Age validation of juvenile Shortfin Mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California

R. J. David Wells (contact author)[1,2]
Susan E. Smith[1]
Suzanne Kohin[1]
Ellen Freund[1]
Natalie Spear[1]
Darlene A. Ramon[1]

Email address for contact author: wellsr@tamug.edu

[1] Fisheries Resources Division
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
8901 La Jolla Shores Drive
La Jolla, California 92037

[2] Department of Marine Biology
Texas A&M University at Galveston
1001 Texas Clipper Rd.
Galveston, Texas 77553

Present address for contact author: Department of Marine Biology
Texas A&M University at Galveston
1001 Texas Clipper Rd.
Galveston, Texas 77553

Abstract—The purpose of this study was to validate aging results of juvenile Shortfin Mako (*Isurus oxyrinchus*) by vertebral band counts. Vertebrae of 29 juvenile Shortfin Mako marked with oxytetracycline (OTC) were obtained from tag-recapture activities to determine centrum growth-band deposition. Tagging occurred off southern California from 1996 to 2010, and time at liberty of the 29 sharks ranged from 4 months to 4.4 years (mean=1.3 years). Growth information also was obtained from length-frequency modal analyses (MULTIFAN and MIXDIST) by using a 29-year data set of commercial and research catch data, in addition to a tag-recapture growth model (e.g, the GROTAG model). For vertebrae samples used for age validation, shark size at time of release ranged from 79 to 142 cm fork length (FL) and from 98 to 200 cm FL at recapture. Results from band counts of vertebrae distal to OTC marks indicate 2 band pairs (2 translucent and 2 opaque) are formed each year for Shortfin Mako of the size range examined. Length-frequency analyses identified 3 age-class modes. Growth rate estimates from 26.5 to 35.5 cm/year were calculated for the first age-class mode (85 cm FL) and from 22.4 to 28.6 cm/year for the second age-class mode (130 cm FL). Results from the tag-recapture growth model revealed fast growth during time at liberty for tagged fish of the 2 youngest age classes. Collectively, these methods suggest rapid growth of juvenile Shortfin Mako in the southern California study area and indicate biannual deposition of growth bands in vertebrae for the first 5 years.

Manuscript submitted 23 August 2012.
Manuscript accepted 20 February 2013.
Fish. Bull 111:147–160 (2013).
doi 10.7755/FB.111.2.3

For almost 3 decades, researchers in various parts of the world have focused on the problem of accurately interpreting age and growth in the Shortfin Mako (*Isurus oxyrinchus*) (e.g., Cailliet and Bedford, 1983; Cailliet et al., 1983; Pratt and Casey, 1983; Casey and Kohler, 1992; Campana et al., 2002; Bishop et al.[1]; Ribot-Carballal et al., 2005; Bishop et al., 2006; Natanson et al., 2006; Ardizzone et al., 2006; Maia et al., 2007; Cerna and Licandeo, 2009; Okamura and Semba, 2009; Semba et al., 2009). Driving these efforts is the need to better assess the vulnerability of Shortfin Mako to harvest in commercial and recreational fisheries and as bycatch in longline and driftnet fisheries from high-seas fleets (Stevens, 2008). Studies of the demographic dynamics of sharks have shown that average age at first maturity and the relative rate of growth that determines this parameter is one of the leading factors that affect the ability of most sharks to rebound from harvest pressures (Smith et al., 1998; Cortés, 2002; Garcia et al., 2008). Accurate age determinations also are necessary for calculations of growth and mortality rates, age at recruitment, and longevity.

The Shortfin Mako is an epipelagic species distributed in temperate and tropical seas worldwide (Compagno, 2001) and seldom found in water temperatures lower than 13–17°C (Casey and Kohler, 1992; Stevens, 2008). Shortfin Mako occur off the U.S. West Coast principally off California and Oregon, and catches are associated primarily with warm sea-surface temperatures from 15° to 25°C (PFMC, 2011). Most Shortfin Mako off the U.S. West Coast are sexually immature, and high recapture rates for tagged juveniles show that young individuals remain for about 2 years in nearshore California waters (Taylor and Bedford, 2001), where they are more frequently taken in the summer months and are only

[1] Bishop, S. D. H., M. P. Francis, and C. Duffy. 2004. Age, growth, maturity, longevity and natural mortality of the Shortfin Mako shark (*Isurus oxyrinchus*) in New Zealand waters. Working Paper SCTB17, BIO-4, National Institute of Water and Atmospheric Research, New Zealand, Ministry of Fisheries, NZ, 34 p. Presented at the 17th Meeting of the Standing Committee on Tuna and Billfish (SCTB), Majuro, Marshall Islands, 9–18 August 2004.

rarely found below the thermocline (Holts and Bedford, 1993). Large fish approaching 200 cm fork length (FL) disappear from the catch and presumably move offshore to a more oceanic and highly migratory existence, where most males are mature but females are not (Mollet et al., 2000; Joung and Hsu, 2005; Semba et al., 2011).

Researchers who study the age and growth of this species have used pairs of alternating bands of different mineralization in vertebral centra to estimate age. These estimates differ depending on assumptions about the number of band pairs that represent a single year of growth. Bishop et al. (2006) noted that despite different conclusions in these studies, all of them appear to have produced relatively similar growth curves if the same rate of band deposition was assumed. This finding indicates that techniques used by different research groups to identify countable band pairs are generally alike, with the greatest difference being assumptions about rates of band deposition. Smaller disparities may be due to ontogeny, geographic variability, divergent methods of preparing and interpreting vertebral banding patterns, difficulties in interpreting banding patterns, differences in sample sizes, or limitations of the growth models used (Bishop et al., 2006).

Although considerable advances have been made in determination of age and growth of Shortfin Mako, questions remain as to why current length-at-age models underestimate growth of young fish, especially fish ≤200 cm FL (Pratt and Casey, 1983; Bishop et al.[1]; Maia et al., 2007). Bishop et al. (2006) suggested that this discrepancy may be due to the inability of commonly used growth models to reconcile such rapid juvenile growth with the slow growth predicted for subadults and adult sharks. Direct age-validation techniques, such as oxytetracycline (OTC) marking and recapture of an adequate sample size of Shortfin Mako ≤200 cm FL, therefore, are needed to help resolve the issue of band-deposition rates in juvenile Shortfin Mako vertebrae.

In this study, we examined OTC-marked vertebrae of 29 juvenile Shortfin Mako (≤200 cm FL) released off California and later recaptured from 2000 to 2010 (at liberty from 145 days to 4.4 years). OTC is deposited at sites of active calcification, such as vertebral centra, and is known to remain distinct for at least 20 years in certain finfish, such as the Sablefish (*Anoplopoma fimbria*) (Beamish and McFarlane, 2000), and sharks, such as the Leopard Shark (*Triakis semifasciata*) (Smith et al., 2003). The combination of tag-recapture and chemical marking is thought to be the most robust method of age validation (Campana, 2001; Goldman, 2005). These methods test the accuracy of the counts of vertebral band pairs as annual indicators through observation of the banding pattern deposited distally to the OTC mark during the known time at liberty. To supplement this information, we also conducted analyses of at-liberty growth of tagged-recaptured sharks and length-frequency data from 3 decades of length data from commercial and research sources.

Materials and methods

Tagging methods

Sharks for tagging and OTC injection were captured in the Southern California Bight (SCB) (Fig. 1) with baited pelagic longlines and identified as Shortfin Mako through the method described by Compagno (2001). Leaders were unsnapped from the main line, and sharks were guided into a semisubmerged metal tagging cradle at the stern of the vessel. The cradle was then raised to facilitate tagging, measuring, and OTC injection, while the eyes of the shark were covered with a wet chamois cloth and a saltwater ventilation hose continuously ran water over the shark's gills. Each shark was tagged on the dorsal fin with a plastic Rototag[2] (Dalton ID, Henley-on-Thames, UK) labeled with contact and reward information in English and Spanish and with instructions to measure the fish and save the vertebrae. Most sharks also were double-tagged with a spaghetti tag placed in the dorsal musculature beneath the first dorsal fin.

At tagging, the sex of each shark was determined and each shark was measured (straight line FL or total length [TL]) to the nearest centimeter with a stationary meter stick fitted to the shark tagging cradle. Sharks were given an intraperitoneal injection of OTC at a dose rate of 25 mg/kg of body weight; the dose was estimated with a length-weight dose table developed from length-weight measurements of Shortfin Mako measured by NOAA scientific observers for the California drift gillnet fishery (Rasmussen[3]).

