Age validation of the blue shark (Prionace glauca) in the eastern Pacific Ocean

R. J. David Wells\textsuperscript{A,B,D}, Natalie Spear\textsuperscript{A} and Suzanne Kohin\textsuperscript{C}

\textsuperscript{A}Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, TX 77553, USA.
\textsuperscript{B}Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA.
\textsuperscript{C}Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA.
\textsuperscript{D}Corresponding author. Email: wellsr@tamug.edu

Abstract. The blue shark (Prionace glauca) is subjected to high levels of fishery catch and by-catch worldwide; thus, knowledge of their productivity and population status is vital, yet basic assumptions of band-pair deposition rates in vertebrae used for age and growth models are being made without direct validation studies in the Pacific Ocean. As such, the purpose of the present study was to validate vertebral band-deposition rates of blue sharks tagged and recaptured in the eastern Pacific Ocean. Vertebræ of 26 blue sharks marked with oxytetracycline (OTC) were obtained from tag–recapture activities to determine timing of centrum growth-band deposition. Results from band counts distal to the OTC mark on each vertebra indicated that a single band pair (1 translucent and 1 opaque) is formed per year for blue sharks ranging from 1 to 8 years of age. Length–frequency modal analysis was also used to obtain growth estimates from a dataset spanning 26 years of research and commercial catch data. Results provide support for annual band-pair deposition in blue shark vertebrae and will aid in future blue shark age and growth studies in the Pacific Ocean.

Additional keywords: length frequency, OTC, oxytetracycline, vertebrae.

Received 26 February 2016, accepted 8 August 2016, published online 23 September 2016

Introduction

The blue shark (Prionace glauca) is one of the most abundant pelagic shark species worldwide in tropical and subtropical seas (Compagno 1984), where it is found throughout oceanic and neritic waters (Pratt 1979; Nakano and Stevens 2008). Blue shark is subjected to high levels of fishery catch and by-catch (Campana et al. 2009; James et al. 2016) and is caught in large numbers in the California and Oregon drift gill-net fishery targeting swordfish, where most is discarded at sea because of a lack of market value (Hanan et al. 1993; NMFS 2016). In that fishery through the mid-1990s, blue shark was caught in equal or greater numbers than the targeted swordfish, and the majority of blue sharks were discarded dead (Holts et al. 1998). An understanding of the productivity and population status is necessary from both a single-species and ecosystem-based perspective, to ensure sound management of this ecologically valuable resource.

Accurate size-at-age determinations form the basis for calculations of growth and mortality rates, age-at-maturity, age-at-recruitment and estimates of longevity. Blue shark growth rates are presumed to be moderately fast, with males and females in the North Pacific reaching sexual maturity at estimated ages of 5 and 6 years respectively (Nakano 1994). Growth studies have documented size-at-maturity of ~200-cm total length (TL; ~170-cm fork length, FL) for both sexes in the North Pacific (Suda 1953; Nakano et al. 1985; Nakano and Seki 2003). In the North-west Atlantic, the size at 50% sexual maturity for male blue sharks averages 180 cm FL, and females are fully mature by 185 cm FL (Pratt 1979). Similarly, Montealegre-Quijano et al. (2014) found the size at 50% maturity of blue sharks in the South-west Atlantic to be 171 and 180 cm FL for females and males, respectively. Longevity of blue sharks is estimated at ~20–26 years (Skomal and Natanson 2003) with a maximum size of 383 cm TL (320 cm FL) reported from the North-west Atlantic Ocean (Bigelow and Schroeder 1953). These studies used various approaches to determine blue shark ages, commonly relying on length-at-age models derived by counting vertebral band pairs and applying an annual band-pair deposition rate.

