# Age, growth and maturity of the roundel skate, *Raja texana*, from the Gulf of Mexico, USA

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**Abstract.** The roundel skate (*Raja texana*) inhabits near-shore waters throughout the Gulf of Mexico. Despite such a wide distribution, very little is known about its biology. In order to gain insight into the life history of this species, the age, growth and maturity of 231 skates ranging in size from 277 to 630-mm total length (TL) were examined. Based on vertebral band counts, the oldest age estimates obtained were 8 years for males and 9 for females, which corresponded to 495-mm TL and 630-mm TL respectively. Age-bias plots and coefficient of variation suggested that our ageing method represents a non-biased and precise approach to age assessment. Marginal increment and edge analyses suggested that growth bands are formed annually with a distinct trend of increasing growth at the beginning of March. Back calculations suggested a birth size of 113–118-mm TL. Observed and back-calculated length-at-age data were used to assess growth with four different models, including the von Bertalanffy (VBGM), von Bertalanffy with size at birth (VB with $L_0$), Gompertz and Francis models. Male and female growth was significantly different. The VBGM and the Francis model produced similar results and provided the best fit. Curves fitted with observed and back-calculated data suggested slightly faster growth than curves fitted with only observed data. Maturity occurred at 444-mm TL and 4.95 years for males, whereas females matured at 537-mm TL and 5.8 years.

**Additional keywords:** elasmobranch, marginal increments, Rajiformes, shell gland, spermatocyst.

## Introduction

The roundel skate (*Raja texana* Chandler, 1921) is a small skate ($\leq$630-mm total length, TL) endemic to the Gulf of Mexico, USA. This skate has been recorded to a depth of 183 m, within a temperature range of 14–28°C (Smith 1997), although it is most commonly caught at 15–110 m (McEachran and Fechhelm 1998), with young skates occurring in shallow bays, while adults tend to live offshore (Smith 1997). Many skates, including *Raja texana*, are caught as bycatch/byproduct of the butterfish (*Peprilus burti* Fowler, 1944) trawl fishery (J. K. Carlson, personal observation) and the shrimp trawl fishery (Shepherd and Myers 2005) that operates in the Gulf of Mexico. In the butterfish fishery, all fishes (including skates) are snap frozen soon after being caught and therefore suffer 100% mortality (J. K. Carlson, personal observation).

It is well documented that directed fisheries have been the cause of stock collapse in many elasmobranch species (Musick 1999; Stevens *et al*. 2000; Musick 2004). However, an equal, if not greater, threat is indirect fishing mortality through bycatch (Bonfil 1994; Musick 2004). In many fisheries, skates are becoming increasing popular as a commercially viable byproduct. A contemporary case history in the north-west Atlantic can be used to illustrate the potential threat to skate populations when taken as bycatch. Before 1980, skates caught by trawl fisheries were discarded (Sosebee 2000), although they are now retained for the rapidly expanding markets for skate pectoral fins, commonly referred to as 'wings' (Sulikowski *et al*. 2003, 2005*a*, 2005*b*). Until 2003, skate exploitation continued without biological/productivity data or management. As a result, several skates were depleted to a potentially unsustainable level (Casey and Myers 1998). Unsustainable fishing practices have seen the depletion of many other skate species, including the well-documented disappearance of the common skate, *Dipturus batis*, from the Irish Sea (e.g. Dulvy and Reynolds 2002).

Age information forms the basis for the calculations of growth rate, mortality rate and productivity, making it one of the most important variables for estimating a population's status and assessing the risks associated with its exploitation. In order to provide insight into these parameters, the objectives of the
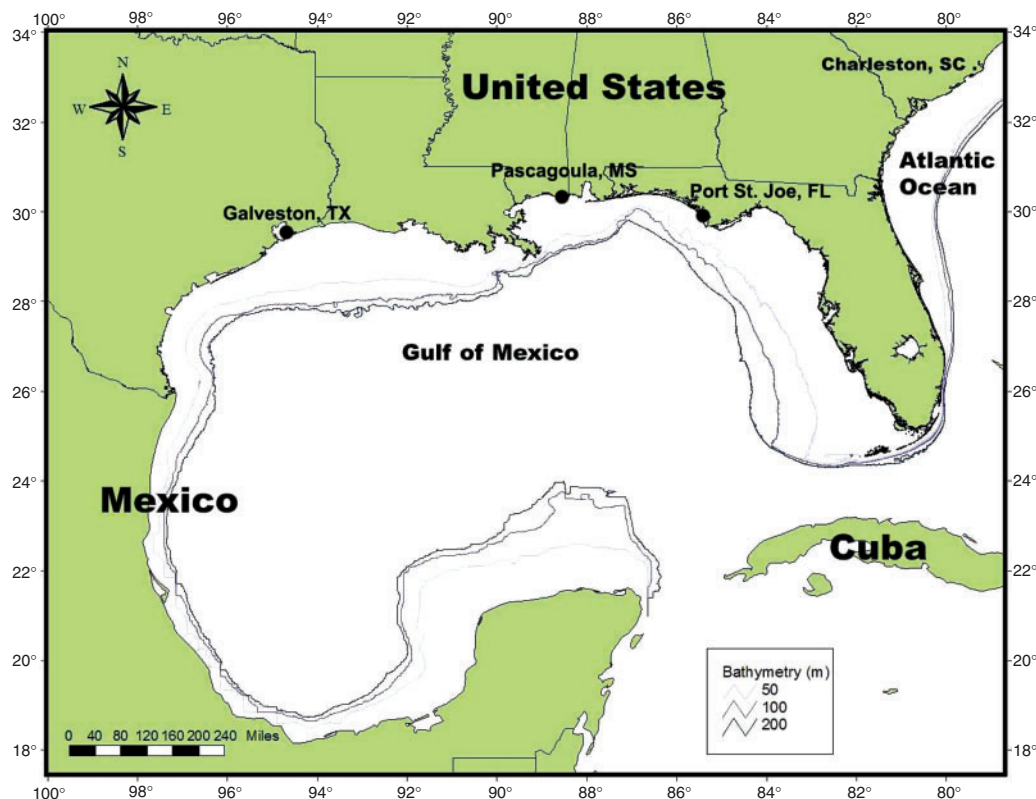
**Fig. 1.**  Map of the sampling area for *Raja texana* within the Gulf of Mexico showing areas and locations stated in the text.

present study were to examine the sex-specific age, growth and size and age at maturity for this species.

## Materials and methods

### Sampling

Roundel skates were collected in January, February, March, April, June and October 2005 during the National Marine Fishery Service (NMFS) trawl surveys (Pascagoula, Mississippi), or from Raffield Fisheries Inc., commercial butterfish trawl catches (Port St. Joe, Florida). These months represent the times of the year when specific NMFS groundfsh surveys are conducted and/or there are peaks in the commercial butterfish fishing season. During the other months of the year, roundel skates were inaccessible from either sampling source. The central catch area ranged from Port St. Joe Bay, Florida to Galveston, Texas (Fig. 1). All skates were captured by trawl, snap frozen and stored for up to 1 month. Frozen skates were then transported to the University of Florida for processing. Skates were thawed, sexed and measured for total length (TL ± 1 mm) and disc width (DW ± 1 mm). Total length was measured as a straight-line distance from the tip of the rostrum to the end of the tail and DW was measured as a straight-line distance between the tips of the widest portion of pectoral fins. Total wet weight (± 1 g) was also recorded. Total length was related to DW and weight for each sex, and an analysis of covariance (ANCOVA) was used to investigate differences between the sexes.