Laboratory methods for processing vertebrae

Past studies have shown that band counts are consistent throughout the vertebral column in the Shortfin Mako, indicating that vertebrae from any region can be used in age analysis, although the larger central vertebrae are easier to read because of wider band spacing (Bishop et al.[1]; Bishop et al., 2006; Natanson et al., 2006). OTC-marked vertebrae were obtained from Shortfin Mako recaptured on research cruises and commercial and recreational fishing vessels between 2000 and 2010. The widest diameter vertebral centra in a given sample were chosen for sectioning. We used only OTC-marked vertebrae from tag recaptures at liberty longer than 124 days (or ~4 months) to incorporate one full season into band-pair counts.

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Rasmussen, R. 1995. Unpubl. data. Southwest Fisheries Science Center, NOAA, La Jolla, CA.

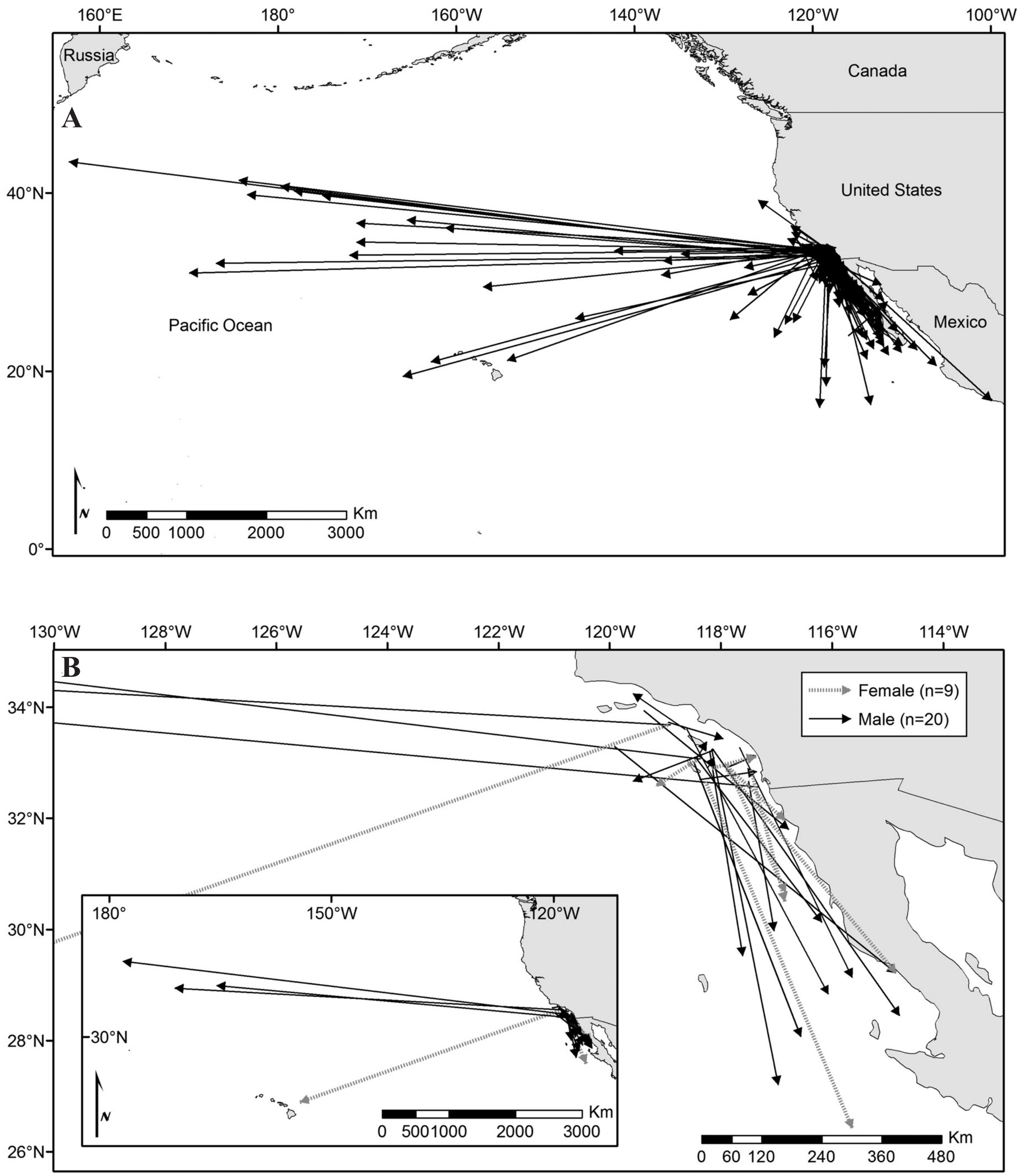

Figure 1

Map of study area in the Southern California Bight with tag and recapture locations (triangles) for (**A**) all recaptured Shortfin Mako (*Isurus oxyrinchus*) (OTC-marked and unmarked (n=317) and (**B**) recaptured OTC-injected juvenile Shortfin Mako (n=29) during the study period from 1996 to 2010. In panel B, black and gray arrows represent males and females, respectively, and the inset shows the more distant recapture locations.

To elucidate the vertebral bands, we chose to duplicate the "hard" (high-frequency) X-radiography technique of Cailliet and Bedford (1983) and Cailliet et al. (1983), which was used in the only centrum aging study of Shortfin Mako off California to date. This type of high-resolution radiography, with industrial, fine-grain, high-contrast film for sharpness and sensitivity, operates in the range of

10–110 kV at 3 mA and penetrates the highly calcified vertebrae.

Samples were stored frozen until processed and kept from light and excessive UV exposure to preserve the OTC time mark. Whole centra were separated, cleaned of excess tissue, rinsed and air-dried. Once dry, 2 centra from each sample were chosen, and 2 types of sections were prepared with a low-speed circular saw (IsoMet, Buehler, Lake Bluff, IL). To duplicate the Cailliet et al. (1983) method of X-raying the whole centrum face and to avoid the double image of the anterior and posterior face superimposed in X-ray images, a transverse cut was made through the centrum to create 2 equal halves of the centrum face. Additionally, longitudinal (sagittal) sections, 0.3–1.0 mm thick, were taken from the center of the second vertebrae to further elucidate banding patterns, especially growth zones along the centrum edge that are sometimes difficult to read on centrum face X-rays (Cailliet et al., 1983). Sections were then mounted and examined under a dissecting microscope at 7.5–10.0× magnification, with reflected long-wave UV light (365 nm) to illuminate the OTC mark. A metal pin was glued into place to visualize the position of the brightest, most distal edge of the OTC mark before it was X-rayed. Samples were X-rayed with a General Electric (Fairfield, CT) Mobile 100-15 X-ray unit for exposures between 15 and 45 s at 5 mA and 20–40 kV by using Kodak Industrex M100 film (Readypack II; Eastman Kodak Co., Rochester, NY). X-radiographs were photographed with a Leica Z16 APO dissecting microscope with substage illumination and a Leica DFC420 digital camera (Leica Microsystems, Wetzlar, Germany).

Standardization of band-reading techniques and terminology

We examined data collected by commercial drift gillnet observers and from research longline surveys and determined the peak in abundance of postpartum-size Shortfin Mako <70 cm FL to identify peak parturition time off southern California. Most individuals (90%) were collected between August and November, providing a tentative parturition time in our study region. Size at birth has been estimated at approximately 63 cm FL (70 cm TL), with parturition occurring year-round according to Mollet et al. (2000); parturition may occur primarily in summer in the South Pacific (Duffy and Francis, 2001) and eastern North Atlantic (Maia et al., 2007). The birth band for counting purposes was identified as the most pronounced calcified first band distal to the centrum focus and indicated by a change in the angle of the centra (Bishop et al., 2006). Seasons were defined according to solstice and equinox periods in the Northern Hemisphere.