While blue shark growth has been studied in all oceans, no studies have validated band-pair deposition rates in the Pacific Ocean. Multiple band-enhancement techniques have been used...
in studies of elasmobranch vertebrae, including digital images of vertebral sections (Natanson et al. 2002; MacNeil and Campana 2002), X-ray radiography (Cailliet et al. 1983; Liu et al. 1998; Wells et al. 2013) and staining of vertebrae (Stevens 1975). For blue sharks, several researchers have used silver nitrate staining on vertebrae (Cailliet and Bedford 1983; Nakano 1994; Blanco-Parra et al. 2008), haematoxylin–eosin staining (Tanaka et al. 1990) and microscopy of sectioned vertebrae bow ties (Skomal and Natanson 2003). Chemical marking methods are some of the most robust age-validation techniques used for teleost and elasmobranch fishes (Campana 2001; Goldman 2005). Validation of annual band-pair deposition for blue sharks up to 4 years of age has been confirmed using vertebrae from two oxytetracycline (OTC)-injected sharks in the North Atlantic (Skomal and Natanson 2003). Supporting migratory and life-history information was used as a plausible explanation of annulus formation. The primary objective of the present study was to validate the periodicity of band-pair deposition in blue shark vertebrae collected in the eastern Pacific Ocean. Consequently, blue sharks were OTC-injected and the vertebrae returned from recaptured sharks were examined to determine the number of band pairs deposited distal to the OTC mark during the known time at liberty. In addition, length–frequency modal analysis from two datasets spanning a 26-year time period was used to corroborate growth rates derived from hard parts.

Materials and methods

Sharks tagged and injected with OTC were captured in the Southern California Bight (SCB) using baited pelagic longlines, as part of a fishery-independent survey that began in 1993. On capture, the gangion was unsnapped from the mainline and the shark was guided into a semi-submerged tagging cradle at the side or stern of the vessel. The cradle was then raised to facilitate tagging, measuring and OTC injection. The eyes of the shark were covered with a wet cloth, and a seawater ventilation hose was used to continuously suffuse water slowly over the shark’s gills. Each shark was tagged on the dorsal fin with a plastic gills. Each shark was tagged on the dorsal fin with a plastic rototag (Dalton, Henley-on-Thames, UK) labelled with contact tags and time at liberty. Readers consulted each other on criteria for counts before readings. Samples for which there was disagreement were counted a second time and counts with similar readings were blind-counted without knowledge of the fish length, sex or time at liberty. Each sample was read independently by two readers. Bands were blind-counted without knowledge of the fish length, sex or time at liberty. Readers consulted each other on criteria for counts before readings. Samples for which there was disagreement were counted a second time and counts with similar readings between readers were deemed final. A least-squares linear regression analysis was performed and the null hypothesis that the slope (b) of the relationship between the number of bands and time at large (in portions of years) was equal to one (a situation occurring if one opaque and one translucent band were deposited each year) was tested using a two-tailed Student’s t-test (Kushner et al. 1992).

Length–frequency data were analysed using the MIXDIST package (Macdonald and Pitcher 1979; Macdonald and Green 1988) in R, ver. 2.8.0 (R Foundation for Statistical Computing, Vienna, Austria). This analysis uses a maximum-likelihood method to estimate proportions of fish at age, with the added benefit of fitting non-normally distributed data. MIXDIST analyses histograms of different statistical distributions by identifying sets of overlapping component distributions to best fit a histogram (Macdonald and Green 1988). A goodness-of-fit test ($\chi^2$ approximation to the likelihood-ratio statistic) is generated for the final fit of each model run, indicating how well the mixture distribution fits the overall...
histogram. In many cases, using length–frequency data, the components highly overlap towards the tail end (larger or older individuals) and the model is not sensitive to identify unique distributions. For purposes of the present analysis, each unique mode within the histogram was assumed to represent one age class. Data for blue shark lengths originated from the following two sources: (1) fishery-dependent data from scientific observers of the California Drift Gill-net fishery (1990–2014), which operates between May and January, and (2) fishery-independent data from juvenile-shark longline research surveys conducted by the NOAA Southwest Fisheries Science Center (SWFSC) (1993–2015) primarily between June and August of each year. A mixture of length measurements was taken across study years and surveys, including TL, FL and alternate length (AL, straight-line distance between the origin of the first and the second dorsal fins), and these were therefore standardised to FL. The following length conversions were obtained on the basis of data from fish measured by the fishery observer program and fishery-independent research (NOAA SWFSC, unpubl. data) and used to standardise data for subsequent length–frequency analyses:

\[
\text{FL} = 0.829 \times (\text{TL}) - 1.122
\]

where \( r^2 = 0.987 \) and \( n = 13,799 \).

\[
\text{FL} = 2.746 \times (\text{AL}) + 11.803
\]

where \( r^2 = 0.941, n = 9,504 \).

