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

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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. Vertebrae 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.

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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 rototag (Dalton, Henley-on-Thames, UK) labelled with contact and reward information in English and Spanish and instructions to measure the fish and save the vertebrae. Most sharks were also tagged with a conventional spaghetti tag (Floy Tag and Manufacturing, Seattle, WA, USA) placed in the dorsal musculature beneath the first dorsal fin. At tagging, each shark was sexed and measured (straight-line FL or TL) to the nearest centimetre by using a rigid calliper. Sharks were given an intraperitoneal injection of OTC (Valley Vet, Marysville, KS, USA) at a dose rate of ~25 mg kg^{-1} of bodyweight, and then released.

Oxytetracycline (OTC)-marked vertebrae were obtained from blue sharks recaptured by recreational and commercial fishers between 2007 and 2010. Samples were stored frozen until processed, and kept from light and ultraviolet (UV) exposure to preserve the OTC time mark. The vertebrae with the widest diameters in a given sample were chosen for sectioning and each was cleaned of excess tissue, rinsed and air-dried. To elucidate the vertebral bands, we attempted several techniques to determine the most suitable method for contrasting opaque and translucent bands on blue shark vertebrae. Techniques included the high-frequency X-radiography technique of Cailliet *et al.* (1983) and Wells *et al.* (2013), whole centrum faces and sectioned vertebrae bow ties viewed under a light microscope and digitally photographed (MacNeil and Campana 2002; Skomal and Natanson 2003) and staining with Alizarin red. For staining experiments, vertebrae were decalcified for 15–30 min by using the rapid decalcifier RDO (Apex Engineering Products Corporation, Aurora, IL, USA), then bowtie sections were cut (frontal slices 80–140 μm) using a microtome and stained using Alizarin red solution. Some samples were not decalcified (to preserve OTC mark) and cut to 0.1–0.3 mm with an Isomet (Beuhler, Lake Bluff, IL, USA) low-speed saw. In all techniques, UV light was used to fluoresce the OTC mark on the vertebrae. Digital photographs of whole centrum faces of vertebrae were determined to provide the best overall image quality for counting band pairs and were therefore chosen as the primary technique for the study, similar to methodology used by MacNeil and Campana (2002) and Jolly *et al.* (2013). Samples were photographed using a Leica Z16 APO dissecting microscope (Wetzlar, Germany) with substage illumination and a digital camera.

Band pairs were counted from digital images of centrum faces on a computer screen. We referred to the original vertebrae under the microscope if more detail was desired. As in Bishop *et al.* (2006), counts excluded the birth band, which represents age zero. Alternating pairs of translucent and opaque bands were assumed to represent one complete 'growth increment' or 'band pair' (terms we use synonymously). A partial translucent zone was counted as a half band pair. Two separate band counts were made, including (1) total band pairs, or bands distal to the presumed birth band, and (2) band pairs distal to the OTC mark. Increment counting for the former began at the distal edge of the first opaque band beyond the birth band, and, for the latter, at the distal edge of the first opaque band beyond the OTC mark.

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 (Kusher *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 (χ^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:

$$\mathrm{FL} = 0.829 \times (\mathrm{TL}) - 1.122$$

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

$$\mathrm{FL} = 2.746 \times (\mathrm{AL}) + 11.803$$

where $r^2 = 0.941$, $n = 9504$.

Lengths are in centimetres. Size data were combined between sexes because no significant differences by sex existed for either dataset (*t*-test, $n = 17\,421$, $P > 0.05$) 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).

