# The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia

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# The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia

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The life histories of two globally endangered hammerhead sharks, *Sphyrna lewini* and *Sphyrna mokarran*, were examined using samples collected from a range of commercial fisheries operating along the east coast of Australia. The catch of *S. lewini* was heavily biased towards males, and there were significant differences in von Bertalanffy growth parameters ($L_\infty$ and $k$) and maturity [stretched total length ($L_{ST}$) and age ($A$) at which 50% are mature, $L_{ST50}$ and $A_{50}$] between those caught in the tropics ($L_\infty = 2119$ mm, $k = 0.163$, $L_{ST50} = 1471$ mm, $A_{50} = 5.7$ years) and those caught in temperate waters ($L_\infty = 3199$ mm, $k = 0.093$, $L_{ST50} = 2043$ mm, $A_{50} = 8.9$ years). The best-fit estimates for a three-parameter von Bertalanffy growth curve fit to both sexes were $L_\infty = 3312$ mm, $L_0 = 584$ mm and $k = 0.076$. Males attained a maximum age of 21 years and grew to at least 2898 mm $L_{ST}$. The longevity, maximum length and maturity of females could not be estimated as mature animals could not be sourced from any fishery. Length at birth inferred from neonates with open umbilical scars was 465–563 mm $L_{ST}$. There was no significant difference in length and age at maturity of male and female *S. mokarran*, which reached 50% maturity at 2279 mm $L_{ST}$ and 8.3 years. *Sphyrna mokarran* grew at a similar rate to *S. lewini* and the best-fit estimates for a two-parameter von Bertalanffy equation fit to length-at-age data for sexes combined with an assumed mean length-at-birth of 700 mm were $L_\infty = 4027$ mm and $k = 0.079$. Females attained a maximum age of 39.1 years and grew to at least 4391 mm $L_{ST}$. The oldest male *S. mokarran* was 31.7 years old and 3691 mm $L_{ST}$. Validation of annual growth-band deposition in *S. mokarran* was achieved through a mark, tag and recapture study.  © 2011 The Authors

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Key words: age and growth; age validation; maturity; *Sphyrna*.

## INTRODUCTION

The scalloped hammerhead *Sphyrna lewini* (Griffith & Smith 1834) and great hammerhead *Sphyrna mokarran* (Rüppell 1837) are two species of large, coastal–pelagic, semi-oceanic sharks found in tropical and warm temperate waters circumglobally

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(Compagno *et al.*, 2005). Both are a target or by-catch species in a wide variety of fisheries throughout their range and substantial population declines are suspected to have occurred in many areas as a result of fishing (Dudley & Simpfendorfer, 2006; Ferretti *et al.*, 2008; Hayes *et al.*, 2009; de Jong, 2009). Clarke *et al.* (2006) estimated that fins from hammerheads *S. lewini*, *S. mokarran* and *Sphyrna zygaena* (L. 1758) made up around 6% of the Hong Kong shark-fin trade. The ongoing demand for hammerhead fins, which are among the most highly valued of all shark fins, suggests that depletion is likely to continue at current levels of fishing. This inference is supported by an 80% increase in global reported catch of hammerheads between 2000 and 2007 (Lack & Sant, 2009). Consequently, both *S. lewini* and *S. mokarran* have been assessed as 'endangered' by the International Union for the Conservation of Nature (IUCN) (Baum *et al.*, 2007; Denham *et al.*, 2007).

In Australian waters, *S. lewini* and *S. mokarran* are considered to be less affected by fisheries than in other parts of the world and were assessed as 'least concern' in a regional IUCN assessment (Cavanagh *et al.*, 2003). There are few long-term indices of hammerhead abundance in Australian waters, however, so this should be viewed cautiously. Indeed, Australian stocks are subject to fishing pressures similar to those in other parts of the world. On the east coast of Australia for example, *S. lewini* and *S. mokarran* make up around *c*. 7 and 10% of the biomass of elasmobranchs caught in inshore, small-mesh, gillnet fisheries in the Great Barrier Reef World Heritage Area (GBRWHA) (Harry *et al.*, 2011). Both are also killed in bather protection programmes at metropolitan beaches along the coast using drum-lines and large-mesh gillnets (Dudley, 1997). A mid-shelf, demersal, longline fishery targets adults and sub-adults of these species south of the GBRWHA (Macbeth *et al.*, 2009), and a small number of hammerheads (probably *S. lewini* and *S. mokarran*) are also caught by pelagic longline fisheries operating offshore (AFMA, 2008). Trawl and recreational fisheries also affect these species to some extent throughout their range on the east coast of Australia. Fishing pressures across other parts of northern Australia are similar to those on the east coast (Bensley *et al.*, 2010) while an unknown but potentially high level of illegal, unreported and unregulated (IUU) fishing for sharks also occurs in waters off northern Australia (Lack & Sant, 2008; Field *et al.*, 2009).

As with many elasmobranch species, Australian and global management of *S. lewini* and *S. mokarran* stocks suffers from a critical lack of life-history data that is necessary for informed and effective management of these species. The wide distribution of *S. lewini* and its large contribution to a range of fisheries has led to numerous studies on its life history (Stevens & Lyle, 1989; Chen *et al.*, 1990; Hazin *et al.*, 2001; Tolentino & Mendoza, 2001; de Bruyn *et al.*, 2005; Piercy *et al.*, 2007; White *et al.*, 2008). Despite extensive study, life-history information available for *S. lewini* is still fragmentary. This may be partly due to the complex patterns of spatial organization and migration of this species. Indeed, few studies have been able to obtain adequate samples from all components of the population, with adult females, adult males and juveniles often residing in different areas (Klimley, 1987; White *et al.*, 2008). Studies on growth rates for *S. lewini* in particular are confounded by a number of factors including probable methodological differences, a lack of validation and intraspecific differences between populations (Branstetter, 1987; Chen *et al.*, 1990; Tolentino & Mendoza, 2001; Piercy *et al.*, 2007). In the case of *S. mokarran*, its particularly large size and inherently low abundance in most areas has resulted in few studies on the life history of this species, and the first estimates of growth

rates have only recently become available (Piercy *et al.*, 2010). Given the ongoing exploitation of these species throughout the world and especially in the Asia-Pacific region, along with the urgent requirement for life-history data to inform fisheries managers, this study examined the age, growth and maturity of *S. lewini* and *S. mokarran* in eastern Australian waters. In addition to providing a general growth model for *S. lewini* off eastern Australia, this study examined apparent spatial differences in growth and maturity of males between tropical and temperate waters.

# METHODS

## SAMPLE COLLECTION

Biological samples were collected between December 2005 and May 2010 from a number of fishery-dependent sources along the east coast of Australia from Princess Charlotte Bay, Queensland (13° 54′ S) to the waters off Laurieton, New South Wales (31° 36′ S) (Fig. 1). The majority of samples were obtained from a fishery observer programme monitoring the commercial gillnet sector of the Queensland east coast inshore finfish fishery (ECIFF) (Harry *et al.*, 2011), in shallow waters up to 25 m depth. Additional fishery-dependent samples were sourced opportunistically from: the Queensland east coast otter trawl fishery (unknown depth); mid-shelf, demersal longline fisheries operating in both Queensland and New South Wales waters (30–110 m depth) (Macbeth *et al.*, 2009) and the Queensland shark control programme. Shark length was measured as stretched total length ($L_{ST}$) in mm following Compagno (1984): the animal was placed ventral side down and the upper lobe of the caudal fin was depressed in line with the body axis. Additional measurements of fork ($L_F$) and pre-caudal ($L_{PC}$) length were recorded for a sub-sample of animals.
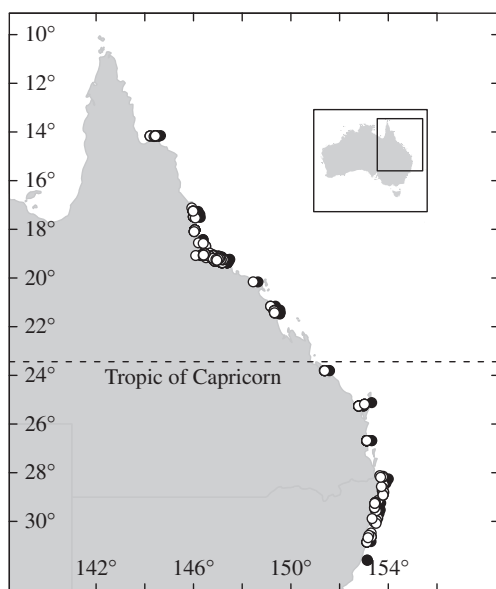


FIG. 1. Location of the study area showing sampling locations of *Sphyrna lewini* (○) and *Sphyrna mokarran* (●) off eastern Australia. Apparent spatial differences in growth and maturity of male *S. lewini* were examined by including region as a factor in growth and maturity analyses. Region was a two-level factor (tropic and temperate) with samples separated into the two nominal regions by the Tropic of Capricorn.

