Age and Growth of the Round Stingray *Urotrygon rogersi*, a Particularly Fast-Growing and Short-Lived Elasmobranch

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Abstract

We examined the age and growth of *Urotrygon rogersi* on the Colombian coast of the Eastern Tropical Pacific Ocean by directly estimating age using vertebral centra. We verified annual deposition of growth increments with marginal increment analysis. Eight growth curves were fitted to four data sets defined on the basis of the reproductive cycle (unadjusted or adjusted for age at first band) and size variables (disc width or total length). Model performance was evaluated using Akaike’s Information Criterion (AIC), AIC weights and multi-model inference criteria. A two-phase growth function with adjusted age provided the best description of growth for females (based on five parameters, \(DW_1 = 20.1 \text{ cm}, k = 0.22 \text{ yr}^{-1}\)) and males (based on four and five parameters, \(DW_1 = 15.5 \text{ cm}, k = 0.65 \text{ yr}^{-1}\)). Median maturity of female and male *U. rogersi* is reached very fast (mean ± SE = 1.0 ± 0.1 year). This is the first age and growth study for a species of the genus *Urotrygon* and results indicate that *U. rogersi* attains a smaller maximum size and has a shorter lifespan and lower median age at maturity than species of closely related genera. These life history traits are in contrast with those typically reported for other elasmobranchs.

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Introduction

Knowledge of age and growth characteristics allows construction of age-based population models and, together with the consideration of other life history aspects and removal rates by fisheries, can eventually lead to an assessment of the population status of a given species [1]. While target species have often been intensely studied, bycatch species are often ignored. These commercially unimportant species, such as the stingrays in the Family Urotrygonidae, are also impacted by fisheries and commercial unimportant species, such as the stingrays in the Order Elasmobranchii, are also impacted by fisheries and commercial fisheries management decisions.

The round stingray *Urotrygon rogersi* (Jordan and Starks 1895) is an endemic batoid of the Eastern Tropical Pacific Ocean that occurs on soft bottoms in coastal and shallow zones at depths of 2 to 30 m [2]. It is the most abundant elasmobranch species in the bycatch of artisanal and industrial prawn trawl fisheries on the Colombian Pacific coast and does not have any commercial value [3].

This species is a specialist that feeds mainly on crustaceans and polychaetes, showing a strong diet overlap between sexes and size classes [4]. This aaplacentiviviparous species attains a maximum size of 20 cm disc width (DW), its median size at maturity is 11.5–11.8 cm DW in males and 11.8–12.3 cm DW in females, size at birth is 7.5–8.2 cm DW and 11.5–14.7 cm total length, gestation lasts about 5–6 months, and the reproductive cycle is triannual and aseasonal [5].

Seasonally reproducing species usually have relatively well-defined birth dates [6] and therefore the age of individuals can be determined with reasonable accuracy [7]. In contrast, non-seasonally reproducing species can have several reproductive peaks or reproduce throughout the year [6], and consequently the age at which the first growth band is formed in a vertebra is unknown. Therefore, age determination based on vertebral growth bands in these species requires that the data be adjusted, specifically by averaging the time between births and the formation of the first growth band [7].

Important considerations when fitting growth curves to observed size-at-age data include the metric of body size and the type of growth curve used. Most studies use total length, yet other metrics may be more relevant for some shark and batoid species [8–10]. Although the von Bertalanffy growth curve has been most extensively used to describe growth in fishes, use of more than one growth function to adequately characterize the growth of a given species has been recommended [11] and used in different elasmobranch species [10,12–15]. However, few elasmobranch studies [13,15,16] have used multi-model inference, as proposed by Katsanevakis [17], to determine a model-averaged set of
parameters across competing models incorporating uncertainty in model selection.

The objective of the present study was to use a multi-model approach to estimate age and growth parameters for *U. rogersi* from the coast of Colombia in the Eastern Tropical Pacific Ocean. To that end we considered four data sets based on: 1) two body size metrics (disc width and total length) as suggested by Cailliet et al. [11] for batoids; and 2) inclusion or not of the reproductive cycle of *U. rogersi*, specifically the time between births and month of first band formation. For each data set we compared eight growth models with varying number of parameters and used multi-model inference when necessary. Finally, median age at maturity of female and male *U. rogersi* was estimated from the best-fit growth curve.

Materials and Methods

Sample collection and study area

*Urotrygon rogersi* specimens were collected between 2006 and 2009 from the bycatch of the artisanal prawn trawl fishery in four locations of the Pacific coast of Colombia between 3° 56’ N - 77° 25’ W and 3° 00’ N - 77° 10’ W. This area is characterized by shallow waters (≤ 10 m depth) and sandy and muddy bottoms. Sex and maturity stage were recorded and disc width (DW, cm) and total length (TL, cm) measured in a straight line for each specimen. The stage of maturity (0-immature, 1-mature) was assigned from measurement and macroscopic examination of specimen. The distance of reader 1 [23]; Bowker’s test of symmetry [24], which determines whether differences between readers are systematic or a result of random error; and finally, the average percentage error (*APE*), which was calculated as:

\[
APE = \frac{1}{N} \sum_{i=1}^{N} \left( \frac{1}{R} \sum_{j=1}^{R} \left[ X_{ij} - X_{j} \right] \right) \times 100
\]

where *N* is the number of samples, *r* the number of readings, *X* is the *ith* age determination of the *jth* fish, and *X*_ _j_, the average age calculated for the *jth* fish.

Marginal increment

Verification of the annual periodicity of band formation was performed using marginal increment ratio analysis (*MIR*) following Natanson et al. [26] and the simplified equation of Conrath et al. [27], as:

\[
MIR = \frac{(R - R_{a})}{(R_{n} - R_{n-1})} = \frac{MW}{PBW}
\]

where *MW* is the margin width, and *PBW* is the previous band pair width. When only one band was present, *MIR* was calculated as the proportion between the outer edge of the translucent zone and *R*. Mean *MIR* was plotted against month of capture to determine trends in band formation and a non-parametric Kruskal–Wallis one-way analysis of variance was used to test for differences in *MIR* between months; Dunn post-hoc tests were used when differences were found. *MIR* was plotted considering the number of bands of each vertebra (1–2, 3–4, ≥5 and overall sample).

Growth curves

Eight models were fitted to the individual disc width and total length of each female and male *U. rogersi* at their estimated age at capture to estimate growth parameters. The models fitted were: von Bertalanffy with two (VBG-2) and three (VBG-3) parameters [28], Gompertz with two (GG-2) and three (GG-3) parameters [29], logistic with two (LG-2) and three (LG-3) parameters [29], and the two-phase model with five (TPG-5) and four (TPG-4) parameters [30] (Table S1). In all cases, growth parameters were estimated by fitting the model to the observed data through

As a preliminary training exercise, two readers (P.A. Mejía-Falla and A.F. Navia) counted the growth bands on a subsample (*n* = 100) both on digital images and under a microscope for discussion and interpretation. Subsequently, the two readers read vertebral sections simultaneously, but independently and without knowledge of sex or length of specimens. The process was repeated twice. Vertebral-age estimates were compared and ages that differed were re-read simultaneously by both readers; when an agreement could not be reached on an age, the sample was discarded and excluded from the age analysis [21].
maximum likelihood, using SAS software (version 9, SAS Institute, Inc.).

