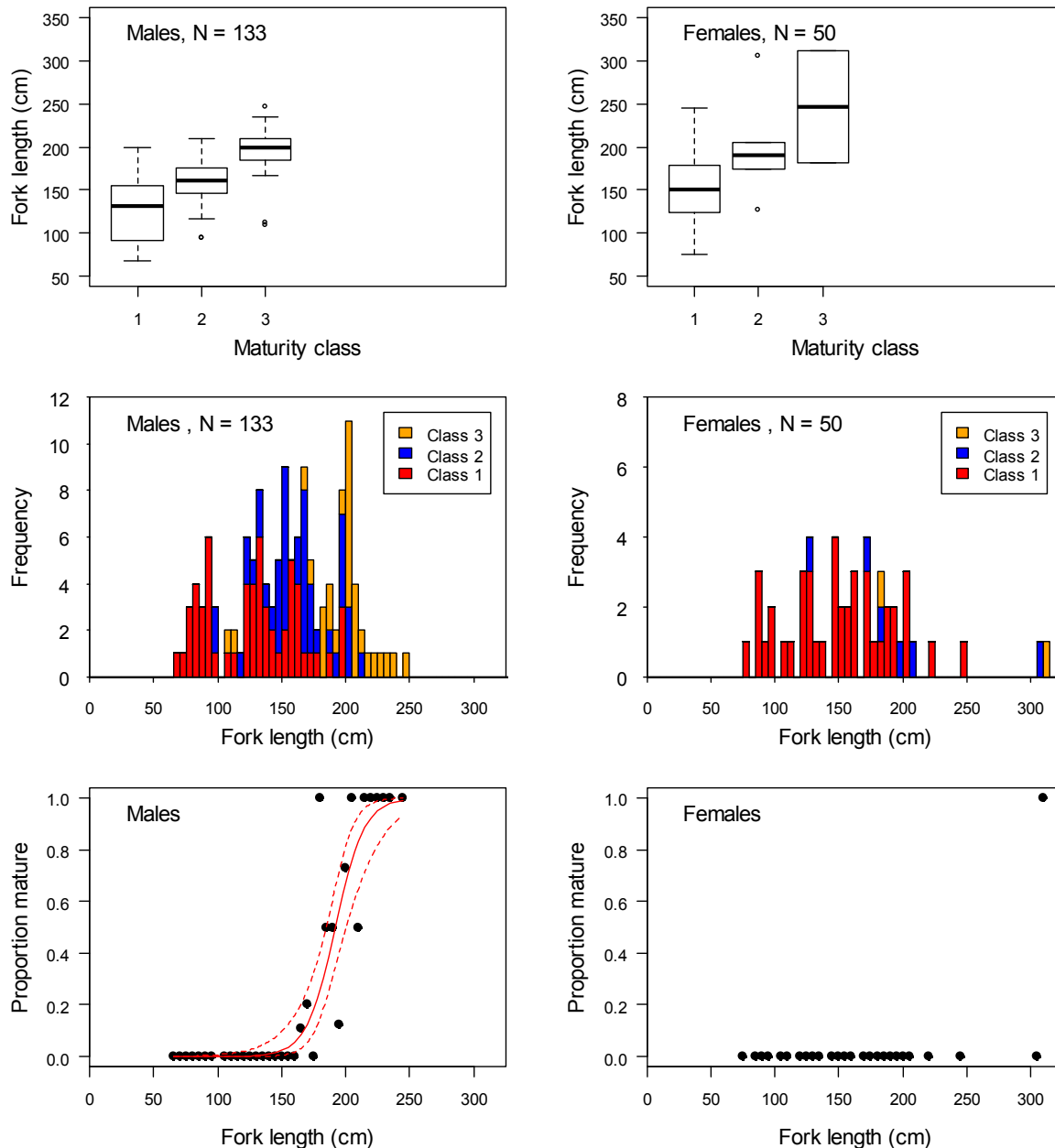


Figure 8: Maturity data collected from male and female mako sharks, 2011–15. Top panels: Box plots of fork length classified by maturity stage (see Appendix 1 for stages). The central black bar is the median, the box spans the first to third quartiles, and the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. Middle panels: Length-frequency distributions classified by maturity class. Bottom panels: Proportion of sharks that were mature (in 5 cm length intervals) with fitted logistic regression for males (no fit was possible for females). Dashed lines are 95% confidence intervals. Two small males and one small female classified as maturity class 3 were omitted from the bottom panels because they were probably mis-classified.