## VERTEBRAL PROCESSING AND GROWTH ANALYSIS

A section of five vertebrae was removed from the anterior region of the vertebral column between the gills and the first dorsal fin and stored frozen. A scalpel was used to remove the neural and haemal arches and soft tissue leaving only the vertebral centra. Centra were then soaked in a solution of 5% sodium hypochlorite (bleach) for *c*. 30 min to remove remaining tissue, then rinsed thoroughly under tap water, and placed in a drying oven at $60°$ C for 24 h. One of the five centra prepared from each individual was selected for ageing. A single $400–600$ µm longitudinal section was taken through the focus of the centrum using a slow-speed saw with a diamond-tipped blade (Buehler; www.buehler.com) (Cailliet & Goldman, 2004). Centra $<10$ mm in diameter were cast in a clear polyester resin prior to sectioning as they were too small to fit in the vice of the saw. The vertebral section was fixed to a glass slide using Crystal Bond adhesive (SPI Supplies; http://www.2spi.com/).

Sectioned centra were examined under a dissecting microscope using transmitted light and the age of an animal was determined by counting the pairs of opaque and translucent (hyper- and hypomineralized) growth bands deposited on the corpus calcareum (Cailliet & Goldman, 2004) (Fig. 2). The birth mark (age 0) was identifiable by a change of angle on the corpus calcareum (Fig. 2). Data from the present study suggested that *S. lewini* pups were being born throughout the year, so partial ages could not be assigned for this species although neonates with unhealed umbilical scars were given an age of zero. For *S. mokarran*, which has a well-defined, seasonal, reproductive cycle (Stevens & Lyle, 1989), partial ages were assigned using a mean population birth date of 1 November. Prior to ageing all centra, a random sub-sample of 50 individuals was read by two readers to ensure that a consensus was reached regarding interpretation of the banding pattern. Inter-reader precision was evaluated using Chang's (1982) method of the coefficient of variation (C.V.) and per cent agreement following the method of Goldman *et al*. (2006). Inter-reader bias was evaluated statistically using Bowker's test of symmetry (Evans & Hoenig, 1998). A single reader then aged each vertebra twice. Intra-reader precision and bias were evaluated as described for two readers above.

A multi-model inference (MMI) information theoretical approach was used to determine the most appropriate growth model for each species (Burnham & Anderson, 2001; Katsanevakis & Maravelias, 2008). Following Thorson & Simpfendorfer (2009), an *a priori* set of five candidate models was fitted to the length-at-age data, with each model representing an alternative hypothesis for growth (Katsanevakis, 2006). The candidate set consisted of a three-parameter
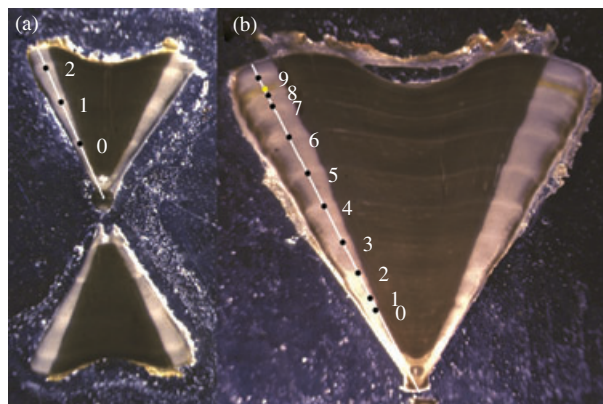


FIG. 2. Sectioned vertebral centrum from (a) an 1145 mm stretched total length ($L_{ST}$) male *Sphyrna lewini* with two growth-band pairs visible, and (b) a 2598 mm $L_{ST}$ male *Sphyrna mokarran* with nine growth-band pairs visible. The vertebral centrum in (b) is from individual GHH4 (Table I) that was injected with calcein and recaptured after 467 days at liberty. Translucent bands on the vertebrae are denoted by ● and the calcein mark denoted by ●. Age 0 corresponds to the birth mark.

version of the von Bertalanffy growth model (VB3), $L_t = L_0 + (L_\infty - L_0)[1 - e^{(-kt)}]$ where $L_t$ is length at age $t$ and $L_0$ (length at birth), $L_\infty$ (asymptotic length) and $k$ (growth completion coefficient) are fitted parameters. A two-parameter version of the von Bertalanffy growth model with a fixed length at birth for each species was also used (VB2). In the VB2 model, $L_0$ was fixed at 525 mm $L_{ST}$ for *S. lewini* and 700 mm $L_{ST}$ for *S. mokarran*. The three-parameter Gompertz model was given by the equation $L_t = L_\infty e^{[-\lambda e^{(-kt)}]}$, where $L_\infty$, $\lambda$ and $k$ are estimated parameters. The three-parameter logistic growth model was given by the equation $L_t = (L_\infty \lambda e^{kt})(L_\infty + \lambda [e^{(kt)} - 1])$, where $L_\infty$, $\lambda$ and $k$ are estimated parameters. Finally, the four-parameter Schnute model was given by the equation $L_t = L_\infty (1 - [\lambda e^{(-kt)}])^\gamma$, where $L_\infty$, $\lambda$, $k$ and $\gamma$ are estimated parameters. Although the parameter $L_\infty$ is common to all models, all other parameters are not directly comparable among models.

Models were fitted using the method of non-linear least squares in the statistical package R (R Development Core Team; www.r-project.org) and model performance evaluated using Akaike's information criteria (AIC). Because of the relatively small sample sizes in the present study, the small-sample, bias-adjusted form of AIC ($x$) was calculated as $AIC_c$ ($y$) from $y = x + 2K(K+1)(n - K - 1)^{-1}$, where $K$ is the total number of estimated parameters + 1 for variance ($\sigma^2$), $n$ is the sample size and $x = n \ln(\sigma^2) + 2K$. The best model was the one with the lowest $AIC_c$ value, $AIC_{min}$ ($x_{min}$). AIC differences were calculated as $\Delta_i = y_i - x_{min}$ and used to rank the support of the remaining models ($i = 1-5$) relative to the best model. Models with $\Delta$ of 0–2 had substantial support, while models with $\Delta$ of 4–7 had considerably less support and models with $\Delta > 10$ had essentially no support (Burnham & Anderson, 2002). Akaike weights ($w_i$), were calculated as the weight of evidence in favour of a model being the best model in the set of candidate models (Burnham & Anderson, 2002). The 95% C.I. around the best-fit parameter estimates were derived from 10 000 re-sampled data sets using the bias-corrected accelerated bootstrap method (Efron & Tibshirani, 1993).

## SPATIAL VARIATION IN GROWTH OF MALE *S. LEWINI*

The spatial extent of the study area was large (*c*. 18° of latitude) and differences in the biology of *S. lewini* were apparent between northern and southern samples (Fig. 1). These were confounded, however, by gear selectivity; northern samples were mainly collected from a small-mesh, inshore, gillnet fishery, while southern samples were mainly collected from a mid-shelf, demersal longline fishery. Further confounding the analysis of growth was the poorly documented spatial ecology of this species. For example, females >1000 mm $L_{ST}$ and males >2000 mm $L_{ST}$ were almost entirely absent from northern regions yet present in southern regions. It was unclear if this was due to a southerly migration of larger animals or related to other factors such as gear type, depth, temperature or habitat characteristics. Given the limitations of the sampling, which was opportunistic, it was not possible to fully reconcile these issues. For males, however, there were sufficient data available to investigate potential spatial effects on growth between northern and southern regions.

Analysis of growth data proceeded as follows: a general growth model of *S. lewini* was first established using data pooled for both sexes and from all regions along the coast. A second analysis was then undertaken on males only to examine potential spatial effects on growth, where region was included as a two-level term: tropical and temperate. Samples were separated into the two nominal regions by the Tropic of Capricorn (23° 26′S) (Fig. 1). Following Kimura (1980), likelihood ratio tests were then used to statistically compare parameters between growth curves from each region. The most appropriate growth model used for the spatial comparison was determined from the initial MMI analysis with all samples pooled.

## AGE VALIDATION AND VERIFICATION

To validate the assumption that growth-band pairs were deposited annually on the centra, a fishery-independent mark, tag and recapture study was carried out. Fishery-independent sampling using experimental multi-hook longlines was conducted between January 2008 and

June 2010 in Cleveland Bay (19° 12′ S; 146° 54′ E) and Halifax Bay (19° 6′ S; 146° 40′ E) near Townsville in north Queensland. The $L_{ST}$ and sex of captured fishes were recorded and individuals were then tagged externally on the first dorsal fin using Rototags or Jumbotags (Dalton, Worldwide; www.dalton.co.uk). The vertebral centra of captured fishes were marked using the fluorescent dye calcein ($C_{30}H_{26}N_2O_{13}$). A pH-buffered, isotonic solution of 12·5 mg ml$^{-1}$ calcein was injected intramuscularly behind the first dorsal fin at a dosage of 5 mg kg$^{-1}$ (McAuley *et al.*, 2006). The body mass of fishes was estimated using published $L_{ST}$ and mass relationships for these species off northern Australia (Stevens & Lyle, 1989).

The method of centrum edge analysis (CEA) described by Okamura & Semba (2009) was used as an additional tool to statistically verify the timing and frequency of translucent growth-band deposition on vertebral centra. During age determination, the centrum edge of each vertebra was classed as either opaque or translucent. The monthly proportion of centra with translucent edges was then fitted to three models corresponding to hypotheses that translucent band formation occurs on an annual cycle, on a biannual cycle or without a cycle. The best-fit model was the one with the lowest AIC$_c$ value. Given the relatively low sample sizes, both sexes and all age classes were pooled. Age 0 year animals were excluded from the analysis because they lacked any fully formed band pairs, while individuals >2500 mm $L_{ST}$ were also excluded because the band pairs were tightly spaced in those older animals.

