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Age and growth of *Neotrygon picta, Neotrygon annotata* and *Neotrygon kuhlii* from north-east Australia, with notes on their reproductive biology

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Vertebral band formations were used to define age and growth in three *Neotrygon* species caught regularly as by-catch in prawn trawl fisheries in north-east Australia. Centrum edge and marginal increment ratio analyses were used to validate annual band formations. Age estimates ranged from 1 to 18 years, with the von Bertalanffy growth function considered to have the best fit to *Neotrygon picta* (males, $W_{D\infty} = 271$ mm, $k = 0{\cdot}12$; females, $W_{D\infty} = 360{\cdot}5$ mm, $k = 0{\cdot}08$) and *Neotrygon kuhlii* (males, $W_{D\infty} = 438{\cdot}6$ mm, $k = 0{\cdot}08$; females, $W_{D\infty} = 440{\cdot}6$ mm, $k = 0{\cdot}08$) disc width (W_D)-at-age data. The Gompertz growth function had the best fit to *Neotrygon annotata* W_D-at-age data (males, $W_{D\infty} = 230{\cdot}4$ mm, $k = 0{\cdot}20$; females, $W_{D\infty} = 265{\cdot}5$ mm, $k = 0{\cdot}31$). Age at sexual maturity ranged from 3 to 6 years, with *N. picta* having the smallest size at birth (100 mm W_D), smallest W_D at 50% maturity (W_{D50}: male, 172 mm, female, 180·7 mm) and lowest age at sexual maturity (3–4 years). This study helps redefine and improve the accuracy of fisheries-based risk assessments for these small species with relatively conservative life-history variables.

Key words: Gompertz function; maskray biology; Myliobatiformes; stingray.

INTRODUCTION

The speckled maskray *Neotrygon picta* Last & White, the plain maskray *Neotrygon annotata* (Last) and the blue spotted maskray *Neotrygon kuhlii* (Müller & Henle) belong to a small genus within the myliobatoid family Dasyatidae, which are commonly referred to as 'maskrays' (Last & White, 2008). The term maskray is in reference to the presence of a distinct dark band surrounding the eyes of each species (Last & Stevens, 2009). All three are small demersal species and are frequently caught as by-catch in prawn trawl fisheries in north-east Australia. As a consequence, they have been the subject of a number of risk assessments examining their susceptibility to overfishing (Stobutzki *et al.*, 2002; Salini *et al.*, 2007; Zhou & Griffiths, 2008). The accuracy of these assessments though has been restricted by the paucity of information on *Neotrygon* age, growth and reproduction.

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For long-lived species such as elasmobranchs (Branstetter, 1990; Cailliet & Goldman, 2004), documenting a species' age and growth has become increasingly important. Often used in conjunction with reproductive analysis, it provides the basis for examining growth rate, life span, mortality rate and age at sexual maturity. As such, age and growth analysis remains a pivotal area of research when determining a species' ability to rebound after potential declines (Branstetter, 1990; Stevens *et al.*, 2000). When compared to other elasmobranch families though, information on batoid age and growth remains poorly documented (Cailliet, 1990; Cailliet & Goldman, 2004; Cailliet *et al.*, 2006; Smith *et al.*, 2007).

This study is an examination of age, growth and reproduction in *N. picta*, *N. annotata* and *N. kuhlii* and provides important information on the life-history constraints of these species, including growth rates, life span, reproductive fecundity and age and size at sexual maturity. It represents the first detailed biological analyses of *N. picta* and *N. annotata*.

MATERIALS AND METHODS

Specimens were obtained from prawn trawl by-catch monitoring programmes (Ye *et al.*, 2006; Brewer *et al.*, 2007) and research vessels (Pitcher *et al.*, 2007*a*, *b*; Queensland Department of Primary Industries and Fisheries 2006*a*, *b*) between November 2003 and April 2007 (Fig. 1). Disc length (L_D) and disc width (W_D) of each animal were measured to the nearest mm and body mass (M) recorded to the nearest g. Specimens were collected and processed in accordance with the University of Queensland Animal Ethics Committee requirements.