Lengths are in centimetres. Size data were combined between sexes because no significant differences by sex existed for either dataset (\( t \)-test, \( P > 0.05 \)) or over time (ANOVA, \( P > 0.05 \)).

### Results

In total, 514 blue sharks were tagged and injected with OTC in the eastern Pacific Ocean during research surveys between 2007 and 2009. Average size of OTC-injected blue sharks was 104.7 cm FL (±33.5 standard deviation, s.d.) and ranged from 60 to 250 cm FL, with 44% being females and 56% males. Vertebrae from 44 of the OTC-injected blue sharks were returned to the laboratory by fishers for processing. Of the 44 returned vertebrae, 26 fluoresced and were used for the present study (Fig. 1, Table 1). The remaining vertebrae that did not fluoresce may have come from other sharks that were not injected with OTC. Time at liberty ranged from 20 to 587 days, with an average of 220 days (±159.3 s.d.). In all, 15 of the 26 individuals were at large for over 6 months, and 5 individuals exceeded 1 year (390–587 days). The majority of blue sharks used in the study were juveniles; however, one OTC-injected adult male blue shark measured 231 cm FL at the time of tagging. The average size at the time of tagging was 97.3 cm FL (±31.8 s.d.). Size estimates at recapture ranged from 89 to 235 cm FL; however, size estimates of recaptured individuals should be treated with caution because of the variability in measurement techniques used. For example, eight recaptured individuals had size estimates reported to the nearest-centimetre FL, eight were measured using straight TL, and for ten, no recapture measurement or an unreliable value was reported (Table 1).

Results supported annual band-pair (1 translucent and 1 opaque) deposition on vertebrae of blue sharks in the eastern Pacific Ocean. The slope of the relationship between the number of band pairs and years at large was not significantly different from the expected value of one (\( P > 0.05, r^2 = 0.63 \)). Agreement between readers during the first blind read was 73% for all vertebrae samples and 92% following the second blind read. Two samples were not agreed on after the second blind read and were therefore discussed and agreed on by the two readers. Two blue sharks at large for 1.32 and 1.61 years had two completed band pairs on vertebrae distal to the OTC mark. In addition, 12 individuals at large from 170 days to 1.3 years had one translucent zone (half band pair) or incomplete band pair development. All sharks were tagged in summer months (June through August) and the OTC mark was located within a translucent zone (light, presumed fast growth). For sharks with one fully developed band pair post OTC, the translucent zone containing the OTC mark was followed by an opaque zone (dark, presumed slow growth) and an additional translucent zone that had been deposited completely (Fig. 2). Findings here supported formation of the opaque zone (slow growth) from late autumn through to winter months, with
In total, 17,421 blue sharks ranging in size from 21 to 273 cm FL were used for length–frequency analysis. Median size of all blue sharks was 106.0 cm FL and mean size was 109.9 cm FL (±31.6 s.d.). A total of 12,275 blue sharks collected from the drift gill-net fishery had a median size of 113.0 cm FL, with a mean of 115.4 cm FL (±29.6 s.d.; Fig. 3). Smaller sharks were collected during the NOAA juvenile shark survey, with a total of 5,146 measured individuals; median size was 97.0 cm FL, with a mean of 97.0 cm FL (±32.4 s.d.; Fig. 3). No significant differences in length occurred over time (drift gill-net: $P > 0.05$, $r^2 = 0.141$, juvenile survey: $P > 0.05$, $r^2 = 0.003$), or by sex within each data source ($P > 0.05$). Thus, length–frequency analysis was collapsed across quarters, data sources, years and sexes to identify size modes in the dataset. The rationale behind collapsing across both data sources was due to the size selectivity of each survey. The NOAA juvenile shark survey targeted small individuals, in contrast to the drift gill-net survey targeting larger sharks. By combining both datasets, the MIXDIST model can identify progressive modes that would not be possible by using a single data source alone. Results from MIXDIST identified three distinct size modes at 80, 110 and 132 cm FL (Fig. 3). Estimated growth rates of 30 and 22 cm FL per year were therefore calculated by taking the difference in size from the first to second mode and second to third mode, respectively. Goodness-of-fit tests indicated that modes beyond the first three were not possible to identify because of the high overlap of individual sizes towards the tail end of the histogram. Consequently, only the first three modes were used for the study.