These models involve as one of their parameters the theoretical asymptotic size ($L_{\infty}$). The VBG models include a relative growth rate parameter ($k_2$, yr$^{-1}$) and the theoretical age at zero disc width or length ($t_i$). The GG models include the ratio of exponential decrease ($k_2$, yr$^{-1}$) of the relative growth rate ($k_2$) with age and a parameter $t_2 = (\ln k - \ln k_2)/k_2$. The LG models include a relative growth rate parameter ($k_3$, yr$^{-1}$) and an inflection point of the sigmoidal curve ($t_3$) [31]. The TPG models consider as additional parameters, the age at which the transition between the two phases occurs ($t_4$, inflection point), and the maximum difference in length-at-age between the VBG and the TPG models at the point $t_5$ [8; Table S1]. Models with two parameters require the mean size-at-birth ($L_0$) instead of $l$ values; we used a mean size-at-birth of 8.0 cm DW and 13.5 cm TL for U. rogersi, estimated from observed near-term embryos and smallest free-swimming individuals during this study and recorded by Mcjia-Falla et al. [5].

Four data sets were built using two different size metrics and considering or not reproductive seasonality, following the recommendations of Gailliet et al. [11] and Harry et al. [7], respectively. Disc width and total length of female and male U. rogersi were used as size metrics. In terms of reproduction, it was assumed that the first band is formed one year after birth, irrespective of reproductive seasonality (unadjusted analysis), but the time between birth and first band formation was also considered, adjusting it to the reproductive cycle of the species (adjusted analysis). In the Colombian Pacific U. rogersi has three birth peaks per year (September, January and May; [5]) and the month of band formation is January (see Results below), thus the time between births and formation of the first band is 4, 12 and 8 months, respectively, with a mean of 0.67 years; in this case, the age at first band (AAFB) is adjusted to the mean value for the population.

Thus, the eight growth models were fitted to two data sets for each size metric: 1) DW (or TL-Unadjusted) and 2) DW (or TL)-Adjusted. In the unadjusted data sets for example, BB = 0+; AAFB = 1, age at the second band (AASB) = 2, whereas in the adjusted data sets BB = 0.67, AAFB = 1.67, and AASB = 2.67.

Model selection

A maximum likelihood (ML) method combined with Akaike’s Information Criterion (AIC) [32] was used to select the model that best fitted U. rogersi size-at-age data [33,34]; additionally, the error sum of squares (SSE) and the residual mean square error (MSE) were also considered to evaluate model goodness-of-fit. The model with the lowest AIC, SSE and MSE values was considered as the most probable for the data. AIC, computed as $2p - 2\ln(ML)$, penalizes the complexity of the model, given by the number of parameters ($p$), by attaining an optimum between parsimony and accuracy [35]. AIC differences ($\Delta = \text{AIC}_{i} - \text{AIC}_{\text{min}}$) were used to rank the support of the remaining models relative to the best-fit model. Models with $\Delta_c$ of 0–2 had substantial support, models with $\Delta_c$ of 4–7 had considerably less support, and models with $\Delta_c > 10$ had essentially no support [33]. The probability of choosing the true model among $k$ models, termed AIC weight ($w_i$), was also computed from $\Delta_c$, as follows [33,34]:

$$w_i = \frac{e^{-0.5\Delta_c}}{\sum_{k=1}^{k} e^{-0.5\Delta_k}} \quad (3)$$

Based on multi-model inference [33], when a model had $w_i \leq 90\%$, or more than one model had substantial support, average $L_\infty$ ($L_{\infty}$) values may be estimated across those models with substantial support from the data, as well as their unconditional standard errors $\text{SE}(L_{\infty})$, as follows:

$$L_{\infty} = \sum_{i=1}^{k} w_i \times \widehat{L}_{\infty,i} \quad (4)$$

$$\text{SE}(L_{\infty}) = \sqrt{\frac{\sum_{i=1}^{8} w_i \times (\text{var}(\widehat{L}_{\infty,i} - L_{\infty,i}))}{C^2}} \quad (5)$$

where var($\widehat{L}_{\infty,i}$) is the variance of the estimated asymptotic length according to model $m_i$.

Finally, differences in growth curves between sexes for the selected model were tested using chi-square tests of likelihood ratios [36,37].

Longevity

Because theoretical longevities calculated from the k value obtained from growth functions are likely overestimates [38], we followed the proposal of Barnett et al. [39] to define longevity. These authors defined the upper range of longevity ($\omega$) from maximum observed age ($T_{\text{max}}$) and the average percentage error (APE) calculated using empirical data from the greatest 20% of age classes sampled, thus:

$$\omega = T_{\text{max}}(c + \text{APE}) \quad (6)$$

where $c$ is an arbitrary constant ($c = 1.4$) to account for the likelihood that the absolute maximum age of each species was not observed in the life history study. For this study, we calculated the APE from the greatest 18% of age classes sampled (corresponding to individuals with six or more growth bands).

Age at maturity

Median age-at-maturity ($A_{50}$) was estimated for females and males from directly aged individuals (i.e., not back-transforming length into age) by fitting a logistic regression model to binomial maturity data (0-inmature, 1-mature) [40] using maximum likelihood. The equation used was:

$$P_{Ai} = \frac{1}{1 + e^{-b_{Ai} - A_{50}}} \quad (7)$$

where $P_{Ai}$ is the proportion of mature individuals at the $i$th age class and $b$ is a model parameter. Differences in logistic models between sexes were tested with chi-square likelihood ratio tests [36,37].

Results

Treatment of vertebrae and reading of bands

A total of 503 specimens (256 male and 247 female) were initially used for the ageing study. Growth bands were distinguishable both along the intermedialia and the corpus calcareum, hence band pair counts were derived from bands on the corpus calcareum; in general, little difficulty was encountered in estimating the age of U. rogersi. Of the processed vertebrae, 466 were readable (92.6%), from 232 males ranging in size from 7.9 to
17.0 cm DW (mean ± SD = 12.8 ± 1.5) and 234 females ranging from 8.2 to 18.8 cm DW (14.4 ± 2.2; Figure 1). Band pair counts of these individuals ranged between 0 and 8 in females and 0 and 6 in males.

Significant, non-linear relationships between DW and R (P = 0.001) were found for both sexes (females: DW = 12.3 + 18.9 * logR, r² = 0.91; males: DW = 12.3 + 17.0 * logR, r² = 0.74), verifying vertebral centra as useful ageing structures. ANCOVA showed significant differences between sexes for the regression of DW vs. R (F = 614.81, d.f. = 244, P = 0.001); therefore, the data were treated separately for each sex.