### Age and growth

#### Vertebral collection and preparation

A block of 10 vertebral centra were taken from above the abdominal cavity of 251 roundel skates (141 females and 110 males), labelled and stored frozen. Vertebrae were thawed and cleaned of excess tissue then washed in tap water and stored in 70% ethanol. Three vertebrae from each sample were randomly removed from the alcohol and air dried. Each vertebra was fixed to a clear glass slide using resin (Crystol bond 509 or thermo-plastic cement, Electron Microscopy Sciences, Hatfield, PA). Sagittal sections (0.6-mm thick) were taken using a Buehler 82 Isomet low-speed saw (Buehler, Lake Bluff, IL, USA). Growth bands were enhanced on one of three sections from each sample by staining with 0.01% crystal violet following Johnson (1979). Sections were then mounted on microscope slides using clear resin (Cytoseal 60, Fisher Scientific, Pittsburg, PA).

#### Band counts

Vertebral sections were examined using reflected light under a compound microscope (25–40× magnification). Centrum diameter (CD ± 0.1 mm) was measured using an ocular micrometer. One growth band was defined as an opaque and translucent band pair that traversed the intermedialia and clearly extended into the corpus calcareum (e.g. Sulikowski *et al.* 2003, 2005*a*; Cailliet and Goldman 2004). The birth mark (age zero) was defined as the first distinct mark distal to the focus that coincided

with a change in the angle of the corpus calcareum (e.g. Wintner and Cliff 1996; Cailliet and Goldman 2004).

### Precision and bias

Vertebrae were examined by two readers (reader 1 = JAS and reader 2 = KCD). Reader 1 made two non-consecutive band counts of all vertebrae sections without prior knowledge of the skate's length or previous counts. Reader 2 made two consecutive counts from 50 randomly selected vertebrae sections. Samples that had a variability of more than 2 years between each reading were eliminated from further analyses. Count reproducibility was estimated using the Index of Average Percentage Error (IAPE) described by Beamish and Fournier (1981). Pair-wise age–reader comparisons (Natanson *et al.* 2002) were independently generated by the two readers by making non-consecutive band counts from a random sample of 50 vertebral sections. Intra-reader bias and precision of annulus counts were examined using age-bias plots and the coefficient of variation (Campana *et al.* 1995; Campana 2001). A Tukey's test was used to test for differences between ages. Precision estimates of each reader were calculated using the coefficient of variation (CV) as described by Chang (1982), Campana *et al.* (1995) and Campana (2001).

### Verification

The periodicity of band-pair formation was investigated using marginal increment ratio (MIR) and edge analysis (EA) (e.g. Sulikowski *et al.* 2003). A sub-sample of vertebrae was randomly selected comprising both juvenile and adult specimens collected in the months of January, February, March and April. As a result of the lack of specimens, all available vertebrae were used from skates collected in June and October. The MIR was calculated as the ratio of the distance between the last and penultimate opaque bands as measured with an optical micrometer. Average MIR was plotted by month of capture to identify trends in band formation and a Kruskal–Wallis test on ranks was used to test for differences in marginal increment by month (Simpfendorfer *et al.* 2000; Sulikowski *et al.* 2005a). The EA was classified using the criteria of Yudin and Cailliet (1990) and each band edge type was compared with the month of capture.

### Back calculation

Because our sample lacked smaller individuals, lengths at previous ages were back calculated from centra measurements for both sexes. The relationship between CD and TL was investigated to determine the most appropriate method for back calculating previous lengths at age. Different proportional methods have been found to vary in their similarity to observed size-at-age data (Carlson *et al.* 2004; Goldman and Musick 2006). We applied the linear modified Dahl–Lea method (Francis 1990) because this method provided better biological accuracy for modelling growth:

$$L_i = L_c[(a + bCR_i)/(a + bCR_c)]$$

where 'a' and 'b' are the linear fit parameter estimates, $L_i$ is length at ring, $L_c$ is length at capture, $CR_c$ = centrum radius at capture and $CR_i$ = centrum radius at ring '$i$'.

### Modelling growth

Observed length-at-age data were used with several growth models to predict the growth of *R. texana* males and females. The von Bertalanffy (1938) growth model (VBGM) is described as:

$$L_t = L_\infty(1 - e^{-k[t-t_0]})$$

where $L_t$ is the expected length at age $t$ years, $L_\infty$ is the asymptotic (average maximum) length, $k$ is the growth coefficient and $t_0$ is the theoretical age at zero length.

A modified form of the von Bertalanffy equation that uses a size-at-birth intercept (VB with $L_0$) (Fabens 1965; see Simpfendorfer *et al.* 2000; Carlson and Baremore 2005) was also fitted to the observed length-at-age data and is described as:

$$L_t = L_\infty + (L_\infty - L_0)(1 - e^{-kt})$$

where $L_0$ is the length at time zero (size at birth as estimated from back-calculations), $L_t$ is the length at time $t$, $L_\infty$ is the asymptotic average maximum length and $k$ is the growth coefficient. The theoretical age at zero length ($t_0$) could be calculated by substituting $L_t = 0$ and solving for $t$.

The third model fitted to the observed length-at-age data was the reparameterised von Bertalanffy model of Francis (1988a) and is described as:

$$L_t = l_\phi + (l_\psi - l_\phi)(1 - r^{2(T-\phi)/(\psi-\phi)})/(1 - r^2)$$

where the three VBGM parameters ($L_\infty$, $t_0$ and $k$) are replaced with $l_\phi$ (mean length at reference age $\phi$), $l_\psi$ (mean length at reference age $\psi$), $l_\chi$ (mean length at reference age $(\phi + \psi)/2$) and $r = (l_\psi - l_\chi)/(l_\chi - l_\phi)$. In order to directly compare growth between each sex and avoid unnecessary extrapolations, the same reference ages ($\phi = 2$, $\psi = 8$) were chosen for each sex. Conventional VBGM parameters were calculated from the Francis model parameters using:

$$L_\infty = l_\phi + (l_\psi - l_\phi)/(1 - r^2)$$
$$k = -(2\log_e r)/(\psi - \phi)$$
$$t_0 = \phi + (1/k)\log_e((L_\infty - l_\phi)/L_\infty)$$

To determine if band deposition was related to an increase in animal weight, the Gompertz growth (Ricker 1975) equation was used with observed weight-at-age data.

$$w_t = w_0 e^{G(1-e^{-gt})}$$

where $w_t$ is mass at age $t$, $w_0$ is weight at age zero, $G$ is the initial exponential growth rate and $g$ is exponential rate of decline in growth rate.

The VBGM, VB with $L_0$ and Francis models were re-fit using back-calculated length data combined with observed length data to investigate the effect of back-calculated data on the fit of the growth curve.

All growth models were fitted with the non-linear regression function in Systat 8.0 (Systat Software Inc., Point Richmond, CA). The goodness-of-fit of each model was assessed by the residual mean square error (MSE) and coefficient of determination ($r^2$). Confidence intervals (95%) around the Francis parameters give a direct measure of the heterogeneity in length at age. Confidence intervals for each parameter were calculated using Systat 8.0.

