

Growth of Tropical dasytid Rays Estimated Using a Multi-Analytical Approach

Owen R. O'Shea^{1,2*}, Matias Braccini³, Rory McAuley³, Conrad W. Speed¹, Mark G. Meekan¹

1 Australian Institute of Marine Science, Crawley, Western Australia, Commonwealth of Australia, **2** School of Veterinary and Life sciences, Murdoch University, Perth, Western Australia, Commonwealth of Australia, **3** Shark and Ray Sustainability Group, WA Fisheries and Marine Research Laboratories, Hillary's Boat Harbour, Western Australia, Commonwealth of Australia

Abstract

We studied the age and growth of four sympatric stingrays: reticulate whipray, *Himantura uarnak* (n=19); blue mask, *Neotrygon kuhlii* (n=34); cowtail, *Pastinachus atrus* (n=32) and blue-spotted fantail, *Taeniura lymma* (n=40) rays at Ningaloo Reef, a fringing coral reef on the north-western coast of western Australia. Age estimates derived from band counts within sectioned vertebrae ranged between 1 and 27 years (*H. uarnak*, 1 - 25 yrs.; *N. kuhlii*, 1.5 - 13 yrs.; *P. atrus*, 1 - 27 yrs. and *T. lymma*, 1 -11 yrs.). Due to limitations of sample sizes, we combined several analytical methods for estimating growth parameters. First, we used nonlinear least squares (NLS) to identify the growth model that best fitted the data. We then used this model, prior information and the data within a Bayesian framework to approximate the posterior distribution of the growth parameters. For all species the two-parameter von Bertalanffy growth model provided the best fit to size-at-age datasets. Based on this model, the Bayesian approach allowed the estimation of median values of W_{∞} (cm) and k (yr⁻¹) for the four species (*H. uarnak*: 149 and 0.12; *N. kuhlii*: 42 and 0.38; *P. atrus* 156 and 0.16, and *T. lymma* 33 and 0.24, respectively). Our approach highlights the value of combining different analytical methods and prior knowledge for estimating growth parameters when data quality and quantity are limited.

Citation: O'Shea OR, Braccini M, McAuley R, Speed CW, Meekan MG (2013) Growth of Tropical dasytid Rays Estimated Using a Multi-Analytical Approach. PLoS ONE 8(10): e77194. doi:10.1371/journal.pone.0077194

Editor: Sharyn Jane Goldstien, University of Canterbury, New Zealand

Received: November 9, 2012; **Accepted:** September 5, 2013; **Published:** October 11, 2013

Copyright: © 2013 O'Shea et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This study was funded by the Australian Institute of Marine Science. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript."

Competing interests: The authors have declared that no competing interests exist.

* E-mail: oshea@ceibahamas.org

Introduction

Elasmobranchs face increasing fishing pressure on a global scale due to a combination of rising consumer demand and life history characteristics that make them vulnerable to overfishing [1,2]. In Australian waters, batoids have been largely overlooked by researchers and managers involved in commercial fisheries primarily due to their low commercial value in comparison to sharks. However, they are still significant components of fisheries bycatch, particularly in penaeid fisheries [3]. In a wider Indo-Pacific context, many demersal rays such as dasytids are targeted in artisanal and small-scale fisheries for their meat and leather [4] yet for the most part, there is a lack of even the most basic life-history information for these taxa. Given that knowledge of growth rates and age structures are essential for determining the ability of populations to sustain and recover from overfishing, studies on the age and growth of batoids are urgently required.

Chondrichthyans have been aged by counting growth band pairs in vertebrae for over 90 years [5]. While such techniques

are generally reliable, accurate and common-place, the acquisition of adequate sample sizes remains a major challenge [6], particularly for those species that are poorly represented in commercial fisheries (the most common method for sourcing specimens) [7] due to gear selectivity [8,9] and/or spatially/temporally restricted sampling [10]. Low sample sizes hinder age and growth studies because they present challenges for the estimation of growth parameters using conventional analytical approaches. For example, low sample sizes may result in techniques such as nonlinear regression providing estimates that are not an accurate reflection of growth patterns [11]. Combining analytical methods to increase accurate estimation in such cases is useful and using a Bayesian framework is one such approach which can aid in overcoming these issues by guiding the estimation of parameters through the use of prior knowledge [11].

Here, we determined the ages and growth parameters of four abundant stingrays in a coastal, coral reef environment at Ningaloo Reef, Western Australia. Our approach combined different analytical methods for estimating model parameters in

a situation where only limited sample sizes were available. We provide the first account of age and growth parameter estimates for these rays at Ningaloo Reef, including three species for which no age and growth information has previously been reported. Our approach has relevance to studies of other elasmobranchs where collection sizes may be restricted due to the difficulty of sampling (e.g. deep sea and no-take areas) or the rarity and/or protected status of the subject animals.

Materials and Methods

Study sites and sample collection

A total of 170 individuals (*H. uarnak*, Forsskål 1775, n=24; *N. kuhlii*, Müller and Henle, 1841, n=36; *P. atrus*, Macleay 1883, n=43; *T. lymma*, Forsskål 1775, n=54 and *U. asperrimus*, Bloch and Schneider 1801, n=13) were collected for aging between February 2010 and February 2011 in the shallow (2–10 m water depth) lagoons of the Ningaloo Reef Marine Park (Figure 1). Due to logistical constraints, sampling was restricted to the months of February (38% of total catch) and August and September (62%). Small rays were caught with hand nets and larger individuals were caught using spear guns following methods outlined in [12]. Logistic, environmental and ethical constraints resulted in small sample sizes, in contrast to other studies that have been able to use large seine nets over sand flats or sourced individuals from commercial fishers [13]. This was not possible at Ningaloo Reef where commercial fishing activities are not permitted within the marine park and the lagoon and nearshore intertidal areas are dominated by coral reef. All animals were collected under WA fisheries exemption permit # RS457/98-05 and Murdoch University animal ethics licence #U6/2010-2011 and Murdoch University ethics permit #R2275/09.