## DURATION OF FIRST GROWTH INCREMENT

In addition to validating the frequency of growth-band pairs throughout life, establishing the duration of the first growth increment (and therefore the age of individuals when the first growth-band pair is formed) is an important consideration in age and growth studies (Campana, 2001; Harry *et al.*, 2010). To establish the duration of the first growth increment, the occurrence and $L_{ST}$ of age 0 year animals and neonates throughout the year was examined using a plot of month against $L_{ST}$.

## MATURITY AND REPRODUCTION

Reproductive staging of animals was determined based on the descriptions of Walker (2005). Maturity in males was determined by examining the claspers: stage 1 (immature), claspers pliable with no calcification; stage 2 (immature), claspers partly calcified; stage 3 (mature), claspers fully calcified. Female maturity was determined by visual examination of the uterus: stage 1 (immature), uniformly thin tubular structure; stage 2 (immature), thin tubular structure partly enlarged posteriorly; stage 3 (mature), uniformly enlarged tubular structure; stage 4 (mature), *in utero* eggs present without macroscopically visible embryos present; stage 5 (mature), in utero embryos macroscopically visible; stage 6 (mature), enlarged tubular structure distended. Maturity stage data were converted into binary form for statistical analysis (immature = 0, mature = 1).

Population estimates of $L_{ST}$ and age at maturity were established using logistic regression analysis (Walker, 2005). $L_{ST}$ and age were modelled separately as a function of maturity stage (logit transformed) using generalized linear models (GLM). For male *S. lewini*, there were sufficient data to examine the potential spatial effects on maturity by incorporating region and the interaction of region as terms in the GLM analysis. Region was a term with two levels (tropical and temperate) as used above in the spatial analysis of growth. For *S. mokarran*, the effect and interaction of sex on maturity was examined by including sex as a term in the GLM analysis. The effect of terms and interactions was examined and the most parsimonious model was the one with the lowest AIC. The small-sample, bias-corrected variation of AIC (AIC$_c$) was used following Burnham & Anderson (2002). The 95% C.I. of the best-fit parameter estimates and population estimates of $L_{ST}$ and age at 50% maturity ($L_{ST50}$, $A_{50}$) were derived from 10 000 re-sampled data sets using the bias-corrected accelerated bootstrap method (Efron & Tibshirani, 1993).
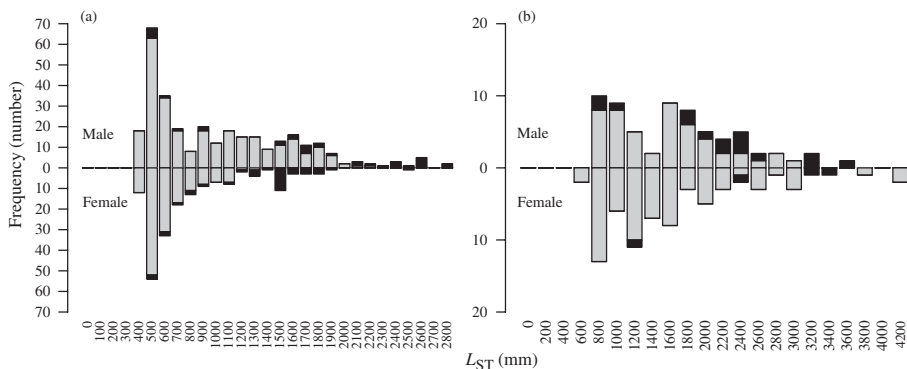
FIG. 3. Stretched total length ($L_{ST}$)-frequency distributions of (a) *Sphyrna lewini* ($n = 519$) and (b) *Sphyrna mokarran* ($n = 142$) specimens collected off eastern Australia between December 2005 and May 2010 [location: tropical (☐) or temperate (■)].

## RESULTS

### SAMPLE COLLECTION AND LENGTH EQUATIONS

Length measurements were obtained from a total of 522 *S. lewini* comprising 324 males (465–2898 mm $L_{ST}$), 195 females (465–2600 mm $L_{ST}$) [Fig. 3(a)] and three animals of unknown sex (530, 600 and 700 mm $L_{ST}$). The majority of samples were obtained in the tropics ($n = 432$) (Fig. 1) *via* the ECIFF, where catches were composed mainly of neonates and juveniles of both sexes and small adult males up to *c*. 2000 mm $L_{ST}$. Larger adult males (up to 2900 mm $L_{ST}$) and juvenile females (1500–2000 mm $L_{ST}$) were predominantly encountered in the demersal longline fishery in temperate waters. Forty-one individuals were tagged, marked with calcein and released using fishery-independent sampling methods. These individuals were mainly small adult males 1400–2000 mm $L_{ST}$. The relationships among $L_{ST}$, $L_F$ and $L_{PC}$ for *S. lewini* (sexes combined) were: $L_{ST} = 15 \cdot 38 + 1 \cdot 30 L_F$ ($r^2 = 0 \cdot 99$, $P < 0 \cdot 001$, d.f. $= 372$) and $L_{ST} = 15 \cdot 49 + 1 \cdot 43 L_{PC}$ ($r^2 = 0 \cdot 99$, $P < 0 \cdot 001$, d.f. $= 250$).

Length measurements were obtained from 146 *S. mokarran* comprising 65 males (801–3693 mm $L_{ST}$), 77 females (795–4397 mm $L_{ST}$) [Fig. 3(b)] and four animals of unknown sex (890, 1100, 1210 and 1220 mm $L_{ST}$). The majority of samples were from the tropics ($n = 123$) (Fig. 1) and were obtained from the ECIFF. Tropical samples were biased towards females and included animals of all lengths except neonates, while the demersal longline fishery samples in temperate waters were mainly larger males ($>2000$ mm $L_{ST}$). Thirty-eight individuals were tagged, marked with calcein and released during the study and were mostly immature males (1600–2000 mm $L_{ST}$). The relationships between $L_{ST}$, $L_F$ and $L_{PC}$ for *S. mokarran* (sexes combined) were $L_{ST} = 49 \cdot 01 + 1 \cdot 29\ L_F$ ($r^2 = 0 \cdot 99$, $P < 0 \cdot 001$, d.f. $= 98$) and $L_{ST} = 74 \cdot 19 + 1 \cdot 39\ L_{PC}$ ($r^2 = 0 \cdot 99$, $P < 0 \cdot 001$, d.f. $= 50$).

### VALIDATION OF GROWTH-BAND PATTERN

Recapture rates of *Sphyrna* spp. tagged during fishery-independent sampling were high. Seven of the 41 marked *S. lewini* were recaptured including three on multiple
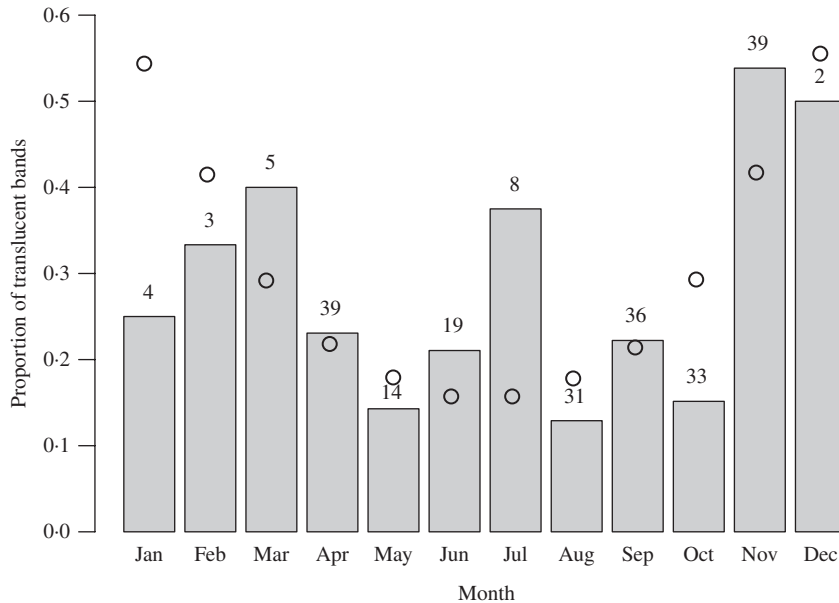
FIG. 4. Monthly proportions of translucent bands present on the outer margin of vertebral centra for *Sphyrna lewini*. Total sample sizes in each month are denoted by numbers above bars. O, the best-fit model suggesting an annual cycle of band formation.

occasions. All recaptures were considered to be too soon after the original tagging date, so the animals were re-released and as a result no calcein-marked vertebrae were recovered from this species. Consequently, centrum edge analysis was used to verify the periodicity of band-pair formation. Two hundred and thirty-three centra had at least one growth-band pair and were therefore available for the analysis (Fig. 4). Using the method proposed by Okamura & Semba (2009), $AIC_c$ values were: 262·48 for the model of an annual cycle, 267·07 for the biannual cycle model and 269·94 for the model hypothesizing no cycle in translucent band formation. The greatest proportion of translucent bands occurred in November followed by December (Fig. 4), but high values also occurred during March and July. Although the annual model was statistically the best-supported, computed $AIC_c$ differences, $\Delta$, were 4·59 and 7·46, implying that there was still some support for the models of a biannual cycle or no cycle. In the absence of a conclusively verified banding pattern for *S. lewini*, growth analysis proceeded with the assumption of an annual cycle. The implications of this are examined further.

