# Comparison of life histories of two deep-water sharks from eastern Australia: the piked spurdog and the Philippine spurdog

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**Abstract.** Deep-water sharks have low biological productivity and are vulnerable to exploitation with species-specific regional life history required to enable effective management. The present study describes the life history of two squalids collected from Australia: (1) the piked spurdog (*Squalus megalops*) from the tropical Great Barrier Reef; and (2) the Philippine spurdog (*S. montalbani*) from New South Wales. Maximum observed ages for males and females were 18 and 25 years for *S. megalops* and 28 and 27 years for *S. montalbani*. Multiple growth models were all well supported and indicated very slow growth rates for both species. The tropical *S. megalops* population was smaller and older at maturity than previously reported temperate populations. Males were mature at 352-mm stretched total length ($L_{ST}$) and 12.6 years, whereas females were mature at 422 mm $L_{ST}$ and 19.1 years. *Squalus montalbani* males were mature at 700 mm $L_{ST}$ and 21.8 years, whereas females were mature at 800 mm $L_{ST}$ and 26 years. Fecundity was lower for *S. megalops* than *S. montalbani* with two to three compared with nine to 16 embryos. Both species have a conservative life history, although in the event of overfishing the longer-lived, later-maturing and deeper-dwelling *S. montalbani* is likely to take longer to recover than *S. megalops*.

**Additional keywords:** age, growth, reproduction.

## Introduction

Deep-water sharks are generally slower growing, later maturing and longer lived than sharks from shelf and pelagic habitats (García *et al.* 2008; Rigby and Simpfendorfer 2015). The resulting lower biological productivity that makes them more vulnerable to exploitation decreases with depth and is evident in marked population declines because of fishing, with population recovery expected to take decades or even centuries (Dulvy *et al.* 2003; Simpfendorfer and Kyne 2009; Daley *et al.* 2015).

Dogfishes (Squaliformes) account for 46% of the deep-water chondrichthyan fauna (Kyne and Simpfendorfer 2010), are frequently targeted for their liver oil and taken as bycatch and are among those species most affected by fishing (Compagno *et al.* 2005). This includes many *Squalus* species (squalids) and, given this group is one of the most taxonomically problematic (Last *et al.* 2007*b*) with regional variability evident in their age and growth parameters (Braccini *et al.* 2007), their effective management requires an understanding of the species-specific life histories at a regional scale.

The piked spurdog *Squalus megalops* (Macleay, 1881) is a small squalid that is wide-ranging across the Atlantic and Indo-West Pacific and inhabits the shelf and upper continental

slope in tropical and temperate waters to at least 732 m (Compagno *et al.* 2005). The widespread distribution and variability in morphometrics have raised the question whether there are different populations of *S. megalops* or whether it is a complex of similar species (Last and Stevens 2009); until this is resolved, it is considered a single species. The medium-sized Philippine spurdog *S. montalbani* Whitley, 1931, occurs solely in the Indo-West Pacific and is restricted to the upper continental slope from 295 to 670 m in mainly tropical and subtropical latitudes (Last and Stevens 2009) of Australia, Indonesia and the Philippines. It was resurrected as a valid species in 2007, before which it was considered part of the *S.* '*mitsukurii* group' (Last *et al.* 2007*a*). Hence, little is known of the life history of *S. montalbani*.

Studies of *S. megalops* life history to date indicate considerable regional variability in size, age and maturity. The populations from the Atlantic have a larger maximum size and size at maturity and are longer lived than populations from the Indo-West Pacific. However, across these oceans, populations from temperate regions have a similar age at maturity, which is younger than that of the population from the subtropical Canary Islands (Table 1; Watson and Smale 1999; Braccini *et al.* 2007;

**Table 1.    Life history traits of *Squalus megalops* in different regions**

$L_{max}$, maximum size; $L_{50}$, size at maturity; $A_{50}$, age at maturity; $^OL_{max}$, observed longevity; $k$, von Bertalanffy growth function; $S_{birth}$, size at birth; $l$, litter size; $I_i$, interbirth interval

| Country | Ocean | $L_{max}$ (mm) | | $L_{50}$ (mm) | | $A_{50}$ (years) | | $^OL_{max}$ (mm) | | $k$ (year$^{-1}$) | | $S_{birth}$ (mm) | $l$ | $I_i$ (years) | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female | | | | |
| Australia | Indo-West Pacific | 470 | 635 | 386 | 484 | 10.0 | 15.5 | 15 | 28 | 0.158 | 0.042 | 218 | 3.0 | 2 | Braccini *et al.* (2006*a*, 2007) |
| Australia | Indo-West Pacific | 510 | 630 | 383 | 483 | | | | | | | | 2.0 | | Graham (2005) |
| South Africa | Atlantic | 572 | 782 | 400 | 490 | 9.0 | 15.0 | 29 | 32 | 0.089 | 0.033 | 255 | 3.0 | 2 | Watson and Smale (1998, 1999) |
| Canary Islands | Atlantic | 640 | 825 | 490 | 647 | 12.0 | 20.0 | 26 | 32 | 0.053 | 0.040 | 226 | 3.5 | 2 | Pajuelo *et al.* (2011) |
| Brazil | Atlantic | 645 | 890 | 445 | 590 | | | | | | | | 4.1 | | Hazin *et al.* (2006) |
| Tunisia | Atlantic | 690 | 760 | 444 | 564 | | | | | | | | | | Marouani *et al.* (2014) |

Pajuelo *et al.* 2011). Other life history parameters are common across regions, including low growth rates, small litters and a 2-year reproductive cycle. The studies concur that *S. megalops* has low biological productivity and is a species vulnerable to the effects of fishing.

The demersal habit of both *S. megalops* and *S. montalbani* exposes them to capture by a variety of commercial fishing gear, including trawl, Danish seine nets, gillnets, longlines and droplines (Braccini *et al.* 2007; Graham *et al.* 2001). *Squalus megalops* is a major bycatch in the Indian Ocean and the South Atlantic (Oliver *et al.* 2015). In Australia, it is a significant bycatch in the Southern and Eastern Scalefish and Shark Fishery (SESSF) and a small bycatch component of line and gillnet fisheries in the Coral Sea, Queensland and Western Australia (Graham *et al.* 2001; Furlani *et al.* 2007; Georgeson *et al.* 2014). It is also captured in the Queensland East Coast Otter Trawl Fishery (ECOTF), where the lack of information on squalids and other bycatch taken in the deep-water eastern king prawn sector of the ECOTF led to a precautionary assessment that trawling in that sector could pose a high risk to bycatch species and the habitat (Pears *et al.* 2012). The sector operates within a poorly known upper slope habitat of the southern Great Barrier Reef Marine Park and there is need for further biological information to facilitate a more confident assessment of the fishery risks. *Squalus montalbani* is now rarely reported from Australian fisheries, having suffered marked declines in the SESSF, although it may be taken in some Australian Commonwealth trawl fisheries and in relatively unmanaged deep-water demersal longline fisheries off Indonesia and the Philippines (Graham *et al.* 2001; White 2009; Sembiring *et al.* 2015).

Life history information is required for the tropical *S. megalops* population and *S. montalbani* to improve their regional management. To address this need, the aims of the present study were to: (1) describe and compare the life histories of the two squalids; (2) compare life history parameters of the tropical *S. megalops* population with temperate Australian and global populations; (3) consider the extent that differences in the life history of the two species and regional differences within *S. megalops* were linked to depth and latitude; and (4) relate the life histories of the two species to the potential effects of fishing.

## Materials and methods

This research was performed under James Cook University Ethics Approval A1566, Great Barrier Reef Marine Park Authority Permit G10/33603.1 and Department of Fisheries, Agriculture and Forestry Permits 55105 and 147714.