For age validation, fifty-two individuals (*H. uarnak*, n=8; *N. kuhlii*, n=11; *P. atrus*, n=19; and *T. lymma*, n=14) were caught at Skeleton (n = 30; 23° 8.378'S 113° 46.240'E) and Mangrove (n = 22; 21°58.385' S 113°56.99' E) Bays in the Ningaloo Marine Park between November 2009 and November 2010. Each ray was weighed, measured (disc width, W_D , and total length, T_L), fitted with a T-bar spaghetti tag, injected with calcein at 3-ml/kg body weight and then released.

Vertebrae preparation

Vertebrae were removed posterior to the cranium at the widest point of the animal and stored in a freezer within 8 hours of excision for transport to the laboratory. In the lab, centra were cleaned of connective tissue before being placed in a 5% sodium hypochlorite solution for between 0.5 - 2 hours depending on their size. The samples were then soaked in distilled water for ten minutes before being air-dried overnight. Next, three centra were embedded in clear polyester casting resin and left to set overnight, after which sagittal sections (350 µm) were cut from the resin blocks using an isomet 2000 linear precision saw. Sections were placed under a dissecting microscope and covered in methyl salicylate liniment APF to remove imperfections and cracks created by the saw. Each centrum was photographed under reflected light up to five

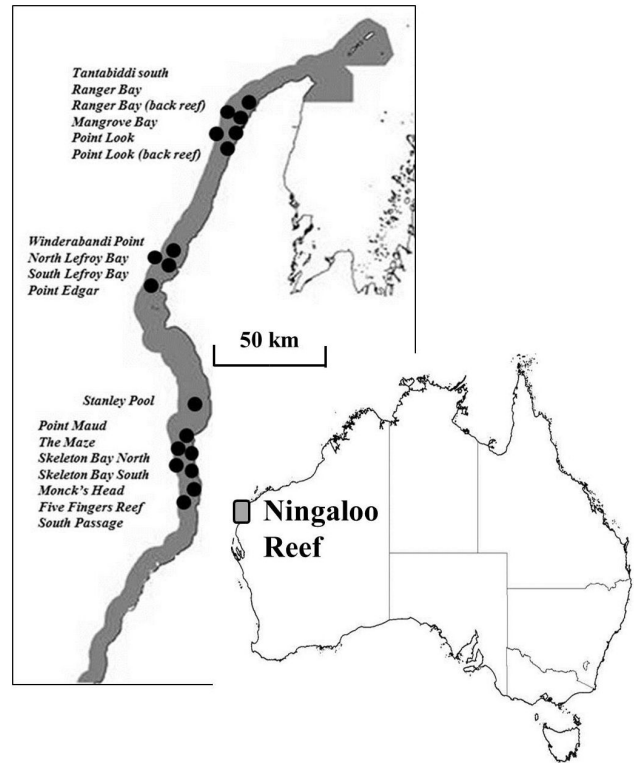


Figure 1. Map of the eighteen sites accessed for sampling within the Ningaloo Reef Marine Park, Western Australia.

doi: 10.1371/journal.pone.0077194.g001

times using a mounted camera. Images were edited using QuickTime (V.7.6.6) image capture software.

Age Estimation

Alternating opaque and translucent bands representing one band pair were visible in all samples with the exception of those from *U. asperrimus*. For this latter species, no further analysis was possible. The position of the birthmark in the section was evaluated from the angle change on the outer edge of the corpus calcareum [14] (Figure 2A). Pre-birth banding was not present in any of the neonate samples; consequently the first band pair was regarded as age one. Age was determined by counting the band pairs on the outer edge of the corpus calcareum and 0.5 years was added if a translucent or opaque band was forming on the outer centrum edge [15,16]. Biases in sampling effort between seasons and unconventional band formation within seasons (i.e. both translucent and opaque bands formed in each season) justified this approach. Two training counts were conducted to achieve fluency in interpreting banding pairs but these scores were not included in the final results. Three blind, independent counts were then made of each sample using three different readers. Final age estimates were achieved when the same age estimate was obtained from two or more readers. A qualitative readability score from one to three was given to each sample, where one meant all bands were clear and unambiguous; two,

bands visible but difficult to interpret; and three, bands were unreadable (modified from [17]). Samples ($n=45$) with readability scores of 3 were excluded from the analyses. The index of average percentage error (IAPE) (Table 1) was calculated, after Beamish & Fournier [18], to estimate the precision of age determination among readers. When averaged across multiple counts for multiple rays, the index provided an estimate of average percent error [19]. In addition, the coefficient of variation (CV) [20] was also calculated (Table 1).