*Comparing growth between sexes*

The Francis growth parameters were directly compared between sexes and $\chi^2$ tests on each likelihood ratio were used to compare the data between sexes for VBGM and VB with $L_0$. This method, advocated by Kimura (1980), is a reliable means of assessing any difference in growth. Likelihood ratio and $\chi^2$ tests were performed in Microsoft Excel as outlined by Haddon (2001).

*Longevity*

Band counts provided an initial estimate of longevity, although these values may be underestimated if the population has been commercially fished. Therefore, theoretical longevity was also estimated based on the age at which >95% of $L_\infty$ is reached ($5 \cdot (\ln 2)/k$ (Ricker 1979)) using the growth coefficients from the VBGM and Francis models.

*Sexual maturity*

*Males*

Testes (including epigonal tissue) were removed, blotted dry and weighed ($\pm 1$ g). Clasper length (CL $\pm 1$ mm) was measured as a straight-line distance from the posterior opening of the cloaca to the posterior tip of the clasper. Relative clasper length (CL/TL) was calculated as the clasper length divided by total length.

Maturity was also assessed using spermatogenic development (Maruska *et al.* 1996). Histological processing followed the protocol of Sulikowski *et al.* (2005a, 2005c). Mature spermatocysts were identified by the organisation of spermatozoa into tightly shaped packets that were arranged spirally along the periphery of the spermatocysts (Sulikowski *et al.* 2004, 2005a, 2005c). The mean proportion of mature spermatocysts was measured along a straight-line distance across a cross section of one representative full testes lobe.

Males were considered mature and reproductively capable of copulating when claspers had elongated (CL/TL $\geq 0.20$) and calcified, and the testes were $\geq 1$ g with $\geq 23\%$ mature spermatocyts (Sulikowski *et al.* 2004, 2005c; Ebert 2005; Oddone and Vooren 2005).

The relationships between TL and mean relative clasper length, mean testes weight and mean percentage mature spermatocysts were examined using 20-mm TL size classes. Mean corresponding ages at TL were used to assess the chronological reproductive development of males.

*Females*

Shell glands were removed, blotted dry and weighed ($\pm 1$ g). Unfortunately, the freeze and thaw process caused unforeseen and detrimental effects on follicles within the ovaries. As a consequence, large vitellogenic follicles often burst during attempts to remove the ovary and accurate gonad weights could not be obtained. To prevent further damage, the diameter of follicles >1 mm was measured with calipers *in situ* (within the skate body cavity). From these measurements, the size of the largest follicle in the left and right ovary was averaged. The presence of egg cases in various stages of formation was also noted.

Females were considered sexually mature (reproductively capable of egg encapsulation and oviposition) when ovarian follicles were $\geq 18$ mm and the shell gland was $\geq 4$ g. These morphological sizes represented the minimum sizes observed for roundel females bearing egg cases in their uteri as outlined by Sulikowski *et al.* ( 2004, 2005b).

*Statistics*

The differences in morphological reproductive parameters between age groups were analysed by using an analysis of variance (ANOVA) followed by a Tukey's post hoc test. Statistical significance was accepted at $P < 0.05$. The proportion of mature spermatocysts was transformed to arcsine values before the aforementioned statistical analyses were performed. To determine if a relationship existed between the measured morphological parameters, a Pearson correlation analysis (denoted as *r*) was performed. The length and age at which 50% of the roundel skate population reached sexual maturity was estimated by fitting maturity ogives to length (at 20-mm intervals) and age (1-year intervals) by sex using probit analyses (Pearson and Hartley 1970).

## Results

*Size composition*

In total, 251 (141 females and 110 males) skates were collected. Males ranged from 277 to 495 mm and 50 to 600 g, whereas females ranged from 285 to 630 mm and 50 to 1100 g. The power relationship between weight (Wt) and total length (TL) differed significantly with sex ($P < 0.05$); Male: Wt $= (0.001)$TL$^{3.434}$ ($r^2 = 0.67$, $n = 110$), Female: Wt $= (0.002)$TL$^{3.234}$ ($r^2 = 0.86$, $n = 141$). The linear relationship between TL and DW differed significantly with sex ($P < 0.006$); Male: DW $= 0.522$TL $+ 3.494$ ($r^2 = 0.897$, $n = 99$), Female: DW $= 0.616$TL $+ 0.787$ ($r^2 = 0.910$, $n = 133$).

*Age and growth*

Regression equations for centrum diameter and total length did not differ significantly between sexes (ANCOVA: $P = 0.845$). The linear relationship for combined sexes was CD $=$ TL$(0.832) + (0.526)$ ($r^2 = 0.814$, $n = 229$). The relationships between CD and weight differed significantly between sexes (ANCOVA: $P < 0.05$). The power relationships were Female: CD $= 4.38$TL$^{0.2865}$ ($r^2 = 0.520$, $n = 95$); Male: CD $= 3.419$TL$^{0.286}$ ($r^2 = 0.584$, $n = 65$).

*Bias and precision*

Vertebral sections were easy to interpret and false bands (those bands that did not completely encircle the centra) were easily distinguished from complete bands. Of the 251 examined vertebrae, 231 (92%) were readable (males $= 99$; females $= 132$). The IAPE for these band counts was 7.2% for reader one. The IAPE for reader two was 7.7%. No appreciable bias was indicated when comparing the counts between the two readers, and

the coefficient of variance was 4.8% (Fig. 2). In the absence of bias, the level of precision was considered acceptable (Campana 2001). Subsequently, the counts generated by reader one were used for all ageing analyses (Natanson *et al.* 2002).

### Back calculation

A mean size at birth of 113 mm for females and 118 mm for males was estimated using back calculation (Table 1). Lee's phenomenon (Ricker 1979) was not evident. The back-calculated lengths were ≤7.4% of the observed length-at-age for each age class (Table 1).

### Verification

Marginal increments were significantly different between months (Kruskal–Wallis $P < 0.001$) with a distinct decrease in monthly increment growth in March (Fig. 3). Centrum EA

revealed that the vertebrae of skates captured in early January contained either a translucent band forming on the centrum edge or a large opaque band width emulating from the penultimate band (Fig. 4a). This banding pattern persisted in to February, when the centrum edge was marked with a translucent band or a small opaque band that was just anterior to a newly formed translucent band (Fig. 4b). The pattern of an increasing opaque band continued in skates captured in the months of March, April, June and October (Fig. 4c). Based on this information, the MIR and EA analyses support the likelihood that a single opaque band may form annually during January or February.