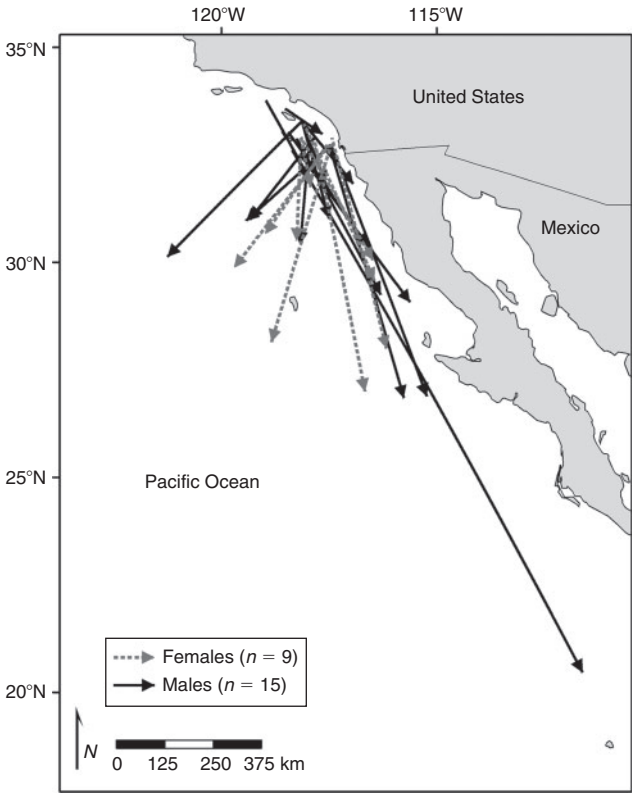

Fig. 1. Map of tag and recapture locations (arrows) for recaptured oxytetracycline (OTC)-injected blue sharks (n = 24 of 26). Recapture locations were not provided for two of the sharks used in the study.

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 to one and a half fully developed band pairs past the OTC mark (Table 1). Remaining individuals at large from 20 to 269 days either 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

Table 1. Summary table of oxytetracycline (OTC)-labelled vertebrae 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

Fish ID	Time at liberty (days)	Tag date	Recapture date	Tagging length (cm FL)	Recapture length (cm FL)	Sex	Number of band pairs after OTC	Number of band pairs after birth band
A039329	587	22 July 2007	28 Feb. 2009	86	123[A]	F	2	3
A039514	503	17 June 2008	2 Nov. 2009	112	140[A]	M	1	3
A039424	482	22 June 2008	17 Oct. 2009	73	98[A]	M	2	3
A039396	473	18 July 2007	2 Nov. 2008	109	121[A]	M	1	2
A039427	390	22 June 2008	17 July 2009	109	151[A]	M	1	3
A039428	309	22 June 2008	27 Apr. 2009	83	111	M	1	1
A039872	292	20 June 2008	8 Apr. 2009	87	NL	F	1	2
A040274	273	6 Aug. 2009	6 May 2010	83	123[A]	F	1	1
A039864	269	20 June 2008	16 Mar. 2009	76	NL	M	0.5	1
A040270	223	6 Aug. 2009	17 Mar. 2010	88	90[A]	M	1	2
A040740	215	17 Aug. 2009	20 Mar. 2010	82	NL	F	1	2
A040276	212	6 Aug. 2009	6 Mar. 2010	83	108	M	1	2
A039786	211	16 June 2008	13 Jan. 2009	110	NL	M	0.5	2
A040735	194	16 Aug. 2009	26 Feb. 2010	87	99[A]	M	1	2
A039844	182	20 June 2008	19 Dec. 2008	81	91	M	1.5	2.5
A039924	177	2 Aug. 2007	26 Jan. 2008	137	163	M	1	5
A039842	170	20 June 2008	7 Dec. 2008	73	NL	M	1	1
A039322	121	17 July 2007	15 Nov. 2007	231	235	M	0.5	8
A040250	113	4 Aug. 2009	25 Nov. 2009	81	89	F	0	1
A040248	89	4 Aug. 2009	1 Nov. 2009	89	NL	F	0.5	1
A038861	71	30 July 2009	9 Oct. 2009	129	NL	F	0	3
A039422	47	22 June 2008	8 Aug. 2008	83	90	M	0.5	1
A040750	43	17 Aug. 2009	29 Sep. 2009	77	NL	F	0	1
A040824	41	25 Aug. 2009	5 Oct. 2009	88	NL	M	0	1
A039438	22	23 June 2008	15 July 2008	98	100	M	0	1
A040803	20	24 Aug. 2009	13 Sep. 2009	95	NL	F	0	1

[A]FL was converted from total length (TL).