Growth parameter estimation

We used a three-step approach to optimise the estimation of growth parameters of each species. First, we pooled male and female samples and used Ford-Walford plots [21,22] to determine adequate starting values for parameter estimation. We then used nonlinear least squares to compare a range of growth models to determine if a particular model best described the growth data [23]. Estimated ages and observed sizes (W_D), were fitted to four commonly used models (Table 2): the three-parameter von Bertalanffy (VBGF) [24,25], the modified two-parameter von Bertalanffy (2VBGF) [26], the logistic (after [9]) and the three-parameter Gompertz (GGF) [27]. Akaike's information criterion (AIC) with a bias correction (AIC_c) due to small sample sizes (<200) was used to determine the best model fit [9,28]. Models were ranked according to AIC differences (Δ) where models with a Δ value of between zero – two were considered to have the highest support, while any higher Δ values were considered to have lower support [29].

Once the model with the best fit was determined, we adopted a Bayesian approach with a penalised likelihood to approximate the posterior distribution of the growth parameters for each of the species (see justification for adopting a Bayesian approach in Appendix S1). Markov Chain Monte Carlo (MCMC) methods using the Metropolis Hastings algorithm were used to sample the posterior distributions [11,30,31]. We used a chain of two million iterations with a burn-in period of 100,000. Owing to the high auto-correlation in the MCMC chain, we used a thinning of 100. We used informative priors for $W_{D\infty}$ (asymptotic size expressed as disc-width) and K (yr^{-1}) (growth coefficient – the rate at which asymptotic size was reached) based on all recently published estimates for sub-tropical/tropical dasyatid species ($n=7$) that were also derived from vertebral sections [13,15,32–35]. Given that age and growth in dasyatids may not conform to the general pattern that larger species live longer and grow more slowly when compared to smaller species [13], we decided to use one prior for each parameter that took large and small species into consideration as opposed to setting one prior for large and one for small species. The prior for $W_{D\infty}$ was lognormal with mean 77 cm and standard deviation of 0.5 (in log space). We used a beta distribution as a prior for K (yr^{-1}) (Beta; 21.9; 162.3). The prior on the variance term was non-informative, defined by an inverse Gamma distribution (IGamma 0.01, 0.01). Preliminary sensitivity tests using informative or non-informative priors for $W_{D\infty}$ and K (yr^{-1}) showed that the data were able to update the priors. Evidence of convergence of the MCMC chains was warranted by standard convergence diagnostics (visual inspection of the

trace plots, the Geweke diagnostic test and from comparing summary statistics for the first 10% of the chain and the second half of the chain). All analyses were conducted using the statistical package R [37].

Results

Of the 170 rays sampled, the vertebrae of 29% ($n=50$) achieved readability scores of one, while 44% ($n=75$) achieved scores of two, and 26% ($n=45$) were assigned scores of three. The 13 *U. asperrimus* vertebral samples were excluded from analyses with only one sample attaining a readability score of <3. In this species, the cartilaginous matrix of the centra was very brittle and it was therefore problematic to obtain accurate counts of band pairs (Figure 2B). The remaining samples that proved difficult to age were typically from very small individuals and full term pups, where calcification within the centra was either insufficient to obtain counts or was not present. The index of average percentage error (IAPE) and coefficient of variation (CV) for the selected samples generally showed low inter-reader variability, particularly for the larger bodied species (*H. uarnak* and *P. atrus*) compared to the two smaller species (*N. kuhlii* and *T. lymma*) (Table 1).

Recaptures and seasonal edge deposition

Of the 52 rays caught and marked with calcein, only two *P. atrus* individuals were recaptured after 83 and 91 days. These rays had both grown 5 cm (W_D) during this period and both had laid down translucent bands of 0.2 cm in width after a very pronounced calcein mark (Figure 2C). Unfortunately, the time at liberty was insufficient for validation of band pair periodicity. Variation in sampling effort resulted in 48 rays being caught in summer and 77 in winter. Of the 48 individuals caught in February, 28 (58%) had opaque bands forming at the edge of the centra, while during the winter months, 51 rays (66%) had translucent bands forming on the centrum edge.

Estimation of ages

Estimated ages ranged from one to 25 years for *H. uarnak* (25–145.4 cm W_D), 1.5 to 13 years in *N. kuhlii* (17–47 cm W_D), one to 27 years in *P. atrus* (36.5–177 cm W_D), and one to 11 years in *T. lymma* (14–34.5 cm W_D) (Figure 3). According to AIC, the 2VBGF was the model of choice, though the other models show very similar fits (Table 3 and Figure 3).

Estimation of growth parameters

Diagnostic tests indicated MCMC chain convergence for all growth parameters for three species (*N. kuhlii*, *P. atrus* and *T. lymma*). Convergence for $W_{D\infty}$ for *H. uarnak* was less obvious, reflecting the less than ideal nature of the data (i.e. few large/old individuals). Growth data were informative for all species, updating the priors for K (yr^{-1}) and $W_{D\infty}$ in all cases (Figure 4). The Bayesian approach provided more precise estimates of K (yr^{-1} median with 95% credibility intervals) for *P. atrus* ($K = 0.16 \text{ yr}^{-1}$, 0.12–0.21 yr^{-1}) than for the remaining species (*H. uarnak*: $K = 0.12 \text{ yr}^{-1}$, 0.04–0.22 yr^{-1} ; *N. kuhlii*: $K = 0.38 \text{ yr}^{-1}$, 0.25–0.53 yr^{-1} ; and *T. lymma*: $K = 0.24 \text{ yr}^{-1}$, 0.1–0.38 yr^{-1}). For $W_{D\infty}$, more precise estimates were obtained for *N.*