### Table 1. Summary table of oxytetracycline (OTC)-labelled vertebra samples from blue sharks

Data are sorted by time at liberty and also include tag and recapture dates, fish lengths (fork lengths, FL), sex and number of band pairs (based on two independent readers) both after OTC and birth band. NL indicates either no length estimate or an unreliable estimate. F, female; M, male.

<table>
<thead>
<tr>
<th>Fish ID</th>
<th>Time at liberty (days)</th>
<th>Tag date</th>
<th>Recapture date</th>
<th>Tagging length (cm FL)</th>
<th>Recapture length (cm FL)</th>
<th>Sex</th>
<th>Number of band pairs after OTC</th>
<th>Number of band pairs after birth band</th>
</tr>
</thead>
<tbody>
<tr>
<td>A039329</td>
<td>587</td>
<td>22 July 2007</td>
<td>28 Feb. 2009</td>
<td>86</td>
<td>123$^A$</td>
<td>F</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>A039514</td>
<td>503</td>
<td>17 June 2008</td>
<td>2 Nov. 2009</td>
<td>112</td>
<td>140$^A$</td>
<td>M</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>A039424</td>
<td>482</td>
<td>22 June 2008</td>
<td>17 Oct. 2009</td>
<td>73</td>
<td>98$^A$</td>
<td>M</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>A039396</td>
<td>473</td>
<td>18 July 2007</td>
<td>2 Nov. 2008</td>
<td>109</td>
<td>121$^A$</td>
<td>M</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>A039427</td>
<td>390</td>
<td>22 June 2008</td>
<td>17 July 2009</td>
<td>109</td>
<td>151$^A$</td>
<td>M</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>A039428</td>
<td>309</td>
<td>22 June 2008</td>
<td>27 Apr. 2009</td>
<td>83</td>
<td>111</td>
<td>M</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A039872</td>
<td>292</td>
<td>20 June 2008</td>
<td>8 Apr. 2009</td>
<td>87</td>
<td>NL</td>
<td>F</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>A040274</td>
<td>273</td>
<td>6 Aug. 2009</td>
<td>6 May 2010</td>
<td>83</td>
<td>123$^A$</td>
<td>F</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A039884</td>
<td>269</td>
<td>20 June 2008</td>
<td>16 Mar. 2009</td>
<td>76</td>
<td>NL</td>
<td>M</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>A040270</td>
<td>223</td>
<td>6 Aug. 2009</td>
<td>17 Mar. 2010</td>
<td>88</td>
<td>90$^A$</td>
<td>M</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A040470</td>
<td>215</td>
<td>17 Aug. 2009</td>
<td>20 Mar. 2010</td>
<td>82</td>
<td>NL</td>
<td>F</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>A040276</td>
<td>212</td>
<td>6 Aug. 2009</td>
<td>6 Mar. 2010</td>
<td>83</td>
<td>108</td>
<td>M</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>A039786</td>
<td>211</td>
<td>16 June 2008</td>
<td>13 Jan. 2009</td>
<td>110</td>
<td>NL</td>
<td>M</td>
<td>0.5</td>
<td>2</td>
</tr>
<tr>
<td>A039844</td>
<td>182</td>
<td>20 June 2008</td>
<td>19 Dec. 2008</td>
<td>81</td>
<td>91</td>
<td>M</td>
<td>1.5</td>
<td>2.5</td>
</tr>
<tr>
<td>A039924</td>
<td>177</td>
<td>2 Aug. 2007</td>
<td>26 Jan. 2008</td>
<td>137</td>
<td>163</td>
<td>M</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>A039842</td>
<td>170</td>
<td>20 June 2008</td>
<td>7 Dec. 2008</td>
<td>73</td>
<td>NL</td>
<td>M</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A039322</td>
<td>121</td>
<td>17 July 2007</td>
<td>15 Nov. 2007</td>
<td>231</td>
<td>235</td>
<td>M</td>
<td>0.5</td>
<td>8</td>
</tr>
<tr>
<td>A040250</td>
<td>113</td>
<td>4 Aug. 2009</td>
<td>25 Nov. 2009</td>
<td>81</td>
<td>89</td>
<td>F</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A040248</td>
<td>89</td>
<td>4 Aug. 2009</td>
<td>1 Nov. 2009</td>
<td>89</td>
<td>NL</td>
<td>F</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>A038861</td>
<td>71</td>
<td>30 July 2009</td>
<td>9 Oct. 2009</td>
<td>129</td>
<td>NL</td>
<td>F</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>A039422</td>
<td>47</td>
<td>22 June 2008</td>
<td>8 Aug. 2008</td>
<td>83</td>
<td>90</td>
<td>M</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>A040750</td>
<td>43</td>
<td>17 Aug. 2009</td>
<td>29 Sep. 2009</td>
<td>77</td>
<td>NL</td>
<td>F</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A040824</td>
<td>41</td>
<td>25 Aug. 2009</td>
<td>5 Oct. 2009</td>
<td>88</td>
<td>NL</td>
<td>M</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A039438</td>
<td>22</td>
<td>23 June 2008</td>
<td>15 July 2008</td>
<td>98</td>
<td>100</td>
<td>M</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A040803</td>
<td>20</td>
<td>24 Aug. 2009</td>
<td>13 Sep. 2009</td>
<td>95</td>
<td>NL</td>
<td>F</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