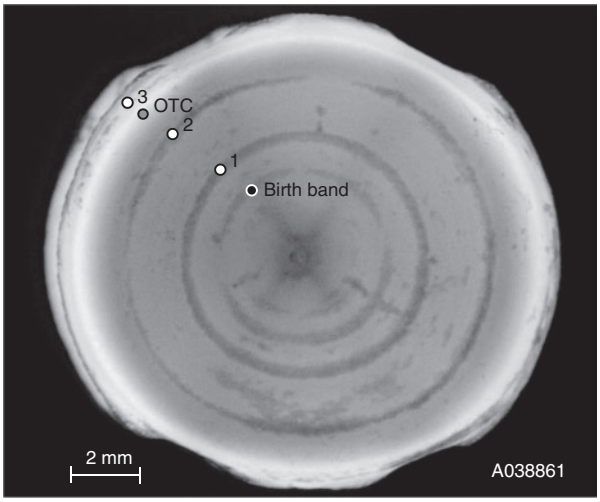

Fig. 2. Image of whole blue shark vertebra (Sample A038861), showing the birth band (black dot), three opaque bands (white dots) and oxytetracycline (OTC) mark (grey dot) under ultraviolet light.

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*a*). Smaller sharks were collected during the NOAA juvenile shark survey, with a total of 5146 measured individuals; median size was 86.8 cm FL, with a mean of 97.0 cm FL (±32.4 s.d.; Fig. 3*b*). 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.

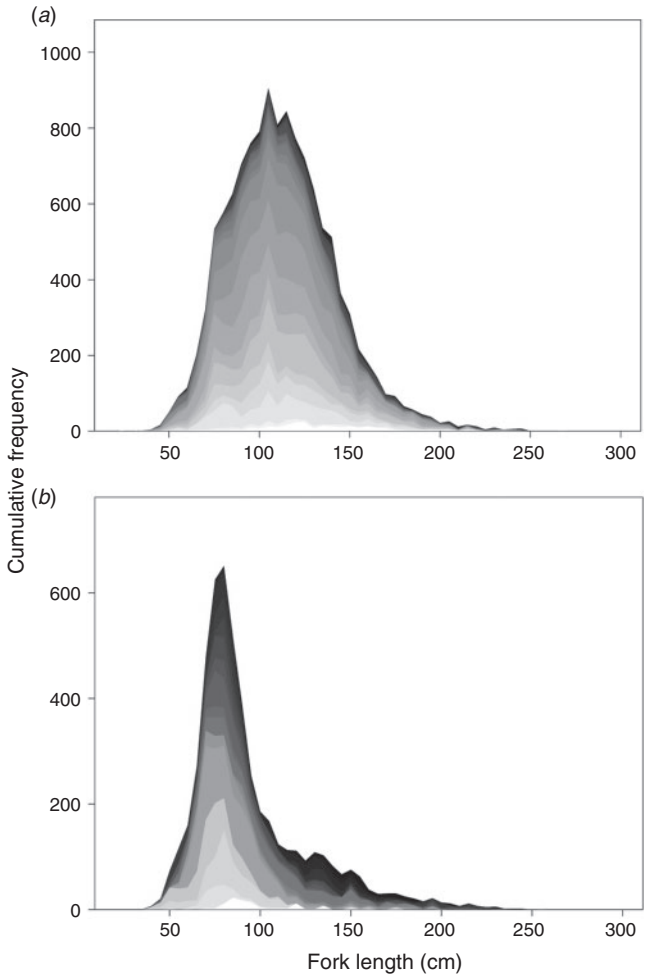

Fig. 3. Cumulative length–frequency plots by survey and year: (*a*) drift gill-net (1990–2014) and (*b*) NOAA juvenile surveys (1993–2015). Data are binned by 5-cm fork length increments and cumulative years are shaded from white (oldest) to black (most recent).

Discussion

Age validation of blue sharks using OTC-marked vertebrae confirmed annual band-pair deposition for blue sharks in the eastern Pacific Ocean. Although our results are limited to blue sharks tagged and recaptured near the Southern California Bight study area, these findings coincided with the annual band-pair deposition rate for two OTC-returned blue sharks at large for 0.7 and 1.5 years in the North Atlantic Ocean up to 4 years of age (Skomal and Natanson 2003). In addition, a bomb radiocarbon-dating study of two adult blue sharks in the Indian Ocean confirmed annual deposition rates in vertebrae (Romanov and Campana 2011). Those two fish were collected in the 1980s and measured 270 and 273 cm FL, with corresponding age estimates of 23 and 19 years, respectively. Collectively, juveniles and the single adult in the present study, combined with the aforementioned studies, suggested that annual deposition may be widespread across ocean basins and with respect to ontogeny.