Precision and bias

Age estimates agreed closely between readers. The first set of band pair counts resulted in an APE between readers of 3.5%, with a PA of 82.1%, PA ± 1 band of 99.3%, and PA ± 2 bands of 100%. When grouped by 4-cm DW intervals, agreement was reached for 95.9% and 100% ± 1 band for rays ≤ 11.4 cm DW, 85.4 and 99.4% ± 1 band for rays > 11.4 cm and ≤ 15.5 cm DW, and 68.7 and 98.8% ± 1 band for rays > 15.5 cm DW of samples initially read. The age-bias plot indicated there was no systematic bias between readers (Figure 2) and Bowker’s test of symmetry indicated no systematic disagreement between readers (χ² = 5.90, df = 11, P = 0.12). These precision and bias values indicated a high level of reproducibility.

Marginal increment

Marginal increments were significantly different among months (Kruskal-Wallis H₁₁,₁₂₅₁ = 27.2, P = 0.004), with an increasing trend from January to a peak in November (Figure 3d). Post-hoc tests showed significant differences between February and March (P < 0.0001) and overestimated merce values. In contrast, the 5-parameter TPG model had the lowest AIC and highest w values in data sets based on DW and TL for females, with substantial empirical support (Δ₁ < 2) and reasonable estimates of k and DWo values. Values of L were very high in all models based on TL and comparatively higher in the unadjusted than in the adjusted data sets (Table 1). Similarly in males, TPG-5 and TPG-4 had the lowest AIC values for unadjusted and adjusted data sets, respectively, based on both DW and TL (Table 2). Although the unadjusted-DW data set had the highest w value (92% in TPG-5), DWw was high, whereas the corresponding value obtained with the adjusted-DW data set was closest to observed size at birth. For this reason, and based on multi-model inference, an average parameter value from the two TPG models was estimated from the adjusted-DW data set (joined w = 97%; Table 2).

Based on statistical results (MSE, SSE, AIC and w values) and biological interpretation (k, L, and L values), the 5-parameter TPG based on the adjusted-DW data set was deemed to provide the best description of growth for females (w = 80%) with DWo = 20.1 cm (SE = 0.10) and k = 0.22 yr⁻¹ (SE = 0.03; Table 1). For males, the asymptotic disc width (Dw) estimated through multi-model inference from TPG-5 and TPG-4 was 15.5 cm (SE = 0.63) and k was 0.65 yr⁻¹ (SE = 0.001). To allow comparison with the TPG-5 model for females, t₀, t₀, k and Dw were estimated by fitting this function to the adjusted-DW data set and fixing Dww; these values were, -1.14, 3.2 years, 0.25 and 7.99 cm, respectively.

Two-phase growth curves were significantly different between sexes (likelihood ratio χ² = 36.04, df = 5, P < 0.0001). Female U. rogersi had a lower growth coefficient than males and a larger asymptotic size (Figure 4a,b). The model estimated well the size-at-birth for males (8.0 cm DW), but overestimated that of females (9.4 cm DW), although less than the other models (except those with two parameters in which this value was fixed). For females, the change in growth rate (t₀ inflection point of the curve) occurred later (5.1 ± 0.3 years) than in males (3.2 ± 0.2 years), corresponding to 15.7 and 13.6 cm DW, respectively (Figure 4a,b). Sizes corresponding to maximum observed ages also differed between sexes, with the oldest aged female being near 8 years and 19 cm DW, and the oldest male, near 6 years and 17 cm DW.

Figure 1. Length-frequency distributions for female (gray bars) and male (black bars) U. rogersi used in this study (n = 466).

Figure 2. Age-bias plot of reader band pair counts. Dots with error bars are the mean counts of reader 2 (upper and lower 95% confidence limits) relative to reader 1. The diagonal line indicates a one-to-one relationship. doi:10.1371/journal.pone.0096077.g002
Longevity

The APE value of the greatest 18% of age classes sampled was 3.01%. Thus, from this value and based on the Barnett et al. [39] equation, the longevity for *U. rogersi* was calculated at 11 years for females and 8 years for males.

Maturity

Estimates of $A_{50}$ were low and equal for females and males (1.0 year; SE = 0.1; 95% CI = 0.9–1.2; Figure 5). Likelihood ratio tests showed no differences between sexes in the relation between maturity and age (logistic curve: $\chi^2 = 0.54$, d.f = 2, $P = 0.765$; $A_{50}$: $\chi^2 = 0.18$, d.f = 1, $P = 0.67$; $b$: $\chi^2 = 0.46$, d.f = 1, $P = 0.50$).

Discussion

Age and growth studies of batoids have been conducted mainly on skates and to a lesser extent on stingrays [19]. These studies have been carried out in only five of 24 species of stingarees (family Urolophidae) and one of 16 species of American round stingrays (family Urotrygonidae; Table 3). The present is the first age and growth study for the genus *Urotrygon*, and its results are in contrast with the generalization that elasmobranchs are slow-growing, long-lived species. This finding has considerable implications for the population assessment and management of *U. rogersi* in particular and suggests reconsidering the previously mentioned generalization about elasmobranch growth.

Despite their small size, vertebrae are good structures to evaluate and estimate the age and growth of *U. rogersi*, as used for other species of Urotrygonidae and Urolophidae [40–43]. Based on our results and those of other studies of urolophids and urotrygonids, we suggest that the technique used in this study (0.4 mm sections and unstained vertebrae) is appropriate as a starting point for other species of *Urotrygon* or *Urobatis*, but recommend testing thicknesses between 0.3 and 0.5 mm.

Formation of one annual band pair has also been verified through marginal increment analysis in closely related species from other geographical areas, such as *U. lobatus*, *Trygonoptera personata* and *T. mucosa* from the South West coast of Australia [37,38] and *U. hallieri* from the West coast of the USA [33,44]. Although marginal increment analysis has been considered as a validation method [45], in this study we use it as a verification method as proposed by Cailliet and Goldman [19] to verify the frequency of band deposition. However, marginal increment analysis has proven problematic owing to technical difficulties related to resolving the margins of growth bands [45] and because the number of deposited bands and time of deposition may vary with age. In this regard, verification of the periodicity of band deposition should be conducted by age class [45–47], as in the present study. Verification of annual band formation in *U. rogersi* was likely facilitated by the fast growth and short lifespan of the species, and an adequate sample size.

Growth curves

In viviparous species, and particularly in *U. rogersi*, disc width has been associated with reproductive aspects. For instance, disc width is thought to limit fecundity and embryo maximum size [5,48]. Thus, the use of disc width is more sensible than that of total length from a biological standpoint, and is recommended for age and growth studies of myliobatiform batoids (i.e. the families Dasyatidae, Urotrygonidae, Urolophidae, Gymnuridae, Myliobatidae, and Potamotrygonidae).