Band-pair counts

Band pairs were counted from digital images of X-ray photographs on a computer screen. We referred to the original X-rays if more detail was desired. As in Bishop et al.[1] and Bishop et al. (2006), counts excluded the birth band, which represents age 0. Alternating pairs of translucent bands (hypomineralized; appearing dark in X-ray) and opaque bands (hypermineralized; appearing light in X-ray) were assumed to represent one complete band pair. Two separate band counts were made: 1) total band pairs, or bands distal to the presumed birth band, and 2) band pairs distal to the OTC mark. Band-pair counting began for the former at the distal edge of the first translucent zone beyond the birth band and for the latter at the distal edge of the first translucent zone beyond the OTC mark. In many cases, the OTC mark was directly on a translucent zone, but this zone was not included in the distal-to-OTC counts because only partial growth occurred during this period. This method results in counts that are conservative; counts are lower than they would be if this zone were included. If a count ended with a partial band pair (observed when the centrum edge was opaque), a plus sign was appended to the count number. For statistical analyses, the plus sign was converted to an arbitrary partial band count of 0.5. The corpus calcareum (centrum "arm") was used as a primary counting surface, and bands in the intermedialia were used for confirmation of a band pair, although we were not always successful in acquisition of sections with the fragile intermedialia intact (Goldman, 2005; Branstetter and Musick, 1994).

Each sample was examined and counted independently by 3 readers. Bands were "blind "counted without knowledge of Shortfin Mako length, sex, or time at liberty. Readers consulted with each other on criteria for counts before readings. Samples for which there was disagreement were counted a second time with X-ray images from which corresponding sample numbers had been removed and placed in a random order. Counts with similar readings among readers were deemed final; however, several samples did not have similar counts. For those samples without similar counts, the average number of band pairs was reported because differences were minor and no readings were deemed irreconcilable.

Differences among final readings of each of the 3 independent readers were examined through an analysis of variance (ANOVA) with readers as the dependent variable. A least-squares linear regression analysis was performed, and the null hypothesis that the slope (b) of the relationship between the number of band pairs and time was 1:1 (a situation that occurred if one opaque and one translucent band were deposited each year) was tested with a two-tailed t-test (Kusher et al., 1992). Age bias was investigated with age-bias plots and chi-square tests of symmetry by using the contingency table methods of Bowker (1948) and Hoenig et al. (1995). Differences in band-pair counts among readers were evaluated by the average percent error (APE) (Beamish and Fournier, 1981) and coefficient of variation (CV) (Chang, 1982) for readings distal to both the OTC mark and birth band.

Length-frequency analysis

Length-frequency distributions of juvenile Shortfin Mako were analyzed to estimate size at age of the first 3 age classes and to compare to vertebrae readings. The MULTIFAN model (Fournier et al., 1990) was one of 2 techniques used to analyze length-frequency data on the basis of size distributions. This model simultaneously analyzes multiple length-frequency distributions using a maximum likelihood method to estimate the number of age classes and proportions of fish at age. Tests for significance (best-fit growth parameters) were made through the use of likelihood ratio tests. First, a systematic search was performed to estimate the number of age classes and to hold the standard deviations of length constant across all age classes. Next, standard deviations of length were allowed to vary across age classes. The MIXDIST package (MacDonald and Pitcher, 1979) in R, vers. 2.8.0 (R Development Core Team, 2008) was the second length-frequency analysis used. This analysis uses a maximum likelihood method to estimate proportions of fish at age with the added benefit of fitting non-normally distributed data.

Data for both techniques were analyzed annually and came from 2 sources: 1) fishery-dependent data from the California drift gillnet fishery (1981–2009), which operates between May and January, and 2) fishery-independent data from longline research surveys of juvenile Shortfin Mako conducted by the NOAA Southwest Fisheries Science Center (1993–2009) between June and August of each year. A mixture of length measurements taken across study years: TL, FL and alternate length (AL, straight line distance between the origins of the first and second dorsal fins) were standardized into FL for this study to allow for comparison of our results with the results of other studies. The following length conversions were obtained from the 2 sources and used to standardize data for subsequent length-frequency analyses:

$$FL = 0.913 \times (TL) - 0.397, \text{ coefficient of determination } (r^2) = 0.986 \ (n=2177)$$

$$FL = 2.402 \times (AL) + 9.996, \ r^2=0.957 \ (n=3250).$$

Size data were combined between sexes because no significant difference existed ($P=0.769$), and size bins of 5 cm, ranging from 55 to 265 cm FL, were used.

Growth of tagged and recaptured mako sharks

Growth rates were calculated for 1) recaptured, OTC-marked sharks and 2) angler- and research-released, unlabeled sharks for which reliable length estimates were available (n=62 of 317 returns) (Fig. 1A). Growth was estimated with the tag-recapture growth model GROTAG (Francis 1988a, 1988b) on the basis of length and time-at-liberty. This model was chosen because age-based and length-based growth models often differ, and it is a useful alternative for comparison of growth rates at particular sizes (Francis, 1988a; Natanson et al., 2006; Claisse et al., 2009). We used a maximum likelihood approach with this model to estimate growth rates (g_α and g_β) at 2 selected lengths (α and β), a CV of growth variability, mean measurement error and standard deviation, and outlier probability. Therefore, estimated growth of a Shortfin Mako, i, was calculated with the following equation:

$$\Delta L_i = ((\beta g_\alpha - \alpha g_\beta) / (g_\alpha - g_\beta) - L_i) / (1 - (1 + (g_\alpha - g_\beta) / \alpha - \beta)^{\Delta Ti}),$$

where L_i = length at release; and
ΔT_i = the tag deployment time.

Results

Tagging and recapturing oxytetracycline-marked sharks

Off southern California from 1996 to 2010, 940 OTC-injected Shortfin Mako were tagged and released (Fig. 1, A and B). Of the subset of released sharks for which sexes were determined, 67% were males and 33% were females. Average size at release was 110 cm FL (±0.80 SE). Of the released OTC-marked sharks, 35 were recaptured from 2000 to 2010. Of these 35 sharks, 29 fish were selected for this study because they had been at liberty for ≥4 months and OTC marks in the vertebrae fluoresced (Table 1, Fig. 1B). Five samples were excluded from analysis because of a short time-at-liberty (within a range from 24 to 60 days), provided no information on band-pair progression, and in the case of 1 shark, the vertebrae did not fluoresce.

For the 29 fish used in this study, average time-at-liberty was 522 days (±71.0 SE), within a range from 145 to 1594 days, and average size was 109 cm FL (±2.9 SE) at tagging and 148 cm FL (±5.0 SE) at recapture (Table 1). The average displacement distance (great-circle distance from tagging to recapture location) for the 29 OTC-marked Shortfin Mako was 902 km (±291 km SE), within a range from 2 to 5295 km (Fig. 1B). According to results from analyses with linear regressions, no significant effects of time-at-liberty or size-at-tagging existed in relation to total displacement distance ($P>0.05$).

Age validation results

Results from readings of the OTC-marked vertebrae indicated that 2 band pairs are deposited each year in samples analyzed in this study. The observed slope of the relationship between the number of band pairs each year and years-at-liberty significantly differed from the 1:1 relationship ($P<0.01$). Specifically, the average number of band pairs predicted each year was modeled with the following linear regression: average *number of band pairs* = 1.988 × (*number of years-at-large*) – 0.136, $r^2=0.942$ ($P<0.05$) (Fig. 2).

Table 1

Summary table of OTC-marked vertebrae samples from juvenile Shortfin Mako (*Isurus oxyrinchus*) recaptured from 2000 to 2010 in the Southern California Bight for this study. Samples are sorted by time at liberty, and information includes tag and recapture dates and fish lengths and sex. The average number of band pairs (from 3 independent readers) is provided for after the OTC mark and birth band mark (±1 standard error [SE]). NL=either no length estimate or an unreliable one. *=fork length (FL) was converted from total length or alternate length (first dorsal to second dorsal fin).