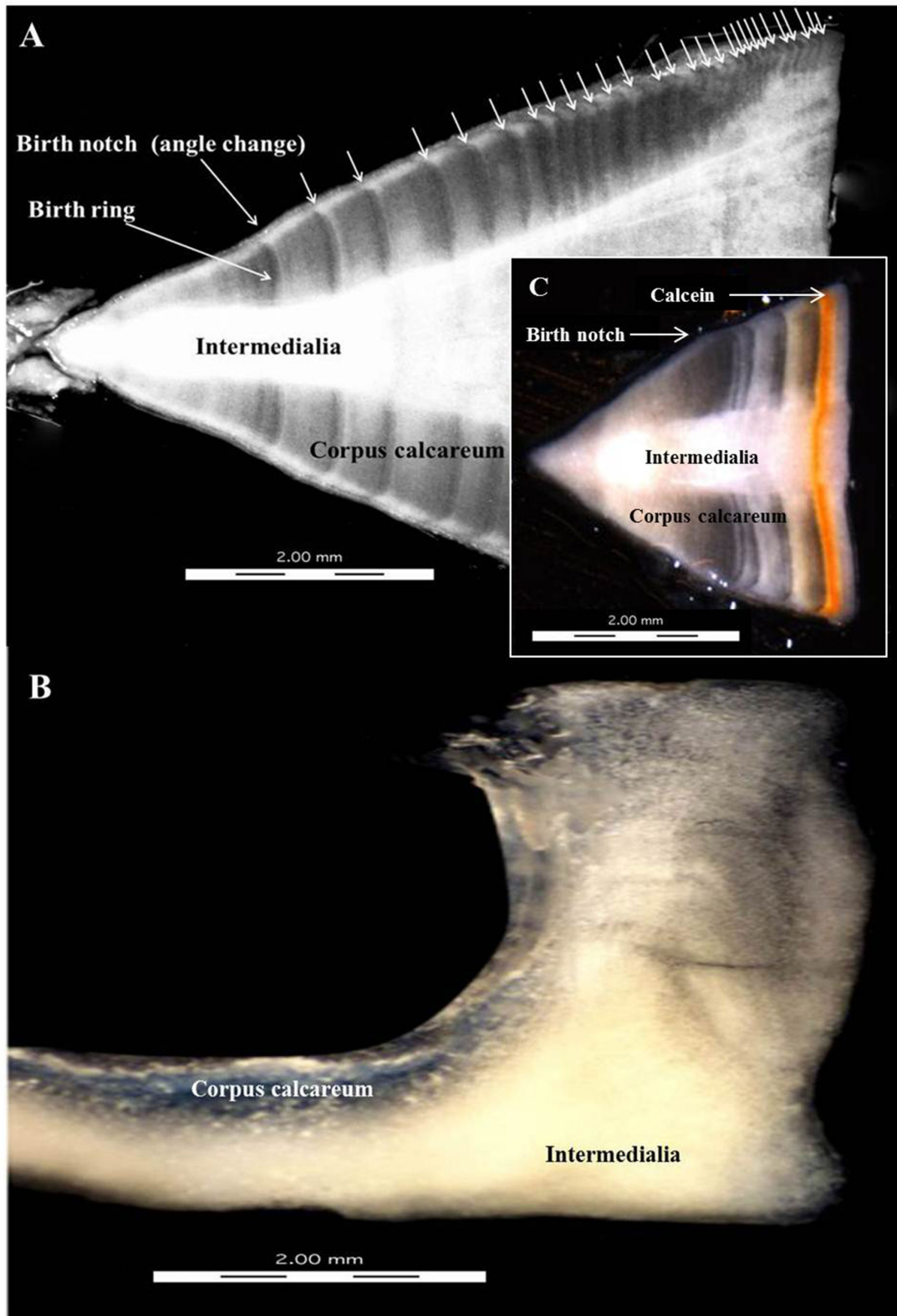


Figure 2. Photographic images of sagittal centrum sections from (A) *Pastinachus atrus* with 27 band pairs (B), example of difficult to read section from *Urogymnus asperrimus* and (C) example of calcein marked centra from 91 days at liberty for *P. atrus*.

doi: 10.1371/journal.pone.0077194.g002

Table 1. Index of average percentage error (IAPE) and coefficient of variance (CV) values for inter-reader precision of age determination (i = reader).

Species	IAPE $i=1$	IAPE $i=2$	IAPE $i=3$	CV $i=1$	CV $i=2$	CV $i=3$
<i>Himantura uarnak</i> *	1.69	1.66	2.92	2.64	2.29	4.03
<i>Neotrygon kuhlii</i> **	2.19	2.84	5.25	3.12	4.04	7.47
<i>Pastinachus atrus</i> *	1.43	2.45	4.66	2.07	3.55	6.75
<i>Taeniura lymma</i> **	2.09	2.15	3.61	2.80	2.88	4.84

* denotes larger bodies species, ** smaller bodies species

doi: 10.1371/journal.pone.0077194.t001

Table 2. Growth models and associated formulas used to fit size-at-age data for four species of dasyatid rays.

Model	Growth Function
3 parameter von Bertalanffy (VBGF)	$W_{Dt} = W_{D\infty} [1 - e^{-k(t-t_0)}]$
2 parameter von Bertalanffy (2VBGF)	$W_{Dt} = W_{D\infty} (1 - be^{-kt}), b = (W_{D\infty} - W_{D0})/W_{D\infty}$
Logistic (LOG)	$W_{Dt} = ((W_{D\infty} - W_{D0} e) / (W_{D\infty} + W_{D0} (e^{kt} - 1)))$
Gompertz (GGF)	$W_{Dt} = W_{D\infty} = e^{(-W_{D0} e^{-kt})}$

doi: 10.1371/journal.pone.0077194.t002

kuhlii, ($W_{D\infty}$ =42 cm, 38–46 cm) and *T. lymma*, ($W_{D\infty}$ =33 cm, 28–41 cm) than for *P. atrus* ($W_{D\infty}$ =156 cm, 133–181 cm) and *H. uarnak* ($W_{D\infty}$ =149 cm, 107–231 cm), with the latter showing a much broader posterior distribution of values (Table 4 and Figure 4).