### Sampling

Specimens of *S. megalops* were obtained from the bycatch of commercial prawn trawlers operating at Swain Reefs in the deepwater eastern king prawn sector (EKP) of the ECOTF (Fig. 1). Demersal trawl fishing gear comprised three otter trawl nets of 15 fathoms each (i.e. head rope length of 27 m) with cod end meshes of 44.5 mm and turtle excluder and bycatch reduction devices. Trawling was from dusk until dawn, with each trawl in one direction with an average duration of 2.5 hand speed of 5.4 km h$^{-1}$. All *S. megalops* landed during two 5-week
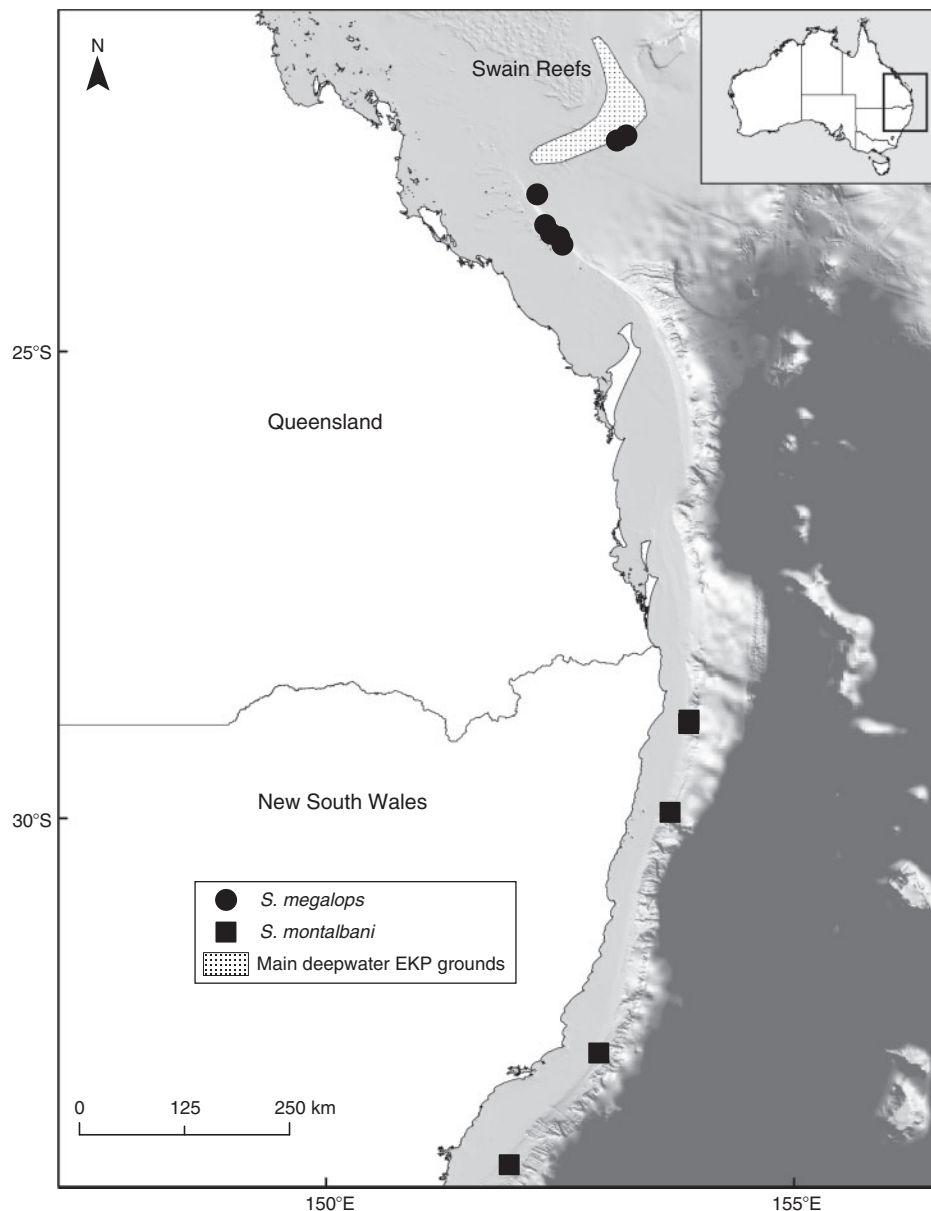
**Fig. 1.** Sampling locations for *Squalus megalops* and *Squalus montalbani*. EKP, eastern king prawn sector.

trawl trips (June–July 2011 and March–April 2012) were retained and frozen whole. They were collected over the depth range 187–280 m. The *S. montalbani* specimens were provided from a CSIRO research survey of gulper sharks along the upper slopes of New South Wales (NSW) onboard the *F. V. Diana* in September 2009. A subsample of the *S. montalbani* captured was retained and frozen whole from depths of 440–590 m (Fig. 1). The fishing gear was auto-longline (1500 × 12/0 Mustad hooks per set) baited with squid and mostly set at approximately 0430 hours for a soak time of 2–4 h (Williams *et al.* 2012).

### Specimen identification

Identification of *S. megalops* was confirmed by taxonomists at the Australian National Fish Collection, CSIRO Hobart

(Tas., Australia) and by molecular techniques based on the structure of the *NADH2* gene of two specimens (Naylor *et al.* 2012). To confirm the identification of *S. montalbani*, the denticles on a dorsal skin sample from each specimen were examined under a dissecting microscope to distinguish it from the morphologically similar *S. chloroculus* (Last *et al.* 2007a; K. Graham, Australian Museum, pers. comm., 2015).

### Sample preparation

All *S. megalops* and *S. montalbani* were sexed, thawed, body total weight ($W_{BT}$; ±0.1 g) recorded and measured for stretched total length ($L_{ST}$) and fork length ($L_F$; ±1 mm) following Francis (2006). Differences in the sex ratio were tested by a Chi-Square test with Yates' correction. Relationships between $L_{ST}$ and $L_F$

were examined using linear regression, with differences in the slopes of the relationships between the sexes tested by analysis of covariance (ANCOVA). The entire first and second dorsal fin spines (DFS) were removed from each individual by making a horizontal cut just above the vertebral column to ensure the spine base and stem were intact (Beamish and McFarlane 1985; Irvine *et al.* 2006*a*). A segment consisting of five vertebrae was excised from under the first dorsal fin of each individual and the neural and haemal arches removed. The retained centra and both DFS were cleaned by trimming off cartilage and tissue after immersion in hot water for 1 min. The centra were then soaked in 4% sodium hypochlorite for 10–20 min to remove any remaining tissue and rinsed thoroughly in tap water. Both centra and DFS were air dried and stored in vials.

*Age estimation*

Many squalids have DFS with visible growth bands and these are generally the structure used to estimate age because the vertebrae tend to be poorly calcified and lack visible growth bands (Holden and Meadows 1962; Irvine *et al.* 2006*b*; Goldman *et al.* 2012). An enamel cap with visible growth bands covered a large portion of the DFS of both species. To ensure optimum readability and reliability of age estimation, we investigated the other two growth band areas of DFS: the stem base and internal sections (Clarke and Irvine 2006). Base bands apparent on the DFS stem of *S. megalops* (but not *S. montalbani*) were enhanced by Alizarin Red S stain and appeared to match the number of bands on the enamel cap, but they were not used for age estimation because, unlike the enamel cap bands, their annual deposition has not been verified. Braccini *et al.* (2007) found agreement between *S. megalops* internal DFS sections and external enamel cap band counts, and internal band counts have proved useful for other dogfishes (McFarlane and Beamish 1987; Tanaka 1990; Clarke *et al.* 2002). Three *S. megalops* and three *S. montalbani* DFS were embedded in polyester resin and serial transverse sections (~300 μm) taken with a low-speed diamond blade saw, rinsed in tap water, air dried, resin mounted on glass slides and examined under a compound microscope (100 and 200×). Bands on the internal dentine layer of both species were clearest but were more difficult to read than the external enamel bands and so the age estimation of both species was done using the external enamel cap.

The bands were counted using reflected light and a dissecting microscope (10×), with a band defined as an alternating translucent and opaque zone or ridge, or both (Holden and Meadows 1962; Beamish and McFarlane 1985; Clarke and Irvine 2006; Braccini *et al.* 2007). The bands and ridges on the enamel cap of S. *megalops* DFS were not as marked as those of the temperate Australian *S. megalops* population (M. Braccini, Western Australian Fisheries, pers. comm., 2014), although they became more distinctive after the enamel was rubbed with fine wet sandpaper and polished, as reported in other dogfishes studies (Irvine *et al.* 2006*b*; Watson and Smale 1999; Braccini *et al.* 2007). Sanding and polishing also highlighted the DFS bands and ridges of *S. montalbani.* Annual band pair deposition had been previously verified for temperate Australian *S. megalops* by enamel edge analysis of whole spines collected throughout the year, and comparison of internal and

**Table 2. Readability scores for dorsal fin spine band counts (from Braccini *et al.* 2007)**

| Readability score | Definition |
|---|---|
| 1 | Band count unambiguous with clear bands |
| 2 | Band count unambiguous with bands of diminished clarity |
| 3 | Two band counts possible but indicated count most likely |
| 4 | More than two interpretations possible; count is best estimate |
| 5 | No band count possible; unreadable |

external band counts over the age range 1–28 years (Braccini *et al.* 2007). Because there were no previous age studies of *S. montalbani*, it was assumed that the enamel bands or ridges formed annually. This assumption was made because other squaloids have been validated or verified as having annual band deposition (Beamish and McFarlane 1985; Tucker 1985; McFarlane and Beamish 1987; Campana *et al.* 2006; Coelho and Erzini 2007, 2008). A subjective readability score was noted for each DFS, following Braccini *et al.* (2007; Table 2).