### Growth

Each growth model was fitted to the observed age data and the combined observed and back-calculated age data (length only). Those models that used observed length-at-age data fitted the
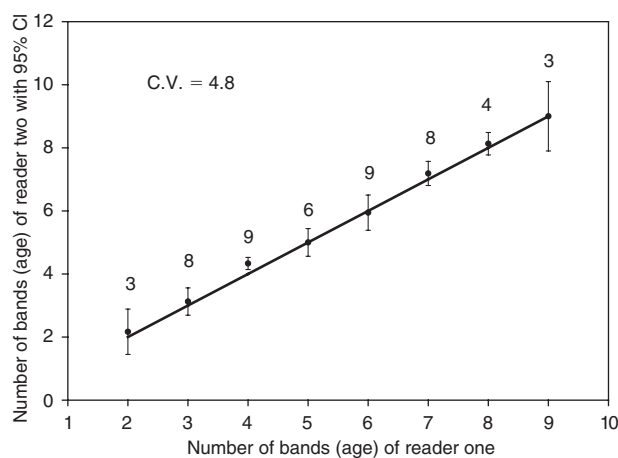


**Fig. 2.** Age-bias graph for pair-wise comparison of 50 *Raja texana* vertebral counts by two independent readers. Each error bar represents the 95% confidence interval for the mean age assigned by reader 2 to all fish assigned a given age by reader 1. The diagonal line represents the one-to-one equivalence line. Sample sizes are given above each corresponding age.
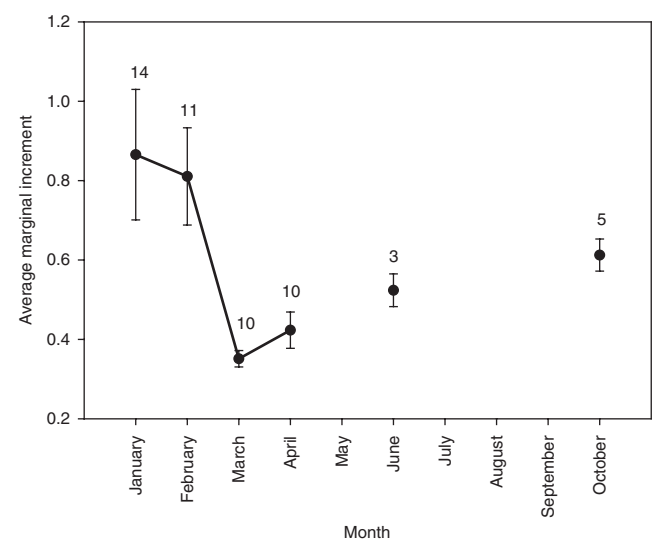


**Fig. 3.** Mean monthly marginal increments for *Raja texana* from the Gulf of Mexico. Sample sizes are given above each corresponding month. Error bars represent $1 \pm$ s.d.

**Table 1. Back-calculated mean total length (TL; mm) and observed mean total length (mm) at band formation for male and female *Raja texana***
s.d. = Standard deviation, $n$ = sample size

| Band number | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|---|
| Male | | | | | | | | | | |
| Back calculated TL | 118 | 198 | 277 | 337 | 381 | 413 | 437 | 453 | 461 | – |
| s.d. | 12.8 | 20.3 | 44.6 | 25.2 | 24.6 | 20.4 | 22.8 | 13.1 | 8.7 | – |
| $n$ | 99 | 99 | 99 | 90 | 74 | 50 | 30 | 17 | 5 | – |
| Observed TL | – | – | 299 | 358 | 405 | 433 | 457 | 474 | 475 | – |
| s.d. | – | – | 20.9 | 29.2 | 24.2 | 17.3 | 25.8 | 12.0 | 5.0 | – |
| $n$ | – | – | 5 | 20 | 24 | 20 | 13 | 12 | 5 | – |
| Female | | | | | | | | | | |
| Back calculated TL | 113 | 209 | 292 | 366 | 431 | 479 | 524 | 552 | 568 | 582 |
| s.d. | 13.6 | 18.9 | 26.7 | 34.8 | 38.5 | 37.9 | 33.2 | 21.1 | 14.5 | 17.9 |
| $n$ | 130 | 130 | 130 | 125 | 104 | 75 | 50 | 33 | 14 | 7 |
| Observed TL | – | – | 309 | 361 | 444 | 479 | 529 | 565 | 577 | 598 |
| s.d. | – | – | 19.9 | 33.5 | 43.5 | 38.3 | 39.4 | 23.5 | 13.2 | 19.5 |
| $n$. | – | – | 5 | 20 | 29 | 25 | 21 | 18 | 7 | 7 |
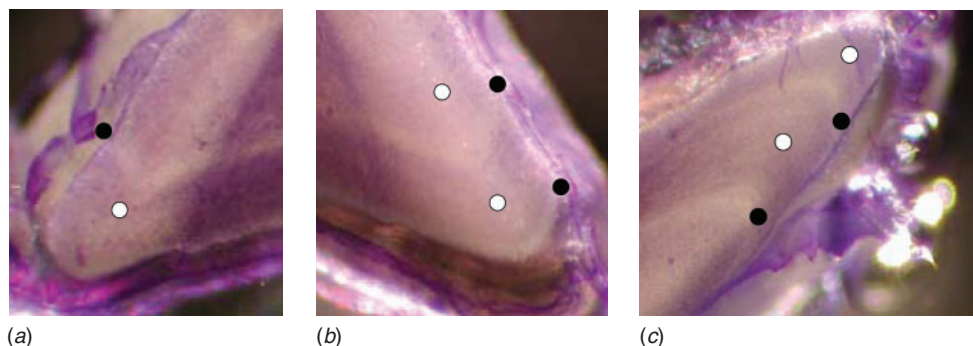
**Fig. 4.** Representative centrum edge analyses for *Raja texana* vertebrae captured during different temporal periods. (*a*) centrum edge from a specimen captured in early January; (*b*) centrum edge from a specimen captured in late January; and (*c*) centrum edge from a specimen captured in March. Black dots denote translucent bands and white dots denote opaque bands.

data well and exhibited a high coefficient of determination for males ($r^2 \geq 0.808$) and females ($r^2 \geq 0.831$) (Fig. 5), whereas models that also used back-calculated data exhibited higher coefficient of determinations for both sexes (Table 2). The three length-based models were considered superior to the Gompertz model. The Gompertz model fitted the female weight-at-age data well ($r^2 = 0.790$), although it provided a poor fit to male weight-at-age data ($r^2 = 0.351$) and this model was not used for further growth analysis.

Male and female growth was significantly different (Kimura's coincident curve: $\chi^2 = 125.03$, $P < 0.001$), with females growing faster than males throughout life. Direct comparison of Francis model parameters found that males grew 122 mm in the 3 years from age two to age five, compared with 194 mm for females. In the 3 years between the ages of five and eight, males grew only 52 mm and females grew 97 mm.

The Francis model predicted the same growth as the VBGM (Fig. 5), and both curves predicted the same size at birth with a *y*-axis intercept of 150 mm for males and 66.2 mm for females. These estimates are considerably different to the birth size of 113–118 mm predicted using back calculation. The VB with $L_0$ had a set intercept of 115 mm and the predicted growth after 2 years was similar to the VBGM and Francis model.

For males, growth parameters were similar for all three length-at-age based models, whereas female growth parameters differed between each model (Table 2). Interestingly, the female asymptotic size was considerably different between models, with the VB with $L_0$ model predicting a much larger asymptotic size than the maximum observed size (Table 2).

*Longevity*

Based on direct age estimates the oldest male in our sample was 8+ years and the oldest female was 9+ years. Using the growth coefficients from the VBGM and Francis models (Table 2), theoretical longevity (Ricker 1975) was estimated as 8.7 years for males and 15.1 years for females.