Although no analyses of vertebrae of near-term embryos were included in this study, the smallest free-living *U. rogersi* (an 8.2 cm DW female captured in August, and two 7.9 cm DW males captured in August and January) did not have any evidence of bands, indicating that the first band is formed after birth. This supports our use of an adjusted data set, especially for tropical species with multiannual reproductive cycles or even those with no seasonal reproductive cycles. Age data of aseasonal species with reproductive events throughout the year can be adjusted by...
Table 1. Growth model parameter estimates of female *U. rogersi* using two different values for the first growth band deposited (unadjusted and adjusting the time between months of births and band formation; see text for details), two metrics (disc width, DW, and total length, TL) and eight models (see Table S1 and methods for details).

| Dataset     | Model | $L^\infty$ | $k$  | $L_0$ | MSE  | SSE  | AIC  | $\Delta_i$ | $w$  |
|-------------|-------|------------|------|-------|------|------|------|------------|------|
| Unadjusted- DW | VBG-3 | 19.41      | 0.22 | 10.91 | 1.20 | 280.45 | 712.44 | 3.29 | 0.15 |
|             | VBG-2 | 16.69      | 0.64 | 8.00  | 2.22 | 519.96 | 854.90 | 145.75 | 0.00 |
|             | GG-3  | 18.79      | 0.29 | 10.95 | 1.21 | 282.39 | 714.05 | 4.90 | 0.07 |
|             | GG-2  | 16.41      | 0.85 | 8.00  | 2.30 | 537.18 | 862.52 | 153.37 | 0.00 |
|             | LG-3  | 18.39      | 0.37 | 11.00 | 1.22 | 284.45 | 715.75 | 6.60 | 0.03 |
|             | LG-2  | 17.38      | 0.42 | 11.29 | 1.28 | 298.58 | 725.09 | 15.94 | 0.00 |
|             | TPG-5 | 20.07      | 0.23 | 10.79 | 1.16 | 271.85 | 709.15 | 0.00 | 0.76 |
|             | TPG-4 | 17.29      | 0.68 | 8.00  | 2.07 | 484.53 | 842.38 | 133.24 | 0.00 |
| Adjusted- DW | VBG-3 | 19.36      | 0.22 | 9.63  | 1.14 | 267.06 | 700.98 | 3.54 | 0.14 |
|             | VBG-2 | 17.46      | 0.40 | 8.00  | 1.25 | 292.95 | 720.64 | 23.19 | 0.00 |
|             | GG-3  | 18.74      | 0.30 | 9.80  | 1.15 | 269.55 | 703.16 | 5.71 | 0.05 |
|             | GG-2  | 17.00      | 0.54 | 8.00  | 1.32 | 307.95 | 732.32 | 34.88 | 0.00 |
|             | LG-3  | 18.34      | 0.37 | 9.94  | 1.16 | 272.08 | 705.35 | 7.90 | 0.02 |
|             | LG-2  | 17.13      | 0.35 | 11.17 | 1.49 | 349.20 | 761.74 | 64.29 | 0.00 |
| TPG-5       | 20.08 | 0.22      | 9.40 | 1.11 | 258.59 | 697.45 | 0.00 | 0.80 |
| TPG-4       | 17.98 | 0.40      | 8.00 | 1.18 | 275.22 | 710.03 | 12.58 | 0.00 |
| Unadjusted- TL | VBG-3 | 35.27      | 0.26 | 19.84 | 5.02 | 1174.18 | 1047.51 | 3.20 | 0.15 |
|             | VBG-2 | 30.87      | 0.72 | 13.50 | 9.81 | 2296.55 | 1202.48 | 158.18 | 0.00 |
|             | GG-3  | 34.30      | 0.33 | 19.93 | 5.05 | 1181.73 | 1049.01 | 4.70 | 0.07 |
|             | GG-2  | 30.33      | 0.97 | 13.50 | 10.13 | 2370.03 | 1209.85 | 165.55 | 0.00 |
|             | LG-3  | 33.66      | 0.41 | 20.04 | 5.09 | 1190.00 | 1050.64 | 6.33 | 0.03 |
|             | LG-2  | 32.48      | 0.45 | 20.50 | 5.21 | 1220.01 | 1054.47 | 10.16 | 0.00 |
| TPG-5       | 35.63 | 0.29      | 19.57 | 4.87 | 1138.59 | 1044.30 | 0.00 | 0.74 |
| TPG-4       | 32.32 | 0.74      | 13.50 | 9.16 | 2413.16 | 1190.31 | 146.00 | 0.00 |
| Adjusted-TL | VBG-3 | 35.16      | 0.26 | 17.12 | 4.77 | 1115.93 | 1035.60 | 2.61 | 0.19 |
|             | VBG-2 | 32.06      | 0.45 | 13.50 | 5.28 | 1235.00 | 1057.32 | 24.33 | 0.00 |
|             | GG-3  | 34.20      | 0.34 | 17.51 | 4.81 | 1126.36 | 1037.78 | 4.79 | 0.07 |
|             | GG-2  | 31.03      | 0.64 | 13.50 | 5.51 | 1277.87 | 1058.23 | 25.24 | 0.00 |
|             | LG-3  | 33.58      | 0.42 | 17.83 | 4.86 | 1137.03 | 1039.98 | 6.99 | 0.02 |
|             | LG-2  | 31.99      | 0.38 | 20.27 | 5.93 | 1388.21 | 1084.69 | 51.70 | 0.00 |
| TPG-5       | 35.60 | 0.28      | 16.52 | 4.62 | 1080.23 | 1032.99 | 0.00 | 0.72 |
| TPG-4       | 33.25 | 0.45      | 13.50 | 4.92 | 1150.49 | 1044.74 | 11.75 | 0.00 |  

$L^\infty$ is the theoretical asymptotic size, $k$ is the coefficient of growth, $L_0$ is the birth size, MSE is the mean square error of the residuals, SSE is the error sum of squares, AIC is Akaike’s Information Criterion, $\Delta_i$ is the Akaike difference, and $w$ is the AIC weight.