Fish ID	Time at liberty (days)	Tagging date	Recapture date	Tagging length (cm FL)	Recapture length (cm FL)	Sex	Average number of band pairs after OTC mark (±1SE)	Average number of band pairs after birth band mark (±1SE)
A037789	1594	7/11/2000	11/21/2004	108	200	F	7.3 (0.9)	9.3 (0.7)
A037559	1512	6/21/2001	8/11/2005	110*	190*	M	8.7 (0.3)	11.7 (0.3)
A038423	1198	7/9/2005	10/19/2008	91	157*	M	7.8 (0.6)	11.5 (0.3)
A037655	1133	7/06/2001	8/12/2004	89*	157*	F	5.3 (0.2)	8.2 (0.2)
A038734	836	7/5/2004	10/19/2006	106*	172*	M	5.0 (0.0)	9.0 (0.0)
A038611	733	6/19/2004	6/22/2006	111*	152	F	4.0 (0.0)	6.0 (0.0)
A039992	730	7/28/2007	7/27/2009	92	146	M	4.0 (0.0)	6.0 (0.0)
A039946	555	8/1/2007	2/6/2009	109	150	M	2.5 (0.0)	4.5 (0.0)
A038623	531	6/22/2004	12/05/2005	130*	154	M	2.3 (0.2)	7.3 (0.2)
A058923	463	6/30/2002	10/06/2003	108*	139*	M	2.5 (0.0)	5.2 (0.7)
A058969	446	6/23/2003	9/11/2004	98*	125*	M	2.3 (0.2)	4.7 (0.4)
A040354	407	8/13/2009	9/24/2010	98	137*	M	2.3 (0.2)	3.8 (0.2)
A039341	400	7/24/2007	8/27/2008	131	160*	M	1.5 (0.0)	5.5 (0.0)
A058916	382	7/01/2002	7/18/2003	137*	162*	F	1.5 (0.0)	4.5 (0.0)
A038924	373	7/21/2005	7/29/2006	129	163*	M	2.0 (0.0)	5.5 (0.3)
A039374	364	7/15/2007	7/13/2008	129	154	M	2.0 (0.0)	7.0 (0.0)
A038091	350	6/24/2005	6/9/2006	128	135	M	2.0 (0.0)	7.5 (0.3)
A038404	335	7/8/2005	6/8/2006	117	NL	M	1.5 (0.0)	5.0 (0.3)
A040327	323	8/11/2009	6/30/2010	96	114*	M	2.0 (0.0)	5.0 (0.6)
A038589	313	8/14/2004	6/23/2005	124	141*	M	1.5 (0.0)	7.5 (0.6)
A040251	298	8/4/2009	5/29/2010	105	141*	F	1.0 (0.0)	3.3 (0.3)
A040374	298	8/15/2009	6/9/2010	100	NL	F	1.2 (0.2)	3.2 (0.2)
A040302	277	8/8/2009	5/12/2010	89	103	M	1.2 (0.2)	3.5 (0.3)
A039912	270	8/2/2007	4/28/2008	79	98	F	2.3 (0.2)	3.3 (0.2)
A040788	253	8/23/2009	5/3/2010	124	164*	M	0.8 (0.2)	5.3 (0.2)
A038854	211	7/29/2009	2/25/2010	108	NL	F	0.8 (0.2)	2.7 (0.2)
A039669	206	6/14/2008	1/6/2009	92	NL	M	1.0 (0.0)	3.0 (0.0)
A040798	193	8/24/2009	3/5/2010	122	NL	F	1.0 (0.0)	4.3 (0.2)
A038445	145	7/10/2005	12/2/2005	88	NL	M	1.0 (0.0)	3.3 (0.3)

Results of the vertebral centrum analysis are summarized in Table 1, including time at liberty, average number of band pairs observed distal to the OTC mark, and average number of band pairs observed distal to the birth band. In addition, Figure 3 shows banding patterns and band-pair counts for 5 vertebrae from Shortfin Mako at liberty from 206 to 1512 days.

Visual band-pair counts (identified by arrows in Fig. 3) were agreed upon post hoc by all 3 readers, and 3 samples had full agreement among readers during independent readings; however, 2 samples did not have complete agreement during independent readings. Band-pair counts distal to the OTC mark for sample A037559 were 9, 9, and 8, and distal counts to the birth band were 12, 12, and 11. Sample A039912 had band-pair counts of 2.5, 2.5, and 2 distal to the OTC mark and 3.5, 3.5, and 3 distal to the birth band.

All tagging activities occurred during summer months when translucent zones appeared in the vertebrae (Fig. 3). In contrast, both translucent and opaque zones were found at the outer edge of vertebrae for samples collected throughout the year without any apparent seasonal patterns.

There were no significant differences among band-pair counts distal to the OTC mark (ANOVA; P=0.978) or among total counts distal to the birth band (ANOVA; P=0.955). Age bias was negligible: age-bias plots (Fig. 4) and chi-square tests of symmetry showed no systematic bias (P>0.05), confirming that differences were due to random error. Variability among reader counts was low with an APE of 4.36% and CV of 5.71% for counts distal to the OTC mark and with an APE of 5.65% and CV of 7.73% for counts distal to the birth band. Among readers, 93% (27 of 29) of the final band-pair estimates distal to the OTC were within 1 band pair of each other, and 86% (25 of 29) of the estimates distal to the birth band were within 1 band pair.

The readings distal to the OTC that differed by more than one band pair were from sharks that had been at liberty for the longest time, indicating that variability in band-pair counts increases with age, likely because of disagreement among readers caused by structural artifacts. For example, sample A037789 was from a shark that was at liberty for 1594 days and band-pair estimates distal to the OTC varied from 6 to 9 among the 3 readers for this shark (Table 1).

Length-frequency analysis

A total of 14,720 individual Shortfin Mako were used for the length-frequency analysis that was completed with fishery-dependent data from the California drift gillnet fishery (1981–2009) and fishery-independent data from juvenile Shortfin Mako surveys (1993–2009) (Fig. 5). No differences in length-frequency modes were detected when analyzed by season or sex; therefore, parameter estimates were generated by grouping across factors (season and sex) with age-dependent standard deviation incorporated into the model. Average size of Shortfin Mako used in growth modeling was 121.3 cm FL (±0.25 SE). The majority of fish (85%) ranged in size from 80 to 160 cm FL with 3 identifiable modes consistently present in annual length frequencies regardless of survey type or sex.

Results from MULTIFAN showed these 3 modes at 86, 112, and 134 cm FL, and average modal sizes from MIXDIST were 83, 118, and 147 cm FL. Taking the difference between modal sizes from MULTIFAN analysis provided average annual growth rates of 27 and 23 cm FL for the period from the first to second mode and for the period from the second to third modes, respectively (Table 2). Similarly, annual growth rates from MIXDIST averaged 36 and 29 cm FL for the same 2 periods (Table 2).

Growth of tagged and recaptured sharks

No difference was observed between growth rates calculated from at-liberty OTC-injected sharks (28 and 21 cm per year at 85 and 130 cm FL, respectively) and tag-recaptured sharks not injected (29 and 19 cm per year at 85 and 130 cm FL, respectively); therefore, these data were pooled. The growth rates that resulted from GROTAG analysis of lengths of tagged and recaptured sharks were similar to the growth rates from length-frequency calculations, averaging 29 and 20 cm per year at 85 and 130 cm FL, respectively (Table 2).

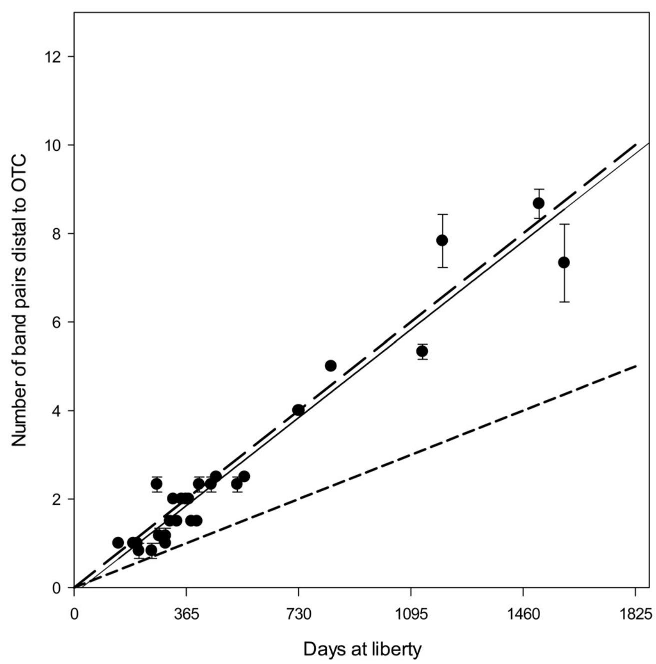

Figure 2

Average number of band-pairs (translucent and opaque) for the number of days at liberty, determined from the oxytetracycline (OTC) mark to the outer centrum edge on vertebrae of juvenile Shortfin Mako (*Isurus oxyrinchus*) (n=29) tagged from 2000 to 2010 in the Southern California Bight for this study. Readings were based on 3 independent readers (±1 standard error [SE]). The solid line shows the linear regression of number of band pairs relative to days at liberty, and the lines with short and long dashes show predicted number of band pairs for 1 band pair/year and 2 band pairs/year, respectively.