*Maturity*

*Males*

Relative clasper length (CL/TL), testes weight and percentage mature spermatocysts increased steadily with total length until
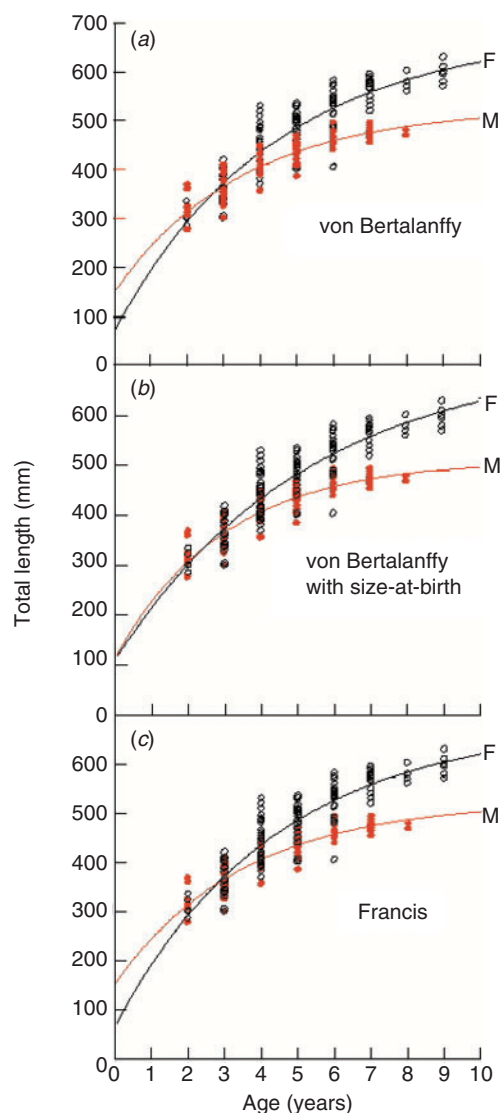


**Fig. 5.** Predicted growth of male and female *Raja texana* from the Gulf of Mexico using various models: (*a*) von Bertalanffy; (*b*) size at birth von Bertalanffy; and (*c*) Francis.

**Table 2.    Estimates of growth parameters and goodness of fit for four growth models fitted to observed size-at-age data for male and female *Raja texana* from the Gulf of Mexico**

VBGM = Bertalanffy (1938) growth model; $L_\infty$ is the asymptotic average maximum length (mm), $k$ is the growth coefficient and $t_0$ is the theoretical age at zero length. VB with $L_0$ = von Bertalanffy with size at birth (Fabens 1965); Francis = reparameterised model from Francis (1988a), $l_2$ is length at age two; $l_5$ is length at age five; $l_8$ is length at age eight; von Bertalanffy parameters estimates from Francis conversion equations. Gompertz (Ricker 1975) model using weight-at-age data; $W_0$ is weight at age zero, $G$ the initial exponential growth rate and $g$ is the exponential rate of decline in growth rate. $r^2$ = coefficient of determination; 95% confidence = 95% Wald Confidence Interval. $L_0$ = size at birth (mm)

| Growth model | Sex | | Observed data only | | | | Observed and back-calculated data | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Parameter | Estimate | Standard error | 95% confidence | Parameter | Estimate | Standard error | 95% confidence |
| VBGM | Male | $r^2$ | 0.808 | – | – | $r^2$ | 0.960 | – | – |
| | | $L_\infty$ | 525.8 | 23.17 | 45.99 | $L_\infty$ | 540.4 | 7.61 | 14.94 |
| | | $k$ | 0.286 | 0.062 | 0.123 | $k$ | 0.249 | 0.009 | 0.017 |
| | | $t_0$ | −1.174 | 0.565 | 1.120 | $t_0$ | −0.942 | 0.034 | 0.067 |
| | | $L_0$ | 150.0 | – | – | $L_0$ | 113.0 | – | – |
| | Female | $r^2$ | 0.831 | – | – | $r^2$ | 0.959 | | |
| | | $L_\infty$ | 682.4 | 73.11 | 36.95 | $L_\infty$ | 731.6 | 12.67 | 24.87 |
| | | $k$ | 0.229 | 0.084 | 0.043 | $k$ | 0.179 | 0.006 | 0.013 |
| | | $t_0$ | −0.446 | 0.096 | 0.402 | $t_0$ | −0.903 | 0.033 | 0.066 |
| | | $L_0$ | 66.2 | – | – | $L_0$ | 109.2 | – | – |
| VB with $L_0$ ($L_0$ = 115 mm) | Male | $r^2$ | 0.806 | – | – | $r^2$ | 0.960 | – | – |
| | | $L_\infty$ | 512.07 | 0.995 | 1.975 | $L_\infty$ | 542.8 | 7.18 | 14.10 |
| | | $k$ | 0.334 | 0.020 | 0.040 | $k$ | 0.246 | 0.007 | 0.014 |
| | | $t_0$ | −0.759 | | | $t_0$ | −0.963 | – | – |
| | Female | $r^2$ | 0.798 | – | – | $r^2$ | 0.958 | – | – |
| | | $L_\infty$ | 721.8 | 51.92 | 27.20 | $L_\infty$ | 744.9 | 12.34 | 24.21 |
| | | $k$ | 0.187 | 0.029 | 0.015 | $k$ | 0.171 | 0.005 | 0.010 |
| | | $t_0$ (*) | −0.925 | – | – | $t_0$ (*) | −0.976 | – | – |
| Francis | Male | $r^2$ | 0.808 | – | – | $r^2$ | 0.960 | – | – |
| | | $l_2$ | 313.8 | 7.60 | 15.1 | $l_2$ | 289.9 | 1.26 | 2.47 |
| | | $l_5$ | 436.0 | 2.90 | 0.58 | $l_5$ | 417.6 | 1.28 | 5.89 |
| | | $l_8$ | 487.8 | 6.70 | 15.33 | $l_8$ | 482.3 | 3.00 | 2.51 |
| | | $L_\infty$ (*) | 485.95 | – | – | $L_\infty$ (*) | 480.1 | – | – |
| | | $k$ (*) | 0.286 | – | – | $k$ (*) | 0.249 | – | – |
| | | $t_0$ (*) | −1.650 | – | – | $t_0$ (*) | −1.529 | – | – |
| | | $L_0$ | 150.0 | – | – | $L_0$ | 113.2 | – | – |
| | Female | $r^2$ | 0.831 | – | – | $r^2$ | 0.959 | – | – |
| | | $l_2$ | 292.5 | 23.74 | 12.00 | $l_2$ | 297.1 | 1.34 | 2.63 |
| | | $l_5$ | 486.2 | 8.20 | 4.14 | $l_5$ | 477.9 | 1.32 | 5.75 |
| | | $l_8$ | 583.7 | 12.82 | 6.48 | $l_8$ | 583.5 | 2.93 | 2.58 |
| | | $L_\infty$ | 581.2 | – | – | $L_\infty$ | 580.1 | – | – |
| | | $k$ | 0.228 | – | – | $k$ | 0.179 | – | – |
| | | $t_0$ | −1.058 | – | – | $t_0$ | −1.99 | – | – |
| | | $L_0$ | 66.2 | – | – | $L_0$ | 109.5 | – | – |
| Gompertz | Male | $r^2$ | 0.351 | – | – | – | – | – | – |
| | | $W_0$ | 0.003 | 0.011 | 0.022 | – | – | – | – |
| | | $G$ | 5.335 | 3.495 | 6.939 | – | – | – | – |
| | | $g$ | 0.635 | 0.247 | 0.491 | – | – | – | – |
| | Female | $r^2$ | 0.790 | | | – | – | – | – |
| | | $W_0$ | 0.008 | 0.007 | 0.015 | – | – | – | – |
| | | $G$ | 4.993 | 0.825 | 1.632 | – | – | – | – |
| | | $g$ | 0.341 | 0.060 | 0.119 | – | – | – | – |