Examination of the whole centrum face of blue shark vertebrae was the preferred method to obtain band-pair counts post OTC. Sectioned vertebrae using both X-radiography and Alizarin red staining techniques did not produce readable images because both tended to produce non-contrasting band pairs along the bowtie section. MacNeil and Campana (2002) compared reading whole versus sectioned vertebrae by using light microscopy for blue sharks ranging in size from 145 to 282 cm FL and found no systematic difference in age estimates between the two methods. The authors did find that whole vertebrae 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

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.

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References

Bigelow, H. B., and Schroeder, W. C. (1953). 'Fishes of the Gulf of Maine.' Fishery Bulletin 53. (US Fish and Wildlife Service: Washington, DC, USA.)

Bishop, S. D. H., Francis, M. P., Duffy, C., and Montgomery, J. C. (2006). Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research* **57**, 143–154. doi:10.1071/MF05077

Blanco-Parra, M. D. P., Galvan-Magana, F., and Marquez-Farias, F. (2008). Age and growth of the blue shark, *Prionace glauca* Linnaeus, 1758, in the northwest coast of Mexico. *Revista de Biologia Marina y Oceanografia* **43**, 513–520.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A.-L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., Henry, R. W., and Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**, 86–90. doi:10.1038/NATURE10082

Cailliet, G. M. (1990). Elasmobranch age determination and verification; an updated review. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries'. (Eds H. L. Pratt Jr, S. H. Gruber, and T. Taniuchi.) NOAA Technical Report 90, pp. 157–165. (US Department of Commerce: Honolulu, HI, USA.)

Cailliet, G. M. (2015). Perspectives on elasmobranch life-history studies: a focus on age validation and relevance to fishery management. *Journal of Fish Biology* **87**, 1271–1292. doi:10.1111/JFB.12829

Cailliet, G. M., and Bedford, D. S. (1983). The biology of three pelagic sharks from California waters: and their emerging fisheries: a review. *California Cooperative Oceanic Fisheries Investigations Reports* **24**, 57–69.

Cailliet, G. M., Martin, L. K., Harvey, J. T., Kusher, D., and Welden, B. A. (1983). Preliminary studies on the age and growth of blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. In 'Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks'. (Eds E. D. Prince, and L. M. Pulos.) NOAA Technical Report NMFS, pp. 179–188. (US Department of Commerce: Miami, FL, USA.)

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197–242. doi:10.1111/J.1095-8649.2001.TB00127.X

Campana, S. E., Joyce, W., and Manning, M. J. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series* **387**, 241–253. doi:10.3354/MEPS08109

Compagno, L. J. V. (1984). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis 125, Vol. 4, Part 1 – Hexanchiformes to Lamniformes. (FAO: Rome, Italy.) Available at http://www.fao.org/3/a-ad122e.pdf [Verified 17 September 2016].

Goldman, K. J. (2005). Age and growth of elasmobranch fishes. In 'Management Techniques for Elasmobranch Fisheries'. (Eds J. A. Musick, and R. Bonfil.) Fisheries Technical Paper 474, pp. 76–102. (FAO: Rome.)

Hanan, D. A., Holts, D. B., and Coan, A. L., Jr (1993). The California drift gill net fishery for sharks and swordfish, 1981–1982 through 1990–91. *California Department of Fish and Game Fish Bulletin* **175**, 1–95.

Holts, D. B., Julian, A., Sosa-Nishizaki, O., and Bartoo, N. W. (1998). Pelagic shark fisheries along the west coast of the United States and Baja California, Mexico. *Fisheries Research* **39**, 115–125. doi:10.1016/S0165-7836(98)00178-7

James, K. C., Lewison, R. L., Dillingham, P. W., Curtis, K. A., and Moore, J. E. (2016). Drivers of retention and discards of elasmobranch non-target catch. *Environmental Conservation* **43**, 3–12. doi:10.1017/S0376892915000168

Jolly, K. A., da Silva, C., and Attwood, C. G. (2013). Age, growth and reproductive biology of the blue shark *Prionace glauca* in South African waters. *African Journal of Marine Science* **35**, 99–109. doi:10.2989/1814232X.2013.783233

Kusher, D. I., Smith, S. E., and Cailliet, G. M. (1992). Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environmental Biology of Fishes* **35**, 187–203. doi:10.1007/BF00002193

Liu, K. M., Chiang, P. J., and Chen, C. T. (1998). Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. *Fishery Bulletin* **96**, 482–491.