Discussion

Results of this study indicate that 2 band pairs are deposited each year in juvenile Shortfin Mako tagged and released in southern California. The fast growth rates collectively obtained through the use of OTC-marked vertebrae, MULTIFAN and MIXDIST length-frequency analyses, and tag-recapture growth models were consistent, providing strength to our results beyond the usefulness possible with the employment of a single method alone. Further, a sample size of 29 OTC-marked vertebrae of Shortfin Mako at liberty from 4 months to more than 4 years is the most comprehensive OTC tag-return data set reported for this species. We also compared our total band-pair counts at length with those of Cailliet et al. (1983), the only other Shortfin Mako age and growth study completed

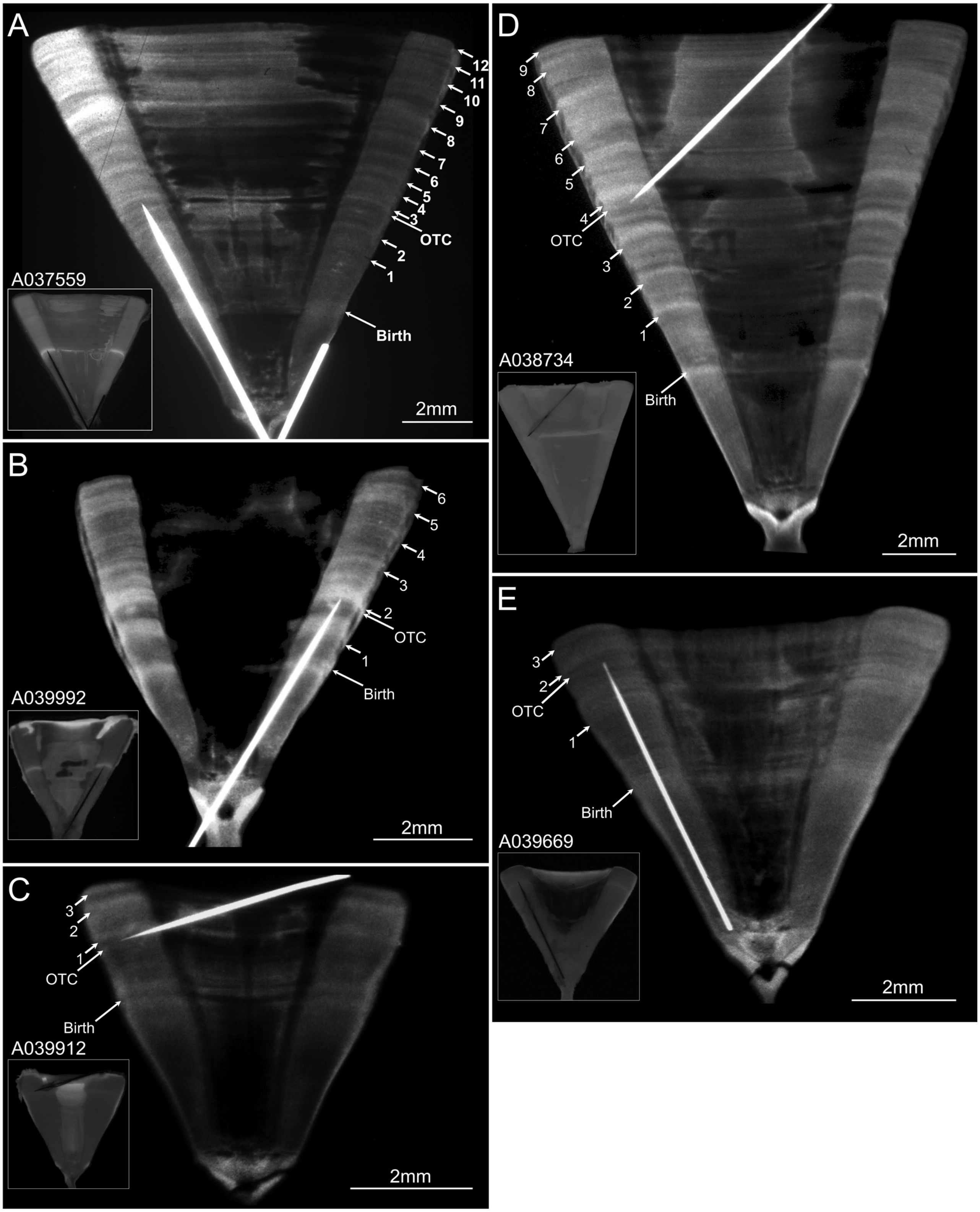

Figure 3

X-ray images of vertebrae sections that show band-pair progression of 5 OTC-marked juvenile Shortfin Mako (*Isurus oxyrinchus*) recaptured during this study off southern California. The small inset in each image shows the OTC fluorescence under UV light. Translucent or hyaline (rapid growth) bands or darker areas of vertebrae show periods of rapid growth, and opaque bands or lighter areas of vertebrae show periods of slow growth. Arrows indicate band-pair counts.

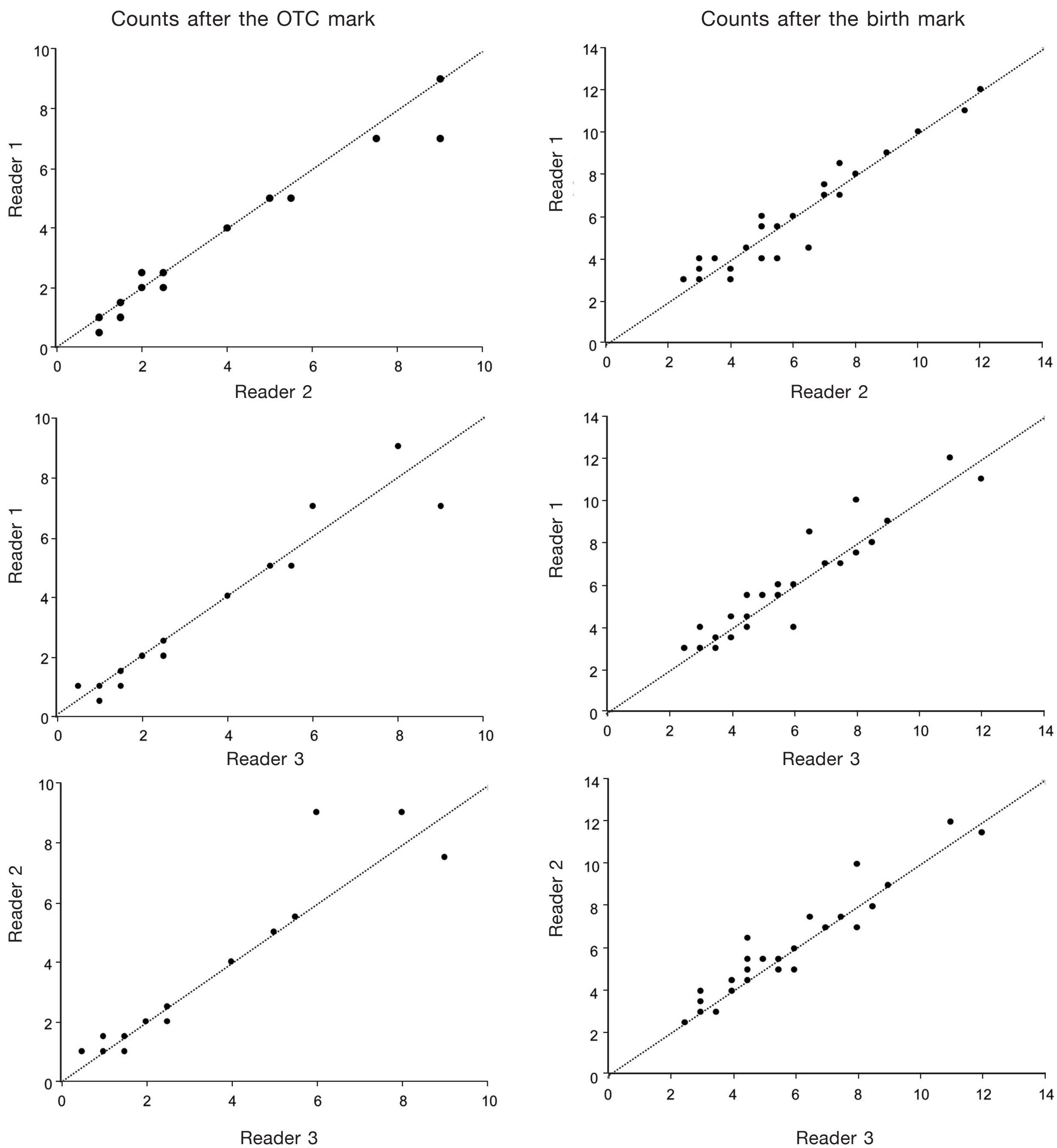

Figure 4

Age-bias plots for all OTC-marked juvenile Shortfin Mako (*Isurus oxyrinchus*) independently aged by 3 readers during this study. Graphs in the left column represent total band-pair counts distal to the OTC mark, and graphs in the right column represent total band-pair counts distal to the birth band.

in this region, to determine if vertebral readings or assumptions about growth-band deposition differed. Total band-pair counts relative to fish size in this study were very similar to the average band-pair counts, relative to fish size, obtained by Cailliet et al. (1983) (Fig. 6). This finding indicates that vertebral readings were similar between the 2 studies and only the assumption about deposition rates differed.