The first and second DFS of two *S. megalops* full-term embryos were examined for prebirth bands (no full-term embryos of *S. montalbani* were collected), but none were observed. Thus, it was assumed that the first band was laid down just before or after birth, which has been reported previously for *S. megalops* (Braccini *et al.* 2007) and other dogfishes (Holden and Meadows 1962; Irvine *et al.* 2006*a*). Hence, the estimated age for both species was calculated as the total number of band counts minus one. To assess whether the first or second DFS was better for age estimation, a random subsample of first and second DFS from 68 *S. megalops* was read three times. Similar to Braccini *et al.* (2007), the first DFS of *S. megalops* had better readability scores and higher precision between readings (based on the index of average percentage error (APE); Beamish and Fournier 1981; see below). Therefore, the first DFS was used for age estimation. *Squalus montalbani* had a high proportion of damaged first DFS, so the second DFS was used for age estimation.

The first DFS of *S. megalops* and the second DFS of *S. montalbani* were read three times by a single reader without prior knowledge of $L_{ST}$, sex or previous counts. To accept a band count for age estimation, the counts of at least two of the three readings had to be identical and the readability score ≤3 (Braccini *et al.* 2007; Coelho and Erzini 2007). Within-reader precision was assessed by APE. A second reader read a random subsample of 40 *S. megalops* first DFS and 15 *S. montalbani* second DFS to evaluate between-reader precision and bias, calculated by APE and age bias plots (Campana *et al.* 1995).

*Growth estimation*

To determine the most appropriate growth model for each species, a multimodel approach was used, as is recommended for modelling chondrichthyan growth (Cailliet *et al.* 2006; Thorson and Simpfendorfer 2009). Three *a priori* candidate growth models were fitted to the length at age data for the separate sexes and the combined sexes of each species: (1) the three-parameter version of the von Bertalanffy growth function (VBGF;

| Model | Growth function equation |
|---|---|
| VBGF | $L_t = L_0 + (L_\infty - L_0)(1 - e^{(-kt)})$ |
| Logistic function | $L_t = \dfrac{L_\infty L_0 e^{(gt)}}{L_\infty + L_0(e^{(gt)} - 1)}$ |
| Gompertz function | $L_t = L_0(e^{G(1-e^{-gt})})$ |

Bertalanffy 1938); (2) the logistic function (Ricker 1979); and
(3) the Gompertz function (Gompertz 1825; Ricker 1975;
Table 3). Each model represented an alternative hypothesis for
growth and has frequently been used to model elasmobranch
growth. The three models were fitted using a length at birth
parameter ($L_0$) rather than age at zero length ($t_0$) because $L_0$ has
greater biological meaning (Cailliet *et al.* 2006; Goldman *et al.*
2012) and can be directly compared between models. The
asymptotic length ($L_\infty$) was also common between models, but
the growth completion parameters, that is $k$ (VBGF), $g$ (logistic)
and $G$, $g$ (Gompertz), cannot be compared directly. The $L_\infty$
was not a fitted parameter of the Gompertz function and was
calculated from the other parameters after they were estimated
as follows:

$$L_\infty = L_0 e^G$$

where $G$ is the instantaneous growth rate at $L_0$ (Ricker 1979).

Models were fitted using the method of non-linear least-
squares regression in the statistical package 'R' (ver. 3.0.2,
R Foundation for Statistical Computing, Vienna, Austria).
Model performance was evaluated using Akaike's Information
Criteria corrected for small sample size (AIC$_C$; Katsanevakis
2006; Zhu *et al.* 2009), calculated as:

$$\text{AIC}_C = \text{AIC} + \frac{2k(k+1)}{(n-k-1)}$$

where $AIC = n \log(\sigma^2) + 2k$, $k$ is the total number of parameters
+1 for variance ($\sigma^2$) and $n$ is the sample size. The most
appropriate model was that with the lowest AIC$_C$ value
(AIC$_{min}$). The two remaining models were ranked by the AIC
difference ($\Delta$) relative to the best model ($i = 1 - 3$), calculated
for each model as:

$$\Delta_i = \text{AIC}_{C,i} - \text{AIC}_{min}$$

Models with a $\Delta$ of 0–2 had substantial support, those with a
$\Delta$ of 4–7 had considerably less support and models with a $\Delta$ of
>10 had virtually no support (Burnham and Anderson 2001).
Akaike weights ($w_i$) were also calculated because they represent
the probability that the chosen model is the best model from
the candidates (Burnham and Anderson 2001). The $w_i$ were
calculated as:

$$w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{j=1}^{3} \exp(-\frac{\Delta_i}{2})}$$

To ascertain whether models for separate or combined sexes
were more appropriate for each species, the growth curves of
males and females were compared using likelihood ratio tests
(Kimura 1980) as implemented by Haddon (2001).

*Reproductive biology*

All *S. megalops* and *S. montalbani* were dissected to investigate
their reproductive biology. The reproductive staging of both
species was determined using Braccini *et al.* (2007)-modified
indices of Walker (2005). Estimates of population length ($L_{ST50}$)
and age ($A_{50}$) at maturity with 95% confidence intervals (CI)
were determined for males and females separately using a
generalised linear model with a binomial error structure and
logit-link function within the statistical package 'R'. These were
used to determine the life history invariant ratios of relative
size ($L_{ST50}/L_{STmax}$) and age ($A_{50}/A_{max}$) at maturity (Dulvy and
Forrest 2010; Rigby and Simpfendorfer 2015). Male maturity
was based on clasper staging, because the claspers were the
simplest to examine and Braccini *et al.* (2007) had found
agreement for *S. megalops* between maturity ogives based on
indices for claspers, vas deferens and gonad. For both species,
males were classed as mature if the claspers were rigid and fully
calcified with evident hooks. For females, Braccini *et al.* (2007)
found *S. megalops* maturity ogives differed slightly between
indices, although the criteria of large-yolked follicles was
preferred as an index of maturity because vitellogenesis was
advanced and the ogive agreed with those of the other criteria.
Hence, for the present study, females of both species were
considered mature when large-yolked follicles were present.

Because there were two sampling trips for *S. megalops*,
differences in mature male reproductive condition between the
two sampling trips was investigated. The presence or absence of
seminal fluid was noted and the seminal vesicles weighed prior
($W_{SV1}$) and after ($W_{SV2}$) expression of spermatozoa. The testes
($W_T$), stomach ($W_S$) and liver ($W_L$) were also weighed ($\pm0.1$ g).
For individuals with seminal fluid present, three indices were
calculated for each sampling trip, namely the gonadosomatic
index (GSI; $100 \times W_T$/total weight), hepatosomatic index (HSI;
$100 \times W_L$/total weight) and proportion of spermatozoa within
the seminal vesicle (PS; $100 \times (W_{SV1} - W_{SV2}/W_{SV1})$), where
total weight $= W_{BT} - (W_T + W_S + W_L)$ (Hamlett 1999; Awruch
2007; Awruch *et al.* 2009). The significance of differences in
GSI, HSI and PS between trips were determined by ANOVA.
The PS was also calculated for mature *S. montalbani*. To describe
the female reproductive cycle, the maximum width of the left
uteri ($\pm1$ mm) was measured, the number of yolked oocytes
in each ovary counted and the maximum oocyte diameter
(MOD; $\pm1$ mm) recorded. When present, the number of embryos
and the sex, uterus (left or right), presence of internal or external
yolk and total length ($\pm1$ mm) of each embryo were noted.