Five of the 38 calcein-marked *S. mokarran* were recaptured after periods of between 126 and 467 days at liberty (Table I). Vertebrae were recovered from all animals except GHH2, which was recaptured during fishery-independent sampling and re-released given the relatively short time at liberty. Two individuals, at liberty for 353 and 467 days, had each formed a single translucent band after the calcein mark, supporting the hypothesis that band pairs are deposited annually on the vertebrae. The remaining two individuals, at liberty for 126 and 186 days, had not formed any translucent bands. All three animals marked with calcein during October or November (GHH1, GHH3 and GHH4) had formed translucent bands closely preceding the

TABLE I. Recapture details of five calcein-marked *Sphyrna mokarran* at liberty for 126–467 days. Two individuals at liberty for 353 and 467 days formed a single band pair, supportive of an annual cycle for band-pair deposition in this species

| Date released | $L_{ST\ Release}$ (mm) | Date recaptured | $L_{ST\ Recap}$ (mm) | Days at liberty | Growth (mm) | Bands pairs formed |
|---|---|---|---|---|---|---|
| GHH1 18 November 2008 | 2037* | 6 November 2009 | 2160 | 353 | 123 | 1 |
| GHH2 26 November 2008 | 1760 | 28 April 2009 | 1820 | 153 | 60 | |
| GHH3 26 November 2008 | 1820 | 1 April 2009 | 1892* | 126 | 72 | 0 |
| GHH4 16 January 2009 | 2340 | 28 April 2010 | 2598 | 467 | 258 | 1 |
| GHH5 22 October 2009 | 1284 | 26 April 2010 | 1470 | 186 | 186 | 0 |

$L_{ST\ Release}$, stretch total length at release; $L_{ST\ Recap}$, stretch total length at recapture.
*$L_{ST}$ unavailable, estimated *via* back or forward calculation.

calcein mark. Furthermore, animal GHH1, which was recaptured in November, had an translucent band formed on the outer margin of the centrum. This suggests that translucent band formation in *S. mokarran* probably occurs during spring (October to November) in tropical eastern Australian waters.

## DURATION OF FIRST GROWTH INCREMENT

No clear trends in the occurrence or $L_{ST}$ of age 0 year *S. lewini* were observed during the year [Fig. 5(a)] and neonates were present throughout the year. For an aseasonally reproducing species, the mean age of the population when the first growth increment is formed should be 0·5 years (Harry *et al.*, 2010). High abundances of *S. lewini* neonates during November and December suggested, however, that reproduction was probably not completely aseasonal, but rather partially seasonal. Without more detailed knowledge on the timing of parturition, no adjustments could be made to the first growth increment, which was left at 1 year for all individuals.

Examining the occurrence and $L_{ST}$ of age 0 year *S. mokarran* [Fig. 5(b)] showed a pattern concordant with a seasonally reproducing species. Although no neonates were captured, a pregnant female was captured in October with full-term embryos
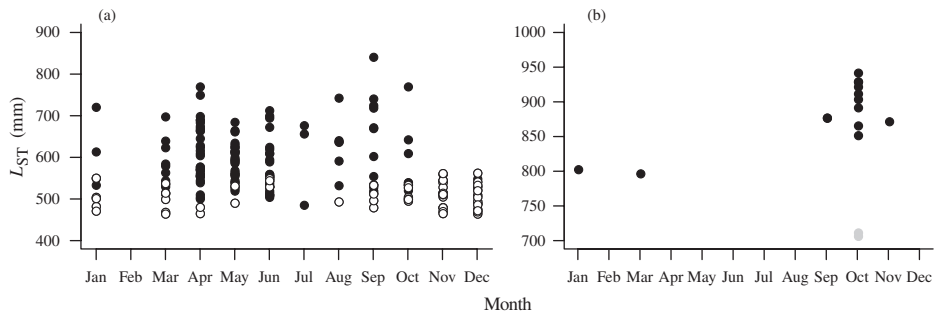


FIG. 5. Occurrence and stretched total length ($L_{ST}$) of age 0 year individuals (●), neonates (○) and near-term embryos (◎) of (a) *Sphyrna lewini* and (b) *Sphyrna mokarran* throughout the year, used to determine the duration of the first growth increment.
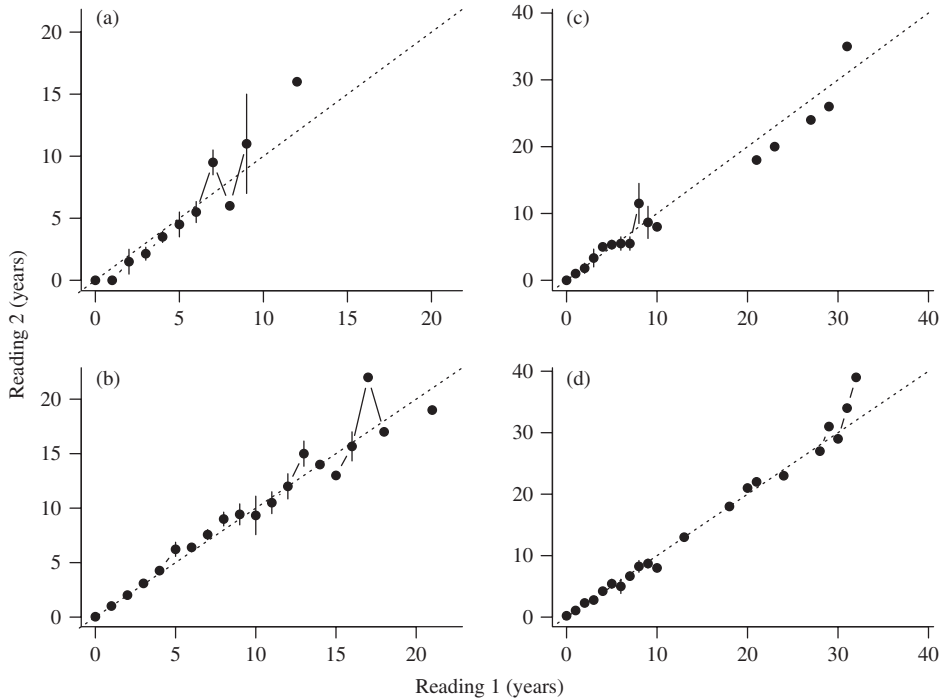
FIG. 6. (a), (c) Inter-reader and (b), (d) intra-reader age-bias plots for (a), (b) *Sphyrna lewini* and (c), (d) *Sphyrna mokarran*. Values are means $\pm$ 2 S.E.

suggesting that birth occurs around this time. Age validation suggested growth bands were formed at a similar time of the year, therefore making the first growth increment *c*. 1 year in duration. The largest age 0 year individuals (850–950 mm $L_{ST}$) were captured between September and November, further supporting this [Fig. 5(b)].

## PRECISION AND BIAS IN AGE ESTIMATION

Inter-reader mean per cent agreement (PA) and PA $\pm$ 1 year summed across 100 mm $L_{ST}$ groupings was 46 and 80·7% for *S. lewini*, while Chang's coefficient of variation (C.V.) was 17·9%. Bowker's test of symmetry indicated there was no systematic bias ($\chi^2 = 18\cdot33$, d.f. = 12, $P > 0\cdot05$) [Fig. 6(a)]. Intra-reader precision for *S. lewini* was similar; mean PA and PA $\pm$ 1 year was 50 and 79%, while C.V. was 14·64%. There was no systematic intra-reader bias ($\chi^2 = 40\cdot09$, d.f. = 31, $P > 0\cdot05$) [Fig. 6(b)]. Measures of precision and age-bias plots indicated *S. lewini* vertebrae could be accurately (*c*. 80% of the time) aged to within 1 year both between and among readers without bias [Fig. 6(a), (b)].

For *S. mokarran*, inter-reader measures of precision were somewhat lower (PA = 35%, PA $\pm$ 1 year = 64%, C.V. = 16·84%), although there was no systematic inter-reader bias ($\chi^2 = 15\cdot33$, d.f. = 18, $P > 0\cdot05$) [Fig. 6(c)]. Intra-reader precision for *S. mokarran* was considerably higher (PA = 48%, PA $\pm$ 1 year = 86%, C.V. = 17·23%), again with no systematic bias between reads ($\chi^2 = 21\cdot67$, d.f. = 22, $P > 0\cdot05$) [Fig. 6(d)]. Given that measures of precision were within the usual range for

elasmobranch studies and there was no systematic bias [Fig. 6(c), (d)], it was concluded that an acceptable and repeatable interpretation of the banding pattern had been achieved.

## GROWTH ANALYSIS

Vertebral samples were obtained from a total of 392 *S. lewini*, comprising 230 males (465–2898 mm $L_{ST}$), 159 females (465–2600 mm$L_{ST}$) and three animals of unknown sex (540–700 mm $L_{ST}$). Male *S. lewini* reach at least 3010 mm $L_{ST}$ in Australian waters (Stevens & Lyle, 1989) and vertebral samples close to this length were obtained. Given, however, that females attain a length of at least 3460 mm $L_{ST}$ in Australian waters and that the largest sample obtained was 2600 mm $L_{ST}$, the samples were unlikely to provide a full representation of growth in females. The oldest male and female *S. lewini* aged in the present study were 21 years (2617 mm $L_{ST}$) and 15 years (2600 mm $L_{ST}$), respectively. In the initial growth analysis with data pooled between regions and sexes, the three-parameter von Bertalanffy (VB3) growth model had the greatest support and was considered most appropriate given the data [Tables II and III and Fig. 7(a)]. The AIC differences ($\Delta$) between the other candidate models were high ($>10$), indicating negligible support for those models.