Discussion

Our study shows that growth parameters of tropical dasyatids can be estimated in data-limited situations using a combination of statistical methods, a result relevant for other studies of elasmobranchs particularly where the species of interest are rare and/or protected, or occur in areas where conventional methods that yield large sample sizes may not be used. Importantly, our samples included a range of size classes, enabling the estimation of growth parameters without the need to resort to other methodologies (e.g. back calculation).

Validation of age estimates

Although we attempted age validation through the recapture of chemically-marked individuals [19] we failed to obtain any rays after a sufficient period at liberty. For this reason we assumed that band pairs were deposited on an annual basis in order to analyse growth patterns. This approach appeared reasonable given that annual patterns of deposition within vertebrae have been reported for the majority of elasmobranchs examined to date [14].

Growth models and parameter estimates

While the use of an information criterion method (AIC) suggested that the two-parameter von Bertalanffy function (2VBGF) provided the best fit to growth data of all species, selection was only marginal and other growth models we trialled showed similar fits. Parameter estimates from the 2VBGF model were also comparable to recently published estimates for other tropical dasyatid rays aged in the same manner [13,15,32–37]. Given that L_0 is generally well documented for sharks and rays, the use of the 2VBGF – where only the k and $W_{D\infty}$ parameters were estimated – was an intuitive choice over the traditional VBGF model, particularly since sample sizes were small and some age classes, particularly younger individuals, were poorly represented [6,8]. Due to the requirement of estimating an additional parameter, the highly correlated nature of growth parameters and the less than ideal representation of age and size data, it was not surprising that the 2VBGF outperformed the other models when ranked using AIC. However, since parameter estimates derived from this model may under-estimate $W_{D\infty}$ and overestimate k (yr^{-1}), our results should be treated with caution [8].

Underlying biases within age and growth data are a common problem for studies of elasmobranchs due to factors that affect the sample collection process such as selectivity of sampling gear and the heterogeneous spatial and temporal patterns of abundance of this mobile group of animals. In our study, even though sample sizes were small and not all age classes were well represented, the application of a multi-staged method based on the 2VBGF and Bayesian estimation allowed a reasonable approximation of the growth parameter metrics. These estimates were close to those obtained through a nonlinear least squares (NLS) analysis however, the NLS was more sensitive to the initial parameter values used in the estimation and it produced more uncertain estimates of growth parameters (Appendix A).

Studies of related species suggest that no particular growth model outperforms any other when describing the growth of dasyatids. For brown stingrays (*Dasyatis lata*) the LOG growth model provided the best fit to age at size data [37], whereas growth of the black whipray (*Himantura astra*) [13] and the diamond stingray (*Dasyatis dipterura*) [15] were described with greater certainty by GGF and the VBGF models respectively. Given that outputs from age and growth studies are limited by their sample size, size range distribution, validation techniques and model constraints [6,15,38], a preferred growth model and parameter estimates can exhibit considerable variation among both studies and species of the same family, as is the case for urolophids [41–44].

Growth rates are defined by the growth coefficient ($k \text{ yr}^{-1}$) that describes the rate at which growth slows as the animal ages [1]. Slow-growing elasmobranchs are defined as having k (yr^{-1}) values <0.1 [38] and it is assumed that these species are more vulnerable to extrinsic pressures such as overfishing [39] than those faster-growing species where k (yr^{-1}) >0.1 . Thus, our findings suggest that of the two largest species we studied, *H. uarnak* was more vulnerable as a slower-growing species ($k \text{ yr}^{-1} = 0.12$), than *P. atrus* ($k \text{ yr}^{-1} = 0.16$), though their posterior