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Table 2. Growth model parameter estimates of male *U. rogersi* using two different values for the first growth band deposited (unadjusted and adjusting the time between months of births and band formation; see text for details), two metrics (disc width, DW, and total length, TL) and eight models (see Table S1 and methods for details).

| Dataset  | Model |  $L^\infty$ |  $k$ |  $L_0$ | MSE | RSS | AIC | $\Delta_i$ | $w$ |
|----------|-------|-------------|------|--------|-----|-----|-----|-----------|-----|
| **Unadjusted- DW** |       |             |      |        |     |     |     |           |     |
| VBG-3    | 15.11 | 0.56        | 10.49| 0.82   | 191.08 | 619.37 | 5.91 | 0.05      |     |
| VBG-2    | 14.22 | 1.28        | 8.00 | 1.65   | 383.08 | 778.74 | 165.28| 0.00      |     |
| GG-3     | 14.97 | 0.65        | 10.51| 0.83   | 192.35 | 620.90 | 7.44  | 0.02      |     |
| GG-2     | 14.12 | 1.55        | 8.00 | 1.66   | 386.04 | 780.52 | 167.07| 0.00      |     |
| LG-3     | 14.86 | 0.75        | 10.53| 0.83   | 193.66 | 622.48 | 9.02  | 0.01      |     |
| LG-2     | 15.30 | 0.69        | 10.36| 0.85   | 197.66 | 625.22 | 11.76 | 0.00      |     |
| TPG-5    | 15.40 | 0.69        | 10.38| 0.79   | 183.09 | 613.46 | 0.00  | 0.92      |     |
| TPG-4    | 15.09 | 1.27        | 8.00 | 1.56   | 362.58 | 769.98 | 156.52| 0.00      |     |
| **Adjusted- DW** |       |             |      |        |     |     |     |           |     |
| VBG-3    | 15.05 | 0.56        | 8.57 | 0.76   | 177.17 | 601.84 | 8.99  | 0.01      |     |
| VBG-2    | 14.80 | 0.66        | 8.00 | 0.77   | 178.23 | 601.22 | 8.37  | 0.01      |     |
| GG-3     | 14.90 | 0.67        | 8.69 | 0.77   | 178.94 | 604.14 | 11.30 | 0.00      |     |
| GG-2     | 14.56 | 0.84        | 8.00 | 0.78   | 181.68 | 605.67 | 12.82 | 0.00      |     |
| LG-3     | 14.79 | 0.77        | 8.86 | 0.78   | 180.78 | 606.52 | 13.67 | 0.00      |     |
| LG-2     | 14.85 | 0.55        | 10.16| 0.87   | 202.82 | 631.20 | 38.35 | 0.00      |     |
| TPG-5    | 15.43 | 0.66        | 7.98 | 0.73   | 169.04 | 594.94 | 2.09  | 0.25      |     |
| TPG-4    | 15.47 | 0.64        | 8.00 | 0.73   | 168.98 | 592.85 | 0.00  | 0.72      |     |
| **Unadjusted- TL** |       |             |      |        |     |     |     |           |     |
| VBG-3    | 28.01 | 0.63        | 19.71| 5.86   | 1358.44 | 1074.41 | 2.91  | 0.16      |     |
| VBG-2    | 26.48 | 1.56        | 13.50| 11.97  | 2777.90 | 1238.38 | 166.88| 0.00      |     |
| GG-3     | 27.78 | 0.74        | 19.74| 5.88   | 1363.37 | 1075.25 | 3.75  | 0.10      |     |
| GG-2     | 26.32 | 1.88        | 13.50| 12.01  | 2787.06 | 1239.14 | 167.64| 0.00      |     |
| LG-3     | 27.59 | 0.85        | 19.76| 5.90   | 1368.42 | 1076.11 | 4.61  | 0.07      |     |
| LG-2     | 31.69 | 0.44        | 20.13| 6.14   | 1424.32 | 1083.40 | 11.90 | 0.00      |     |
| TPG-5    | 28.83 | 0.78        | 19.52| 5.68   | 1318.56 | 1071.50 | 0.00  | 0.67      |     |
| TPG-4    | 28.34 | 1.49        | 13.50| 11.60  | 2691.79 | 1235.07 | 163.57| 0.00      |     |
| **Adjusted-TL** |       |             |      |        |     |     |     |           |     |
| VBG-3    | 27.50 | 0.74        | 14.75| 5.44   | 1263.04 | 1057.52 | 7.00  | 0.02      |     |
| VBG-2    | 27.06 | 0.87        | 13.50| 5.47   | 1268.72 | 1056.56 | 6.04  | 0.03      |     |
| GG-3     | 27.33 | 0.85        | 15.37| 5.49   | 1274.61 | 1059.64 | 9.12  | 0.01      |     |
| GG-2     | 26.65 | 1.12        | 13.50| 5.56   | 1290.87 | 1060.58 | 10.06 | 0.00      |     |
| LG-3     | 27.20 | 0.95        | 15.84| 5.54   | 1285.10 | 1061.54 | 11.02 | 0.00      |     |
| LG-2     | 27.63 | 0.67        | 18.28| 5.79   | 1342.87 | 1069.74 | 19.22 | 0.00      |     |
| TPG-5    | 28.53 | 0.83        | 13.66| 5.24   | 1214.76 | 1052.48 | 1.96  | 0.25      |     |
| TPG-4    | 28.49 | 0.84        | 13.50| 5.24   | 1214.97 | 1050.52 | 0.00  | 0.68      |     |

$L^\infty$ is the theoretical asymptotic size, $k$ is the coefficient of growth, $L_0$ is the birth size, MSE is the mean square error of the residuals, SSE is the error sum of squares, AIC is Akaike’s Information Criterion, $\Delta_i$ is the Akaike difference, and $w$ is the AIC weight.

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averaging the time between each month of possible birth and the month of band formation [7], resulting in an adjustment of 0.54 years in our case.

Two-parameter models incorporating estimated size at birth were not deemed to be appropriate descriptors of DW-at age data for *U. rogersi* because $DW_\infty$ underestimated observed maximum DW values and appeared to overestimate $k$ values in both females and males, making them a biologically unreasonable choice in most cases. In contrast, models with at least three parameters generally described observed size-at-age data well. Thorson and Simpfendorfer [49] used simulation to show that two-parameter models were only useful for small samples sizes (<100) after which three- or four- parameter models performed better. However, these authors also suggested that sample sizes of 200 are required to consistently achieve good accuracy for growth parameters, which supports the results of this study for both sexes (females, $n = 234$; males, $n = 232$).

Moreau [50], Wang and Milton [51] and Katsanevakis and Maravelias [31] proposed that the choice of the best growth model and the interpretation of estimated parameters should be subjective and, in some cases, based on the decision of the researcher, founded on experience with the species and previous studies. In this study, the TPG-5 model based on unadjusted-DW was not selected as the best model to describe male growth despite having the highest empirical support and AIC weight because the estimated $DW_\infty$ was not reliable. Instead, we opted to use multi-model inference by averaging the TPG-4 and TPG-5 models to produce more robust parameter estimates (with unconditional

![Figure 4. Growth curves for female (a) and male (b) *U. rogersi* using the single (five parameter) and average (5 and 4 parameter) Two-Phase Growth Model, respectively, from the adjusted-DW data set.](doi:10.1371/journal.pone.0096077.g004)
standard errors) for males and allow comparison with the growth model for females [17,31].

For batoids, it has been proposed that the Gompertz model describes growth better than other models, especially in rays that continue to grow in weight but not greatly in length [19] and those with viviparous reproduction [52–54]. Although *U. rogersi* reaches a large adult weight in relative to its juvenile weight and is a viviparous species, decision criteria showed that the Gompertz model was not appropriate in this case, performing worse than the TPG or even the three-parameter VBG models.