Of the 230 male samples for which an age was determined, 200 were obtained from tropical regions and 30 from temperate regions (Fig. 1). Male samples from temperate regions were larger (505–2898 mm $L_{ST}$) and older (0–21 years) than samples obtained from tropical regions (465–1970 mm $L_{ST}$, 0–12 years). Hypothesis testing for the effect of region on growth showed that there were significant differences between $k$ and $L_\infty$, between tropical and temperate samples [Tables III and IV and Fig. 7(b)]. There was no significant difference, however, between $L_0$, between regions, and hence a single parameter was included in the most parsimonious model (Table III). The relatively low sample size from temperate regions led to much higher

TABLE II. Summary of five *a priori* growth models fitted to stretched total length-at-age data for *Sphyrna lewini* and *Sphyrna mokarran*. Models are ranked in terms of performance (best to worst with the best in bold) based on computed values of small-sample, bias-adjusted Akaike's information criteria ($AIC_c$). Akaike differences ($\Delta$) and Akaike weights ($w$) show the relative support for other models. The number of parameters in each model (+1 for variance) is given by $K$

| Species | Model | $K$ | $AIC_c$ | $\Delta$ | $w$ | R.S.E. |
|---|---|---|---|---|---|---|
| *Sphyrna lewini* | **VB3** | **4** | **3647·29** | **0·00** | **1·0000** | **104·13** |
| | Schnute | 5 | 3709·97 | 62·68 | 0·0000 | 120·85 |
| | Gompertz | 4 | 3710·37 | 63·08 | 0·0000 | 113·08 |
| | VB2 | 3 | 3762·96 | 115·67 | 0·0000 | 151·96 |
| | Logistic | 4 | 3943·59 | 296·30 | 0·0000 | 112·65 |
| *Sphyrna mokarran* | **VB2** | **3** | **1043·10** | **0·00** | **0·7262** | **180·25** |
| | VB3 | 4 | 1045·06 | 1·95 | 0·2738 | 180·98 |
| | Gompertz | 4 | 1068·84 | 25·73 | 0·0000 | 203·83 |
| | Schnute | 5 | 1095·69 | 52·58 | 0·0000 | 231·75 |
| | Logistic | 4 | 1097·79 | 54·69 | 0·0000 | 235·59 |

R.S.E., residual standard error.

TABLE III. Best-fit parameter estimates (with 95% C.I.) in preferred growth models for *Sphyrna lewini* and *Sphyrna mokarran*. Parameters are asymptotic stretched total length ($L_\infty$), stretched total length at birth ($L_0$) and growth completion coefficient ($k$). The sample size of each analysis is given by $n$

| Species | Sex | Region | Model | $n$ | $L_\infty$ (mm) | $L_0$ (mm) | $k$ |
|---|---|---|---|---|---|---|---|
| *Sphyrna lewini* | Both | Pooled | VB3 | 392 | 3305 (2924, 3934) | 582 (572, 593) | 0·077 (0·059, 0·094) |
| | Male | Tropic | VB3 | 200 | 2119 (1943, 2304) | 565 (553, 579)* | 0·163 (0·136, 0·196) |
| | Male | Temperate | VB3 | 30 | 3199 (2616, 4042) | | 0·093 (0·026, 0·166) |
| *Sphyrna mokarran* | Both | Pooled | VB2 | 100 | 4027 (3638, 4545) | 700† | 0·079 (0·064, 0·095) |

*$L_0$ was not significantly different in the regional comparison for males.

†$L_0$ was fixed at 700 mm in the best-fit model for *S. mokarran*.

uncertainty around parameter estimates compared to the tropics (Table III). Despite this, comparison of approximate 95% C.I. around $k$ and $L_\infty$ parameters between regions highlighted the large differences in both $k$ and $L_\infty$ [Fig. 7(c)]. On the basis of the model predictions, males from temperate regions grew $c$. 1 m larger and had a $k$ value $c$. half that of males in the tropics.

Vertebral samples were obtained from a total of 100 *S. mokarran*, comprising 43 males (801–3691 mm $L_{ST}$), 51 females (795–4391 mm $L_{ST}$) and six animals of unknown sex (890–1220 mm $L_{ST}$). The oldest male and female aged in the present study were 31·7 years (3691 mm $L_{ST}$) and 39·1 years (4391 mm $L_{ST}$), respectively.
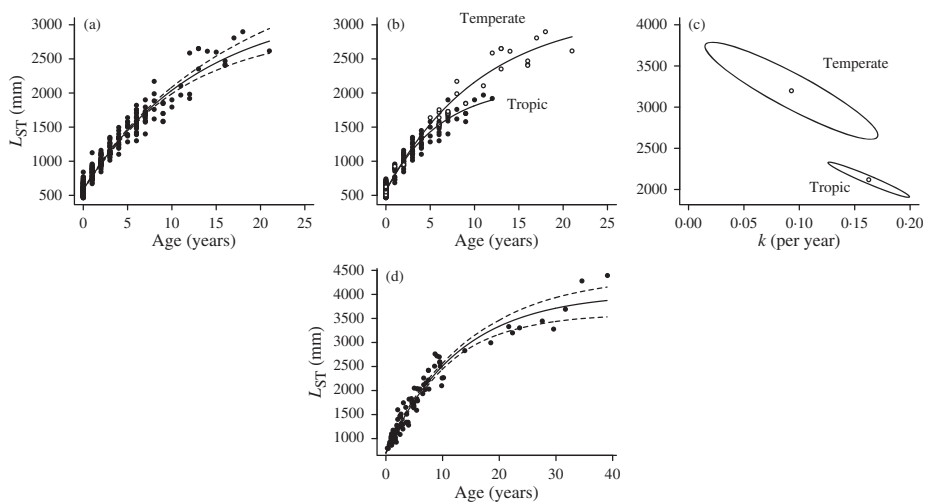


FIG. 7. Stretched total length ($L_{ST}$) at age determined by vertebral analysis for (a), (b) *Sphyrna lewini* and (d) *Sphyrna mokarran*. (b) The difference in growth between male *S. lewini* from temperate (○) and tropical (●) sites. Solid lines are fitted von Bertalanffy growth models and dashed lines in (a) and (d) are 95% C.I. (c) The 95% C.I. for the spatial comparison of male *S. lewini* growth in (b) are provided and highlight the difference in growth rate, $k$ and $L_\infty$ parameters (see Tables II and III).

In the multi-model growth comparison, computed $AIC_c$ values were lowest for the VB2 model and so it was considered most appropriate given the data [Tables II and III and Fig. 7(d)]. The VB3 model was also supported by the data ($\Delta = 1.95$, $w = 0.2738$), however, the VB2 was clearly preferable ($w = 0.7262$) as it reduced the number of parameters and had a similar explanatory power to the VB3 model (Table II).

Values of $k$ were similar between *S. lewini* and *S. mokarran* for the models with data pooled for regions and sex ($k = 0.077$ and $0.079$; Table III) and suggested the two species had similar growth characteristics: both were relatively long lived and slow growing. The regional comparison of growth in male *S. lewini* also indicated, however, that within the overall population some components had considerable variation in their growth characteristics.

## MATURITY ANALYSIS

Stretched total length ($L_{ST}$) and age at maturity data were available for 264 and 187 male *S. lewini*, respectively ($465–2898$ mm $L_{ST}$ and $0–21$ years). The smallest mature male was 1288 mm $L_{ST}$ (unknown age) while the youngest mature male was 3 years old (1320 mm $L_{ST}$); both were captured in the tropics. The largest immature male was 1989 mm $L_{ST}$ (unknown age), while the oldest immature male was 9 years (1846 mm $L_{ST}$); both captured in temperate waters. Logistic regression analysis found that, like growth, region had a strong influence on $L_{ST}$ and age at maturity (Table V). The interaction between $L_{ST}$ or age and region did not, however, improve the overall performance of the model enough to justify its inclusion. The removal of region altogether considerably decreased the explanatory power of the models and the models with the smallest $AIC_c$ values for both $L_{ST}$ and age at maturity included region as a factor. A separate intercept was therefore fitted to account for this factor (Tables V and VI). Estimates of $L_{ST50}$ and $A_{50}$ (with 95% C.I.) for *S. lewini* males differed considerably between regions and occurred at 1471 (1423–1519) mm and 5.7 (5.1–6.2) years in the tropics and 2043 (1934–2182) mm and 8.9 (7.5–10.8) years in temperate waters [Fig. 8(a)–(d)]. The relatively small sample sizes in temperate regions led to greater uncertainty in parameter estimates and this is reflected in the much larger 95% C.I. around $L_{ST50}$ and $A_{50}$ estimates compared with tropical samples. Although $L_{ST}$ and age at maturity data were available for 100 and 93 female *S. lewini*, respectively ($469–2600$ mm $L_{ST}$ and $0–15$ years), only a single