the onset of maturity (Fig. 6a–c). For relative clasper length, a significant difference was found between the ages of 3–4 years (~360–405-mm TL), 4–5 years (~405–440-mm TL) and 5–6 years (~440–460-mm TL). In contrast, significant differences in testes weight and percentage mature spermatocysts were only found at ages 5–6 years (~440–460-mm TL). All parameters remained relatively constant after the age of 6 years (>460-mm TL). Moreover, simultaneous changes in the measured parameters were strongly correlated ($r^2 \cong 0.70 \pm 0.02$) over the course of maturation.

Maturity ogives suggested that 50% maturity occurs at 444-mm TL ($\pm 3.9$) (Fig. 7a) and 4.95 years ($\pm 0.7$) (Fig. 7b). These
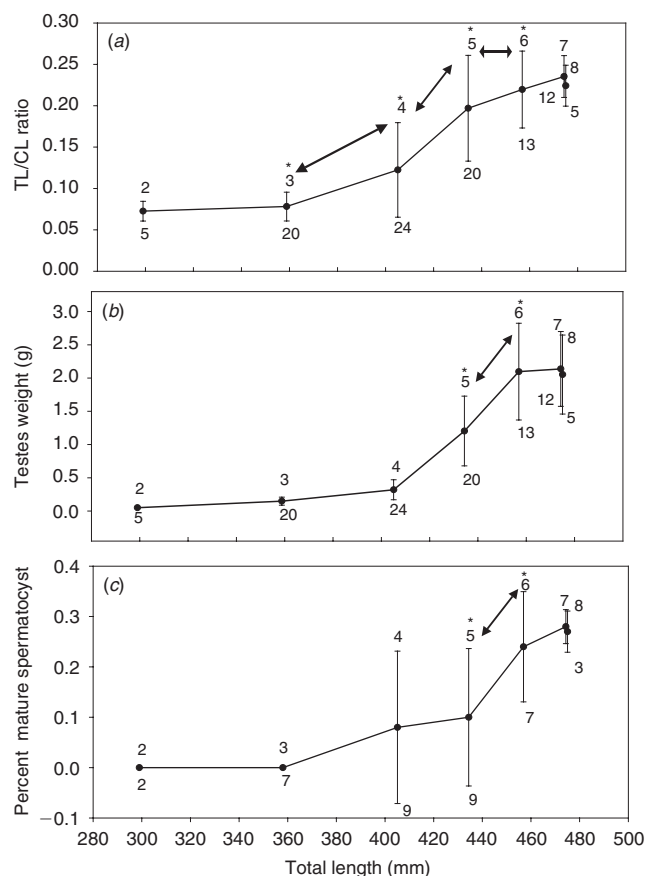
**Fig. 6.** (*a*) The clasper length to total length ratio (CL/TL), (*b*) total length to testis weight and (*c*) the proportion of mature spermatocysts as male *Raja texana* progresses through sexual maturity. Values are expressed as mean ± s.d. Asterisks followed by arrows represent significant differences (*P* < 0.05; ANOVA followed by a Tukey's post hoc test) between skates in consecutive age groups. The average age is given above each representative size class; numbers below the trend line of each graph represent the sample size.



**Fig. 7.** Maturity ogives for (*a*) total length of male and female *Raja texana* given in 10-mm intervals and (*b*) age of male and female *Raja texana*.

data are in overall agreement with our measured morphological parameters, which suggested that maturity occurs at 440-mm TL (± 17 mm) and 5–6 years. Thus, maturity in males occurs at about 88% of their maximum observed total length and 67% of their maximum observed age. The smallest mature male was 400-mm TL and 4 years, and the largest immature male was 454-mm TL and 6 years.

*Females*

Shell gland weight and average follicle size increased steadily until an abrupt increase at maturation. At the onset of maturity and throughout the maturation process, abrupt and significant (*P* < 0.05) increases in shell gland weight were observed (Fig. 8*a*). These increases were detected as female skates matured from ages 5 to 6 (~480–540-mm TL) and from 6 to 7 (~540–560-mm TL). Non-vitellogenic follicles between 1 and 4 mm in diameter were predominant in ovaries of skates aged 2–4 years (~310–445-mm TL; Fig. 8*b*). As skates matured, the quantity of small vitellogenic follicles gradually increased until the
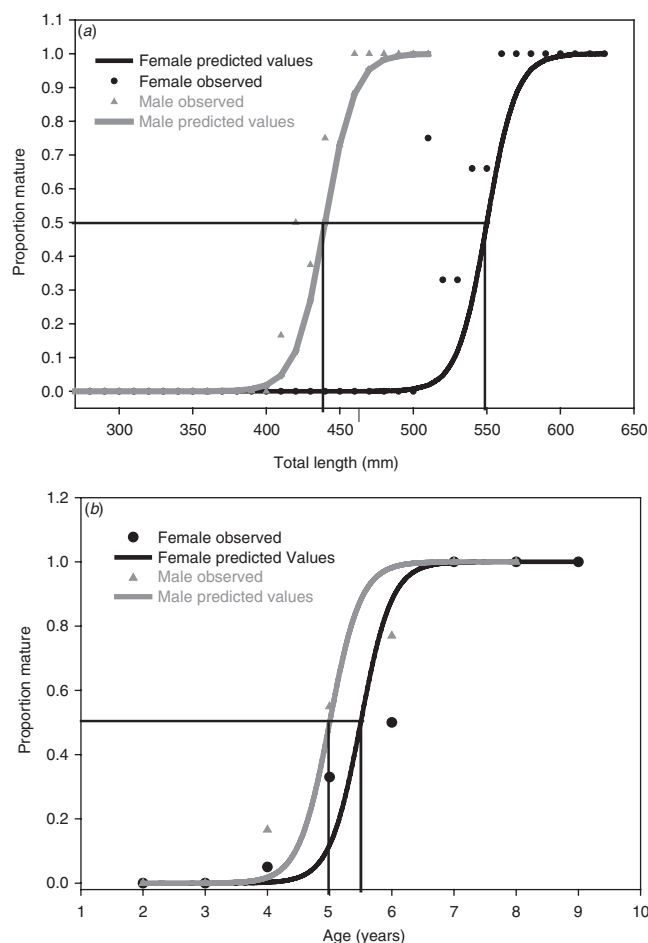
age of 6 years. A notable and significant (*P* < 0.05) change in the mean size of the largest follicle occurred as skates reached 6–7 years. Thereafter, the average size of the largest follicle remained relatively constant. Analogous to males, synchronous changes in the measured parameters were strongly correlated ($r^2 \cong 0.76 \pm 0.03$) over the course of maturation.