$^A$FL was converted from total length (TL).

Fig. 2. Image of whole blue shark vertebra (Sample A038861), showing the birth band (black dot), three opaque bands (white dots) and oxytetracycline (OTC) mark (grey dot) under ultraviolet light.

translucent zone formation (fast growth) occurring during spring and summer periods.

In total, 17,421 blue sharks ranging in size from 21 to 273 cm FL were used for length–frequency analysis. Median size of all blue sharks was 106.0 cm FL and mean size was 109.9 cm FL (±31.6 s.d.). A total of 12,275 blue sharks collected from the drift gill-net fishery had a median size of 113.0 cm FL, with a mean of 115.4 cm FL (±29.6 s.d.; Fig. 3). Smaller sharks were collected during the NOAA juvenile shark survey, with a total of 5,146 measured individuals; median size was 86.8 cm FL, with a mean of 97.0 cm FL (±32.4 s.d.; Fig. 3). No significant differences in length occurred over time (drift gill-net: $P > 0.05$, $r^2 = 0.141$, juvenile survey: $P > 0.05$, $r^2 = 0.003$), or by sex within each data source ($P > 0.05$). Thus, length–frequency analysis was collapsed across quarters, data sources, years and sexes to identify size modes in the dataset. The rationale behind collapsing across both data sources was due to the size selectivity of each survey. The NOAA juvenile shark survey targeted small individuals, in contrast to the drift gill-net survey targeting larger sharks. By combining both datasets, the MIXDIST model can identify progressive modes that would not be possible by using a single data source alone. Results from MIXDIST identified three distinct size modes at 80, 110 and 132 cm FL (Fig. 3). Estimated growth rates of 30 and 22 cm FL per year were therefore calculated by taking the difference in size from the first to second mode and second to third mode, respectively. Goodness-of-fit tests indicated that modes beyond the first three were not possible to identify because of the high overlap of individual sizes towards the tail end of the histogram. Consequently, only the first three modes were used for the study.
Brae was the preferred method to obtain band-pair counts post-spread across ocean basins and with respect to ontogeny. According to studies, suggested that annual deposition may be widespread across adults in the present study, combined with the aforementioned studies, produced higher-quality images with clear bands that were more easily interpreted and required less time than sectioning. Jolly et al. (2013) also found silver nitrate and Alizarin red staining methods to be unsuccessful in enhancing vertebral bands and, therefore, relied on digital images of unstained whole centrum faces.