## Results

*Specimen collection and length equations*

In all, 422 *S. megalops* were collected: 117 males (253–407 mm
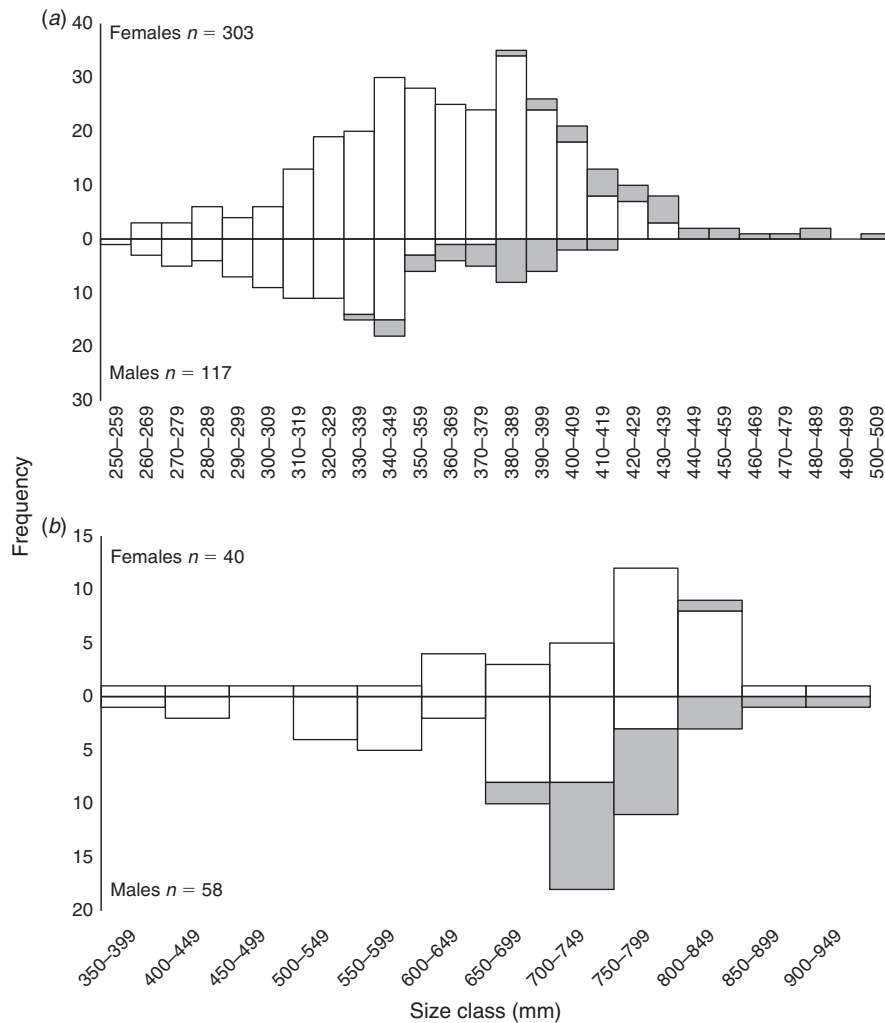$L_{ST}$), 304 females (261–505 $L_{ST}$) and one hermaphrodite

**Fig. 2.** Size frequency of immature (white) and mature (grey) *Squalus megalops* (*a*) and *Squalus montalbani* (*b*) individuals.

(internal male, external female; 370 mm $L_{ST}$). One male and one female were lodged as voucher specimens H7565-01 and H7565-02 at the Australian National Fish Collection (CSIRO). Most *S. megalops* were immature (Fig. 2) and collected when the fisher was trialling the gear in three consecutive trawl shots at depths of 203–280 m south of the main EKP grounds (Fig. 1). One of these shots captured 84 males (19 mature) and 225 females (18 mature, 4 of which were pregnant). Only 31 animals (15 males and 16 females, all immature) were collected within the main EKP grounds. The sex ratio across all the trawls was significantly biased towards females (1 : 2.6; $\chi^2 = 83.06$, d.f. $= 1$, $P < 0.0001$); however, in the main EKP grounds, the sex ratio did not differ significantly from 1 : 1 ($\chi^2 = 0.06$, d.f. $= 1$, $P = 0.86$). The relationship between $L_{ST}$ and $L_F$ was significantly different between the sexes ($n = 420$, $P = 0.030$, ANCOVA) and was described for males by $L_{ST} = 1.129 L_F + 2.49$ ($R^2 = 0.99$, $P < 0.001$, d.f. $= 117$) and females by $L_{ST} = 1.128 L_F + 3.40$ ($R^2 = 0.99$, $P < 0.001$, d.f. $= 301$).

Ninety-eight *S. montalbani* were provided to this study: 58 males (370–920 $L_{ST}$) and 40 females (351–934 $L_{ST}$). The

length frequency was representative of the 465 *S. montalbani* captured in the CSIRO 2009 gulper survey, where males ranged from 300 to 930 mm $L_{ST}$ and females were 310–1110 mm $L_{ST}$ (K. Graham, Australian Museum, pers. comm., 2015). The sex ratio did not differ significantly from 1 : 1 (1.4 : 1; $\chi^2 = 2.93$, d.f. $= 1$, $P < 0.08$) and the individuals were predominantly immature (Fig. 2). The relationship between $L_{ST}$ and $L_F$ was significantly different between the sexes ($n = 97$, $P = 0.021$, ANCOVA) and was described by $L_{ST} = 1.146 L_F - 0.512$ ($R^2 = 0.99$, $P < 0.001$, d.f. $= 57$) for males and by $L_{ST} = 1.138 L_F + 8.66$ ($R^2 = 0.99$, $P < 0.001$, d.f. $= 39$) for females.

## Age estimation

### Squalus megalops

Most first DFS had readability scores of 2 (33.8%) or 3 (60.3%), whereas the majority of the second DFS had poorer readability, with scores of 3 (53.0%) or 4 (42.7%). The APE among readings was 4.00% for the first DFS and 5.32% for the second DFS. Of the 117 males, 17 had a damaged first DFS and
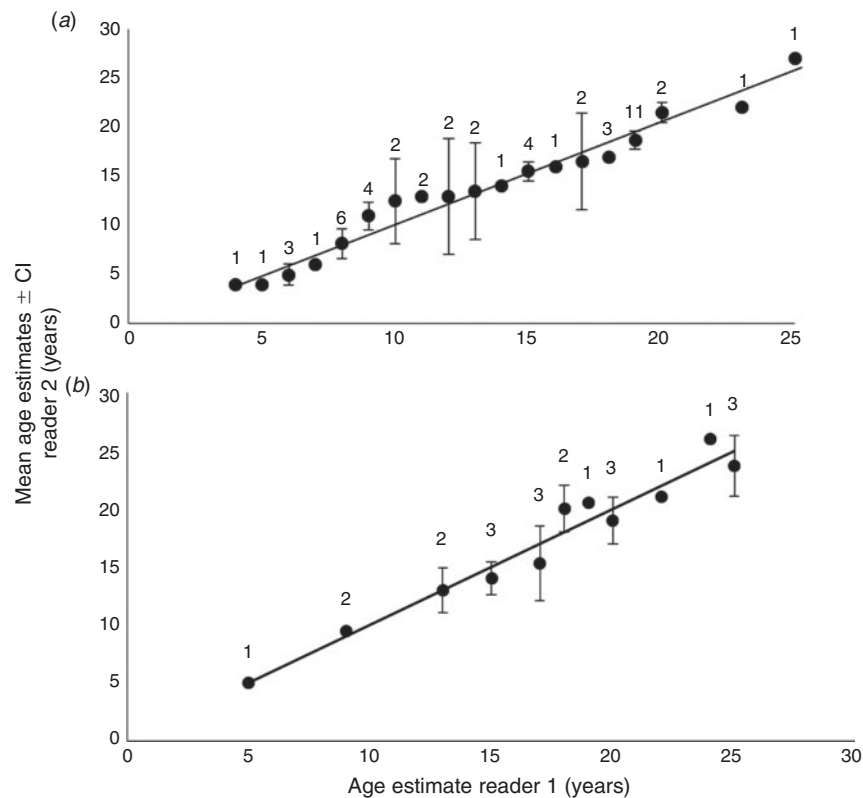
**Fig. 3.** Age bias plots for the comparison of age estimates between readers for (*a*) *Squalus megalops* and (*b*) *Squalus montalbani*. The solid line is the 1 : 1 relationship. Numbers above the data points are sample sizes. Data show mean (±95% confidence intervals) age estimates.

were not used for age reading. A subsample of the 304 female *S. megalops* from across the full size range was used for age reading with only whole spines used (no damaged, broken or worn spines). In all, 202 (100 male and 102 female) first DFS were read three times. Within-reader precision of the three age estimates was high, with an APE of 3.66%. There was no systematic age estimation bias between readers (Fig. 3) and between-reader precision was good, with an APE of 5.11%. Ten DFS were discarded because of poor readability and lack of concordance of counts (five males and five females); consequently, the estimated age from 192 animals was used in the growth models: 95 males ranged from 4 to 18 years and from 253 to 407 mm $L_{ST}$; 97 females ranged from 5 to 25 years and from 262 to 505 mm $L_{ST}$.