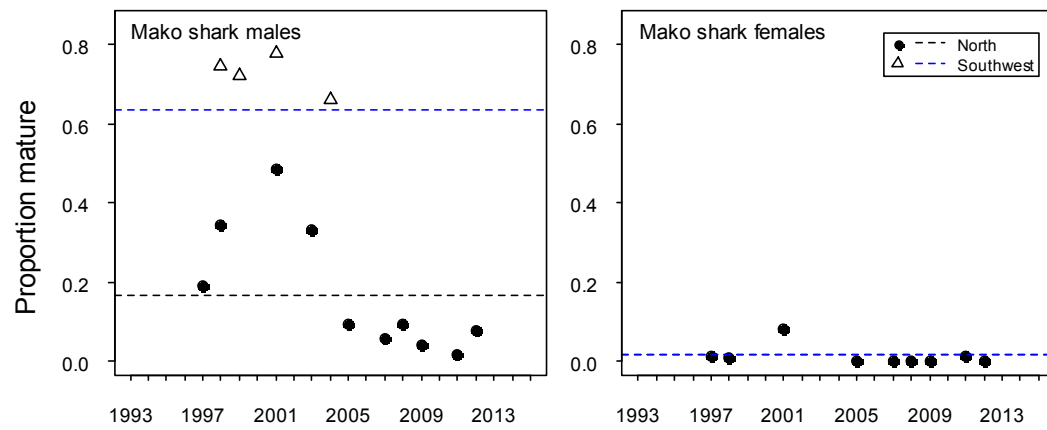


Figure 9: Proportions of observed mako sharks that were estimated to be mature based on length-frequency distributions and median lengths at maturity.

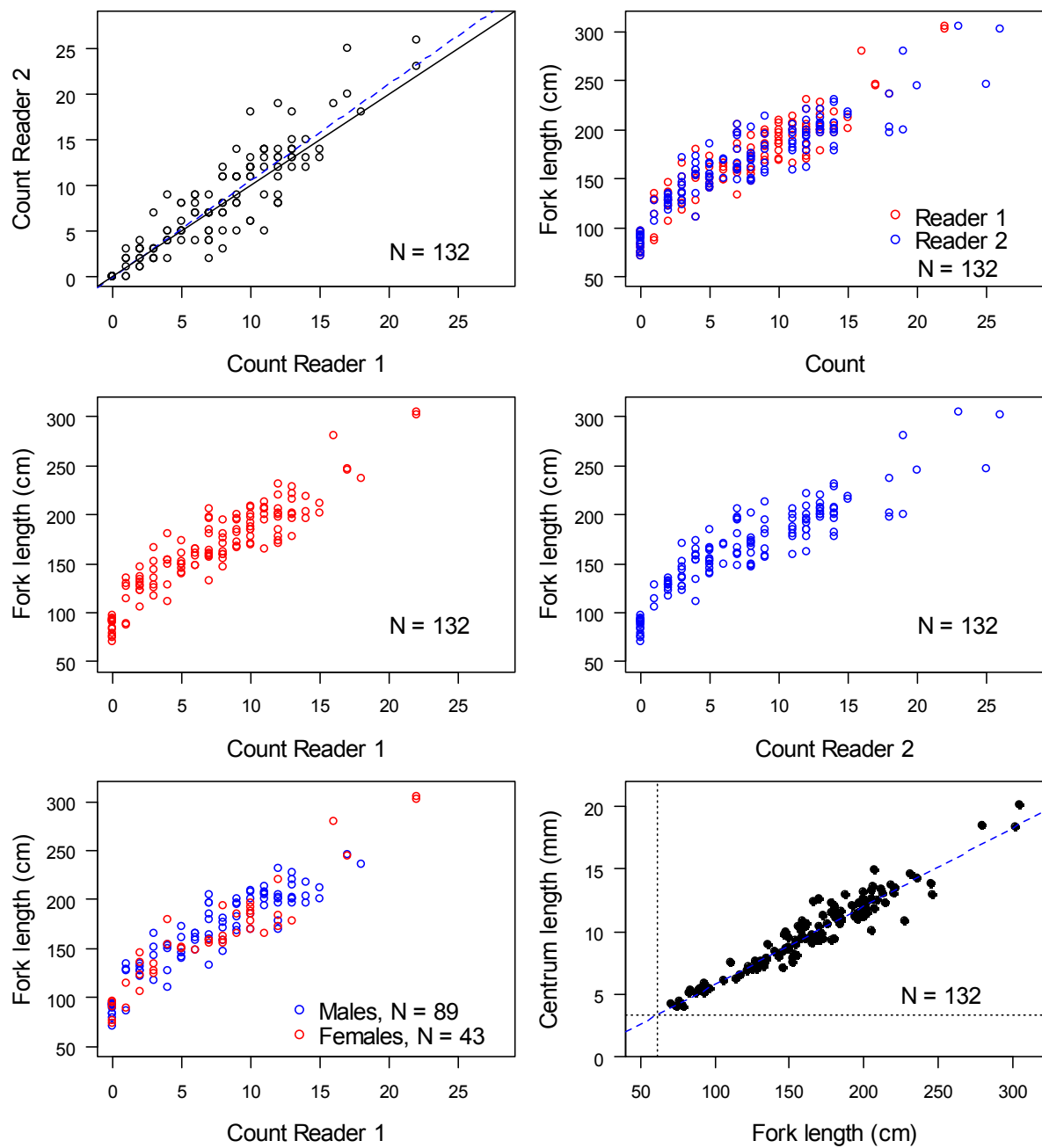


Figure 10: Comparison of vertebral band counts of Readers 1 and 2. Diagonal black line is the 1:1 line; dashed blue lines are fitted linear regressions. The bottom right panel shows the relationship between centrum length and fork length.