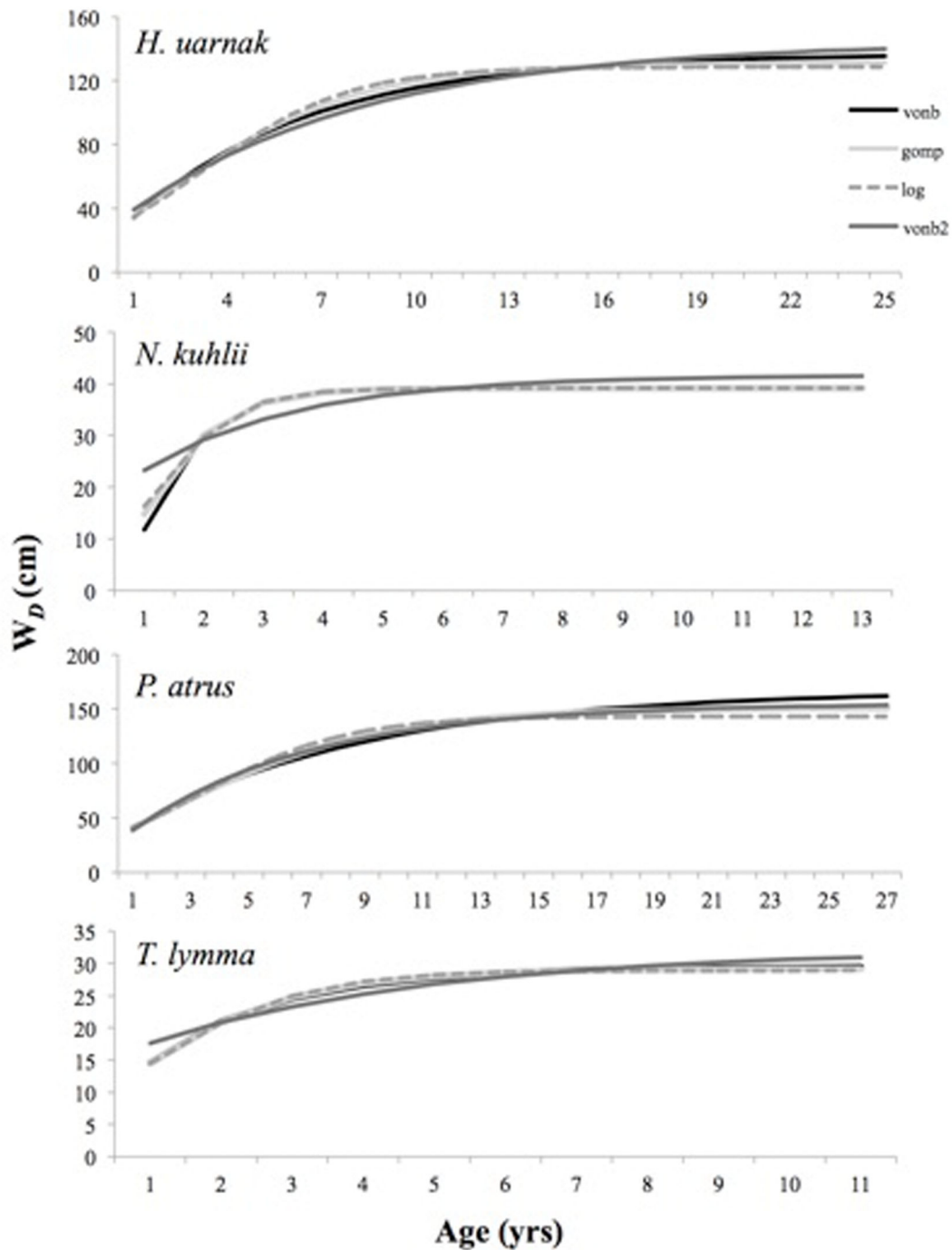


Figure 3. Predicted size at age from four growth models: Vonbertalanffy, Gompertz, Logistic and two-parameter Vonbertalanffy.

doi: 10.1371/journal.pone.0077194.g003

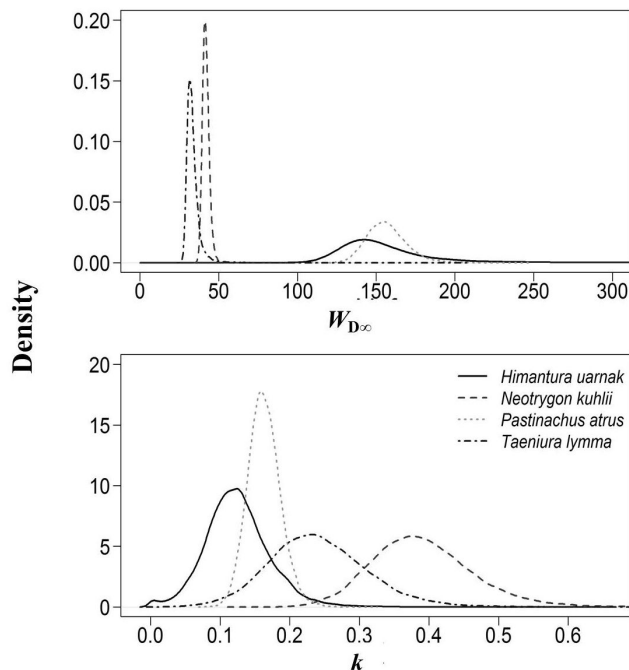
distributions overlapped considerably. As expected, the two smaller-bodied species (*N. kuhlii* and *T. lymma*) both had faster growth rates ($k \text{ yr}^{-1} = 0.38$ and 0.24 respectively) and thus may be less vulnerable. Published studies for other sub-tropical/tropical dasyatid species show similar results, with those

species attaining larger maximum sizes ($W_{D,max} > 100\text{cm}$) having slower growth rates than smaller-bodied species (e.g. [13,40]).

Table 3. Comparison of growth model's fit and parameter estimates.

Species	Model	ΔAIC	$W_{D\infty}$ (cm)	K (yr ⁻¹)	T_0 (yr)
<i>Himantura uarnak</i> N=19	VBGF	3.03	137	0.17	0.68
	GGF	3.93	131	0.29	1.99
	LOG	4.34	128	25	0.43
<i>Neotrygon kuhlii</i> N=34	2VBGF	0	145	0.13	NA
	VBGF	3.03	39	1.12	0.68
	GGF	2.86	39	1.29	0.98
<i>Pastinachus atrus</i> N=32	LOG	2.87	39	5.45	1.48
	2VBGF	0	42	0.38	NA
	VBGF	2.49	167	0.12	-1.25
<i>Taeniura lymma</i> N=40	GGF	2.32	151	0.24	2.12
	LOG	2.87	74	30.35	0.39
	2VBGF	0	155	0.16	NA
<i>Taeniura lymma</i> N=40	VBGF	2.77	29	0.58	-0.22
	GGF	2.81	29	0.73	0.5
	LOG	2.83	29	8.29	0.92
	2VBGF	0	32	0.25	NA

doi: 10.1371/journal.pone.0077194.t003

**Figure 4.** Posterior distributions for $W_{D\infty}$ and k , for the four species where band pairs could be counted.

doi: 10.1371/journal.pone.0077194.g004

Conclusions

The development of methods that produce accurate and robust estimates of growth parameters of elasmobranchs when

Table 4. Summary of growth parameter estimates (median with 95% credibility intervals) from the Bayesian modelling approach.