AGE AND GROWTH

Ten to 15 consecutive thoracic vertebrae were removed from specimens and immersed in a 5% sodium hypochlorite solution (<5 min) (Cailliet *et al.*, 1983; McFarlane & King,

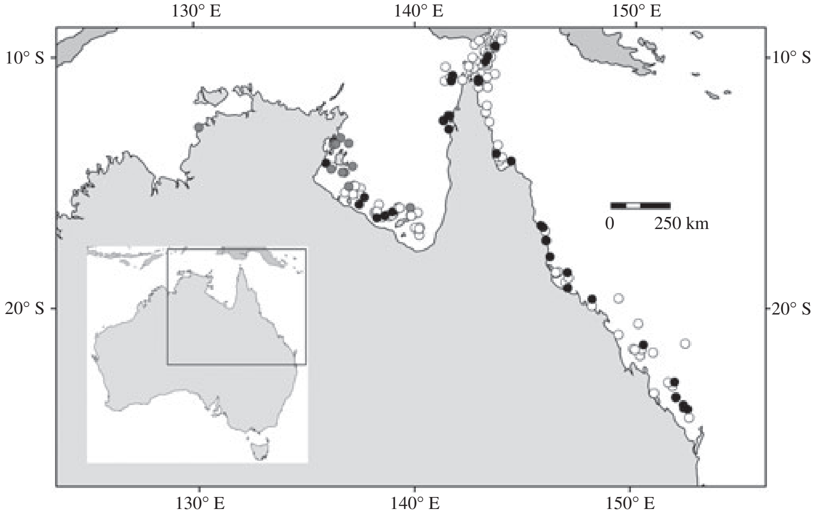

FIG. 1. Sample collection sites for *Neotrygon picta* (○), *Neotrygon annotata* (◉) and *Neotrygon kuhlii* (●) collected from north-east Australia.

2006). Neural and haemal arches were removed and a final clean undertaken to remove any remnants of connective tissue. Due to the inherent difficulties of embedding very small vertebrae, specimens were embedded in polyester resin as a collective unit of three to four consecutive vertebrae. All vertebrae were sectioned using a *Leco VC-50* diamond wafering-saw (www.leco.com). Preliminary investigation found band clarity to be greatest in sagittal sections of 200–300 μm.

Vertebral samples were viewed with a dissection microscope with specimens illuminated from the side (Intralux 5000-1; www.intralux.com.au). Centrum diameter (D_C, mm) was measured using an eyepiece micrometer and plotted against W_D. Vertebral sections were photographed with a digital camera (Nikon Coolpix 995; www.nikon.com) attached to a dissection microscope (WILD-Heerberg M3Z–type S; www.wild-heerbrugg.com). Photographs were subsequently transferred to Adobe Photoshop Editor 7.0 (www.adobe.com) to permit adjustments of the brightness, contrast and colour dynamics of the resulting images to assist in band differentiation. The birth band (B_B) was defined as the outer edge of the first translucent band encountered distal to the focus following an angle change in the intermedialia (Smith *et al*., 2007), with band identification and clarification defined in accordance with Cailliet *et al*. (2006).

Vertebrae were prepared and examined, with age estimates based on three counts (Smith *et al*., 2007; Kume *et al*., 2008). In each instance, band pairs of one sectioned centrum were counted and cross-referenced with that of the two adjacent centra (White *et al*., 2001; Pierce & Bennett, 2009). Vertebrae were also assigned a modified clarity and readability grade as outlined by Officer *et al*. (1996) and Smith *et al*. (2007). All counts were made as a blind study with no prior knowledge of the species, the sex of the animal, L_D, W_D or previous band pair count totals. In instances where agreement could not be reached between counts, the average was taken for specimens with count ranges of ≤ 2 years, *i.e.* 2, 3 and 4 (Cerna & Licandeo, 2009; Cicia *et al*., 2009). Specimens with count ranges of >2 years were omitted from the sample (Sulikowski *et al*., 2007; Cicia *et al*., 2009).

Age estimate reproducibility and precision were assessed using the index of average percentage error (I_{APE}) and the mean coefficient of variation (C.V.) (Beamish & Fournier, 1981; Chang, 1982; Campana, 2001). The I_{APE} was calculated using: $I_{APE} = N^{-1} \sum [R^{-1} \sum (|X_{ij} - X_j| X_i^{-1})\ 100]$, where N is the number of fish aged, R is the number of readings, X_{ij} is the ith age determination for the jth fish and X_i is the average age calculation for the jth fish (Lessa *et al*., 1999; Simpfendorfer *et al*., 2002). Numerically, the C.V. is $\sqrt{2}$ (=1·414) times greater than I_{APE} (Bishop *et al*., 2006; Francis *et al*., 2007).