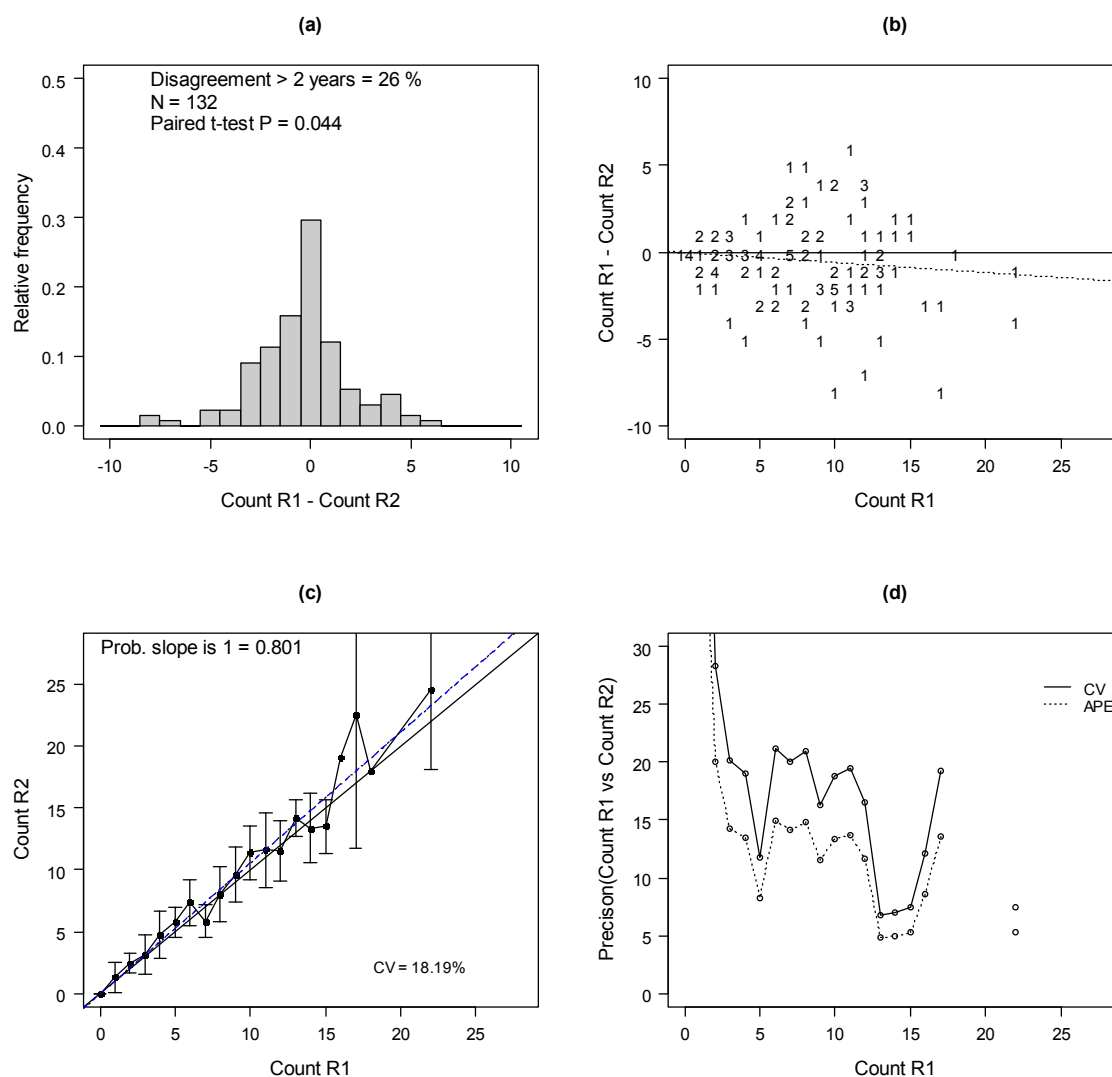


Figure 11: Analysis of vertebral band count differences between Reader 1 and reading 3 of Reader 2. Dotted and dashed lines are fitted linear regressions. CV, coefficient of variation; APE, average percentage error.