Age and growth of the blue shark has been examined using both vertebral band counts and length–frequency modal analyses. In the North Pacific, Cailliet et al. (1983), Tanaka et al. (1990), and Blanco-Parra et al. (2008) used vertebral growth rings or band-pair counts and Nakano (1994) used both vertebrae and length–frequency modes to establish growth curves for the blue shark, assuming an annual vertebral band-pair deposition rate. Moderate differences in size-at-age were shown among studies and were likely based on geography, methodology, sex and the ranges of lengths studied. Generally, length modes most abundant in our fishery and survey samples overlapped with the lengths in the aforementioned studies that were associated with the same estimated ages. Our modes and corresponding growth estimates generated from length–frequency analyses also closely matched size-at-age and growth estimates from previous blue shark studies (Cailliet et al. 1983, Tanaka et al. 1990, Nakano 1994, Blanco-Parra et al. 2008). The majority of samples collected from the drift gill-net fishery ranged between 75 and 160 cm FL, corresponding to an age range of 1–7 years, with a peak in size between 90 and 130 cm FL (~2–4 years of age; Cailliet et al. 1983, Tanaka et al. 1990, Nakano 1994, Blanco-Parra et al. 2008). Similarly, the majority of samples collected from the juvenile survey ranged in size from 60 to 125 cm FL, corresponding to young-of-the-year to 4 years of age, with a peak size range of 75–110 cm FL (~1–3 years of age). These size-at-age estimates suggested that the majority of samples collected from both sources were juveniles and subadults. Assuming an average size-at-maturity of 170 cm FL (Suda 1953, Pratt 1979, Nakano et al. 1985), over 96% of the blue sharks collected in both the drift gill-net fishery and the juvenile shark survey were likely to be sexually immature.

Band-pair deposition rates are species-specific (Cailliet 2015) and researchers have found that deposition patterns in elasmobranch vertebrae vary from no periodicity (Natanson 1984), to annual deposition (Cailliet 1990) and to biannual deposition (Wells et al. 2013). Although specific processes regulating deposition rates in vertebrae are unknown, several factors such as movement, prey availability, temperature exposure and physiological differences are likely to be important. An interesting contrast to the annual deposition rate in the present study was the biannual deposition rate of juvenile shortfin mako (Isurus oxyrinchus) in the same study region (Wells et al. 2013). Horizontal movement patterns from conventional tagging (Fig. 1; Wells et al. 2013) and electronic tagging (Weng et al. 2005; Block et al. 2011) have shown similar movement patterns.
Age validation of the blue shark

Marine and Freshwater Research 1135

between the two species, with the majority of animals moving south along the western coast of Baja Mexico, and a small percentage of animals making longer movements into offshore waters extending to the Hawaiian Islands and beyond. All of the OTC-recaptured blue sharks from the present study were collected along the southern California and Baja California, Mexico coast, similar to the shortfin makos studied by Wells et al. (2013), suggesting that environmental factors may have been similar for both species and may not be the basis for different deposition rates. Despite shortcomings of identifying specific mechanisms regulating deposition rates in elasmobranch vertebrae, the present study has highlighted the importance of species-specific age-validation studies even within similar geographic regions.

Acknowledgements

Personnel of the SWFSC in La Jolla, California, specifically, D. Holts, J. Wraith, J. Hyde, R. Rasmussen, S. Smith, O. Snodgrass, R. Vetter and H. Dewar made this study possible by assisting with tagging and logistical operations. Special thanks go to NOAA/NMFS observers for their diligent work in collecting specimens and length data, and the many anglers and commercial operators for returning OTC-labelled vertebrae. We also thank O. Sosa-Nishizaki of the Center for Scientific Research and Higher Education at Ensenada, Baja California (CICESE), for helping arrange collection and shipping of samples from Mexico, Emily Williams and Tom Timan for assistance with figures, and suggestions from two anonymous reviewers that improved the manuscript.

References