Species	$W_{D\infty}$ (cm) \pm 95% C.I.	K (yr ⁻¹) \pm 95% C.I.
<i>Himantura uarnak</i>	149 (107 - 231)	0.12 (0.04 - 0.22)
<i>Neotrygon kuhlii</i>	42 (38 - 46)	0.38 (0.25 - 0.53)
<i>Pastinachus atrus</i>	156 (133 - 181)	0.16 (0.12 - 0.21)
<i>Taeniura lymma</i>	33 (28 - 41)	0.24 (0.1 - 0.38)

doi: 10.1371/journal.pone.0077194.t004

sample sizes are small and may not be representative of the entire population is critical for determining the conservation status of rare and protected taxa, or any species where the collection of large sample sizes presents logistic or ethical problems. By combining different analytical methods and maximising the use of available information, our approach increased the precision of estimates of growth parameters of tropical shallow water rays.

Supporting Information

Figure S1. Simulated data sets. The upper panel shows the well-represented data set (10 observations for each of the 20 age classes) from where samples were drawn. The middle and lower panels show an example of data-poor sampling. (TIF)

Figure S2. Comparison of the performance of nonlinear least squares (NLS) and Bayesian methods for estimating growth parameters based on simulated data. The broken line indicates the parameter value used for simulating the data. (TIF)

Appendix S1. Performance of NLS and Bayesian methods when estimating growth parameters in data-poor cases. (DOCX)

Acknowledgements

We thank the Department of Environment and Conservation (WA), field volunteers and others, S. Basso, A. Turco, T. Hill, S. Ridley, H. Bowers, T. Schenk, M. Drevander, G. Vianna, D. Ilich, C. Egeberg, K. Brooks, E. Garza-Gisholt, A. Hesp, M. Travers and especially T. Espeland. F. Cerutti-Pereyra for genetic species identification for *Himantura uarnak*.

Author Contributions

Conceived and designed the experiments: ORO MGM. Performed the experiments: ORO RM. Analyzed the data: ORO MB. Contributed reagents/materials/analysis tools: ORO MB. Wrote the manuscript: ORO MB. Sample preparation and analysis: CWS. Assisted in field work (Collection of samples): CWS.