The periodicity and temporal deposition of bands were analysed using two semi-direct methods of validation: centrum edge analysis (CEA) and mean monthly marginal increment ratios (R_{MI}) (Cailliet *et al*., 2006). The centrum edges of vertebrae were classified as narrow opaque (OP1), broad opaque (OP2), narrow translucent (T1) or broad translucent (T2) (Smith *et al*., 2007). The R_{MI} were calculated following protocols outlined by Conrath *et al*. (2002) with $R_{MI} = W_M\ W_{PB}{}^{-1}$ where W_M is the width of the outermost forming band and W_{PB} is the width of the penultimate band pair. As *Neotrygon* spp. at age 0 years have no fully formed band pairs, they were excluded from the R_{MI} analysis. A non-parametric Kruskal–Wallis test by ranks was employed to compare potential differences in mean monthly R_{MI} (Cailliet *et al*., 2006). Pair-wise comparisons using Dunn's (1964) comparison of group rank sums for unequal sample sizes were applied to assess which months provided the greatest degree of variance. The R_{MI} of immature and mature *N. picta* and *N. annotata* were compared for intraspecific variability, with specimens divided into immature (including sub-adult) and mature *Neotrygon* spp.

Three growth models were fitted to W_D-at-age data: a three-parameter von Bertalanffy growth model (VBGF; von Bertalanffy, 1938), a modified two-parameter VBGF (2VBGF; Fabens, 1965; Braccini *et al*., 2007) and the Gompertz growth function (GGF; Ricker, 1975). The three-parameter VBGF was calculated following Beverton & Holt (1957), where $W_{Dt} = W_{D\infty}(1 - e^{-k(t-t_o)})$ and W_{Dt} is the mean W_D-at-age t; $W_{D\infty}$ is the theoretical average asymptotic W_D; k is the rate at which the $W_{D\infty}$ is attained (year^{-1}); t is the estimated age and t_o is the theoretical age at which the fish would have been zero W_D. The modified 2VBGF was calculated using a known size of birth for each species with $W_{Dt} = W_{D\infty}(1 - be^{-kt})$, $b = [W_{D\infty} - (W_{D0}\ W_{D\infty}{}^{-1}]$, where W_{D0} is the known or predefined W_D at birth and the remaining variables are previously defined (Braccini *et al*., 2007). The GGF was fitted to W_D-at-age data following Ricker (1975) where $W_{Dt} = W_{D\infty}\ e^{-e\ [-k(t-t_0)]}$. Model variables were estimated using the least-squares non-linear regression function of the SPSS statistical programme (SPSS Inc; www.spss.com).

Akaike's information criterion (AIC) was used to determine a model's goodness-of-fit with the lowest AIC value providing the best fit for the W_D-at-age data (Buckland *et al*., 1997; Burnham & Anderson, 2002; Braccini *et al*., 2007). The AIC values (y) were calculated as $y = n\ \ln(\sigma^2) + 2p$, where n is the sample size, σ is the residual sum of squares divided by n and p is the number of variables. Inter-model comparisons followed criteria outlined by Braccini *et al*. (2007), which focused on ΔAIC values and Akaike weights (ω_i). The ΔAIC (Z) was calculated as $Z = X_i - X_{min}$, where X_i is the AIC value of model i and X_{min} is the AIC value of the best model. The probability of choosing the correct model was determined using Akaike weight (ω_i) from

$$\omega_i = (e^{-0\cdot 5Z})\left[\sum_{r=1}^{R} e^{(-0\cdot 5Z)}\right]^{-1},$$

where $R =$ the number of candidate models.

Variations in male and female growth curves were compared using a χ^2 test on maximum likelihood ratios (Kimura, 1980; Cerrato, 1990; White *et al*., 2001; Braccini *et al*., 2007).

REPRODUCTION

Individual specimens were assigned a maturity stage using modified criteria adopted from Bass *et al*. (1973) and White *et al*. (2001). Males were assigned to one of three maturity stages based on testis and clasper development: (1) immature, (2) sub-adult (adolescent males) and (3) mature. Females were assigned a maturity stage of one to five based on ovary and uterine tract development: (1) immature; (2) maturing (sub-adult); (3) mature, non-pregnant; (4) mature, pregnant with fertilized eggs or embryos *in utero* and (5) mature, postpartum. By definition, female specimens at maturity stages 1 to 2 were not able to reproduce and therefore are collectively referred to as immature. Females at maturity stages 3 to 5 would have either been gravid or had the capacity to reproduce and are collectively referred to as mature.