TABLE IV. Hypothesis testing for the effect of region on von Bertalanffy growth parameters for male *Sphyrna lewini*. Four hypotheses (H1–H4) were tested against the null hypothesis (H0) using likelihood ratio tests, where LL is the computed negative log-likelihood for a model ($\chi^2$, test statistic)

|  | Potential process | LL | $\chi^2$ | d.f. | $P$ |
|---|---|---|---|---|---|
| H0 | All parameters differ between region | −1369.7 | | 7 | |
| H1 | $L_\infty$ is the same between regions | −1386.2 | 32.896 | 6 | <0.001 |
| H2 | $k$ is the same between regions | −1377.5 | 15.566 | 6 | <0.001 |
| H3 | $L_0$ is the same between regions | −1369.8 | 0.037 | 6 | >0.05 |
| H4 | All parameters are the same between regions | −1407.7 | 75.985 | 4 | <0.001 |

TABLE V. Summary of logistic regression analysis of stretched total length ($L_{ST}$) and age at maturity stage for *Sphyrna lewini* and *Sphyrna mokarran*. The effects of the factors sex and region (tropical and temperate) on maturity stage were also examined, and the best model was chosen as the one that minimized the small-sample, bias-adjusted form of Akaike's information criteria ($AIC_c$). Akaike differences ($\Delta$), Akaike weights ($w$), residual deviance and residual d.f. show the relative performance of competing models. $K$ is the number of estimated regression parameters. The models with the most support are in bold

| Species | Model | $K$ | $AIC_c$ | $\Delta$ | $w$ | Residual deviance |
|---|---|---|---|---|---|---|
| *Sphyrna lewini* | **Stage−$L_{ST}$ + region** | **3** | **52·72** | **0·00** | **0·5449** | **46·63** |
| | Stage−$L_{ST}$ + region + $L_{ST}$:region | 4 | 53·08 | 0·36 | 0·4551 | 44·93 |
| | Stage−$L_{ST}$ | 2 | 95·84 | 43·12 | 0·0000 | 91·80 |
| | **Stage−age + region** | **3** | **45·13** | **0·00** | **0·7348** | **39·00** |
| | Stage−age + region + age:region | 4 | 47·18 | 2·04 | 0·2650 | 38·96 |
| | Stage−age | 2 | 61·22 | 16·08 | 0·0002 | 57·15 |
| *Sphyrna mokarran* | **Stage−$L_{ST}$** | **2** | **23·16** | **0·00** | **0·6231** | **19·01** |
| | Stage−$L_{ST}$ + sex | 3 | 25·11 | 1·95 | 0·2350 | 18·82 |
| | Stage−$L_{ST}$ + sex + $L_{ST}$:sex | 4 | 26·12 | 2·96 | 0·1418 | 17·62 |
| | **Stage−age** | **2** | **20·54** | **0·00** | **0·5948** | **16·35** |
| | Stage−age + sex | 3 | 21·89 | 1·34 | 0·3044 | 15·50 |
| | Stage−age + sex + age:sex | 4 | 24·10 | 3·55 | 0·1008 | 15·44 |

mature female was obtained (2600 mm $L_{ST}$, 15 years). It was therefore not possible to statistically determine $L_{ST}$ or age at maturity of females. The largest and oldest immature female was 1982 mm $L_{ST}$ and 12 years old. Two immature females of 1794 and 1859 mm $L_{ST}$ were 10 and 9 years, respectively.

For *S. mokarran*, $L_{ST}$ and age at maturity data were available for 59 and 42 males (801−3691 mm $L_{ST}$ and 0·25−31·7 years) and 26 and 24 females (795−4280 mm $L_{ST}$ and 0·4−34·6 years). The largest immature male and female were both 2420 mm $L_{ST}$ and aged 7·5 years. The oldest immature male was 9·8 years (2100 mm $L_{ST}$), while the oldest immature female was 7·6 years (2030 mm $L_{ST}$). The smallest and youngest mature female was 2120 mm $L_{ST}$ and 6·7 years old, while the smallest and youngest mature males were 2267 mm $L_{ST}$ (10·2 years) and 8·6 years (2507 mm $L_{ST}$). The $L_{ST}$ and ages over which maturity occurred were variable and there was minimal difference between sexes in the range over which it occurred. Therefore, given the relatively low sample sizes, the most parsimonious models with the lowest values of $AIC_c$ included neither the sex nor the interaction between $L_{ST}$ or age and sex (Tables V and VI). Consequently, data for both sexes were pooled. For *S. mokarran*, $L_{ST50}$ occurred at 2279 (2149−2429) mm and $A_{50}$ occurred at 8·3 (7·4−9·5) years [Table VI and Fig. 8(e), (f)].

## NOTES ON REPRODUCTIVE CYCLE AND LENGTH AT BIRTH

Little could be observed directly on the reproductive cycle of either species due to the absence of adult female *S. lewini* in catches, and the apparent rarity of pregnant *S. mokarran*. Although some of the larger female *S. mokarran* may have been pregnant, the small-scale nature of the inshore net fishery and large size of these animals meant that dissection and examination of the uteri were rarely possible. One

TABLE VI. Summary of preferred logistic regression models used to determine stretched total length ($L_{ST50}$), and age at maturity ($A_{50}$) of *Sphyrna lewini* and *Sphyrna mokarran*. Parameter values (with 95% c.i.) are given for the logistic regression model $P(x) = [1 + e^{(a+bx)}]^{-1}$, where $P(x)$ is the proportion of individuals mature at a given $L_{ST}$ or age $x$, and $a$ and $b$ are fitted regression coefficients

| Species | Model | Sex | Region | $a$ | $b$ | $L_{ST50}$ or $A_{50}$ | $n$ | $N$ |
|---|---|---|---|---|---|---|---|---|
| *Sphyrna lewini* | Stage–$L_{ST}$ + region | Male | Tropic | −25.29 (−38.72, −17.44) | 0.017 (0.026, 0.119) | 1471 (1423, 1519) | 56 | 233 |
| | | | Temperate | −35.12 (−53.83, −23.49) | | 2043 (1934, 2182) | 14 | 31 |
| | Stage–age + region | Male | Tropic | −8.90 (−13.94, −5.75) | 1.575 (1.028, 2.368) | 5.7 (5.1, 6.2) | 25 | 160 |
| | | | Temperate | −14.03 (−23.36, −7.75) | | 8.9 (7.5, 10.8) | 13 | 27 |
| *Sphyrna mokarran* | Stage–$L_{ST}$ | Both | | −22.63 (−39.34, −13.74) | 0.010 (0.006, 0.019) | 2279 (2149, 2429) | 22 | 85 |
| | Stage–age | Both | | −11.76 (−24.07, −5.65) | 1.418 (0.630, 2.818) | 8.3 (7.4, 9.5) | 15 | 66 |

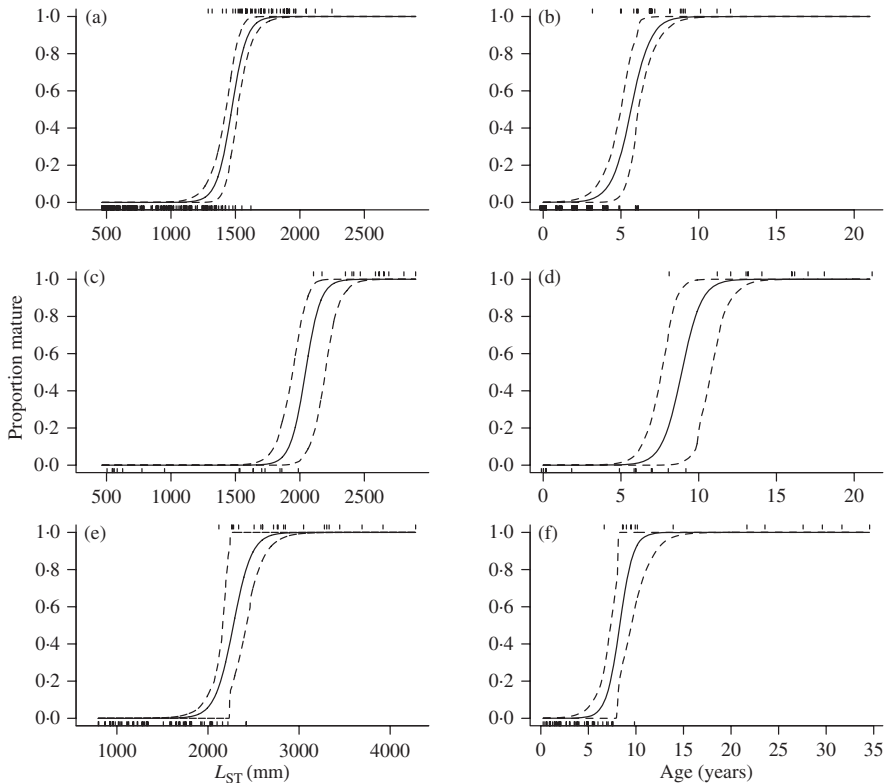$n$, the number of mature animals; $N$, the total number of animals.