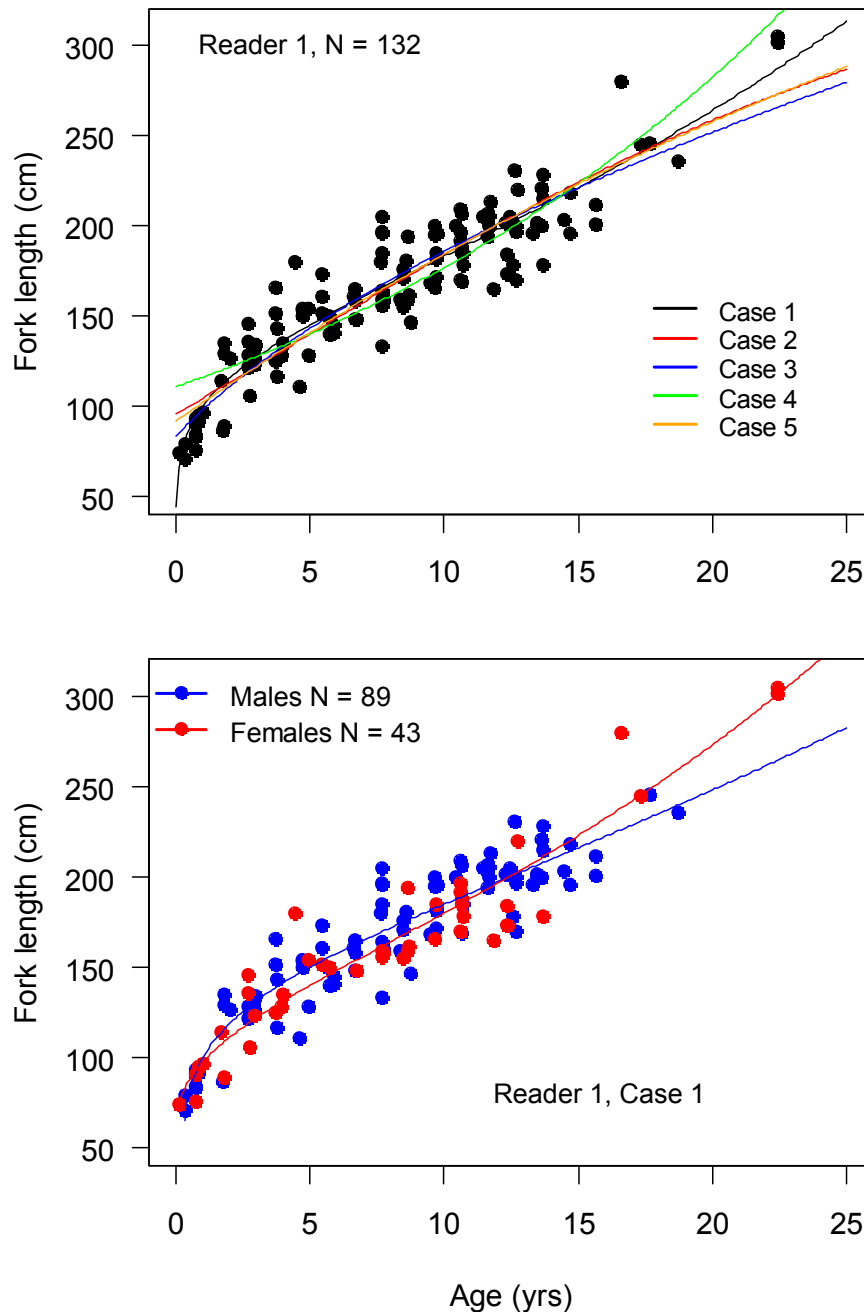


Figure 12: Schnute growth curves for mako sharks based on the age estimates of Reader 1. Top: Cases 1–5, combined sexes. Bottom: Case 1, separate sexes.

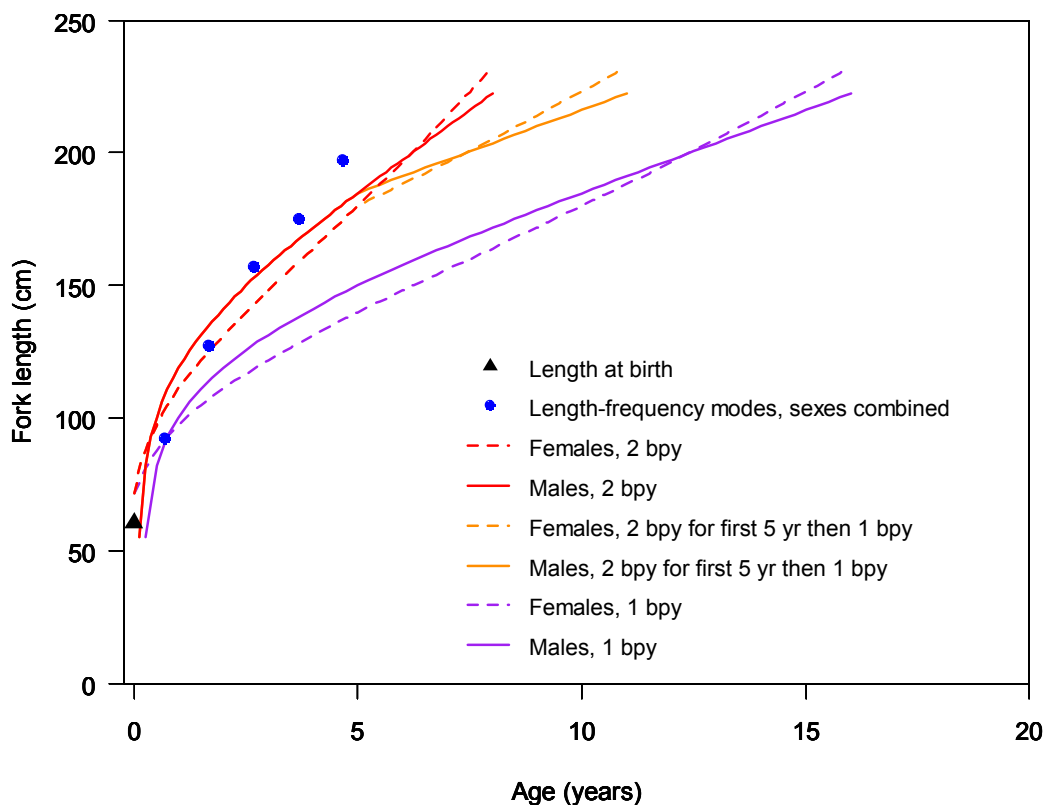


Figure 13: Comparison of three growth hypotheses for mako sharks using band counts from the present study: (1) one band pair per year (1 bpy); (2) two band pairs per year (2 bpy); and (3) two band pairs per year changing to one band pair per year after five years. Curves were truncated at 16 band pairs because few data were available for older sharks. Also shown are the length-at-birth (61 cm on the theoretical birthdate of 1 October) and five length-frequency modes estimated by eye from April–July observer data (see Figure 14; modes are plotted at 1 June, 8 months after the theoretical birthdate).