The W_D at which 50% of males and females attained maturity (W_{D50}) was calculated following protocols outlined by Marshall *et al*. (2007) and White & Dharmadi (2007), with W_{D50} derived for each species using logistic regression analysis where $P_{WD} = P_{max}\{1 + e^{[-\ln\ 19(W_D - W_{D50})(W_{D95} - W_{D50})^{-1}]}\}$ and describes the probability (P_{WD}) that a fish of W_D is mature, where W_{D95} (95% mature) and W_{D50} are constants, with P_{max} defined as 1 (Walker, 2005; Marshall *et al*., 2007). Maximum likelihood estimates of the variables were obtained using the routine SOLVER in Microsoft Excel, with the likelihood of immature and mature individuals calculated as $1 - P_{WD}$ and P_{WD}, respectively. Reproductive data were randomly re-sampled to create 100 sets of bootstrap estimates for variables of the logistic regression analysis. The 95% CL for each variable were estimated as the 2·5 and 97·5 percentiles of the 100 estimates resulting from these re-sampled data (White & Dharmadi, 2007).

RESULTS

AGE AND GROWTH

A total of 336 *N. picta* specimens were collected and had a male to female ratio of 1·07:1 ($Z = 0{\cdot}510$, $P > 0{\cdot}05$). Males ranged from 105 to 249 mm W_D and 30·6 to 679·6 g M. Females recorded W_D and M ranges of 97 to 322 mm and

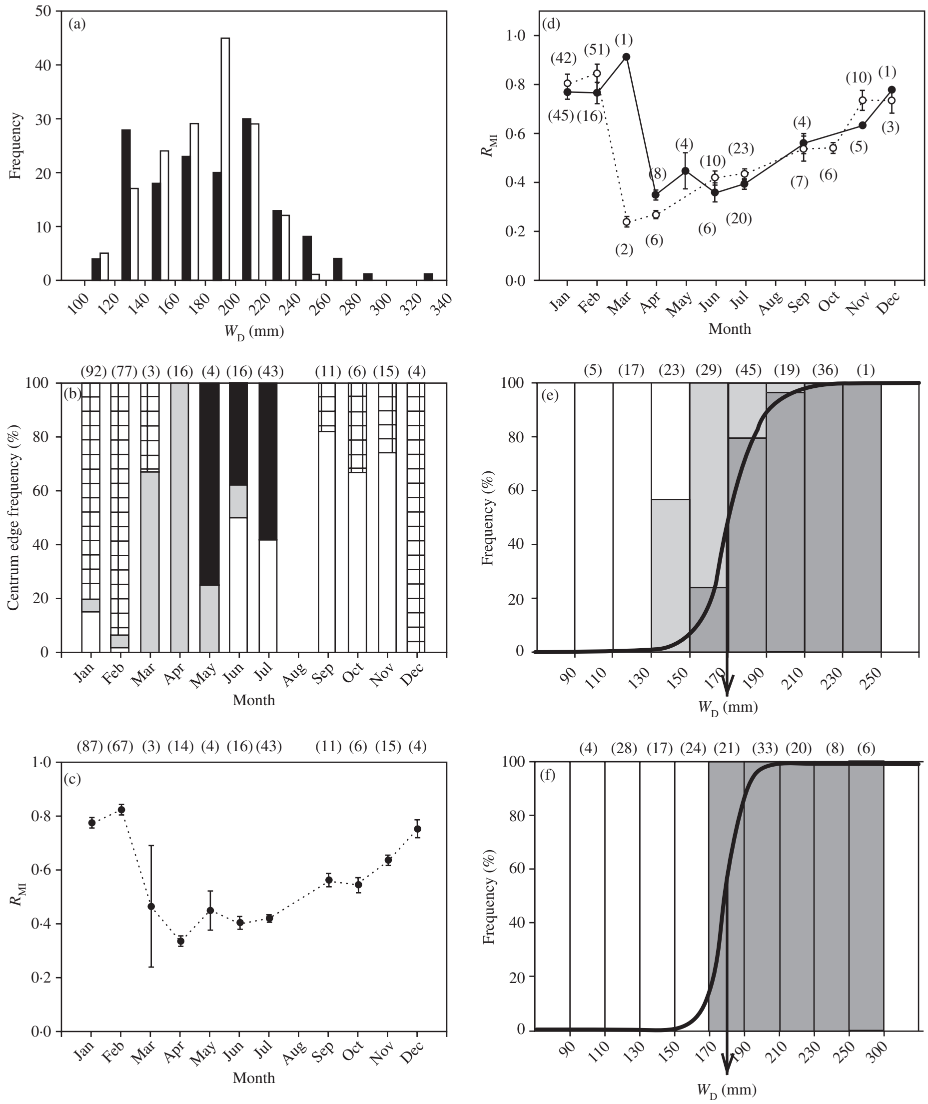

FIG. 2. Age, growth and reproductive summary for *Neotrygon picta*: (a) male (□) and female (■) sample frequency; (b) centrum edge analysis narrow translucent (□), broad translucent (⊞), narrow opaque (▒) and broad opaque (■); (c) mean ± S.E. monthly marginal increment ratios (R_{MI}), analysis; (d) mature (○) *v.* juvenile (●) mean ± S.E. R_{MI}; (e) male per cent frequency of occurrence for immature (□), sub-adult (▒) and mature (▒) fish and (f) female per cent frequency of occurrence for immature (□) and mature (▒) fish. Logistic curves fitted to (e) and (f); ⟶, W_D at which 50% attained maturity (W_{D50}). Numbers in parenthesis represent numbers for each category.