Macdonald, P. D. M., and Green, P. E. J. (1988). 'User's Guide to Program MIX: an Interactive Program for Fitting Mixtures of Distributions. Release 2.3.' (Ichthus Data Systems: Hamilton, ON, Canada.)

Macdonald, P. D. M., and Pitcher, T. J. (1979). Age-groups from size-frequency data: a versatile efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada* **36**, 987–1001. doi:10.1139/F79-137

MacNeil, M. A., and Campana, S. E. (2002). Comparison of whole and sectioned vertebrae for determining the age of young blue shark (*Prionace glauca*). *Journal of Northwest Atlantic Fishery Science* **30**, 77–82. doi:10.2960/J.V30.A5

Montealegre-Quijano, S., Cardoso, A. T. C., Silva, R. Z., Kinas, P. G., and Vooren, C. M. (2014). Sexual development, size at maturity, size at maternity and fecundity of the blue shark *Prionace glauca* (Linnaeus, 1758) in the Southwest Atlantic. *Fisheries Research* **160**, 18–32. doi:10.1016/J.FISHRES.2014.03.003

Nakano, H. (1994). Age, reproduction and migration of blue shark in the North Pacific Ocean. *Bulletin of the National Research Institute of Far Seas Fisheries* **31**, 141–256.

Nakano, H., and Seki, M. P. (2003). Synopsis of biological data on the blue shark, *Prionace glauca* Linnaeus. *Bulletin Fisheries Research Agency* **6**, 18–55.

Nakano, H., and Stevens, J. D. (2008). The biology and ecology of the blue shark, *Prionace glauca*. In 'Sharks of the Open Ocean: Biology, Fisheries and Conservation'. (Eds M. D. Camhi, E. K. Pikitch, and E. A. Babcock.) pp. 140–151. (Blackwell Publishing: Oxford, UK.)

Nakano, H., Makihara, M., and Shimazaki, K. (1985). Distribution and biological characteristics of the blue shark in the central North Pacific. *Bulletin of the Faculty of Fisheries Hokkaido University* **36**, 99–113.

Natanson, L. J. (1984). Aspects of age, growth, and reproduction of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. M.A. Thesis, San Jose State University, San Jose, CA, USA.

Natanson, L. J., Mello, J. J., and 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.

NMFS (2016). NOAA Fisheries West Coast Region Observer Program data summaries and reports. Available at http://www.westcoast.fisheries.noaa.gov/fisheries/wc_observer_programs/sw_observer_program_info/data_summ_report_sw_observer_fish.html [Verified 15 July 2016].

Pratt, H. W. (1979). Reproduction in the blue shark, *Prionace glauca. Fishery Bulletin* **77**, 445–470.

Romanov, E., and Campana, S. (2011). Bomb radiocarbon dating of the Indian Ocean blue shark *Prionace glauca*: a preliminary test of ageing accuracy. Working group report, IOTC-2011-WPEB07-INF33, Indian Ocean Tuna Commission.

Skomal, G. B., and Natanson, L. J. (2003). Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Fishery Bulletin* **101**, 627–639.

Stevens, J. D. (1975). Vertebral rings as a means of age determination in the blue shark (*Prionace glauca*, L.). *Journal of the Marine Biological Association of the United Kingdom* **55**, 657–665. doi:10.1017/S0025315400017318

Suda, A. (1953). Ecological study of blue shark (*Prionace glauca* Linne). *Bulletin of the Nankai Fisheries Research Laboratory* **1**, 1–11.

Tanaka, S., Cailliet, G. M., and Yudin, K. G. (1990). Differences in growth of the blue shark, *Prionace glauca*: technique or population? In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries'. (Eds H. L. Pratt, S. H. Gruber, and T. Taniuchi.) Technical Report 90, pp. 177–187. (NOAA: Honolulu, HI, USA.)

Wells, R. J. D., Smith, S. E., Kohin, S., Freund, E., Spear, N., and 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. doi:10.7755/FB.111.2.3

Weng, K. C., Castilho, P., Morrissette, J. M., Landeira-Fernandez, A. M., Holts, D. B., Schallert, R. J., Goldman, K. J., and Block, B. A. (2005). Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* **310**, 104–106. doi:10.1126/SCIENCE.1114616