The suitability of the TPG model, which incorporates the influences of changes in growth trajectories [32], has been evaluated for some elasmobranch species. Araya and Cubillos [35] associated the change in growth with the onset of maturity. In female and male *U. rogersi*, the inflection points (*t*= 5 and ≈ 3 years, respectively) are higher than the A50 values (one year in both cases); therefore we suggest that the onset of maturity does not influence this change. However, given the small size at which maturity is reached, it is necessary for individuals to invest energy in growth in parallel to reproduction to achieve greater reproductive success in their lifetime. Females may continue growing to a size or age at which fecundity is highest (3 embryos), i.e., 16.0 cm DW [5], which coincides with the inflection point at ≈ 5 years in the TPGM (Figure 3). Thus, this inflection point is associated more with increased reproductive output (i.e., higher fecundity) than with the onset of maturity.

It is possible that other events or discontinuities in development, such as changes in habitat or behavior, may cause changes in growth trajectories [29]. Since no segregation by sex or size is apparent in the area where individuals of all ages and sizes are found throughout the year [5], no changes in habitat are suggested. Changes in feeding habits with size or age can generate changes in behavior; ontogenetic changes in diet were detected in *U. rogersi* from individuals ≤20 cm total length (<11.5 cm DW, ca. 1 year old) compared to larger ones, with a shift from polychaetes to shrimps [4]. This size or age is closer to that corresponding to the onset of maturity than to the inflection point in the growth curve.

As the present study is the first to provide age and growth estimates for *U. rogersi*, no comparisons of growth parameters with other populations within the Eastern Tropical Pacific region are possible. In addition, as this is the first age and growth study for a batoid species on the Colombian Pacific Ocean, no comparisons with sympatric congeners are possible. Comparisons with stingarees or round stingrays from Southwest Australia (genera *Urolophus* and *Trygonoptera*) and American round stingrays of the west coast of the USA (genus *Urolophus*), based on available von Bertalanffy growth model parameters, suggest that female *U. rogersi* complete their growth at a similar rate (k value) than *U. lobatus*, *U. paucimaculatus* [54] and *T. mucosa* and reach a maximum age similar to that of *U. hallieri* ([55], Table 3). Male *U. rogersi* appear to complete their growth at a higher rate and reach a lower maximum age and size than those other species (Table 3). Females of these species have greater DW and lower k values than males, except for *U. hallieri* [9], although this discrepancy may have been caused by the paucity of larger females sampled in that study. Thus, larger sizes, slower growth, and longer lifespan in females than males seems to be a general pattern for the stingarees or round stingrays (families Urolophidae and Urotrygonidae) and the result of an ancestral trait mediated by intrinsic (i.e., advantages in reproduction) rather than extrinsic environmental factors.

Interpretation of growth coefficients for a species is influenced by sample sizes, size ranges, ageing methodology, validation of band formation periodicity, and model fitting techniques [19]. Thus, although growth coefficients are not directly comparable among models, they may still provide a practical but generalized characterization of fundamental life history traits that may be linked to longevity, fecundity, and size or age at maturity [56,57]. According to Holden [58], growth coefficients for batoid elasmobranchs (based on linear relationships or the VBG model) range from 0.1 to 0.3. Based on this, females and males of some species fall within the slow-growing end of this range (i.e., *U. hallieri*, *U. paucimaculatus*, and *U. lobatus*).
Table 3. Comparison of growth parameter estimates of related species of the families Urolophidae and Urotrygonidae obtained with the von Bertalanffy growth model.

| Species                | Study area (Ocean, country) | Sex | DW$_{(cm)}$ | k $(yr^{-1})$ | Maximum age (year) | Maximum DW $(cm)$ | Maturity age (year) | n  | References |
|------------------------|-----------------------------|-----|-------------|--------------|-------------------|------------------|-------------------|----|------------|
| *Urotrygon rogersi*    | TE Pacific, Colombia        | F   | 19.4        | 0.22         | 8.0              | 19.9             | 1.0               | 234| This study |
|                        |                             | M   | 14.8        | 0.63         | 6.0              | 17.0             | 1.0               | 232|            |
| *Urobatis halleri*     | NE Pacific, USA             | F   | 22.5        | 0.15         | 14.0             | 21.3             | 3.8               | 96 | [9]        |
|                        |                             | M   | 28.6        | 0.09         | 14.0             | 23.9             | 3.8               | 84 |            |
| *Urobatis halleri*     | NE Pacific, USA             | F   | 31.0        | –            | 8.0              | –                | 2.6               | 96 | [55]       |
|                        |                             | M   | 25.0        | –            | 8.0              | –                | 2.6               | 84 |            |
| *Urolophus lobatus*    | SE Indian, Australia        | F   | 24.1        | 0.26         | 14.0             | 27.7             | –                 | 330| [42]       |
|                        |                             | M   | 20.3        | 0.36         | 12.0             | 23.7             | –                 | 437|            |
| *Urolophus paucimaculatus* | SE Indian, Australia    | F   | 26.1        | 0.27         | 14.0             | 27.2             | 5.0               | 113| [41]       |
|                        |                             | M   | 24.3        | 0.36         | 11.0             | 25.6             | 3.0               | 99 |            |
| *Urolophus paucimaculatus* | SE Indian, Australia    | F   | 57.3*       | 0.21         | 10.0             | 56.0*            | 3.0               | 113| [54]       |
|                        |                             | M   | 42.8*       | 0.45         | 8.0              | 44.0*            | –                 | 99 |            |
| *Trygonoptera personata* | SE Indian, Australia    | F   | 30.3        | 0.14         | 16.0             | 31.1             | 4.0               | 352| [43]       |
|                        |                             | M   | 26.9        | 0.20         | 14.0             | 26.9             | 4.0               | 303|            |
| *Trygonoptera mucosa*  | SE Indian, Australia        | F   | 30.8        | 0.24         | 17.0             | 36.9             | 5.0               | 324| [43]       |
|                        |                             | M   | 26.1        | 0.49         | 14.0             | 28.3             | 2.0               | 400|            |

TE: Tropical Eastern; NE: North Eastern; SE: South Eastern. F: female, M: male. * Values are total length.
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T. personata), whereas others, notably male U. rogersi, fall outside, toward the fast-growing end of this range.

Beukema [39] suggested that maximum age directly estimated from a population may not provide an adequate measure of species longevity. However, theoretical estimates of longevity derived from the growth coefficient alone are also influenced by the choice of growth model and therefore could be a mathematical artifact rather than reflect biological reality, for which reason we did not use them in this study. Particularly for female U. rogersi, the theoretical longevity, defined as the age at which 95% or 99% of DW is reached, would be 15 or 22 years, respectively, which is very high, as much as three times the corresponding values for males (5 or 7 years). Considering the sample size, age at maturity of the species (about 1 year), and the definition of theoretical longevity, these theoretical values of longevity for females appear to be overestimates, as noted by others authors [38,60]. Thus, we believe the longevity estimates obtained by using the equation proposed by Barnett et al. [39] based on the APE value are more realistic for this species because they approximate the maximum observed age much better.