25·4 to 1100·6 g, respectively [Fig. 2(a)]. Male [$M = 2{\cdot}59\text{E-}05(W_D)^{3{\cdot}027}$, $n = 175$] and female [$M = 1{\cdot}80\text{E-}05(W_D)^{3{\cdot}103}$, $n = 161$] M and W_D relationships differed significantly (ANCOVA, $F = 8{\cdot}32$, d.f. $= 1$, $P < 0{\cdot}01$), however, male and female W_D and D_C relationships did not (ANCOVA, $F = 1{\cdot}240$, d.f. $= 1$, $P > 0{\cdot}05$). The

W_D and D_C relationship for the entire *N. picta* vertebrae sample ($n = 312$) is represented by $W_D = 120{\cdot}2(D_C)^{0{\cdot}714}$.

The majority of sections were assigned a clarity grade of 3: 74·9%, followed by grade 1: 1·0%, grade 2: 5·0% and grade 4: 11·1%. Twenty-five sections (8·1%) were omitted due to poor band clarity or lack of agreement. Translucent band completion occurred in *N. picta* between February and March (Australian late summer) and opaque band completion between June and August (Australian winter) [Fig. 2(b)]. Maximum and minimum R_{MI} for the complete *N. picta* sample occurred in February and April, respectively [Fig. 2(c)], with monthly R_{MI} values differing significantly ($H = 96{\cdot}1$, d.f. $= 8$, $P < 0{\cdot}001$). Pair-wise comparisons identified February and April (Dunn's method, $Q = 3{\cdot}3$, $P < 0{\cdot}05$) and February and May ($Q = 3{\cdot}3$, $P < 0{\cdot}05$) as major contributors of variance. When plotted, R_{MI} trends for juvenile and mature *N. picta* reflected the complete sample [Fig. 2(d)]. Results obtained from the CEA and R_{MI} analysis indicate one band pair comprising one opaque band and one translucent band is formed each year in *N. picta*.

Maximum age estimates for male and female *N. picta* were 11 and 18 years, respectively. Sample counts recorded an I_{APE} of 7·1% and a c.v. of 10·1%. Model performance criteria revealed the VBGF as the best descriptor of female W_D-at-age data and the 2VBGF for male W_D-at-age data (Table I and Fig. 3(a)–(c)]. Significant differences were detected between male and female growth curves for both the VBGF (χ^2, d.f. $= 3$, $P < 0{\cdot}001$) and the 2VBGF (χ^2, d.f. $= 3$, $P < 0{\cdot}001$).

Ninety-four *N. annotata* specimens were collected and had a male to female ratio of 1·24:1 ($Z = 1{\cdot}721$, $P > 0{\cdot}05$). The male sample population ranged from 137 to 240 mm W_D and 73·7 to 391·3 g M [Fig. 4(a)]. Females had a range of 141–278 mm W_D and 77·4–603·9 g M. Male [$M = 1{\cdot}32\text{E-}05(W_D)^{3{\cdot}137}$, $n = 52$] and female [$M = 2{\cdot}66\text{E-}05(W_D)^{3{\cdot}01}$, $n = 42$] M and W_D relationships differed significantly (ANCOVA, $F = 8{\cdot}13$, d.f. $= 1$, $P < 0{\cdot}01$), although W_D and D_C relationships did not (ANCOVA, $F = 1{\cdot}240$, d.f. $= 1$, $P > 0{\cdot}05$). The W_D and D_C relationship for the entire *N. annotata* vertebrae sample is represented by $W_D = 135{\cdot}8(D_C)^{0{\cdot}650}$.