FIG. 8. (a), (c), (d) Stretched total length ($L_{ST}$) and (b), (d), (f) age at maturity ogives for (a)–(d) male *Sphyrna lewini* in (a), (b) tropical and (c), (d) temperate waters and (e), (f) *Sphyrna mokarran* both sexes from all latitudes sampled during this study. ———, the expected proportion of population mature at a given $L_{ST}$; – – –, 95% c.i. Rug plots indicate observed data points.

pregnant female (4280 mm $L_{ST}$) caught in the tropics (17° 5′ S) during May had 39 embryos (18 females and 21 males) with a mean $L_{ST}$ of 376 mm. A second pregnant female (3921 mm $L_{ST}$), caught in October in the tropics (19° 5′ S) had 21 full-term embryos. The $L_{ST}$ for two retained embryos were 705 mm (1·57 kg) and 710 mm (1·59 kg), the two largest recorded for this species. The single adult *S. lewini* (2600 mm $L_{ST}$) was recorded as pregnant with *in utero* eggs, however, no additional measurements were recorded. Neonate *S. lewini* with open umbilical scars indicating recent birth were recorded in small numbers throughout the year as far south as Moreton Bay, but were most abundant in late November and early December. Using those neonates, $L_0$ was inferred at between 465 and 563 mm $L_{ST}$ ($n = 55$) [Fig. 5(a)].

## DISCUSSION

### LIFE HISTORY OF *SPHYRNA LEWINI*

The results of this study increase understanding of the complex life history of this widespread and formerly abundant large shark species that is important to fisheries

throughout its range. The study indicated that off the east coast of Australia, neonates are born in shallow intertidal habitats throughout the year, but there appeared to be a peak in pupping during late spring and early summer (November to December). This suggests that the reproductive cycle is likely to be partially aseasonal with a peak during summer. Stevens & Lyle (1989) found evidence of a similarly protracted pupping season in the Arafura Sea, while the data of White *et al.* (2008) suggest a seasonal reproductive cycle in the waters off Indonesia. The study also indicated that in the tropics many juveniles of both sexes remain in shallow inshore habitats <25 m for the first few years of life, but by age 3 years and *c*. 1000 mm $L_{ST}$ females are almost completely absent from this depth range, presumably having migrated to deeper water. In contrast, many males up to age 10 years and 2000 mm $L_{ST}$, including many sexually mature individuals, were sampled from those inshore waters. Despite extensive fishery-dependent and fishery-independent sampling, however, males >2000 mm were rarely encountered. Sexual segregation at some level is ubiquitous among chondrichthyans and is particularly pronounced and well documented in *S. lewini* (Klimley, 1987; Sims, 2005).

The pronounced sex segregation of *S. lewini* off the coast of Australia precluded detailed study of females, but revealed some striking insights into the life history of males. The $L_{ST50}$ and $A_{50}$ in male *S. lewini* in eastern Australian waters were highly variable. In tropical waters within the inner lagoon of the Great Barrier Reef (GBR), 50% of males were mature at 5·6 years old and 1471 mm $L_{ST}$, one of the smallest lengths reported globally, and concordant with the estimate of Stevens & Lyle (1989) off northern Australia (1400–1600 mm $L_{ST}$). Yet, in more temperate waters south of the GBR and Tropic of Capricorn, males matured both larger ($L_{ST50} = 2043$ mm) and older (8·9 years) than in northern areas, as also was noted by Stevens (1984). Differences in maturity characteristics also extended to differences in growth: males from the tropics grew at a much faster rate and to a much smaller asymptotic length ($k = 0·163$, $L_\infty = 2119$ mm $L_{ST}$) compared to those from temperate regions ($k = 0·093$, $L_\infty = 3199$ mm $L_{ST}$).

Intuitively the differences in maturity and growth characteristics observed in males would appear to be an effect of latitudinal differences within the wide spatial extent of the study area. Yet, sampling for *S. lewini* occurred all along the coast, and in both regions maturation occurred within a discrete length and age range with no apparent overlap or gradient. On the basis of the relatively small sample size from temperate regions, coupled with the differences in gear type, it is also tempting to suggest that the observed differences in male biology were purely methodological. Yet, there is evidence to support the notion that the observed differences in biology are, in fact, real.

It is well established that many life-history variables are correlated and predicted by adult body size (Charnov, 1993). For example, the ratio of length at maturity to maximum length is invariant in many taxa, including fishes (Frisk *et al.*, 2001). This can also be seen in other hammerheads including *S. lewini* [Fig. 9(a)]. It therefore follows that the difference in length at maturity of *c*. 500 mm between tropic and temperate samples probably extends to differences in maximum length (and growth). The extensive length frequency data of male *S. lewini* ($n = 3852$) presented by Stevens & Lyle (1989) were similar to this study and indicate that in tropical waters off northern Australia, male *S. lewini* >2100 mm $L_{ST}$ were rarely captured.
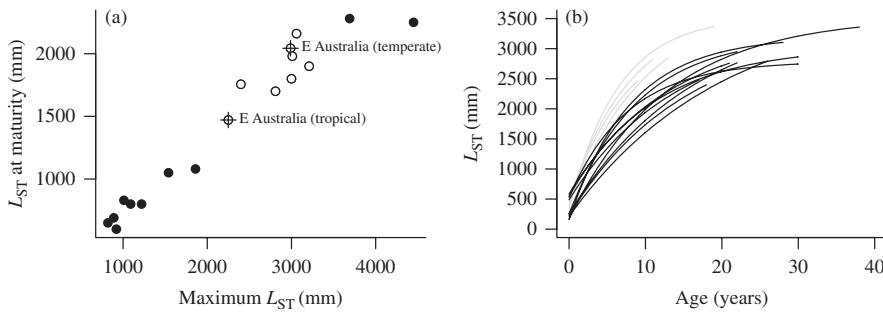
FIG. 9. Synthesis of life-history data from published studies on Sphyrnidae indicating (a) how maximum stretched total length ($L_{ST}$) predicts length at maturity in male hammerhead sharks (where ○ denotes *Sphyrna lewini* and ● denotes all other hammerhead species), and (b) a comparison of all growth estimates for both sexes when growth-band pairs are assumed to be formed annually. Grey lines in (b) are original growth trajectories in studies that have assumed biannual growth-band deposition.

Overall, these findings suggest there is pronounced intraspecific dimorphism among male *S. lewini* in Australian waters. As differences were found between tropical and temperate samples, this indicates temperature could be a driving factor, however, the depth where the samples were collected also differed and this factor could be equally important. Irrespective of the cause, the finding points to the existence of two separate and non-mixing groups of male *S. lewini* in Australian waters. A search of the literature reveals that similar dimorphism of male *S. lewini* seems to occur in other parts of the world, although generally it appears to have been overlooked. For example, Bass *et al*. (1975) found males matured within the range of 1400–1650 mm $L_{ST}$ in southern Mozambique, much smaller than the $L_{ST50}$ of 2160 mm (range 1825–3061 mm $L_{ST}$) reported by de Bruyn *et al*. (2005) just south in Durban, South Africa. Similarly in Brazil, Hazin *et al*. (2001) found males caught by pelagic drift nets were mature at lengths >2000 mm $L_{ST}$, while the observations of Lessa *et al*. (1998) suggest males on the coast matured at lengths <1500 mm $L_{ST}$. These studies suggest that dimorphism in length at maturity of male *S. lewini* may be common.

Recent molecular work on samples from the present study suggests that males on the east coast of Queensland are likely to be composed of a single stock (Welch *et al*., 2010). It is therefore hypothesized that two distinct male forms exist: coastal strategists and pelagic strategists. Although *S. lewini* are born in coastal habitats, it is well documented that females in particular migrate offshore soon after birth, possibly to exploit higher energy pelagic prey (Klimley, 1987; Stevens & Lyle, 1989). Recent work suggests females may regularly inhabit the mesopelagic zone, using depths up to 1000 m (Jorgensen *et al*., 2009). For *S. lewini*, the necessary conditions of the female reproductive strategy are therefore both pelagic and coastal habitats. As reproduction is thought to be annual in *S. lewini* (Chen *et al*., 1988; White *et al*., 2008), this would imply at least annual migration between these habitats for an adult female *S. lewini*.

Males on the other hand, do not have such strict requirements. While it appears all females disperse from their natal grounds, the occurrence of adult males offshore (Hazin *et al*., 2001) and outside of known nursery grounds (de Bruyn *et al*., 2005), as well as in nursery grounds (present study), indicates that some males disperse while others remain. It is hypothesized that the observed dimorphism represents a

trade-off between reproductive success and reproductive opportunity and that males form two distinct groups: pelagic strategists and coastal strategists.

Pelagic strategists are males that disperse from their natal grounds, migrating off-shore like females and also ranging further into temperate waters. Coastal strategists, however, remain in inshore waters for their entire lives. Pelagic strategists attain a large maximum length (*c*. 3000 mm) that is close to that of females and therefore likely to be optimal for reproduction (Cortes, 2000). Coastal strategists, however, may gain an advantage by being able to mate opportunistically with females entering coastal waters to give birth, which has been postulated to occur directly after parturition (Clarke, 1971; Chen *et al*., 1988). If coastal strategists faced less competition, they may be selected to mature at younger ages, potentially explaining their smaller size and lower longevity. Alternatively, their smaller size may be due to restrictions in prey availability in coastal areas. Studies into the spatial ecology of *S. lewini* are needed to further investigate this hypothesis. It may potentially explain, however, the dimorphism between males observed in some parts of the world, especially in areas such as northern Australia where there is a wide continental shelf and where a distance of hundreds or even thousands of kilometres separates female nursery grounds and suitable pelagic habitats.

Although males dominated the catch of Australia's coastal fisheries and hence growth models of this study, female growth was still represented in the general growth model (both sexes and regions) where vertebral ages were obtained from 159 females up to 2600 mm $L_{ST}$. Overall, growth rates of *S. lewini* based on the general model were within the range of previous studies. Yet, hindering any meaningful comparisons of growth rates with other studies was the serious issue of age validation, which has yet to be conclusively resolved for this species. Consequently, all existing growth studies on *S. lewini* fall into two categories based on interpretation of the vertebral banding pattern: those assuming band pairs are formed annually, and those assuming band pairs are formed biannually.