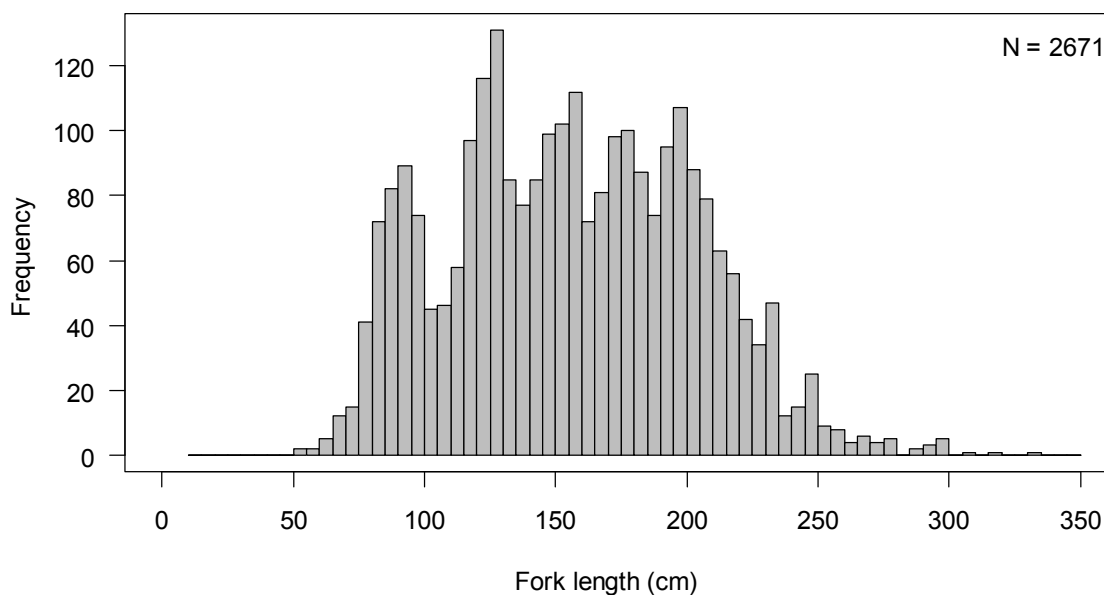


Figure 14: Length-frequency distribution (unscaled) for New Zealand mako sharks sampled by observers in April–July, 1993–2015.

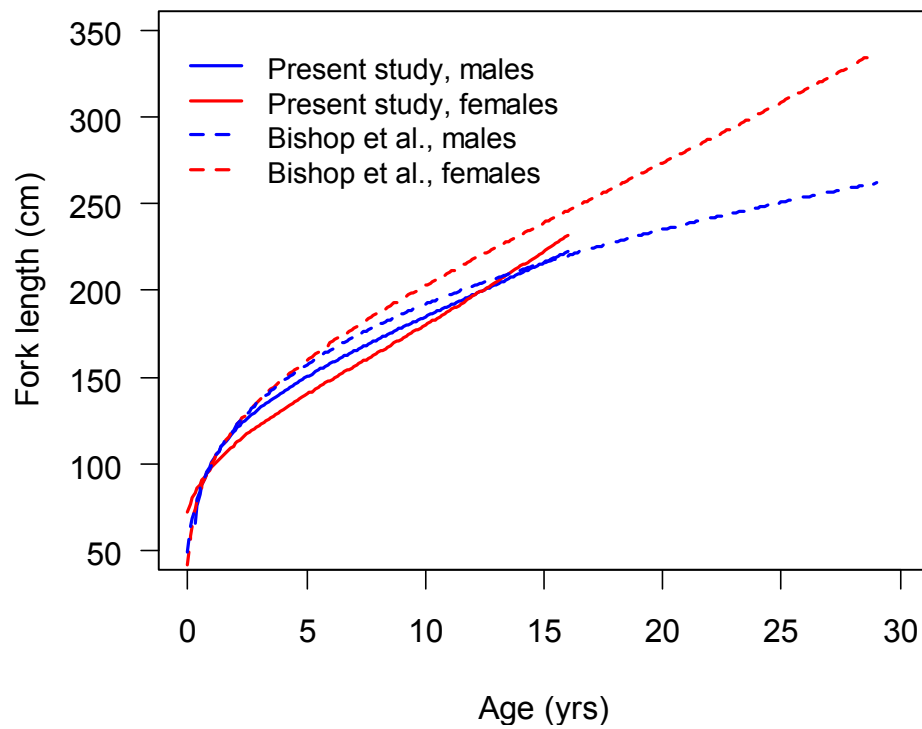


Figure 15: Comparison of Schnute growth curves for mako sharks from the present study with those from Bishop et al. (2006).