References

1. Hoenig JM, Gruber SH (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. NOAA Tech Rep Nmfs 90: 1-16.
2. Dulvy NK, Forrest RE (2010) Life histories, population dynamics and extinction risks in chondrichthyan. In: Carrier JC, Musick JA, Heithaus MR. Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. Boca Raton, FL: CRC Press. 639–679
3. Dell Q, Brewer D, Griffiths S, Heales D, Tonks M (2009) Bycatch in a tropical schooling-penaeid fishery and comparisons with a related, specialised trawl regime. Fish Manag Ecol 16: 191-201. doi:10.1111/j.1365-2400.2009.00655.x.
4. White WT, Last PR, Stevens JD, Yearsley GK (2006) Economically important sharks & rays of Indonesia. Australian Centre for International Agricultural Research (ACIAR).
5. Ridewood W (1921) On the calcification of the vertebral centra in sharks and rays. Philos Trans R Soc Lond B Biol Sci, Containing Papers of a Biological Character 210: 311-407
6. Cailliet G, Goldman K (2004) Age determination and validation in chondrichthyan fishes. In: Carrier JC, Musick JA, Heithaus MR, Biology of sharks and their relatives. Boca Raton, Florida: CRC Marine Biology Series. 399-447
7. Davenport S, Stevens J (1988) Age and growth of two commercially important sharks (*Carcharhinus tilstoni* and *C. sorrah*) from Northern Australia. Mar Freshw Res 39: 417-433. doi:10.1071/MF9880417.
8. Thorson JT, Simpfendorfer CA (2009) Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. Fish Res 98: 75-84. doi:10.1016/j.fishres.2009.03.016.
9. Smart JJ, Harry AV, Tobin AJ, Simpfendorfer CA (2012) Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. Aquat Conserv 23: 124-132.
10. Simpfendorfer C, Poulakis G, O'Donnell P, Wiley T (2008) Growth rates of juvenile smalltooth sawfish *Pristis pectinata* Latham in the western Atlantic. J Fish Biol 72: 711-723. doi:10.1111/j.1095-8649.2007.01764.x.
11. Siegfried K, Sansó B (2006) Two Bayesian methods for estimating parameters of the von Bertalanffy growth equation. Environ Biol Fishes 77: 301-308. doi:10.1007/s10641-006-9112-6.
12. O'Shea OR, Meekan M, van Keulen M (2013) Lethal sampling of stingrays (Dasyatidae) for research. Proceedings of the Australian and New Zealand Council for the Care of Animals In Research and Teaching: Annual Conference on Thinking Outside the Cage: A Different Point of View. Perth, Western Australia, 24th - 26th July, 2012
13. Jacobsen IP, Bennett MB (2011) Life history of the blackspotted whiplay *Himantura astra*. J Fish Biol 78: 1249-1268. doi:10.1111/j.1095-8649.2011.02933.x. PubMed: 21463319.
14. Goldman KJ (2005) Age and growth of elasmobranch fishes. NOAA Tech Rep Nmfs 90: 76.
15. Smith WD, Cailliet GM, Melendez EM (2007) Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura*. Mar Freshw Res 58: 54-66. doi:10.1071/MF06083.
16. Pierce SJ, Bennett MB (2009) Validated annual band pair periodicity and growth parameters of blue spotted maskray *Neotrygon kuhlii* from south east Queensland, Australia. J Fish Biol 75: 2490-2508. doi: 10.1111/j.1095-8649.2009.02435.x. PubMed: 20738504.
17. McAuley RB, Simpfendorfer CA, Hyndes GA, Allison RR, Chidlow JA et al. (2006) Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia. Environ Biol. Fish 77: 385-400. doi:10.1007/s10641-006-9126-0.
18. Beamish R, Fournier D (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38: 982-983. doi: 10.1139/f81-132.
19. Campana S (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. doi:10.1111/j.1095-8649.2001.tb00127.x.
20. Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. Can J Fish Aquat Sci 39: 1208-1210. doi:10.1139/f82-158.
21. Ford E (1933) An account of the herring investigations conducted at Plymouth during the years from 1924 to 1933. J Mar Biol Assoc UK 19: 305-384. doi:10.1017/S0025315400055910.
22. Walford LA (1946) A new graphic method of describing the growth of animals. Biol Bull 90: 141-147. doi:10.2307/1538217. PubMed: 21023417.
23. Cailliet GM, Smith WD, Mollet HF, Goldman KJ (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. Environ Biol. Fish 77: 211-228. doi:10.1007/s10641-006-9105-5.
24. Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws II). Hum Biol 10: 181-213.
25. Beverton RJH, Holt SJ (1993) The dynamics of exploited fish populations. London: Chapman and Hall.
26. Fabens AJ (1965) Properties and fitting of the Von Bertalanffy growth curve. Growth 29: 265-289. PubMed: 5865688.
27. Ricker WE (1975) Computation and interpretation of biological statistics of fish populations 191. Bull Fish Res Board Can. pp. 1-382. PubMed: 1110344.
28. Zhu L, Li L, Liang Z (2009) Comparison of six statistical approaches in the selection of appropriate fish growth models. Chin J Oceanol Limnol 27: 457-467. doi:10.1007/s00343-009-9236-6.
29. Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer-Verlag.
30. Hastings WK (1970) Monte Carlo sampling methods using Markov chains and their applications. Biometrika 57: 97-109. doi:10.1093/biomet/57.1.97.
31. Gelman A, Carlin JB, Stern HS, Rubin DB (2003) Bayesian data analysis. Chapman & Hall/CRC, Boca Raton/London
32. Jacobsen IP, Bennett MB (2010) Age and growth of *Neotrygon picta*, *Neotrygon annotata* and *Neotrygon kuhlii* from north east Australia, with notes on their reproductive biology. J Fish Biol 77: 2405-2422. doi: 10.1111/j.1095-8649.2010.02829.x. PubMed: 21155791.
33. Dale JJ, Wallsgrave NJ, Popp BN, Holland KN (2012) Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. Mar Ecol Prog Ser 433: 221-236.
34. Cowley PD (1997) Age and growth of the blue stingray *Dasyatis chrysonota* from the South-Eastern Cape coast of South Africa. S Afr J Mar Sci 18: 31-38. doi:10.2989/025776197784161054.
35. Ismen A (2003) Age, growth, reproduction and food of common stingray (*Dasyatis pastinaca* L., 1758) in Iskenderun Bay, the eastern Mediterranean. Fish Res 60: 169-176. doi:10.1016/S0165-7836(02)00058-9.
36. Dale J, Holland K (2012) Age, growth and maturity of the brown stingray (*Dasyatis lata*) around Oahu, Hawaii. Mar Freshw Res 63: 475-484. doi:10.1071/MF11231.
37. R Development Core Team (2012) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available: <http://www.R-project.org/>.
38. Branstetter S (1990) Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. Elasmobranchs As Living Resources Advances Biol Ecol Syst and Stat Fisheries 90: 17-28.
39. Musick JA (1999) Life in the slow lane: ecology and conservation of long-lived marine animals: proceedings of the Symposium Conservation of Long-Lived Marine Animals held at Monterey, California, USA 24 August 1997.
40. Yigin CC, Ismen A (2012) Age, growth and reproduction of the common stingray, *Dasyatis pastinaca* from the North Aegean Sea. Mar Biol Res 8: 644-653. doi:10.1080/17451000.2012.659667.
41. Edwards RRC (1980) Aspects of the population dynamics and ecology of the white spotted stingaree, *Urolophus paucimaculatus* Dixon, in Port Phillip Bay, Victoria. Mar Freshw Res 31: 459-467.
42. White WT, Platell ME, Potter IC (2001) Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). Mar Biol 138: 135-147. doi:10.1007/s002270000436.
43. White WT, Hall NG, Potter IC (2002) Reproductive biology and growth during pre and postnatal life of *Trygonoptera personata* and *T. mucosa* (Batoidea: Urolophidae). Mar Biol:140: 135-131.
44. Hale LF, Lowe CG (2008) Age and growth of the round stingray *Urolophus halleri* at Seal Beach, California. J Fish Biol 73: 510-523. doi: 10.1111/j.1095-8649.2008.01940.x.