Given differences in the rates of band-pair deposition of Shortfin Mako in other studies, our findings

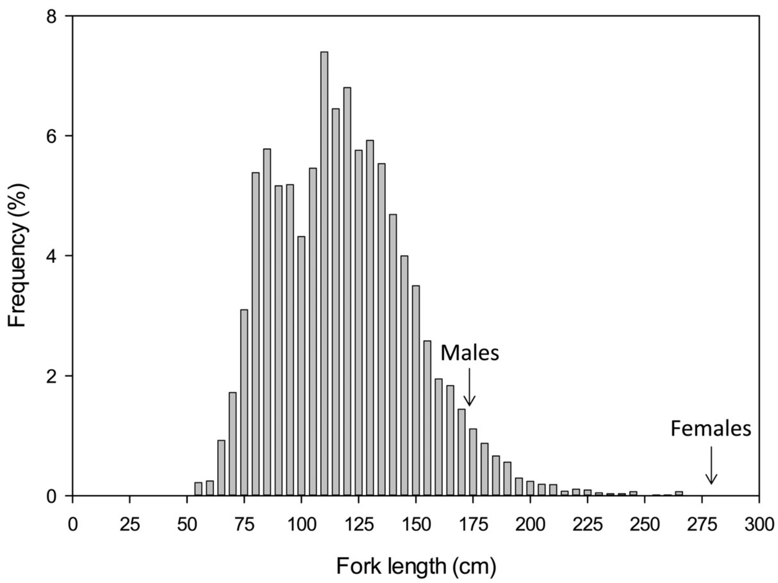

Figure 5

Total percent length-frequency distribution of Shortfin Mako (*Isurus oxyrinchus*) collected from fishery-dependent (1981–2009) and fishery-independent (1993–2009) surveys conducted in the Southern California Bight. Vertical bars are placed in length bins of 5 cm along the x-axis, showing the range of fork lengths (FL) from 55 to 265 cm FL. Arrows show the approximate size at 50% maturity for males and females determined by Semba et al. (2011).

should not be extrapolated beyond our size range and geographic area; however, our results indicate that growth patterns of juvenile and adult Shortfin Mako merit additional research.

The differences in rates of band-pair deposition of Shortfin Mako among studies may be due to a number of factors, including study location, methods, and ontogeny. Rates of band-pair deposition of the Common Carp (*Cyprinus carpio*) vary geographically among similar age classes of the same species; biannual deposition occurs in South Africa (Winker et al., 2010) and annual deposition occurs in Australia (Brown et al., 2004), exemplifying the importance of regional age validation.

In one of the first Shortfin Mako aging studies, Pratt and Casey (1983) read silver-nitrate-stained, whole vertebral centra collected in the northwest Atlantic and suggested that 2 band pairs were deposited annually, after noting that calculated growth under this assumption closely matched direct observations of growth over time for this species (especially for fish ≤200 cm FL). Pratt and Casey's (1983) growth curves were generated from tag-recapture growth data collected in the field, temporal analysis of length-month information, and a vertebral age-based growth curve corroborated and compared with length-frequency mode analyses.

In contrast, Cailliet and Bedford (1983) and Cailliet et al. (1983) used hard (high-frequency) X-radiography and silver nitrate staining of whole centra to elucidate banding patterns of Shortfin Mako in the northeast Pacific. The authors of both studies assumed that only 1 band pair was deposited annually and obtained a growth rate of about half the rate of that of Pratt and Casey (1983), but they did not test the assumption of 1 versus 2 band pairs per year.

Campana et al. (2002) concluded that the hypothesis of a single band pair was the most consistent with the banding pattern obtained from a 21-year-old Shortfin Mako (328 cm FL) collected from the northeast Atlantic and aged with bomb-radiocarbon techniques. Ardizzone

Table 2

Estimates from the tag-recapture growth model with GROTAG for juvenile Shortfin Mako (*Isurus oxyrinchus*) in the eastern Pacific (n=62). Growth estimates from the length-frequency techniques (MULTIFAN and MIXDIST) also are included for the first 2 age classes. K=Brody growth parameter, L_∞=mean asymptotic length.

Parameter	Symbol (unit)	Tag-recapture growth model	Length frequency (MULTIFAN)	Length frequency (MIXDIST)
Growth rate	g_{85} (cm/year)	29	27	36
	g_{130} (cm/year)	20	23	29
K	(per year)	0.19	0.17	
L_∞	(cm)	231.03	252.12	
Growth variability	ν	0.31		
Mean measurement error	m (cm)	2.87		
Standard deviation measurement error	s	4.46		
Log likelihood	λ	–235.8		

et al. (2006) expanded on this study with 54 samples used for radiocarbon chronologies. Their results supported the hypothesis of annual band-pair deposition for older ages, but they did not rule out biannual band-pair deposition for young fish. Similarly, Natanson et al. (2006) reiterated the aforementioned results and presented evidence of annual band-pair formation from an OTC-injected, 241-cm-FL, male Shortfin Mako at liberty for just over 1 year. However, growth curves generated from their tag-recapture and length-frequency data showed a much faster growth rate for young Shortfin Mako than the rate calculated from vertebrae data, and the authors suggested the possibility that rates of band deposition may change with ontogeny.

Bishop et al.[1] and Bishop et al. (2006) examined age and growth of Shortfin Mako from New Zealand waters and assumed a deposition rate of 1 band pair per year on the basis of Campana et al. (2002) and Ribot-Carballal et al. (2005). They obtained a growth curve similar to that of Cailliet et al. (1983), and their best-fit Schnute growth model predicted that growth was fast for the first few years of life (39 cm during year 1), then slowed for older ages to a rate that is similar to juvenile growth rates found in our study. Like Pratt and Casey (1983), they found that length-frequency data indicated considerably faster growth than did estimates from vertebral ages for the younger age classes with the assumption of 1 band pair per year. Through the use of cohort analysis, Maia et al. (2007) also reported fast growth in juvenile Shortfin Mako collected from the longline fishery in the eastern North Atlantic (average growth rate of 61.1 cm/year for the first year, and 40.6 cm/year for the second year).

More recently, Okamura and Semba (2009) and Semba et al. (2009) examined monthly centrum edge patterns with a new statistical method and surface shadow technique to determine periodicity of band-pair formation. Their results indicated that the deposition of band pairs in Shortfin Mako in the western and central North Pacific has an annual cycle, but they also warned about sources of error from inaccuracies in centrum margin readings and from a large variability in the timing and duration of band deposition.

Biannual band-pair deposition is not species-specific to Shortfin Mako; it reportedly has occurred in other shark species as well. Chen et al. (1990) and Anislado-Tolentino et al. (2008) suggested biannual band-pair deposition in the Scalloped Hammerhead (*Sphyrna lewini*). In addition, Parker and Stott (1965) suggested that 2 band pairs were laid down annually in the Basking Shark (*Cetorhinus maximus*); however, those conclusions were questioned by Pauly[4] (2002). Further, Natanson et al. (2008) examined vertebral growth patterns in *C. maximus* as a function of ontogeny and questioned the feasibility of aging this species with vertebral band-pair counts.

Ontogenetic differences may play a critical role in band-pair formation for Shortfin Mako, as well. Unfortunately, none of our OTC-marked vertebrae were from sharks >200 cm FL at tagging or recapture, but the 3 largest sharks at recapture (172, 190, and 200 cm FL) exhibited a pattern consistent with biannual deposition. Two of these sharks (200 and 190 cm FL) were at liberty for more than 4 years and averaged 7.3 and 8.7 band pairs distal to the OTC mark, respectively, indicating that the biannual pattern continues in fish of this size. Both had similar total band-pair counts, averaging 9.3 and 11.7, respectively.