### Squalus montalbani

The second DFS was damaged in 14 animals. Unfortunately, this included the largest male of 920 mm $L_{ST}$ and largest female of 934 mm $L_{ST}$. The second DFS of two animals had very worn enamel and these were also excluded from age reading. A few of the second DFS had slightly worn enamel on the top of the spines but the bands could still be read down the sides of the spines and were included in the age reading. In all, 82 (46 male and 36 female) second DFS were read three times. The within-reader precision of the three age estimates was high, with an APE of 4.60%. There was no systematic age estimation bias between

readers (Fig. 3) and between-reader precision was good, with an APE of 5.43%. Five DFS (6.0%) were discarded because of poor readability (readability >4; four males, 1 female); therefore, 77 animals were used in the growth models: 42 males (5–28 years, 370–866 mm $L_{ST}$) and 35 females (3–27 years, 351–852 mm $L_{ST}$).

### Growth estimation

#### Squalus megalops

The Gompertz growth model was the best fit for males and females with $w_i = 39\%$ for both sexes, although there was little difference in the performance of the three models for each sex and all models were well supported with $\Delta_i < 1$ (Table 4). There was little variation in the estimates of length at birth and growth completion parameters between the models and two sexes, with only the estimates of $L_\infty$ varying substantially for the males (Table 4). Likelihood ratio tests indicated no significant difference between the growth curves of the sexes (d.f. = 3, $\chi^2 = 2.26$, $P = 0.52$); hence, the growth models for the sexes combined were considered the most appropriate. Of these, the VBGF was the best fit with the lowest $AIC_C$, although the Gompertz was also well supported ($\Delta_i = 1.56$). The growth completion rate was very slow at $k = 0.003$ year$^{-1}$ with almost linear growth, which would account for the large value of $L_\infty$ (3922 mm) that was biologically unrealistic (Table 4; Fig. 4). There were no individuals less than 5 years of age collected, which may also have

**Table 4.  Summary of model parameters and Akaike's Information Criteria corrected for small sample size ($AIC_C$) results for the observed length at age data for *Squalus megalops* and *Squalus montalbani***

$n$, sample size; $\Delta_i$, difference in $AIC_C$ values between models; $w_i$ (%), $AIC_C$ weights; RSE, residual standard error; $L_\infty$, asymptotic length parameter; $L_0$, length at birth parameter; $k$, growth rate parameter for the von Bertalanffy growth function (VBGF); $g$, growth rate parameter for Logistic model; $G$ and $g$, growth coefficients of the Gompertz model. Only $L_0$ and $L_\infty$ are comparable between the three models

| Sex | Model | $n$ | $AIC_C$ | $\Delta_i$ | $w_i$ (%) | RSE | $L_\infty$ (mm) | $L_0$ (mm) | $k$ (year$^{-1}$) | $G$ | $g$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *S. megalops* | | | | | | | | | | | |
| Sexes combined | VGBF | 192 | 969.60 | 0 | 60 | 12.39 | 3922 | 234 | 0.003 | – | – |
| | Logistic | 192 | 972.75 | 3.15 | 12 | 12.50 | 855 | 243 | – | – | 0.046 |
| | Gompertz | 192 | 971.16 | 1.56 | 28 | 12.44 | 1249 | 241 | – | 1.646 | 0.021 |
| Male | VGBF | 95 | 445.80 | 0.28 | 34 | | 3921 | 234 | 0.003 | – | – |
| | Logistic | 95 | 438.30 | 0.76 | 27 | | 440 | 213 | – | – | 0.120 |
| | Gompertz | 95 | 437.25 | 0 | 39 | | 455 | 207 | – | 0.788 | 0.093 |
| Female | VGBF | 97 | 518.45 | 0.28 | 34 | | 3921 | 235 | 0.003 | – | – |
| | Logistic | 97 | 518.92 | 0.76 | 27 | | 2202 | 252 | – | – | 0.031 |
| | Gompertz | 97 | 518.16 | 0 | 39 | | 2323 | 247 | – | 2.240 | 0.014 |
| *S. montalbani* | | | | | | | | | | | |
| Sexes combined | VGBF | 77 | 478.78 | 1.15 | 22 | 21.89 | 3624 | 272 | 0.007 | – | – |
| | Logistic | 77 | 477.78 | 0.15 | 38 | 21.82 | 1079 | 287 | – | – | 0.082 |
| | Gompertz | 77 | 477.63 | 0 | 40 | 21.80 | 1285 | 275 | – | 1.54 | 0.046 |
| Male | VGBF | 42 | 274.48 | 3.57 | 10 | | 3624 | 257 | 0.007 | – | – |
| | *Logistic* | *42* | *270.91* | *0* | *60* | | *979* | *249* | – | – | *0.100* |
| | Gompertz | 42 | 271.04 | 1.33 | 30 | | 1100 | 229 | – | 1.569 | 0.062 |
| Female | VGBF | 35 | 203.69 | 0 | 40 | | 3628 | 285 | 0.007 | – | – |
| | Logistic | 35 | 204.58 | 0.89 | 25 | | 1190 | 311 | – | – | 0.069 |
| | Gompertz | 35 | 203.94 | 0.25 | 35 | | 1515 | 303 | – | 1.610 | 0.036 |

accounted for the larger estimate of $L_0$ (234 mm; Table 4) than that observed from near-term embryos (157 mm; Table S1 available as Supplementary material to this paper). Because the growth rate was close to linear, VBGF parameters should be used with caution when compared with other taxa.

### Squalus montalbani

The male length at age data was best fitted by the logistic model at $w_i = 60\%$, and although there was little variation in the $AIC_C$ performance of all three models, the Gompertz was more supported ($w_i = 30\%$ and $\Delta_i = 1.33$) than the VBGF (Table 4). For females, the VBGF was the best fit, although all three models were well supported with comparable performance (Table 4). The $L_\infty$, $L_0$ and growth completion parameters between the respective male and female models were similar (Table 4) and the likelihood ratio tests indicated no significant difference between the growth curves of the sexes (d.f. = 3, $\chi^2 = 2.98$, $P = 0.39$). Consequently, the sexes combined model was used. All three growth models had similar performance, support and estimates of $L_0$, although the Gompertz model had a marginally lower $AIC_C$ value and was considered the best model at $w_i = 40\%$ (Table 4). The growth curve did not reach an asymptote (Fig. 4), although the $L_\infty = 1285$ mm (Table 4) was biologically realistic compared with the observed maximums of 1010 mm (White and Dharmadi 2010) and 1110 mm from the CSIRO 2009 gulper survey (K. Graham, Australian Museum, pers. comm., 2015). $L_0$ (275 mm; Table 4) was also biologically realistic because it was slightly higher than the size of near term pups reported from the CSIRO 2009 gulper survey of $L_0 = 234$–235 mm $L_{ST}$ (Table S1).

### Maturity analyses

#### Squalus megalops

Length and age at maturity data were available for 117 and 95 male *S. megalops* respectively (253–407 mm $L_{ST}$ and 4–18 years). The smallest mature male was 327 mm $L_{ST}$ and the youngest mature male was 10 years old. The largest and oldest immature male was 370 mm $L_{ST}$ and 14 years. Estimates of $L_{ST50}$ and $A_{50}$ (with 95% CI) were 352 (335, 370) mm and 12.4 (10.4, 14.5) years respectively (Fig. 5). Length and age at maturity data were available for 303 and 97 female *S. megalops* respectively (261–505 mm $L_{ST}$ and 5–25 years). The smallest mature female was 380 mm $L_{ST}$ (not aged) and the youngest aged mature female was 18 years old (405 mm $L_{ST}$). The largest and oldest immature female was 436 mm $L_{ST}$ and 20 years. Estimates of $L_{ST50}$ and $A_{50}$ (95% CI) were 419 (400, 439) mm and 19.1 (17.5, 20.7) years respectively (Fig. 5).