Maturity ogives for females predicted that 50% maturity occurs at 537 (± 8.9)-mm TL and 5.8 years (± 0.8) (Fig. 7*a*, *b*). These estimates corroborate the maturity estimates derived from the use of shell gland and follicle size data, which suggest 50% maturity at 540-mm TL and 6 years (Fig. 8*a*, *b*). Thus, female maturity occurs at about 86% of their maximum observed total length and 67% of their maximum observed age. Using the measured reproductive parameters, the smallest mature female was 515-mm TL and aged 5 years, whereas the largest immature female measured 582-mm TL and aged to 6 years.

**Discussion**

The Gulf of Mexico hosts approximately 10% of all extant elasmobranch species, including at least 60 species of sharks, 23 species of skates and 20 species of stingrays (McEachran and Fechhelm 1998). However, biological study of these species has
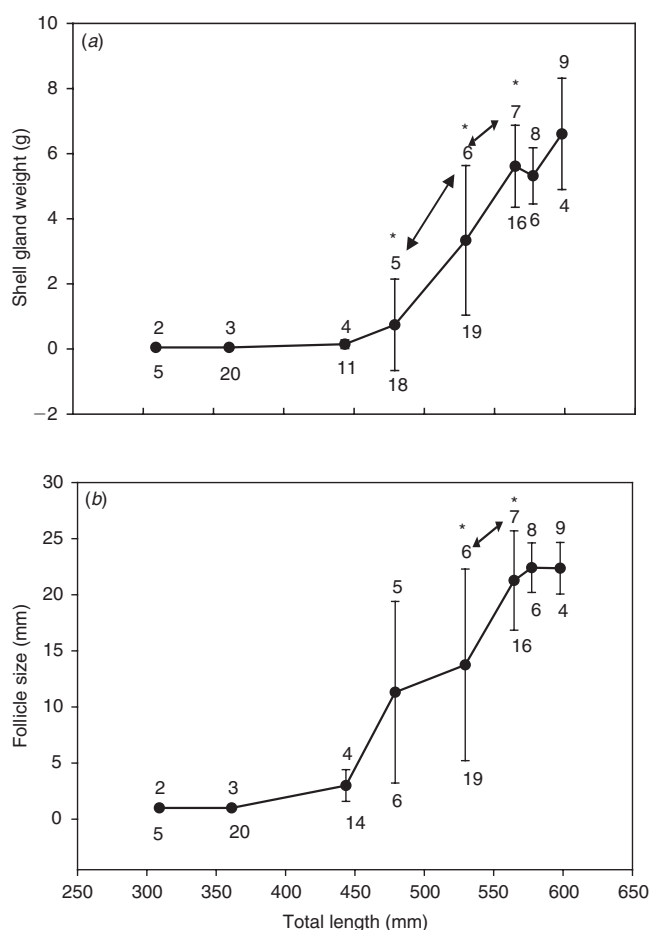
**Fig. 8.** (*a*) The total length to shell gland weight and (*b*) follicle diameter as female *Raja texana* progresses through sexual maturity. Values are expressed as mean ± s.d. Asterisks followed by arrows represent significant differences ($P < 0.05$; ANOVA followed by a Tukey's post hoc test) between skates in consecutive age groups. The average age is given above each representative size class; numbers below the trend line of each graph represent the sample size.

focussed mostly on commercially important sharks (Branstetter 1987; Carlson and Brusher 1999; Carlson *et al.* 1999) and one species of cownose ray (Rogers *et al.* 1990; Neer and Thompson 2005). The present study of *Raja texana* represents the first biological study of a skate species from the Gulf of Mexico, USA.

### Age and growth

The linear relationship between centrum diameter and total length indicates that centra grew proportionally to skate length for all size classes, demonstrating that centra were a suitable structure for growth interpretation. Centrum diameter was only poorly related to animal weight ($r^2 = 0.5201$). Growth bands were easily distinguishable, and the precision estimates (7.3% IAPE and 4.8% CV) suggest that our band interpretation methods represent a precise approach for ageing *R. texana*. Minimal width of the marginal increment for roundel skates captured in March and centrum edge analysis supported the hypothesis that bands are formed annually.

In the present study, the Gompertz model did not fit the data as well as the three models that used length-at-age data. The VBGM and Francis model predicted the same growth, and the variation between these models and the VB with $L_0$ may be due to the paucity of data from age-zero and one skates. The back-calculated size at birth of 115 mm was used for the VB with $L_0$, whereas the VBGM and Francis model predicted a birth size of 59–66 mm. For males, the asymptotic length (average maximum TL at age infinity) was 500 mm for both the VBGM and Francis model, which is very close to the maximum observed length of 495 mm. The VB with $L_0$ predicted a slightly greater asymptotic length of 512 mm. For females, the asymptotic length for the VBGM and Francis model (682 mm) and the VB with $L_0$ (722 mm) were slightly greater than the maximum observed length (630 mm).

Although the VBGM is the most commonly used model to describe fish growth, it does not always provide a particularly good fit and there has been a wide array of criticisms (Roff 1980; Haddon 2001). For instance, several skate ageing studies have reported an overestimation of the asymptotic length using the VBGM (see Sulikowski *et al.* 2005*a* for a full review). The VBGM curve is strongly determined by the values for $L_\infty$ and $t_0$, which are at either end of the curve, generally where there is the least amount of data (Sainsbury 1980). The growth coefficient ($k$) is correlated to $L_\infty$ (Francis 1988*b*), and any inaccuracy (or overestimation) of $L_\infty$ affects the estimate of $k$.

The use of other models to interpret elasmobranch growth from size-at-age data is gaining popularity. The 2-parameter VB with $L_0$ model by Faben (1965) used in the present study replaces the $t_0$ parameter with the size-at-birth parameter $L_0$. This model may provide more realistic parameter estimates when sample sizes are small (Goosen and Smale 1997), and its use is becoming more common (Simpfendorfer *et al.* 2000; Carlson and Baremore 2005). Likewise, the 3-parameter reparameterised model by Francis (1988*b*) has recently been used to interpret the growth of deepwater dogfishes (Irvine *et al.* 2006). The Francis model suggests three alternative parameters that are biologically significant (i.e. average length at a known age). Each parameter is evenly distributed along the curve, unlike the VBGM where two parameters are at either end of the curve.

Despite the variety of growth models available (Haddon 2001), there are few examples of studies that compare various growth models to reveal which model fits best (Neer and Cailliet 2001; Mollet *et al.* 2002; Carlson and Baremore 2005; Neer and Thompson 2005; Neer *et al.* 2005). For example, for the spinner shark (*Carcharhinus brevipinna*), a logistic growth model provided the best fit, whereas the VBGM gave the worst fit (Carlson and Baremore 2005). For the pelagic stingray (*Dasyatis violacea*), the Gompertz model predicted a more realistic size at birth and growth rate than the VBGM (Mollet *et al.* 2002). The present study represents the first to compare various growth models for a skate species.