APPENDIX 1

Observer instructions for sampling pelagic sharks

Collection of pelagic shark vertebrae and maturity and fin weight data

Pelagic sharks (blue, mako and porbeagle sharks) are caught mainly in tuna longline and midwater trawl fisheries around New Zealand. A sampling programme has been initiated to obtain information on the catch composition of these sharks in commercial catches, and to develop improved shark fin conversion factors. Size, sex, and maturity data will be collected, along with vertebrae to enable the sharks to be aged. Fins will be weighed at sea and related to shark green weight to obtain fin weight ratios.

Size and sex composition

For each shark caught, measure fork length and determine sex. Where possible, weigh green weight. For as many sharks as possible, determine maturity status (see shark staging guide below; note that males have a 3-stage maturity scale and females have a 6-stage scale). **Males of all three species can be staged by examining the state of clasper development.** Females have to be opened up to examine the reproductive tract.

MAK and POS

Please record uterus width and check for pregnancy for:

MAK longer than 250 cm fork length

POS longer than 150 cm fork length

For mako and porbeagle sharks (MAK and POS), the ovarian egg size is not a good indicator of maturity. Instead, measurements are required of uterus widths to estimate female maturity. **Measure uterus width about three-quarters of the way along the body cavity.** There are two uteri, one on either side of the backbone, and they are suspended from the roof of the body cavity by a translucent mesentery. **Only measure one uterus, and don't include the mesentery in the measurement (see figures).** The width of the uterus in natural position (flattened, but not squashed) should be measured with a small ruler to the nearest millimetre. For female MAK and POS, record uterus width in the column provided, and try and determine maturity stage from the guide below (staging should be easy for small females (stage 1), and large pregnant or recently-pupped females (stages 4-6), but may be difficult to determine for other females (stages 2-3), hence the need for uterine width measurements). **Check out a few large females first and be sure you know what the uteri look like, before routinely recording widths.** Check for pregnancy in all three species. **If the uteri appear to have objects inside, open the uteri and record pup or uterine egg numbers, and average size of pups, in the 'Comments' field.**

Ageing

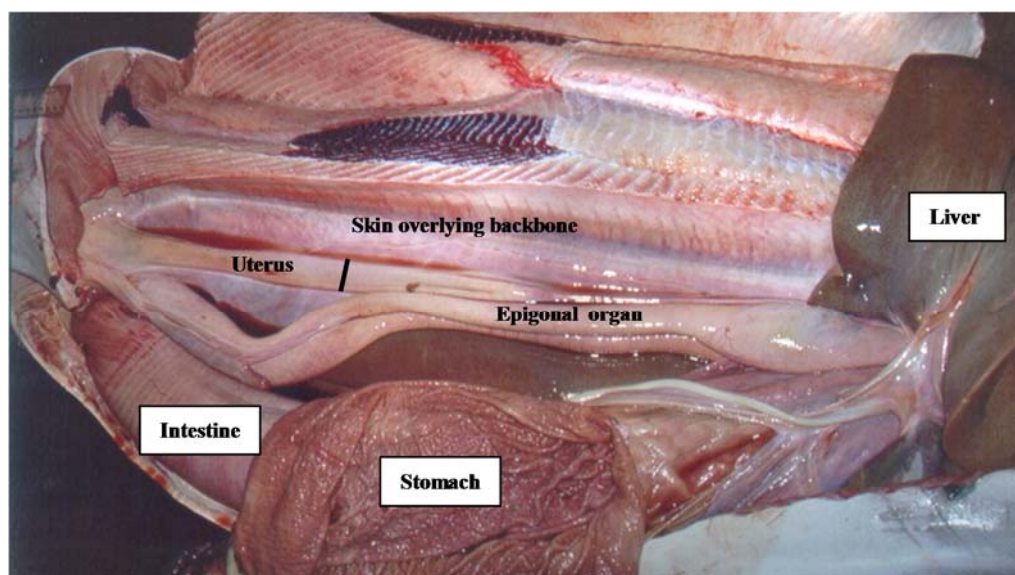
Remove a section of 3-4 vertebrae. For makos, vertebrae should be taken from the front of the fish just behind the head, to avoid damaging the carcass. Put a label in with each specimen giving trip, set/tow number, fork length and sex (or sample number). The vertebrae should then be bagged and frozen. Please ensure that all bags are tightly sealed to reduce desiccation in the freezer.

The numbers of sharks to be sampled has been determined according to a monthly sampling schedule and will be advised by the Observer Programme.