Seventy per cent of all sections ($n = 94$) were assigned a clarity grade 3; 2·2% grade 1; 16·3% grade 2; and 12·0% grade 4. Inconsistent counts resulted in 4·4% of vertebrae being discarded due to a lack of count consistency. Translucent edges were observed between September and April, with opaque edges between March and July [Fig. 4(b)]. Maximum and minimum R_{MI} (entire sample) were recorded in January and April, respectively [Fig. 4(c)] with observed R_{MI} variations differing significantly ($H = 59{\cdot}6$, d.f. $= 6$, $P < 0{\cdot}001$). Pair-wise comparisons identified January and April as the key source of variance (Dunn's method, $Q = 2{\cdot}5$, $P > 0{\cdot}05$). A plot of juvenile and mature R_{MI} produced similar plots to the overall R_{MI} analysis [Fig. 4(d)]. Results obtained from the R_{MI} and CEA support annual band pair deposition in *N. annotata*.

Neotrygon annotata males ranged from 1 to 9 years and females 1 to 13 years. The I_{APE} for the sample was recorded at 7·5% with a c.v. of 10·6%. Model performance criteria indicated that the GGF provided the best fit for *N. annotata* male and female W_D-at-age data [Table I and Fig 3(d)–(f)]. Likelihood ratio tests detected a significant difference (χ^2, d.f. $= 3$, $P < 0{\cdot}01$) between male and female GGF curves [Fig. 2(f)].

A total of 79 *N. kuhlii* were obtained for the study which had a male to female ratio of 0·8:1 ($Z = 0{\cdot}307$, $P > 0{\cdot}05$). The male sample population ranged from 144 to

TABLE I. Growth estimates and model selection criteria for male and female *Neotrygon picta*, *Neotrygon annotata* and *Neotrygon kuhlii*

		Neotrygon picta									
		Females (n = 152)					Males (n = 159)				
Model	Variable	Estimate	r^2	AIC	ΔAIC	ω_i	Estimate	r^2	AIC	ΔAIC	ω_i
VBGF	$W_{D\infty}$	360·5	0·79	1616·5	0	0·97	271	0·74	1756·5	2	0·20
	W_{D0}	123·7					124·9				
	k (year^{-1})	0·08					0·12				
	t_0 (years)	−5·3					−5·0				
2VBGF	$W_{D\infty}$	376·1	0·80	1623·4	6·9	<0·1	271	0·74	1754·5	0	0·70
	k (year^{-1})	0·08					0·12				
	b	0·6					0·5				
GGF	$W_{D\infty}$	326·4	0·80	1629·9	13·4	<0·1	255·8	0·74	1759·3	4·8	0·10
	W_{D0}	126·3					128				
	k (year^{-1})	0·13					0·18				
	t_0 (years)	−0·4					−1·9				

		Neotrygon annotata									
		Females (n = 40)					Males (n = 50)				
Model	Variable	Estimate	r^2	AIC	ΔAIC	ω_i	Estimate	r^2	AIC	ΔAIC	ω_i
VBGF	$W_{D\infty}$	265·5	0·81	437·7	0·2	0·47	230·4	0·60	562·9	9·0	<0·1
	W_{D0}	138·4					130·6				
	k (year^{-1})	0·20					0·31				
	t_0 (years)	−3·6					−2·7				
2VBGF	$W_{D\infty}$	265·5	0·81	491·7	54·2	<0·1	230·2	0·60	622·7	68·8	<0·1
	k (year^{-1})	0·20					0·31				
	b	0·5					0·4				

TABLE I. Continued

		Neotrygon annotata									
		Females ($n = 40$)					Males ($n = 50$)				
Model	Variable	Estimate	r^2	AIC	ΔAIC	ω_i	Estimate	r^2	AIC	ΔAIC	ω_i
GGF	$W_{D\infty}$	261·5	0·82	437·5	0·0	0·53	227·9	0·60	553·9	0·0	0·99
	W_{D0}	140·6					135·7				
	k (year^{-1})	0·25					0·37				
	t_0 (years)	−1·8					−1·7				

		Neotrygon kuhlii									
		Females ($n = 40$)					Males ($n = 35$)				
Model	Variable	Estimate	r^2	AIC	ΔAIC	ω_i	Estimate	r^2	AIC	ΔAIC	ω_i
VBGF	$W_{D\infty}$	440·6	0·86	572·9	8	<0·1	438·6	0·9	381·8	0	0·65
	W_{D0}	119·8					147·6				
	k (year^{-1})	0·08					0·08				
	t_0 (years)	−5·3					−5·3				
2VBGF	$W_{D\infty}$	440·6	0·86	564·8	0	0·84	438·6	0·9	383·1	1·4	0·33
	k (year^{-1})	0·08					0·08				
	b	0·7					0·7				
GGF	$W_{D\infty}$	390·5	0·87	568·3	3·4	0·15	399·6	0·9	388·8	7·1	<0·1
	W_{D0}	125·7					138·4				
	k (year^{-1})	0·15					0·15				
	t_0 (years)	−0·3					−0·4				

n, number of specimens examined; VBGF, von Bertalanffy growth function; 2VBGF, two-parameter von Bertalanffy growth function; GGF, Gompertz growth function; r^2, coefficient of determination; AIC, Akaike's information criterion; ΔAIC, difference from AIC minimum; ω_i, Akaike weight; $W_{D\infty}$, asymptotic disc width (W_D) (mm); W_{D0}, estimated size at birth (mm); k (year^{-1}), growth coefficient; t_0 (years), theoretical age at which the fish would have been zero W_D; b, GGF constant.