Chen *et al*. (1990) first reported that growth-band pairs were formed biannually in *S. lewini.* At the time, this hypothesis was supported by studies reporting biannual deposition of growth bands in *Isurus oxyrinchus* Rafinesque 1810 (Pratt & Casey, 1983) and *Cetorhinus maximus* (Gunnerus 1765) (Parker & Stott, 1965), both of which have since been disproved (Campana *et al*., 2002; Natanson *et al*., 2006, 2008; Semba *et al*., 2009). Two subsequent studies on *S. lewini* growth in the eastern Pacific Ocean have also assumed biannual growth-band deposition (Tolentino & Mendoza, 2001; Tolentino *et al*., 2008). Conversely, two growth studies on *S. lewini* within the Atlantic Ocean have assumed annual growth-band deposition (Branstetter, 1987; Piercy *et al*., 2007). Unfortunately the prevailing feature of *S. lewini* growth studies is that all have used indirect methods to verify growth, and none has proved conclusive. Validation of the periodicity of growth-band formation was attempted in the present study, but was not possible as no long-term recaptures of animals at liberty were made. Although the method of CEA verification statistically supported an annual cycle, like previous studies the results were ambiguous.

The difficulty of achieving validation in wide-ranging sharks is an issue that has been particularly poignant for *S. lewini*. Its implications for both conservation and management are evident in demographic modelling of *S. lewini* populations, where greatly differing estimates of population productivity are obtained depending on whether annual or biannual growth-band pairs are assumed (Liu & Chen, 1999;

Cortes, 2002). In this study, two reasons were used to justify the assumption that band pairs were formed annually. First, annual band pairs have now been validated for two other species of *Sphyrna*, including *S. mokarran* up to 42 years old using both bomb radiocarbon and calcein validation methods (Parsons, 1993; Passerotti *et al.*, 2010). Second, evidence for annual bands has been found in many other chondrichthyan growth studies (Campana *et al.*, 2002; Simpfendorfer *et al.*, 2002; McAuley *et al.*, 2006; Pierce & Bennett, 2009).

Why the various indirect methods (*e.g.* marginal increment ratio, CEA) for verifying band-pair timing in *S. lewini* have failed to produce a convincing pattern is unclear, but it is probably related to small sample sizes. Campana (2001) stressed the limitations of these methods, especially when multiple age groups are combined or sample sizes are insufficient. In this study, the timing of band-pair deposition for *S. mokarran* appeared to coincide with reproduction. It follows that if growth-band formation in *S. lewini* also coincides with reproduction, then the lack of distinct reproductive seasonality in females may have obscured any patterns in the CEA.

If all growth studies on *S. lewini* are transformed to have annual growth-band deposition, then global estimates of growth *S. lewini* are relatively similar [Fig. 9(b)], although it should be noted that the same argument can be made in reverse. In this study, the oldest male aged was 21 years, while the maximum age of females could not be established due to lack of adults. In the north-west Atlantic Ocean, Piercy *et al.* (2007) aged both sexes up to 30·5 years of age. If the data of Chen *et al.* (1990) are transformed to annual bands, maximum ages are 28 and 22 years for females and males, respectively. At present, empirical evidence is lacking to support such longevity in *S. lewini* as none of the above estimates are validated. For example, the maximum time at liberty in any tagging study is *c*. 10 years (Kohler *et al.*, 1998). It is worth noting, however, that extensive study of young-of-the-year individuals in Hawaii indicates that growth rates during the first year are relatively slow (96 mm year$^{-1}$) and are characterized by periods of mass loss immediately after birth (Lowe, 2002; Duncan & Holland, 2006). This is compared with a mean first-year growth of 630 mm in females and 540 mm in male *S. lewini* predicted by the original, untransformed models of Chen *et al.* (1990). Such rapid growth has so far only been observed in captive situations (Clarke, 1971). On the basis of the available evidence, it is hypothesized that *S. lewini* is long lived (at least 20–30 years) and is slow growing throughout its range.

## LIFE HISTORY OF *SPHYRNA MOKARRAN*

This study of *S. mokarran* provides a valuable contribution to understanding the life history of a widely distributed, but poorly understood species that has been heavily affected by fisheries throughout much of its range. On the east coast of Australia, *S. mokarran* was present in shallow tropical waters at a wide range of lengths >795 mm $L_{ST}$. Despite extensive sampling of nearshore habitats, no neonates were captured. This supports the findings of other studies that suggest this species does not use discrete coastal nursery areas and that pupping probably occurs further offshore (Stevens & Lyle, 1989; Hueter & Tyminski, 2007). Few pregnant females were recorded, but from the limited data available, timing of birth would appear to occur around October to November on the east coast, slightly earlier than that reported by Stevens & Lyle (1989) for northern Australia. Sexual segregation in

this species was less pronounced than in *S. lewini*; however, juveniles of both sexes and adult females appear to be much more common in inshore tropical areas (Harry *et al.*, 2011), while adult males may be relatively more common in temperate waters (Macbeth *et al.*, 2009).

The growth coefficient of *S. mokarran* in this study ($k = 0.079$) was considerably slower than found by Piercy *et al.* (2010) for the north-west Atlantic Ocean and Gulf of Mexico ($k = 0.16$, males; and $k = 0.11$, females). The asymptotic length on the east coast of Queensland ($L_\infty = 4027$ mm $L_{ST}$) was also larger than that calculated by Piercy (3346 mm $L_{ST}$, males and 3892 mm $L_{ST}$, females). This difference translated into much faster early growth in Atlantic *S. mokarran*, with growth rates approaching 400 mm year$^{-1}$ in the first year of life compared with *c.* 250 mm year$^{-1}$ off eastern Australia. The slower first-year growth of Australian *S. mokarran* was supported by the existence of age 0 year individuals in the range of *c.* 850–950 mm $L_{ST}$ *c.* 1 year after birth [Fig. 5(b)]. As a direct consequence of this, age at 50% maturity in Australia occurred at 8·3 years compared with an estimated 5–6 years in the Atlantic Ocean. The maximum ages of males (31·7 years) and females (39·1 years) in this study were somewhat lower than those obtained by Piercy *et al.* (2010) (42 years, males; 44 years, females), however, few large animals (especially males) were sampled.

Although this is the first study to statistically establish age at maturity of *S. mokarran*, several studies have previously examined length at maturity. Across northern Australia, Stevens & Lyle (1989) reported that maturity occurred at 2250 mm $L_{ST}$ for males and 2100 mm $L_{ST}$ for females. Although $L_{ST50}$ was not established in that study, length at maturity occurred over a similar length range to the current study and was also highly variable. It is concluded that length at maturity of *S. mokarran* does not appear to differ greatly throughout its range in Australian waters. Elsewhere in its range, however, *S. mokarran* appears to mature at considerably greater lengths. Cliff (1995) found that females matured at 3370 mm $L_{ST}$ and males at 3090 mm $L_{ST}$ off the coast of South Africa, while Piercy *et al.* (2010) reported a median length at maturity of 2850 mm $L_{ST}$ for females and 2380 mm $L_{ST}$ for males in the north-west Atlantic Ocean and Gulf of Mexico.

## FISHERY IMPLICATIONS AND FUTURE WORK

The results of this study suggest that in the waters off eastern Australia *S. lewini* and *S. mokarran* are long-lived and slow-growing species, although some components of the population may grow faster than others (*e.g.* tropical *S. lewini* males). Although both species have high fecundities in comparison with many other shark species (Last & Stevens, 2009), assumptions that this will translate into greater population growth rates should be considered carefully given the lack of empirical measurements of first-year survival rates for sharks in general and these species in particular (Bush & Holland, 2002; Heupel & Simpfendorfer, 2002; Duncan & Holland, 2006). Therefore, despite being assessed by the IUCN as 'least concern' in Australian waters (Cavanagh *et al.*, 2003), these species should be managed cautiously, especially in light of the recently reported declines off eastern Australian (de Jong, 2009) and in many other parts of their range (Dudley & Simpfendorfer, 2006; Ferretti *et al.*, 2008; Hayes *et al.*, 2009). The recent closure of 33% of the Great Barrier Reef World Heritage Area to commercial fishing in 2004 (GBRMPA, 2009) is

likely to be beneficial to populations of these species off eastern Australia, although a better understanding of their movements and distributions relative to protected areas is also necessary. For *S. lewini* specifically, it is not possible to accurately assess the potential threats to this species without first identifying the location of the adult female component of the stock. As females are likely to be more pelagic than males and potentially migratory (Clarke, 1971; Klimley, 1987; Stevens & Lyle, 1989), Australian stocks may be shared with nearby countries (*e.g.* Indonesia and Papua New Guinea) or extend well into the high seas. Future work should therefore prioritize the demarcation of adult female component of the stock.

Additional future work on *S. lewini* must also prioritize age validation of this species. This is a major issue with profound implications for fisheries management and conservation. As all indirect age verification methods have so far proved inconclusive, direct age validation methods (*e.g.* mark, tag, recapture or bomb radiocarbon validation) appear to be the only way to conclusively resolve whether growth bands are formed annually or biannually in this species and therefore confirm its longevity.

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