Age at maturity
Growth and reproduction should not be separated as different aspects of life history because they are inter-related. The onset of maturity involves a reduction in the energy allocated to growth because more energy is shifted towards reproduction [61]. Moreover, it has been suggested that a better strategy is to stop growing once maturity is reached and to invest all available energy into reproduction thereafter (“bang-bang strategy”) than to continue growing while reproducing (“intermediate strategy”); [62,63]. However, male and female U. rogersi seem to follow the latter strategy, wherein growth just slows down two (males) or four (females) years after the onset of maturity (when fecundity can be higher in females), and then speeds up again. Therefore growth and reproduction co-occur and individuals simultaneously invest energy in both processes.

Despite differences in maximum length and theoretical asymptotic size between male and female U. rogersi, both sexes reach maturity at similar sizes [5] and ages. The same occurs in U. hallien [55], T. personata [43], and T. imitata [64], but not in U. lobatus [42] or T. mucosa [43], in which females reach maturity at larger sizes and older ages than males. The very rapid onset of maturity in U. rogersi (< 1 year) is to our knowledge the earliest for any batoid species; only male T. mucosa reaches maturity at a young age of 2 years [43]. This rapid onset of maturity was also found in the Australian sharpnose shark Rhizoprionodon taylori, which matures in one year and is also a tropical species [65].

The growth patterns found in this study indicate that U. rogersi is a relatively short-lived, fast-growing species in which females and males reach 58% and 70% of maximum disc width, respectively, in the first year of life. This, coupled with reproductive aspects such as short gestation period, a triannual reproductive cycle, and low fecundity but with large pups [5], indicates that this species could be more resilient to exploitation than other elasmobranchs for any given level of fishing pressure. However, demographic or other population assessment models are needed to characterize the vulnerability of the studied population to fishing or other stressors.

Supporting Information
Table S1. Equations of the growth models used in the study.

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Author Contributions
Conceived and designed the experiments: PAMF EC FZ. Performed the experiments: PAMF AFN. Analyzed the data: PAMF EC. Wrote the paper: PAMF AFN. Reviewed drafts: EC FZ. Interpreted and discussed of the results: PAMF AFN EC FZ.

References
1. Cortés E (2002) Stock assessment of small coastal sharks in the US Atlantic and Gulf of Mexico. NOAA, National Marine Fisheries Service, Panama City.
2. Robertson DR, Allen G (2008) Shorefishes of the Tropical Eastern Pacific, online information system. Available at: www.stri.org/stfr. Accessed 27 November 2011.
3. Navia AF, Mejía-Falla PA, Zapata LA, Besudo S, Soler G, et al. (2009) Estado del conocimiento de tiburones y rayas del Pacifico Colombiano. In: Puentes V, Corte´s E (2002) Stock assessment of small coastal sharks in the US Atlantic and Gulf of Mexico. NOAA, National Marine Fisheries Service, Panama City.
4. Navia AF, Mejía-Falla PA, C., Diazgranados MC, Zapata LA, editors. Avances en el Conocimiento de Tiburones, Rayas y Quimeras de Colombia. Fundación SQUALUS, Ministerio de Ambiente Vivienda y Desarrollo Territorial, Instituto Colombiano Agropecuario, Conservación Internacional, WWF. pp. 133–194
5. Mejía-Falla PA, Navia AF, Cortés E (2012) Reproductive variables of Urotrygon rogersi in the Colombian Pacific ocean. J Fish Biol 78: 1213–1224.
6. Mejía-Falla PA, Navia AF, Cortés E (2012) Reproductive variables of Urotrygon rogersi (Batoidae: Urotrygonidae): a species with a trimodal reproductive cycle in the Eastern Tropical Pacific Ocean. J Fish Biol 80: 1246–1266.
7. Wourms JP (1977) Reproduction and development in chondrichthyan fishes. Amer Zool 17: 379–410.
8. Harry AV, Tomlinson AJ, Simpfendorfer CA, Tobin AJ (2010) Improving age, growth, and maturity estimates for assessentially reproducing chondrichthians. Fish Res 106: 393–403.
9. Natanson LJ, Cailliet GM (1990) Vertebral growth zone deposition in Pacific angel sharks. Copeia 1990(4): 1133–1145.
10. Hale LF, Low CG (2006) Age and growth of the round stingray Dasyatis alatus at Seal Beach California. J Fish Biol 73: 510–523.
11. Cailliet GM, Smith WD, Mollet HE, Goldman KJ (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environ Biol Fishes 77: 211–220.
12. Chin A, Simpfendorfer C, Tobin A, Heupel M (2013) Validated age, growth and reproductive biology of Carcharhinus melampyurus, a widely distributed and exploited reef shark. Mar Freshw Res 64(10):935–975.
13. Geraghty PT, Macbeth WG, Harry AV, Bell JE, Yerman MN, Williamson JE (2013) Age and growth parameters for three heavily exploited shark species off temperate eastern Australia. ICES J Mar Sci doi:10.1093/icesjms/fst164.
14. Gervella BJ, Natanson I (2013) Age and growth of the common thresher shark in the Western North Atlantic Ocean. Trans Am Fish Soc 142: 1353–1354.
15. Harry AV, Tobin AJ, Simpfendorfer CA (2013) Age, growth and reproductive biology of the spot-tail shark, Carcharhinus sorrah, and the Australian blacktip shark, C. alutus, from the Great Barrier Reef World Heritage Area, north-eastern Australia. Mar Freshw Res 64: 277–293.
16. Barreto RR, Lessa RP, Hazin FH, Santana FM (2013) Age and growth of the blacknose shark, Carcharhinus acronotus (Poey, 1860) off the northeastern Brazilian Coast. Fish Res 110: 170–176.
17. Katsanevakis S (2006) Modelling fish growth: model selection, multi-model inference and model selection uncertainty. Fish Res 81: 229–235.
18. Cailliet GM, Martin LK, Kusler D, Wold P, Welden BA (1983) Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In: Prince ED, Pulso LM, editors. Proceedings international workshop on age determination of oceanic pelagic fishes: Tuna, Billfishes, Sharks. NOAA Technical Report 8. pp. 157–165.
20. Mejía-Falla PA (2012) Historia de vida y demografía de la raya espinosa Urotrygon rogersi en dos áreas con distintos niveles de presión pesquera. [PhD Thesis, Facultad de Ciencias, Universidad del Valle].

21. Carlson JK, Baremore IE (2005) Growth dynamics of the spinner shark (Carcharias taurus) off the United States southeast and Gulf of Mexico coasts: Katsanevakis, S. Modelling and quantitative methods in fisheries. Boca Raton: CRC Press. 465 p.

22. Goldstein KJ (2002) Aspects of age, growth, demographics and thermal biology of two Lamniform shark species. [PhD Thesis, College of William and Mary, Virginia Institute of Marine Science].