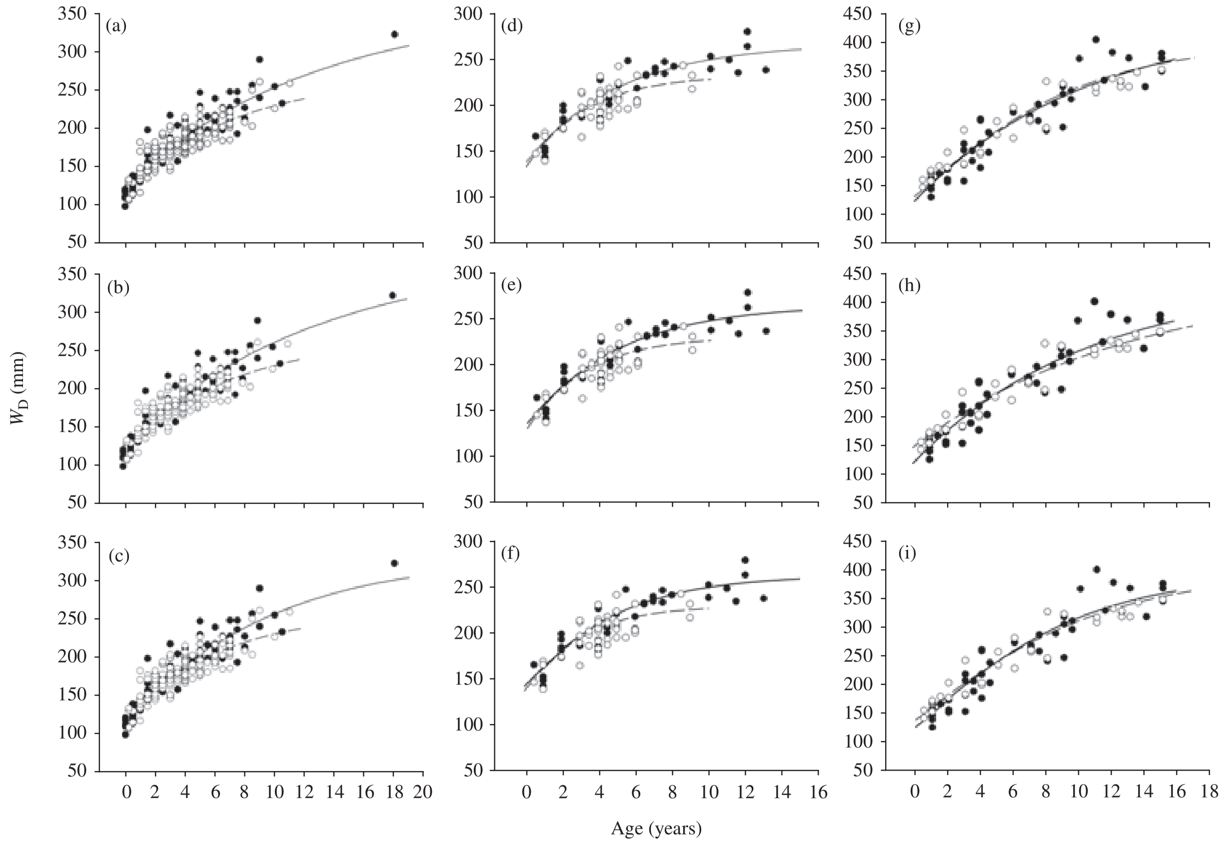

FIG. 3. (a), (d), (g) Three-parameter von Bertalanffy (VBGF); (b), (e), (h) two-parameter VBGF and (c), (f), (i) Gompertz growth function trajectories for male (○) and female (●) *Neotrygon picta* [(a)–(c)], *Neotrygon annotata* [(d)–(f)] and *Neotrygon kuhlii* [(g)–(i)].