If one assumes a biannual pattern, as indicated by our OTC marking results, these fish would range from

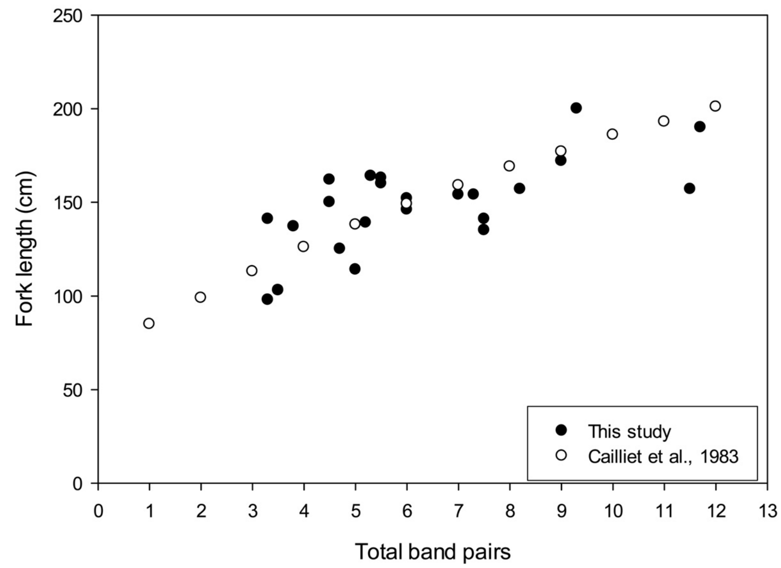

Figure 6

Individual band-pair counts relative to size, shown in fork length (cm), of juvenile Shortfin Mako (*Isurus oxyrinchus*) from this study (*n*=29) compared with the average number of band-pair counts relative to size by Cailliet et al. (1983). Vertebral readings were similar between these 2 studies, and only the assumption about deposition rates differed. Sharks for both studies were captured off southern California.

[4] Pauly, D. 1978. A critique of some literature data on the growth, reproduction and mortality of the lamnid shark, *Cetorhinus maximus* (Gunnerus). ICES Coucil Meeting Doc. 1978/H:17, 10 p.

4.5 to 6 years of age when collected. Examination of vertebral centra from some of our larger, non-OTC-tagged, recaptured Shortfin Mako reveals that as fish approach maturity, banding patterns appear to become more distinct, with both fast and slow growth zones becoming more regular and evenly spaced. Therefore, it is possible that these larger fish, on entering a more oceanic realm, change the periodicity of their banding pattern. On the basis of these results, it appears that Shortfin Mako ≤200 cm FL and found off California grow much faster than previously thought, with observed rapid growth (biannual band deposition) for approximately the first 6 years of life. Slower growth (annual deposition) thereafter may occur but cannot be confirmed by this study.

Mechanisms that drive the observed biannual band-pair deposition may be linked to seasonal migration patterns and subsequent food availability. Through the use of similar OTC tag-recapture methods, Murphy et al. (1998) determined that Black Drum (*Pogonias cromis*) begin to deposit biannual band pairs after 4 years of age because of a shift in migration patterns. Similarly, Shortfin Mako tagged in southern California appear to exhibit a biannual growth cycle, with fast-growth periods (wide, translucent band formation) in summer and winter and slow-growth periods (narrow, opaque band formation) in spring and fall. One possible explanation is that, as coastal waters warm and cool seasonally, juvenile Shortfin Mako move between rich feeding grounds off California in the summer and off Mexico in the winter and spend spring and fall migrating between these feeding areas.

Of the 15 OTC-marked sharks recaptured in Baja Mexico waters (Fig. 1B), only 2 sharks were recaptured during summer months. In contrast, 70% of the returns of OTC-marked sharks in California coastal waters occurred during summer and there were no returns in the winter. In addition, on the basis of data from all tag recaptures (OTC and non-OTC-marked sharks, n=317, senior author, unpubl. data), 40% of all shark recaptures in Mexico (south of 30°N) occurred during winter, but only 7% of sharks were recaptured in Mexico during summer. Likewise, 58% and 7% of all recaptures in California coastal waters occurred during summer and winter seasons, respectively. Preliminary analysis of movements of juvenile (<150 cm FL) Shortfin Mako tracked with satellite tags (2003–10, n=26) also shows high relative densities of Shortfin Mako at reported locations off Baja California, Mexico, in the winter and off California in the summer and more dispersive offshore movements in the spring and fall (S. Kohin, unpubl. data).

Tag-recapture techniques with OTC are among the most powerful methods for validation of age and growth patterns in fishes, but there are difficulties with this method. One disadvantage in the use of chemical marking and recaptures is that the number of band pairs formed for short times between tagging and recapture is often low, resulting in a potentially large relative error if one of the band pairs (such as on the growing edge) is misinterpreted (Campana, 2001). For example, misinterpretation of a single growth zone in a fish at liberty for 2 years would result in a 50% error, but the same misinterpretation in a fish at liberty for 10 years would produce an error of only 10%. Fortunately, the relatively large sample size of 15 sharks at liberty for more than 1 year and 4 sharks at liberty for more than 3 years (2 of them for more than 4 years) allowed us to confirm the consistent banding patterns between both short- and long-term deployments.

An additional problem with the use of chemical marking techniques, such as with OTC, is that growth may be inhibited (Pfizer,[5] 1975; Monaghan, 1993); however, other researchers that have worked with elasmobranchs have shown OTC to have little adverse effects on growth (Tanaka [1990] for the Japanese Wobbegong [*Orectolobus japonicus*] and Gelsleichter et al. [1998] for the Nurse Shark [*Ginglymostoma cirratum*]). Further, this problem does not appear relevant in this study because fast (i.e., not inhibited) growth was observed with our OTC-marked juveniles.

Conclusions

Direct and indirect methods used in this study indicate rapid growth of juvenile Shortfin Mako in southern California and the OTC-marked vertebrae support a pattern of biannual deposition for the first 5 years of life. Accurate age and growth parameters in stock assessment models are important for fisheries management and are necessary for calculations of growth and mortality rates, age at recruitment, and longevity. This article highlights the need to continue life history studies of elasmobranch species throughout different regions and ocean basins.

Acknowledgments

We thank personnel of the Southwest Fisheries Science Center for assistance in tagging and logistical operations to make this study possible: specifically, D. Holts, R. Rasmussen, R. Vetter, and J. Wraith. We also thank NOAA Fisheries observers for their diligent work in collecting specimens and length data and to the many anglers and commercial operators for returning OTC-marked vertebrae. We especially thank O. Sosa-Nishizaki for help with collection and shipment of samples from Mexico, G. Morse for sharing microscope and imaging equipment, and both A. Andrews and M. Francis for valuable suggestions and comments on earlier drafts.

[5] Pfizer, Inc. 1975. Oxytetracycline intramuscular solution leaflet 60-1051-00-8, 2 p. Pfizer Lab. Div., New York.

Literature cited

Anislado-Tolentino, V., M. Gallardo-Cabello, F. Amezcua-Linares, and C. Robinson-Mendoza.
2008. Age and growth of the scalloped hammerhead shark, *Sphyrna lewini* (Griffith & Smith, 1834) from the Southern coast of Sinaloa, México. Hidrobiológica 18:31–40.

Ardizzone, D., G. M. Cailliet, L. J. Natanson, A. H. Andrews, L. A. Kerr, and T. A. Brown.
2006. Application of bomb radiocarbon chronologies to shortfin mako (*Isurus oxyrinchus*) age validation. Environ. Biol. Fishes 77:355–366.

Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Beamish, R. J., and G. A. McFarlane.
2000. Reevaluation of the interpretation of annuli from otoliths of a long-lived fish, *Anoplopoma fimbria*. Fish. Res. 46:105–111.

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

Bowker, A. H.
1948. A test for symmetry in contingency tables. J. Am. Stat. Assoc. 43:572–574.

Branstetter, S., and J. A. Musick.
1994. Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. Trans. Am. Fish. Soc. 123:242–254.

Brown, P., C. Green, K. P. Sivakumaran, D. Stoessel, and A. Giles.
2004. Validating otolith annuli for annual age determination of common carp. Trans. Am. Fish. Soc. 133:133–196.

Cailliet, G. M., and D. S. Bedford.
1983. The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. CalCOFI Rep. 24:57–69.