#### Squalus montalbani

Length and age at maturity data were available for 58 and 42 male *S. montalbani* respectively (370–920 mm $L_{ST}$ and 5–28 years). The smallest and youngest mature male was 674 mm $L_{ST}$ and 17 years. The largest immature male was 785 mm $L_{ST}$ and oldest immature 24 years. Estimates of $L_{ST50}$ and $A_{50}$ (with 95% CI) were 700 (627, 783) mm and 21.8 (19.0, 24.0) years respectively (Fig. 5). Although length and age data were available for 40 and 35 female *S. montalbani* respectively (351–934 mm $L_{ST}$ and 3–27 years), this included only one pregnant female (849 mm $L_{ST}$, not aged). Therefore, it was not possible to determine the female estimates of $L_{ST50}$ and $A_{50}$. There were two females larger than the pregnant 849 mm $L_{ST}$,
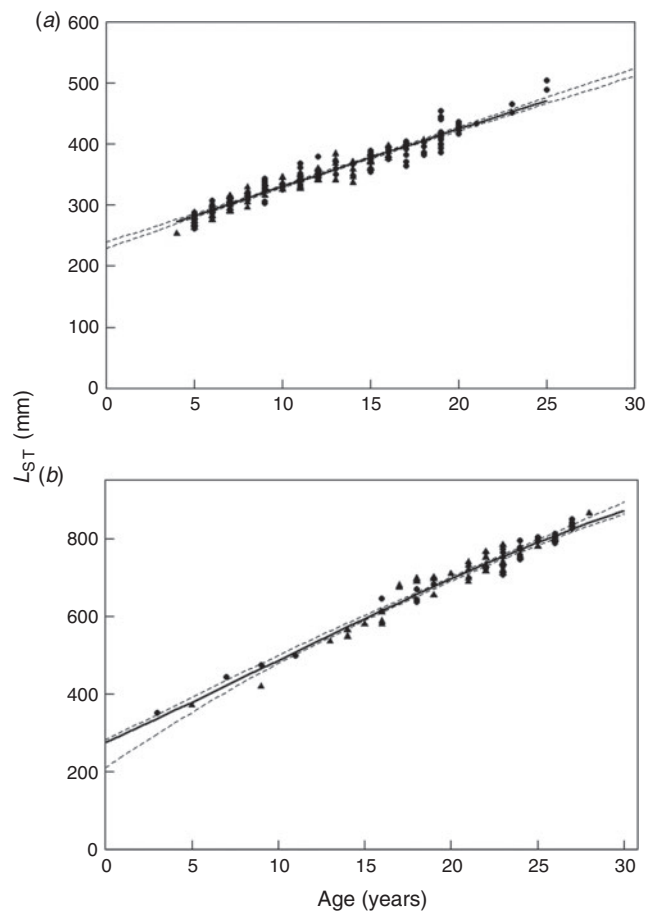
**Fig. 4.** Growth models fitted to length at age data for combined sexes (triangles, males; circles, females) for (*a*) *Squalus megalops* von Bertalanffy growth function (VBGF) and (*b*) *Squalus montalbani* Gompertz. Dashed lines are 95% confidence intervals. $L_{ST}$, stretched total length.

both of which were immature at 852 mm $L_{ST}$ (27 years) and 934 mm $L_{ST}$ (not aged).

### Invariants

The invariants of relative size at maturity were similar for both male and female *S. megalops* (0.86 and 0.84 respectively) but larger than that of *S. montalbani* males (0.76). The relative age at maturity was high for both species at 0.70 and 0.76 for male and female *S. megalops* respectively and 0.87 for male *S. montalbani*.

### Length at birth and reproductive cycle
#### Squalus megalops

In total, 27 of the 117 males collected had seminal fluid present (17 on the first trip and 10 on the second trip). There was no difference in the maturity condition of mature males between the two sampling trips, with similar values of mean GSI ($F_{1,25} = 4.24$, $P = 0.83$), HSI ($F_{1,25} = 4.24$, $P = 0.28$) and PS ($F_{1,25} = 4.24$, $P = 0.82$). Pregnant females were captured on both sampling trips, with a total of 10 collected. The

number of embryos ranged from two to three. One had near-term embryos with umbilical scars and internal yolk sacs (Table S1). At 37.1% of the maternal $L_{ST}$, it is likely they were close to length at birth, because Braccini *et al.* (2007) reported the temperate *S. megalops* mean length at birth as 38.5% (95% CI 35.6–42.4) of maternal total length. The remaining nine pregnant females all had candles with evident embryos and yolked oocytes that, at 12–14 mm in diameter, were smaller than the yolked oocytes of maximum oocyte diameter (MOD) 32 mm in the female with near-term pups (Table S1).

Although there were only limited data for mature and pregnant *S. megalops* females, a comparison of MOD with uterus width for different phases of uterus development suggested a continuous reproductive cycle (Fig. 6). The MOD increased with uterus width for females ovulating for the first time (Uterus Index, UI = 1–3), with ovulation at a MOD of ~35 mm. Pregnant animals had a smaller MOD that increased with embryonic development (UI = 5a) to a size ready for ovulation when embryos were near term (UI = 5b; Fig. 6). The cycle is also likely asynchronous because not all mature females collected each trip were pregnant.

#### Squalus montalbani

Of the 58 males collected, 25 were mature and all but two had seminal fluid present with the proportion of seminal fluid at a mean ($\pm$s.e.) of $50.5 \pm 2.7\%$. The one mature female was pregnant with a litter size of nine. Four other breeding *S. montalbani* have been recorded from eastern Australian with litters of 6–16, with one of these litters near term at 234–245 mm and 29.3–30.6% of maternal $L_{ST}$ (Table S1).

The data were too limited to draw any definite conclusions about the female reproductive cycle. The MOD increased with uterus width in immature females (UI = 1–2) and the pregnant female had developing yolked oocytes (Table S1). Additional data for breeding females indicated one female of 800 mm $L_{ST}$ with near-term embryos and yolked oocytes, whereas two larger pregnant females with less well-developed embryos had no yolked oocytes (Table S1).

### Discussion

The present study demonstrated that both *S. megalops* and *S. montalbani* are slow growing, long lived with a late age at maturity and mostly small litters. These conservative life history traits were similar to those reported in previous studies of *S. megalops* (Watson and Smale 1998, 1999; Braccini *et al.* 2006a, 2007; Hazin *et al.* 2006; Pajuelo *et al.* 2011) and are typical of deep-water squaloids (Compagno *et al.* 2005; Kyne and Simpfendorfer 2007; Graham and Daley 2011; Irvine *et al.* 2012) and deep-water chondrichthyans in general (García *et al.* 2008; Barnett *et al.* 2013; Rigby and Simpfendorfer 2015). This combination of traits is indicative of low productivity and poor resilience to exploitation (Walker 1998; Morato *et al.* 2006), which is of concern for both species. The deeper-dwelling *S. montalbani* may be more vulnerable to fishing pressure than *S. megalops* because it was found to be longer lived and matured later, which are life history differences associated with increasing depth and a reduction in the capacity to recover from
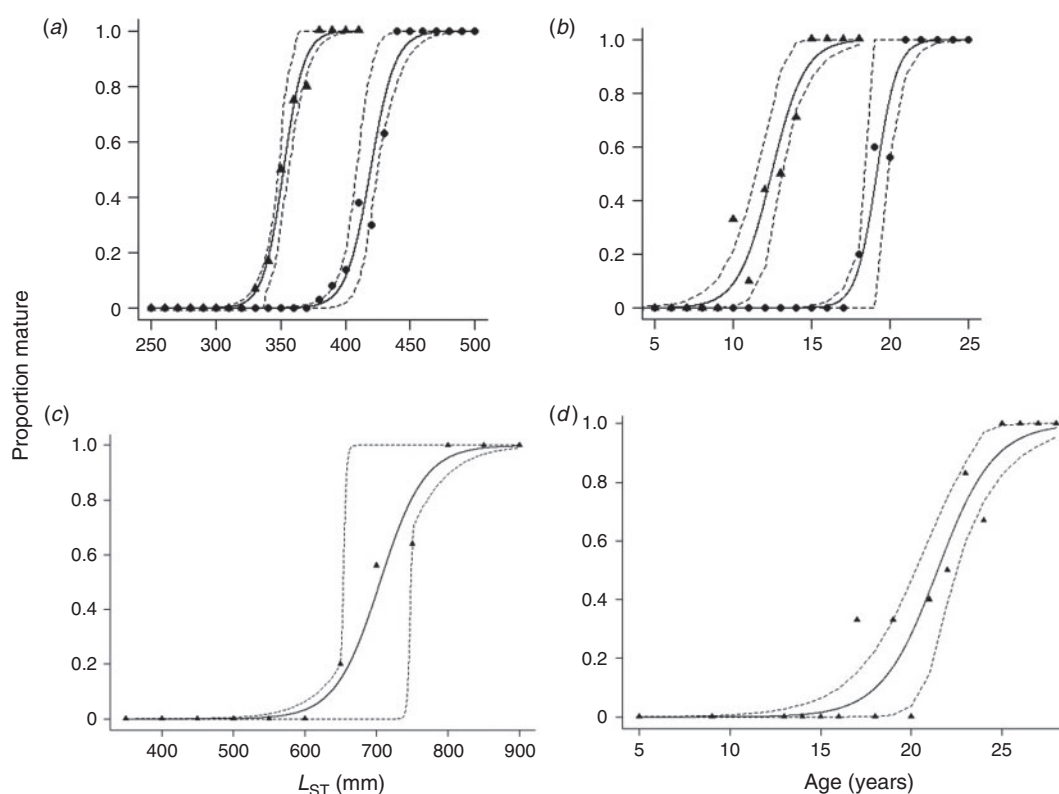
**Fig. 5.** (*a, c*) Length and (*b, d*) age at maturity ogives for male (triangles) and female (circles) *Squalus megalops* (*a, b*) and *S. montalbani* males (*c, d*). Dashed lines are 95% confidence intervals.
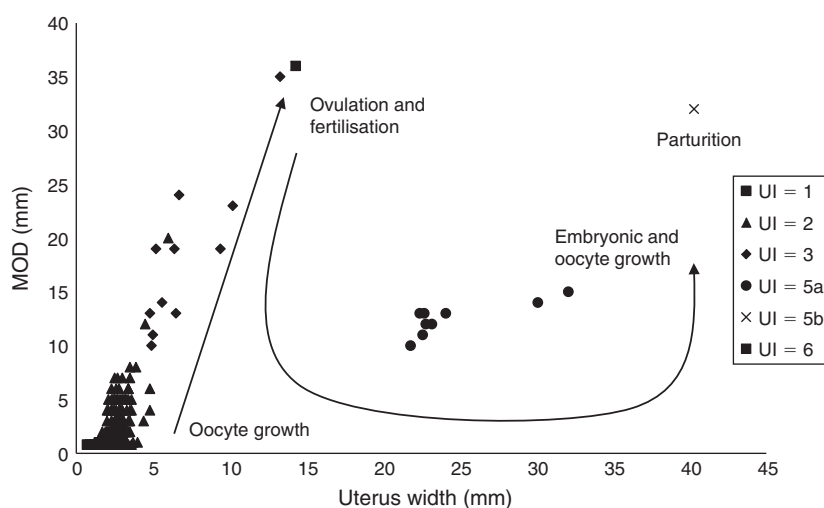