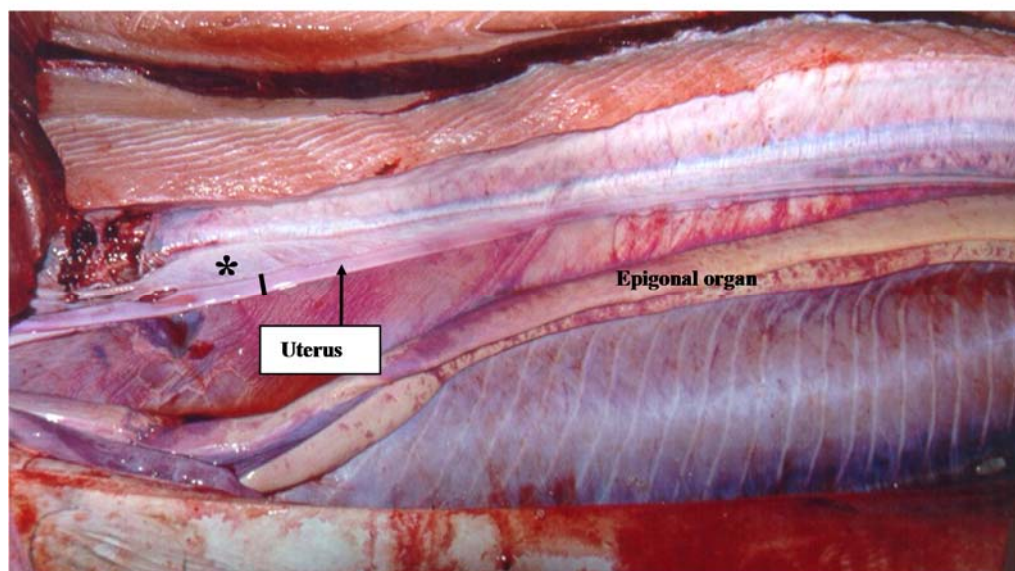
Reproductive staging guide for sharks and skates

Stage	Name	Males	Females
1	Immature	Claspers shorter than pelvic fins, soft and uncalcified, unable or difficult to splay open	BWS: Ovaries small and undeveloped. Ova not visible, or small (pin-head sized) and translucent whitish POS: Uterine width about 4-7 mm MAK: Uterine width about 4-15 mm
2	Maturing	Claspers longer than pelvic fins, soft and uncalcified, unable or difficult to splay open or rotate forwards	BWS: Some ova enlarged, up to about pea-sized or larger, and white to cream. POS: Uterine width about 8-10 mm MAK: Uterine width about 16-30 mm
3	Mature	Claspers longer than pelvic fins, hard and calcified, able to splay open and rotate forwards to expose clasper spine	BWS: Some ova large (greater than pea-sized) and yolky (bright yellow) POS: Uterine width > 10 mm MAK: Uterine width > 30 mm
4	Gravid I	<i>Not applicable</i>	Uteri contain eggs or egg cases but no embryos are visible
5	Gravid II	<i>Not applicable</i>	Uteri contain visible embryos.
6	Post-partum	<i>Not applicable</i>	Uteri flaccid and vascularised indicating recent birth

Uterine width measurements for POS and MAK



Dissection of maturing female mako shark (stage 2) with liver folded back towards head, (right) and stomach (opened) and intestine displaced downwards. The uterus is moderately well developed and of intermediate width; only the right uterus is visible. Black bar shows location of width measurement. Note the paired epigonal organ running the full length of the body cavity – do not confuse this with the uterus. The epigonal organ is soft, mushy, and easily damaged (like the liver but even softer), and usually yellowish and reddened by blood vessels. The uterus is usually cream or white, has fewer blood vessels (except in pregnant and recently pupped females), is tougher (more muscular), and is suspended closer to the backbone than the epigonal organ.



Immature female mako shark with liver, stomach and intestine removed. The uterus is narrow and undeveloped. Black bar shows location of width measurement. Asterisk indicates mesentery supporting uterus – do not include mesentery in width measurement. In both photos the head is to the right and tail to the left.

APPENDIX 2

Inventory of vertebral samples, and maturity and fin weight records, collected by observers for blue, porbeagle and mako sharks in the 2011 to 2015 fishing years.