Cailliet, G. M., L. K. Martin, J. T. Harvey, D. Kusher, and B. A. Welden.
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; 15–18 February 1982 (E. D. Prince and L. M. Pulos, eds.), p. 179–188. NOAA Tech. Rep. NMFS 8.

Campana, S. E.
2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59:197–242.

Campana, S. E., L. J. Natanson, and S. Myklevoll.
2002. Bomb dating and age determination of the large pelagic sharks. Can. J. Fish. Aquat. Sci. 59:450–455.

Casey, J. G., and N. E. Kohler.
1992. Tagging studies on the shortfin mako shark *(Isurus oxyrinchus)* in the western North Atlantic. Aust. J. Mar. Freshw. Res. 43:45–60.

Cerna, F., and R. Licandeo.
2009. Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. Mar. Freshw. Res. 60:394–403.

Chang, W. Y. B.
1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208–1210.

Chen, C. T., T. C. Leu, S. J. Joung, and N. C. H. Lo.
1990. Age and growth of the scalloped hammerhead, *Sphyrna lewini*, in northeastern Taiwan waters. Pac. Sci. 44:156–170.

Claisse, J. T., M. Kienzle, M. E. Bushnell, D. J. Schafer, and J. D. Parrish.
2009. Habitat- and sex-specific life history patterns of yellow tang *Zebrasoma flavescens* in Hawaii, USA. Mar. Ecol. Prog. Ser. 389:245–255.

Compagno, L. J. V.
2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Vol. 2: Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes 1, 269 p. FAO, Rome.

Cortés, E.
2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv. Biol. 16:1048–1062.

Duffy, C., and M. P. Francis.
2001. Evidence for summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. Z. J. Mar. Freshw. Res. 35:319–324.

Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton.
1990. MULTIFAN: a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47:301–317.

Francis, R. I. C. C.
1988a. Are growth parameters estimated from tagging and age-at-length data comparable? Can. J. Fish. Aquat. Sci. 45:936–942.
1988b. Maximum likelihood estimation of growth and growth variability from tagging data. N. Z. J. Mar. Freshw Res 22:43–51.

García, V. B., L. O. Lucifora, and R. A. Myers.
2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimeras. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 275:83–89.

Gelsleichter, J., E. Cortés, C. A. Manire, R. E. Heuter, and J. A. Musick.
1998. Evaluation of oxytetracycline on growth of captive nurse sharks, *Ginglymostoma cirratum*. Fish. Bull. 96:624–627.

Goldman, K. J.
2005. Age and growth of elasmobranch fishes. *In* Management techniques for elasmobranch fisheries (J. A. Musick and R. Bonfil, eds.), p. 76–102. FAO Fish. Tech. Pap. 474. FAO, Rome.

Hoenig, J. M., J. M. Morgan, and C. A. Brown.
1995. Analyzing differences between two age determination methods by tests of symmetry. Can. J. Fish. Aquat. Sci. 52:364–368.

Holts, D. B., and D. W. Bedford.
1993. Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the southern California bight. Aust. J. Mar. Freshw. Res. 44:901–909.
Joung, S. J., and H. H Hsu.
2005. Reproduction and embryonic development of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, in the northwestern Pacific. Zool. Stud. 44:487–496.
Kusher, D. I., S. E. Smith, and G. M. Cailliet.
1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Environ. Biol. Fishes 35:187–203.
MacDonald, P. D. M., and T. J. Pitcher.
1979. Age-groups from size-frequency data: a versatile efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36:987–1001.
Maia, A., N. Queiroz, H. N. Cabral, A. M. Santos, and J. P. Correia.
2007. Reproductive biology and population dynamics of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, off the southwest Portuguese coast, eastern North Atlantic. J. Appl. Ichthyol. 23:246–251.
Mollet, H. F., G. Cliff, H. L. Pratt, and J. D. Stevens.
2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fish. Bull. 98:299–318.
Monaghan, J. P.
1993. Comparison of calcein and tetracycline as chemical markers in summer flounder. Trans. Am. Fish. Soc. 122:298–301.
Murphy, M. D., D. H. Adams, D. M. Tremain, and B. L. Winner.
1998. Direct validation of ages determined for adult black drum, *Pogonias cromis*, in east-central Florida, with notes on black drum migration. Fish. Bull. 96:382–387.
Natanson, L. J., N. E. Kohler, D. Ardizzone, G. M. Cailliet, S. P. Wintner, and H. F. Mollet.
2006. Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ. Biol. Fishes 77:367–383.
Natanson, L. J., S. P. Wintner, F. Johansson, A. Piercy, P. Campbell, A. D. Maddalena, S. J. B. Gulak, B. Human, F. C. Fulgosi, D. A. Ebert, F. Hemida, F. H. Mollen, S. Vanni, G. H. Burgess, L. J. V. Compagno, and A. Wedderburn-Maxwell.
2008. Ontogenetic vertebral growth patterns in the basking shark *Cetorhinus maximus*. Mar. Ecol. Prog. Ser. 361:267–278.
Okamura, H., and Y. Semba.
2009. A novel statistical method for validating the periodicity of vertebral growth band formation in elasmobranch fishes. Can. J. Fish. Aquat. Sci. 66:771–780.
PFMC (Pacific Fishery Management Council).
2011. Fishery management plan for U.S. West Coast fisheries for highly migratory species. As amended through Amendment 2, 106 p. Pacific Fishery Management Council, Portland, OR. [Available from http://www.pcouncil.org/highly-migratory-species/fishery-management-plan-and-amendments/.]
Parker, H. W., and F. C. Stott.
1965. Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). Zool. Meded. 40:305–319.
Pauly, D.
2002. Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. *In* Elasmobranch biodiversity, conservation and management. Proceedings of the international seminar and workshop; Sabah, Malaysia, July 1997 (S. L. Fowler, T. Reid, and F. A. Dipper, eds.), p. 199–208. Occasional Papers of the IUCN Survival Commission, no. 25. Int. Union Conserv. Nature, Gland, Switzerland.
Pratt, H. L., Jr., and J. G. Casey.
1983. Age and growth of shortfin mako, *Isurus oxyrinchus*, using four methods. Can. J. Fish. Aquat. Sci. 40:1944–1957.
R Development Core Team.
2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing. [Available from: http://R-project.org, accessed November 2008.]
Ribot-Carballal, M. C., F. Galván-Magana, and C. Quinonez-Velazquez.
2005. Age and growth of the shortfin mako shark, *Isurus oxyrinchus*, from the western coast of Baja California Sur, Mexico. Fish. Res. 75:14–21.
Semba, Y., H. Nakano, and I. Aoki.
2009. Age and growth analysis of the shortfin mako shark, *Isurus oxyrinchus*, in the western and central North Pacific Ocean. Environ. Biol. Fishes 84:377–391.
Semba, Y. I. Aoki, and K. Yokawa.
2011. Size at maturity and reproductive traits of shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific. Mar. Freshw. Res. 62:20–29.
Smith, S. E., D. W. Au, and C. Show.
1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Mar. Freshw. Res. 49:663–678.
Smith, S. E., R. A. Mitchell, and D. Fuller.
2003. Age-validation of a leopard shark recaptured after 20 years. Fish. Bull. 101:194–198.
Stevens, J. D.
2008. The biology and ecology of the shortfin mako shark, *Isurus oxyrinchus*. *In* Sharks of the open ocean: biology, fisheries and conservation (M. D. Camhi, E. K. Pikitch, and E. A. Babcock, eds), p. 87–94. Blackwell Publ., Ltd., Oxford.
Tanaka, S.
1990. Age and growth studies on the calcified structures of newborn sharks in the laboratory aquaria using tetracycline. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries (H. L. Pratt Jr., S. H. Gruber, and T. Taniuchi, eds.), p. 189–202. NOAA Tech. Rep. NMFS 90.
Taylor, V. B., and D. W. Bedford.
2001. Shortfin mako shark. *In* California living marine resources: a status report (W. S. Leet, C. M. DeWees, R. Klingbeil, and E. J. Larson, eds), p. 336–337. Publication SG01-11, California Dep. Fish Game, Sacramento, CA.
Winker, H., O. L. F. Weyl, A. J. Booth, and B. R. Ellender.
2010. Validating and corroborating the deposition of two annual growth zones in asteriscus otoliths of common carp *Cyprinus carpio* from South Africa's largest impoundment. J. Fish Biol. 77:2210–2228.