**Fig. 6.** Relationship between maximum oocyte diameter (MOD) and uterus width for *S. megalops*. Uterus Index (UI) 1, 2 and 3, immature; UI 5a, developing embryo; UI 5b, near-term embryo; UI6, post partum.

exploitation (García *et al.* 2008; Simpfendorfer and Kyne 2009; Rigby and Simpfendorfer 2015).

### Growth

Both species exhibited almost linear growth with no evidence of an asymptote and a very slow growth completion rate. All three models examined fit the data well and produced very similar growth curves, for both males and females and sexes combined. The lack of difference in growth curves between the sexes is contrary to previous studies of *S. megalops* that have reported significant differences between growth of the sexes, although only for their later years (Watson and Smale 1999; Braccini *et al.*

2007; Pajuelo *et al.* 2011). Growth rates diverged between sexes at 10 years in temperate south-east Australian waters (Braccini *et al.* 2007) and 16 years in the Canary Islands subtropical waters (Pajuelo *et al.* 2011), when male growth slowed, whereas female growth increased steadily. It is possible that this divergence in growth rates does occur in the tropical population of *S. megalops* at a later age than sampled in the present study.

The lack of an asymptote in the growth curves of both species has occurred with other dogfishes, although usually only for females (Wilson and Seki 1994; Taniuchi and Tachikawa 1999; Cotton *et al.* 2011; Irvine *et al.* 2012) and, in one case, in both sexes (Cannizzaro *et al.* 1995). All previous growth studies of *S. megalops* also found fairly linear growth for females, but not for males (Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). The lack of an asymptote may be due to a paucity of older animals in the samples, which was the most commonly suggested reason by previous authors (Wilson and Seki 1994; Watson and Smale 1999; Braccini *et al.* 2007; Cotton *et al.* 2011). The lack of older *S. megalops* may have resulted from some degree of maturity segregation. Although there was some mixing of immature, mature and pregnant animals in the Swain Reefs area, the majority of the samples were of immature animals. In addition, the commercial demersal otter trawl gear used to collect *S. megalops* possibly influenced the sizes collected and caused length-selective sampling bias. The turtle excluder and bycatch reduction devices, mandatory for trawl nets in the Australian tropics (Griffiths *et al.* 2006; Courtney *et al.* 2014), may have had an additional effect and excluded the larger *S. megalops*, although these devices generally only exclude larger sharks >1000 mm in length (Brewer *et al.* 2006; Courtney *et al.* 2014).

*Reproduction*

The maximum age of *S. megalops* in the present study was 25 years, which is less than that in temperate Australian waters, South Africa and the Canary Islands (Table 1; Watson and Smale 1999; Braccini *et al.* 2007; Pajuelo *et al.* 2011). Comparisons with the Atlantic populations are treated with caution because the regional differences may be due to different populations or the possibility that *S. megalops* is a species complex (Compagno *et al.* 2005; Graham 2005; Last and Stevens 2009; Pajuelo *et al.* 2011).

The invariants of relative age at maturity also suggested that the oldest animals of *S. megalops* and *S. montalbani* were not aged, because the invariants were much higher than the average of 0.53 for deep-water chondrichthyans (Rigby and Simpfendorfer 2015), and invariants are known to be consistent across chondrichthyan taxa (Dulvy and Forrest 2010). Although specimens close to the maximum size of *S. montalbani* were provided to this study, the largest animals could not be aged because of their damaged dorsal fin spines. The 934 mm $L_{ST}$ *S. montalbani* in the present study and the 1110 mm $L_{ST}$ female captured in the CSIRO 2009 gulper survey were larger than the previously reported maximum of 910 mm for this species within Australia (Last and Stevens 2009) and 1010 mm for Indonesia (White and Dharmadi 2010). It was unlikely the maximum size of *S. megalops* was sampled; at 505 mm $L_{ST}$, the largest animal in the present study was considerably smaller than the 635 mm recorded from temperate Australia (Braccini *et al.* 2007) and the

Atlantic maximum of 890 mm (Hazin *et al.* 2006). The invariant of relative size at maturity corroborates this, because the 0.84 was greater than the average relative size of maturity of 0.76 for deep-water chondrichthyans (Rigby and Simpfendorfer 2015).

Regional differences in the Australian *S. megalops* size and age at maturity were evident, with the tropical animals smaller and older at maturity than those of temperate waters. The regional differences were greater for females than males. The Swain Reefs population $L_{ST50}$ values for females and males, at 422 and 352 mm respectively were markedly less than those from two studies of temperate Australian *S. megalops* (Table 1; Graham 2005; Braccini *et al.* 2006*a*). It is possible that the sizes and ages at maturity estimates from the present study may be biased because the majority of the samples were of immature animals. This could only be determined from further sampling in a wider area of the tropics to collect more mature animals. Regional size variations in shark population parameters have been linked to latitudinal differences in distribution correlated with water temperature (Yamaguchi *et al.* 2000; Lombardi-Carlson *et al.* 2003; Colonello *et al.* 2007; Gutteridge *et al.* 2013), with the increased size at maturity hypothesised to enable higher-latitude animals to store more energy (Blackburn *et al.* 1999). This may explain the regional size differences, because the temperate waters were on average 5°C cooler than those of the tropics, even in the shallower waters of the 21–238-m depth range across which animals were collected in the temperate region (Integrated Marine Observing System, IMOS 2015).