The VBGM and Francis model predicted the same growth. This similarity is expected because both models use three parameters and *R. texana* only lives to 8–9 years, making variability unlikely. Therefore, it seems acceptable to assume that *R. texana* growth (from the age of 2 years) is adequately interpreted using either the VBGM or Francis model.
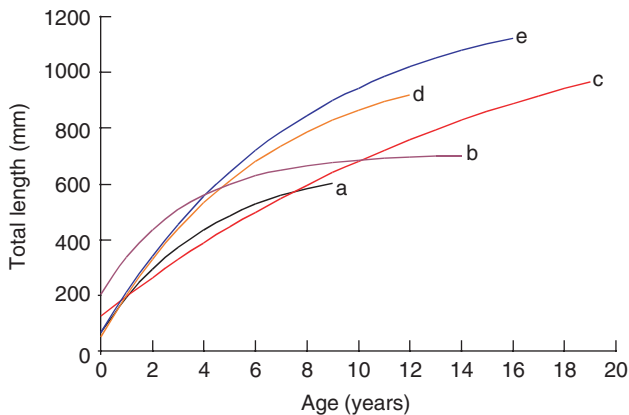
**Fig. 9.** Comparison of various skate growth. (a) Female *Raja texana* (the present study); (b) male and female *Amblyraja georgiana* (Francis and Ó Maolagáin 2005); (c) female *Leucoraja ocellata* (Sulikowski *et al.* 2003); (d) female *Raja rhina* (Zeiner and Wolf 1993); (e) female *A. radiata* (Sulikowski *et al.* 2005*a*).

Growth between species is often compared by directly comparing the growth coefficient ($k$) and asymptotic length ($L_\infty$) (Cailliet and Goldman 2004). However, these two parameters are highly correlated and in the absence of raw data, statistical comparisons (e.g. the analysis of the residual sum of squares (Chen *et al.* 1992) and likelihood ratio tests (Kimura 1980)) are not possible. We therefore compared the growth of *R. texana* with other skate species by fitting growth curves from published VBGM data (Fig. 9). Growth rates for *R. texana* were similar to other skate species of comparable size skate but were faster than larger species.

*Longevity*

Skates have a very wide range of longevities, with most skate species living between 9 and 24 years (Francis and Ó Maolagáin 2001). *Raja texana* is a relatively short-lived skate species, with longevity to 8 years for males and 9 years for females. Larger skate species tend to live longer than smaller species (Frisk *et al.* 2001). A good example of this contrast in longevity is with the blue skate (*Dipturus batis*), which attains 2850-mm TL and lives to approximately 50 years (Du Buit 1972). The theoretical longevity calculated for *R. texana* using the equation by Ricker (1975) was the same for males, although female longevity was estimated as 15 years. The difference of 6 years for female longevity estimates may be explained by the removal of older (and larger) females by commercial fisheries that have operated in the Gulf of Mexico for several year/decades. It is unclear which longevity estimate is more accurate because both estimates are biologically feasible. An increase in female longevity (from 9 to 15 years) would indicate that mature females have 10 years to produce offspring (rather than only 5), and this would increase the productivity estimate of this species.

*Maturity*

In males, sexual maturity is marked by the conspicuous and abrupt increase in clasper length relative to TL and clasper calcification. These criteria are often used to assess maturity in elasmobranchs (e.g. Conrath and Musick 2002; Loefer and Sedberry 2003; Sulikowski *et al.* 2005*a*). In addition, serial changes in development of testes and concomitant increases in spermatogenesis have been shown in a few other elasmobranch species; a correlated increase in these parameters was found during the maturity of the winter skate (Sulikowski *et al.* 2005*b*), yellowspot skate, *R. wallacei*, and the slime skate, *R. pullopunctata* (Walmsley-Hart *et al.* 1999). However, the examination of the reproductive tract for testes weight and the presence of mature spermatocysts may provide a more accurate indication of maturity in males (Sulikowski *et al.* 2005*b*). Based on clasper length, there was a biological push towards maturity in males at 360-mm TL (3 years), whereas both testes weight and spermatogenesis examination suggested maturity began at 435 mm (5 years). Moreover, partial calcification of the claspers (CL/TL ratio of 0.15) was observed in skates just over 4 years of age, whereas the percentage of mature spermatozoa in the testes reached minimum maturity values closer to age 5 years. This type of morphological delay has also been observed in the winter skate, *Leucoraja ocellata* (Sulikowski *et al.* 2005*b*), where the observed differences in age and size between morphological and histological maturity was approximately 1 year and 30-mm TL respectively. A lag period in functional maturity was also described in the bonnethead shark (*Sphyrna tiburo*) (Gelsleichter *et al.* 2002). In this shark species, claspers grew in length continuously during puberty, but did not reach functional maturity until a short period before mating activity commenced. The reason why the increases in the spermatocyst concentration and testes weight lagged behind statistical increases in the CL/TL ratio in the roundel skate is unknown. However, the process of spermatogenesis and testes maturation may require less time than the development of fully functional claspers.

Functional maturity only occurred once the male skates had reached 88% of the observed maximum TL and 63% of the maximum age, suggesting male growth slowed considerably after the onset of maturity. Other skates exhibit similar maturity and growth patterns, with maturity 80–90% of their maximum length (e.g. Zeiner and Wolf 1993; Dulvy *et al.* 2000; Francis *et al.* 2001; Ebert 2005).

For female elasmobranchs, an abrupt increase in ovary weight and follicle size has been shown to mark the onset of sexual maturity (e.g. Francis *et al.* 2001; Conrath and Musick 2002; Ebert 2005; Sulikowski *et al.* 2005*a*). Although ovary weights could not be accurately measured in the present study, the use of shell gland weights provided a good surrogate to assess maturity in this species. This assumption was based on the strong association between shell gland weight and follicle size observed in this study and the analogous correlations between these parameters in other female species (Sulikowski *et al.* 2004, 2005*a*, 2005*b*).

Similar to males, the shift towards maturity occurred once the skates had reached over 85% of the observed maximum TL, with growth slowing considerably after maturity. However, in contrast to male roundel skates, the observed biological shifts towards coordinated functional maturity in females occurred over a broader size range. These shifts occurred within a 35-mm span (ages 6–7 years) when both shell gland weight and follicle sizes displayed significant increases. Both males and females appear to reach maturity at about the same percentage of their observed size (between 86% and 88% respectively).

However, it is quite possible that the wider range at which functional maturity commences in females represents a longer period of gonadal development in order for their reproductive tracts to become fully functional. Since a marked size and growth difference existed between the sexes, the differences in age and size at functional maturity were not unexpected. However, the significance of a shift towards maturity that occurs at a smaller size and younger age in males of this species needs further review.

## Conclusion

The age and growth analysis of the roundel skate demonstrates the potential value of using models other than the commonly used VBGM. This is especially important because demographic models require accurate determinations of the growth coefficient if stock assessments are to be successful in preventing overexploitation of a species (e.g. Cortés 1999; Goldman 2002; Neer and Thompson 2005). The roundel skate possesses life history characteristics that make its populations highly susceptible to exploitation by fisheries (e.g. Casey and Myers 1998; Musick 1999; Dulvy *et al*. 2002), with particular concern on the relatively late size and age of maturity. As this species is a regular bycatch of the butterfish fishery operating in the Gulf of Mexico, there is a need for the development and implementation of a fisheries management plan. We recommend that future management plans should include the accurate recording of species and size composition to assess the level of impact and, when possible, skates should be discarded alive.

## Acknowledgements

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