23. Katsanevakis S, Maravelias CD (2008) Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish Bull 96: 178–187.

24. Hoernig JM, Morgan MJ, Brown CA (1995) Analyzing differences between two age determination methods by tests of symmetry. Can. J Fish Aquat Sci 52: 364–368.

25. Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38: 982–983.

26. Natanson LJ, Casey JG, Kohler NE (1995) Age and growth estimates for the dusky shark, Carcharhinus obscurus, in the western North Atlantic Ocean. Fish Bull 93: 116–126.

27. Conrath CL, Gelsleichter J, Musick JA (2002) Age and growth of the smooth dogfish (Mustelus canis) in the northwest Atlantic Ocean. Fish Bull 100: 674–682.

28. von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws II). Human Biol 10: 181–213.

29. Ricker WE (1979) Growth rates and models. In: Hoar WS, Randall DJ, Brett JR, editors. Fish physiology: bioenergetics and growth. New York: Academic Press. pp. 677–743.

30. Soriano M, Moreau J, Hoenig JM, Pauly D (1992) New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch. Trans Am Fish Soc 111: 486–493.

31. Katsanevakis S, Maravelias CD (2008) Modelling fish growth: multi-model inference as a better alternative to a priori using von Bertalanffy equation. Fish Bull 9: 178–187.

32. Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, editors. Second international symposium on information theory. Budapest: Akadémiai Kiado. pp. 267–281.

33. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer-Verlag. 488 p.

34. Motulsky H, Christopoulos A (2003) Fitting models to biological data using linear and nonlinear regression: A practical guide to curve fitting. Available at: www.graphpad.com. Accessed 25 October 2011.

35. Araya M, Caballero LA (2006) Evidence of two-phase growth in elasmobranchs. Environ Biol Fishes 77: 293–300.

36. Kimura DK (1980) Likelihood methods for the von Bertalanffy growth curve. Fish Bull 89: 93–116.

37. Haddon M (2001) Modelling and quantitative methods in fisheries. Boca Raton: CRC Press. 465 p.

38. Ebert DA, Maurer JR, Ainsley SM, Barnett LK, Cailliet GM (2009) Life history and population dynamics of four endemic Alaskan skates: determining essential biological information for effective management of bycatch and target species. North Pacific Research Board Final Report 715.

39. Barnett LK, Winton MV, Ainsley SM, Cailliet GM, Ebert DA (2013) Comparative demography of skates: Life-history correlates of productivity and implications for management. ResOce 8(3): e63680.

40. Mollet HF, Cliff G, Pratt HL Jr, Stevens JD (2000) Reproductive biology of the female shortfin mako, Isurus oxyrinchus. Environ Biol Fishes 56: 101–110.

41. White WT, Potter IC (2002) Reproductive biology and growth during pre- and postnatal life of Trygonoptera penacea and T. maura (Batoidea: Urolophidae). Mar Biol 140: 699–712.

42. White WT, Hall NG, Potter IC (2002) Reproductive biology and growth during pre- and postnatal life of Trygonoptera penacea and T. maura (Batoidea: Urolophidae). Mar Biol 140: 699–712.

43. Hale LF, Dudgeon JV, Mason AZ, Lowe CG (2006) Elemental signatures in the vertebral cartilage of the round stingray, Urolophus halleri, from Seal Beach, California. Environ Biol Fishes 77: 317–325.

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

45. Cailliet GM, Radkovek R, Welden BA (1989) Elasmobranch age determination and verification: a review. In: Uyeno, T, Ari, T, Tanich, T, Matusura K, editors. Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Tokyo: Ichthyological Society of Japan. pp. 345–359.

46. Ainsley SM, Ebert DA, Cailliet GM (2011) Age, growth, and maturity of the yellowfin thresher shark, Alopias pelagicus (Squaliformes: Alopiidae). Fish Bull 109: 176–185.

47. Brothers EB (1983) Summary of round table discussions on age validation. In: Prince ED, Pule JM, editors. Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Technical Report NMS-8, pp. 35–44.

48. Goodwin NB, Duhky NK, Reynolds JD (2002) Life-history correlates of the evolution of live-bearing in fishes. Philos Trans R Soc Lond B 357: 259–267.

49. Thorson GT, Simpfendorfer CA (2005) Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. Fish Res 80: 73–84.

50. Moreau J (1987) Mathematical and biological expression of growth in fishes: recent trends and further developments. In Summerfelt RC, Hall GE, editors. The age and growth of fish. Ames: Iowa University Press. pp. 81–113.

51. Wang Y, Milton DA (2000) On comparison of growth curves: how do we test whether growth rates differ? Fish Bull 98: 874–880.

52. Neer JA, Cailliet GM (2001) Aspects of the life history of the Pacific electric ray, Torpedo californica (Ayres). Copeia 3: 842–847.

53. Neer JA, Thompson BA (2005) Life history of the cow nose ray, Rhinoptera bonasus, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. Environ Biol Fishes 73: 321–331.

54. Edwards KRC (1980) Aspects of the population dynamics and ecology of the white spotted stingray, Urolophus paccanaculatus Dixon, in Port Phillip Bay, Victoria. Aust J Mar Fresh Res 31: 459–467.

55. Babel JS (1967) Reproduction, life history and ecology of the round stingray, Torpedo rhombus (Ayres). Copeia 3: 842–847.

56. Sibly R, Calow P, Nichols N (1985) Are patterns of growth adaptive? J Theor Biol 112: 553–574.

57. Stearns SC (1992) The evolution of life histories. New York: Oxford University Press. 362 p.

58. Holdren MJ (1974) Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In: Jones E.H, editor. Sea fisheries research. New York: Wiley and Sons. pp. 187–215.

59. Beukema JJ (1989) Bias in estimates of maximum life span, with an example of the edible cockle, Ctenodoma zehli, Neth J Zool 39: 79–85.

60. Ainsley SM, Ebert DA, Cailliet GM (2011) Age, growth, and maturity of the white brow skate, Bathyura microphias, from the eastern Bering Sea. ICES J Mar Sci 68: 1426–1434.

61. Jensen AI (1985) Relations among net reproductive rate and life history parameter for lake Whitefish (Coregonus clupeaformis). Can J Fish Aquat Sci 42: 164–167.

62. Silby R, Calow P, Nichols N (1985) Are patterns of growth adaptive? J Theor Biol 112: 553–574.

63. Perrin N (1989) Reproductive allocation and size constraints in the cladoceran, Daphnia pulex. In Evernden, JF, editor. Reproduction in aquatic communities. New York: Springer-Verlag. 387 p.

64. Nelson JS (1994) Fishes of the world. 3rd ed. New York: John Wiley & Sons. pp. 263–269.

65. Simpfendorfer CA (1995) Age and growth of the Australian sharpnose shark, Rhizoprionodon laticaudatus, from north Queensland, Australia. Environ Biol Fishes 36: 233–241.