The *S. megalops* males and females in the present study were mature at 12.6 and 19.1 years respectively, which is older than previous estimates for temperate Australian waters (Table 1; Braccini *et al.* 2006*a*, 2007). Although there may be a bias because of a smaller proportion of mature animals sampled, there is still a regional difference in age at maturity, particularly for females. This difference could also be the result of the latitudinal separation, although logically it would be expected the *S. megalops* from higher latitudes would mature later because of slower growth in cooler waters. Although comparisons with Atlantic studies were treated with caution, the ages at maturity of the present study were more similar to those in the subtropical Canary Islands than in temperate South Africa (Table 1; Watson and Smale 1999; Pajuelo *et al.* 2011). It seems plausible that the sampling of a smaller proportion of mature animals in temperate studies may have affected the estimates of age at maturity. The temperate studies included shallow shelf waters and the studies reported strong sexual segregation and the possibility that parturition and the majority of the larger females occurred outside the areas sampled (Watson and Smale 1999; Braccini *et al.* 2007). Pajuelo *et al.* (2011) and the present study did not sample depths <190 m and sexual segregation was not as strong as for the temperate studies. Pajuelo *et al.* (2011) found populations were not sex or size segregated at all and although the present study found some segregation, there was still some mixing with immature and mature animals and pregnant females co-occurring in samples. In the Canary Islands, the lack of segregation was attributed to a narrow range of available habitat, but this was not a limiting factor in the Swain Reefs area. *Squalus megalops* is an opportunistic predator (Burrage *et al.* 1996; Braccini *et al.* 2005) and the mixed schools in the present study may have been due to the presence of a large mesoscale

eddy, the 'Capricorn Eddy', which increases the availability of nutrients and food ( Weeks *et al.* 2010, 2015; Jaine *et al.* 2014).

Sexual dimorphism is typical of deep-water squaloids and many chondrichthyans (Cailliet and Goldman 2004; Cortés 2004; Kyne and Simpfendorfer 2007) and was apparent in the *S. megalops* in the present study, whereby the females were of a larger size and size at maturity, matured later and were older than the males. This was also the case, but to a lesser degree, for *S. montalbani*, where the females were larger and older than males at maturity. This dimorphism, previously found for *S. megalops* (Watson and Smale 1999; Graham 2005; Hazin *et al.* 2006; Braccini *et al.* 2007; Pajuelo *et al.* 2011; Marouani *et al.* 2014), has been attributed to the need for females to partition more time and energy into growth before reproductive age is reached to be of sufficient size to support the production of large young (Frisk *et al.* 2001; Cailliet *et al.* 2005; Rigby and Simpfendorfer 2015).

The *S. megalops* reproductive information suggested a continuous and asynchronous breeding cycle for females, with males able to mate at both sampling times. This is a strategy common among outer shelf and upper slope deep-water dogfishes (Cotton *et al.* 2011; Graham and Daley 2011; Rochowski *et al.* 2015) and concurs with other *S. megalops* studies, which found a 2-year ovulation and gestation period, and that males were able to breed throughout the year (Watson and Smale 1998; Graham 2005; Braccini *et al.* 2006a; Hazin *et al.* 2006; Pajuelo *et al.* 2011). It seems reasonable to assume that the Swain Reefs *S. megalops* have a biennial cycle, the same as for other regions (Braccini *et al.* 2006a; Pajuelo *et al.* 2011). If this is the case, then combined with the low fecundity and late age at maturity, the Swain Reefs population has a low biological productivity similar to other populations of *S. megalops*.

The reproductive cycle of the deeper-dwelling *S. montalbani* was difficult to discern from the one pregnant female in the present study and the four reported from the Australian east coast. Although two females had developing oocytes during gestation, there were no such oocytes in other pregnant animals and there were two very large but immature females with immature uteri, oviducal glands and ovaries. These limited data provide some evidence of a non-continuous breeding cycle with a resting phase that is common among the mid-slope ($>$650 m) dogfishes (Kyne and Simpfendorfer 2010; Irvine *et al.* 2012). The larger litter sizes of nine to 16 were also more typical of mid-slope than upper-slope dogfishes (Daley *et al.* 2002). Litter sizes increased with increasing maternal size and were comparable for maternal size to those of four to 16 reported from Indonesia for 12 females of 830–952 mm $L_T$ (White *et al.* 2006; White and Dharmadi 2010). The largest embryos were near term at 234–245 mm, which is similar to the largest embryo observed in Indonesia of 240 mm (referred to as *Squalus* sp. 1; White *et al.* 2006). This extends the known size of birth range to 207–245 mm (Last *et al.* 2007a). Female size at maturity in Indonesia (White *et al.* 2006) and the CSIRO 2009 gulper survey was 800–820 mm (K. Graham, Australian Museum, pers. comm., 2009) which, from the growth curve in the present study, was estimated to be 26 years. Although the pregnant 849 mm $L_{ST}$ specimen of the present study could not be aged because of damaged DFS, from the growth curve it was estimated to be 27–28 years old.

The size of maturity of male *S. montalbani* in the present study was similar to that for Indonesia (600–700 mm; White and Dharmadi 2010) and to that for all males captured in the CSIRO 2009 gulper survey (650–700 mm; K. Graham, Australian Museum, pers. comm., 2009). It was not possible to elucidate the synchronicity or length of the reproductive cycle, although an asynchronous breeding cycle was suggested for the Indonesian *S. montalbani* females (White and Dharmadi 2010). Although *S. montalbani* inhabits the upper slope, it has a reproductive cycle more typical of mid-slope dogfishes, with larger litters and a potential resting period that may enable it to recover between pregnancies, particularly during times of low food supply (Daley *et al.* 2002; Irvine *et al.* 2012). This suggests it may have a long reproductive cycle because the length of the deep-water chondrichthyan cycle increases with depth (Rigby and Simpfendorfer 2015). Even though it has a larger litter size, *S. montalbani* is probably less productive than *S. megalops*, based on later age at maturity, greater longevity and a potentially longer and non-continuous reproductive cycle.

### Effects of fishing

The differences in reproductive cycles and life history traits between the two squalids are typically associated with their different distribution within the deep-water habitat (Rigby and Simpfendorfer 2015). *Squalus megalops* inhabits both the shelf and upper slope, whereas *S. montalbani* lives deeper, is more restricted to the upper slope and likely has a more conservative life history. An increase in depth is known to coincide with an increase in vulnerability to exploitation (García *et al.* 2008; Simpfendorfer and Kyne 2009). This was evident off the east Australian coast, where trawling over two decades caused significant declines of $>$90% in the relative abundance of a suite of dogfishes, including *S. montalbani* off southern NSW, yet an increase by 18% in the relative abundance of *S. megalops* (Graham *et al.* 2001; Kyne and Simpfendorfer 2010). These highly disparate fishery impacts between the two species were mostly attributed to their different depth distributions, although the more conservative life history traits of *S. montalbani* identified in the present study would have also contributed to the differences. The distribution of *S. montalbani* on the upper slope exposed the entire population to fishing impacts, whereas *S. megalops* was abundant in a relatively unfished outer shelf area that was thought to enable recruitment onto the fished upper slope area and help maintain their overall biomass (Graham *et al.* 2001; Walker and Gason 2007). Further south, where the outer shelf areas were much more intensely trawled, there were noticeable effects on *S. megalops*, with some declines evident in their relative abundance (Graham *et al.* 2001).

The management arrangements for the east coast Australian trawl fishery have changed significantly since the surveys that highlighted the declines in upper slope dogfishes. Catch limits and spatial and depth closures were implemented to provide protection to the vulnerable dogfishes and to aid recovery of overfished populations (AFMA 2012). Estimates of recovery times were multiple decades for two upper slope species with ages at maturity similar to *S. montalbani* (AFMA 2012). The life history traits elucidated from the present study of *S. montalbani* of slow growth, late age at maturity, high longevity and a possibly non-continuous breeding cycle indicate their recovery

from overfishing off southern NSW in the east coast Australian trawl fishery is also anticipated to take decades.

*Squalus megalops* likely has a greater capacity to recover from fishery impacts than *S. montalbani*, although it still has low biological productivity that would hinder recovery. A risk assessment of temperate Australian *S. megalops* highlighted the potential vulnerability of this species to the effects of fishing (Braccini *et al.* 2006*b*). In the Swain Reefs area, the main deep-water EKP fishing grounds are limited in their spatial extent and are generally concentrated on the shelf, although there is some fishing on the upper slope habitat. The fishery appears to be interacting with only part of the *S. megalops* population, with low catches within the main fishing grounds. Although the current effects of the fishery appear to be limited, any change in fishing practices in the Swain Reefs area that leads to an increase in catch susceptibility, such as a change in area fished, could place *S. megalops* at risk of depletion.

Both *S. megalops* and *S. montalbani* share life history traits aligned to other deep-water dogfishes that limit their ability to recover in the event of depletion. Their traits were associated with differences in their depth of occurrence, with the deeper-dwelling *S. montalbani* more vulnerable to exploitation and expected to take decades to recover from overfishing. The tropical Great Barrier Reef population of *S. megalops* was smaller and older at maturity than the temperate Australian and global populations and may not be greatly affected by the deep-water trawl fishery in the Swain Reefs area, although to confirm this would require further temporal and spatial sampling.

## Acknowledgements

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