Trip	Year	Months	Method	Fleet	FMA	Target species	Vertebrae				Maturity				Individual fin weights			
							BWS	POS	MAK	Total	BWS	POS	MAK	Total	BWS	POS	MAK	Total
1	2011	Apr-Jun	SLL	C	5, 7	STN	67	11	0	78	492	12	2	506	221	9	2	232
2	2011	Apr-Jun	SLL	C	5, 7	STN	20	8	3	31	0	0	1	1	12	7	3	22
3	2011	Apr-Jun	SLL	C	1, 5, 7	STN/BIG	51	0	5	56	236	5	5	246	0	0	0	0
4	2011	Apr-Jun	SLL	C	5, 7	STN	41	14	2	57	66	5	2	73	149	22	2	173
5	2011	Jun-Aug	SLL	D	1, 2	STN/BIG/SWO	0	0	0	0	385	41	24	450	0	0	0	0
6	2011	Jun-Jul	SLL	D	1, 2	STN	0	0	0	0	23	3	1	27	0	0	0	0
7	2011	Jul-Aug	SLL	D	1	STN/SWO	0	0	0	0	6	15	7	28	0	0	0	0
8	2011	Aug-Sep	TWL	C	6, 7	HOK/SBW	0	5	0	5	0	0	0	0	0	0	0	0
9	2011	Aug-Sep	TWL	D	3, 7	HOK/HAK/BA	0	0	0	0	0	3	0	3	0	3	0	3
10	2012	May-Jun	SLL	D	2	STN	0	0	0	0	229	0	9	238	0	0	0	0
11	2012	Apr-Jun	SLL	C	5,7	STN	125	6	5	136	223	6	4	233	146	6	5	157
12	2012	Apr-Jun	SLL	C	5,7	STN	34	8	7	49	0	0	0	0	0	0	0	0
13	2012	Apr-Jun	SLL	C	5,7	STN	80	1	2	83	63	0	0	63	0	1	0	1
14	2012	Apr-Jun	SLL	C	5,7,9	STN/BIG	150	17	6	173	0	0	0	0	57	10	5	72
15	2012	May-Jul-Aug	SLL	D	7,9,1	STN/SWO	0	0	0	0	79	0	7	86	0	1	3	4
16	2012	May-Jul	SLL	D	2	STN	8	13	9	30	8	12	9	29	0	0	0	0
17	2012	Jun	SLL	D	1,2	STN	0	0	0	0	13	0	6	19	0	0	0	0
18	2012	Jun-Jul	SLL	D	1	STN	19	6	2	27	19	6	2	27	0	0	0	0
19	2012	Jun-Jul	SLL	D	7	STN	0	0	0	0	1	0	0	1	0	0	0	0
20	2012	Aug-Oct	SLL	D	1,9	STN/BIG	3	6	11	20	4	6	11	21	0	0	0	0
21	2013	May-Jun	SLL	C	1,5,7,9	STN/BIG	81	5	11	97	79	4	11	94	0	0	0	0
22	2013	May-Jun	SLL	C	5,7,9	STN	113	26	3	142	0	0	0	0	0	0	0	0
23	2013	May-Jun	SLL	C	5,7	STN	20	10	3	33	0	0	0	0	96	9	5	110
24	2013	May-Jun	SLL	C	5,7	STN	90	11	8	109	88	8	10	106	88	8	10	106
25	2013	May-Jun	SLL	D	1	BIG	4	0	1	5	14	0	4	18	0	0	0	0
26	2013	May-Sep	SLL	D	1,9	STN/SWO	23	0	0	23	61	1	0	62	0	0	0	0
27	2013	Jun	SLL	D	7	STN	1	3	2	6	1	3	2	6	0	0	0	0
28	2013	Jul-Aug	SLL	D	1,2	STN	34	10	4	48	33	7	3	43	0	0	0	0
29	2013	Jul-Aug	SLL	D	1	STN	11	2	0	13	0	0	0	0	0	0	0	0
30	2013	Aug	SLL	D	9	BIG	0	0	0	0	38	0	4	42	0	0	0	0
31	2013	Aug-Dec	SLL	D	1,9	BIG/STN	0	0	1	1	0	0	0	0	0	0	0	0
32	2013	Nov-Dec	SLL	D	1	BIG	0	0	0	0	2	4	0	6	0	0	0	0
33	2014	Jan-Mar	SLL	D	1,9	BIG	1	0	18	19	1	0	23	24	0	0	22	22
34	2014	Apr-Jun	SLL	D	7	STN	0	0	1	1	0	42	12	54	0	0	0	0
35	2014	Apr	SLL	D	1	BIG	0	0	1	1	0	0	0	0	0	0	0	0
36	2014	May-Jul	SLL	C	5,7	STN	21	16	5	42	0	1	0	1	112	22	5	139
37	2014	May-Jun	SLL	C	5,7	STN	34	9	4	47	33	8	4	45	0	0	0	0
38	2014	May-Jun	SLL	C	5,7	STN	61	19	5	85	0	1	0	1	77	20	5	102
39	2014	May-Jun	SLL	C	5,7	STN	7	1	2	10	0	0	0	0	203	3	2	208
40	2014	May	SLL	D	7	STN	0	0	0	0	1	0	0	1	0	0	0	0
41	2014	May-Jun	SLL	D	7	STN	0	0	0	0	34	1	1	36	0	0	0	0
42	2014	Jul-Aug	SLL	D	1,2	STN	21	5	1	27	17	10	1	28	0	0	0	0
43	2014	Aug	SLL	D	1	STN	3	0	0	3	0	0	0	0	0	0	0	0
44	2014	Jul-Aug	SLL	D	2	STN/BIG	1	7	1	9	0	0	0	0	0	0	0	0
45	2014	Sept-Oct	TWL	C	3,6	BAR/SBW	0	3	0	3	0	0	0	0	0	0	0	0
46	2014	Sept-Oct	SLL	D	1,9	BIG	0	1	0	1	0	1	0	1	0	0	0	0
47	2015	Dec-Jan	TWL	C	7,8,9	JMA	2	17	5	24	2	17	5	24	0	0	0	0
48	2015	Jan-Feb	SLL	D	1	BIG,SWO	0	0	1	1	0	0	2	2	0	0	0	0
49	2015	Mar-Apr	SLL	D	1	BIG,SWO	0	0	0	0	2	0	1	3	0	0	0	0
50	2015	Apr-Jun	SLL	C	5,7	STN	14	7	0	21	15	4	0	19	0	0	0	0
51	2015	Apr-Jun	SLL	C	5,7	STN	12	2	0	14	0	0	0	0	0	0	0	0
52	2015	Apr-Jun	SLL	C	5,7	STN	0	0	13	13	0	0	13	13	0	0	13	13
53	2015	Apr-Jun	SLL	C	5,7	STN	0	0	1	1	0	0	0	0	0	0	0	0
54	2015	Jun-Jul	SLL	D	1,2	STN	0	9	3	12	0	2	2	4	0	0	0	0
Total							1152	258	146	1556	2268	228	188	2684	1161	121	82	1364