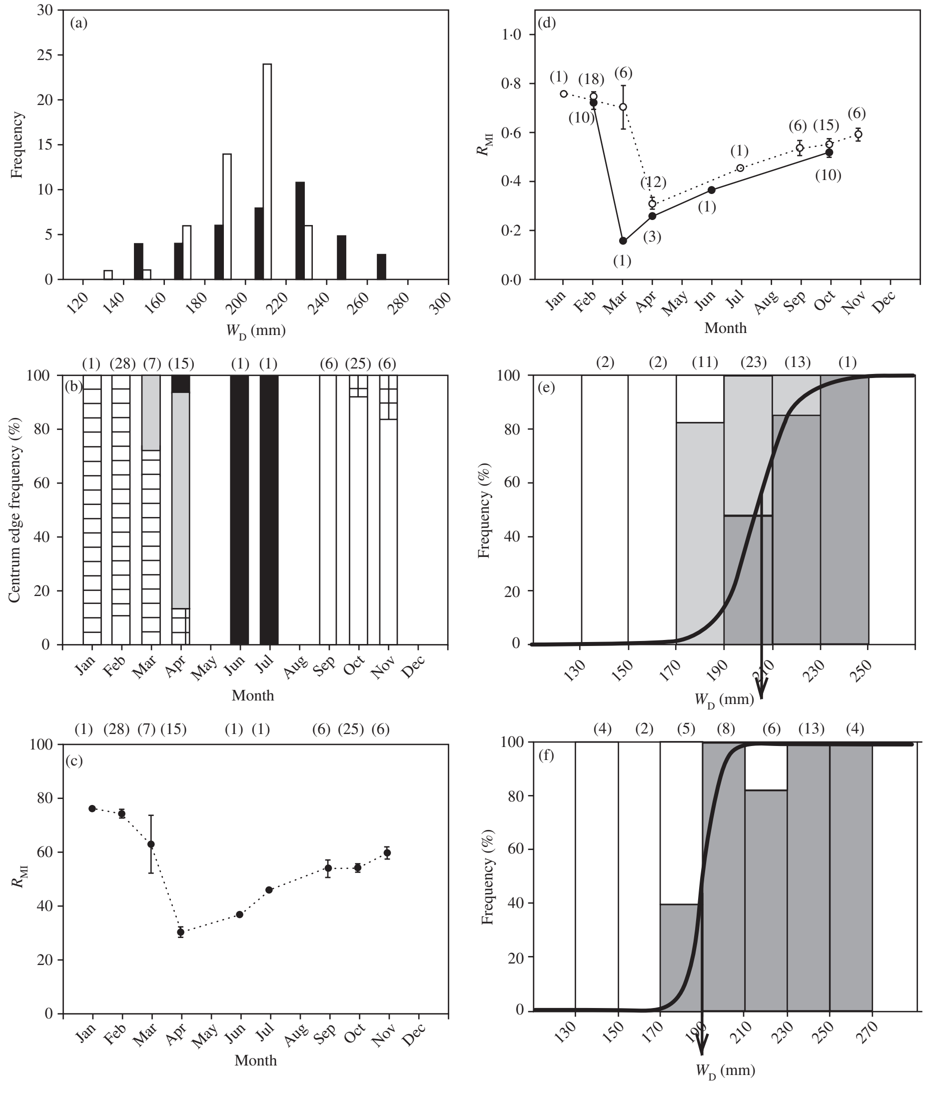

FIG. 4. Age, growth and reproductive summary for *Neotrygon annotata*: (a) male and female sample frequency, (b) centrum edge analysis, (c) mean ± S.E. R_{MI}, (d) mature *v.* juvenile R_{MI} ± S.E., (e) male per cent frequency of occurrence and (f) female per cent frequency of occurrence (Figure descriptions as for Fig. 2).

350 mm W_D and 85·0 to 1229·4 g M. Females ranged from 127 to 402 mm W_D and 55·0 to 2024·7 g M [Fig. 5(a)]. No significant difference was detected between male and female M and W_D (ANCOVA, $F = 2·19$, d.f. = 1, $P > 0·05$) or W_D and D_C relationships (ANCOVA, $F = 0·906$, $P > 0·05$), with the entire *N. kulii* vertebrae sample ($n = 79$) represented by $M = 5·05\text{E-}05(W_D)^{2·913}$ and $W_D = 129·12(D_C)^{0·708}$.

A clarity grade of 3 was assigned to 67·5% of sections; grade 4 to 14·9%; grade 2 to 12·2%; and grade 1 to 1·4%. Inconsistent counts resulted in 3·8% of vertebrae being omitted from the study. CEA indicated translucent band completion occurring

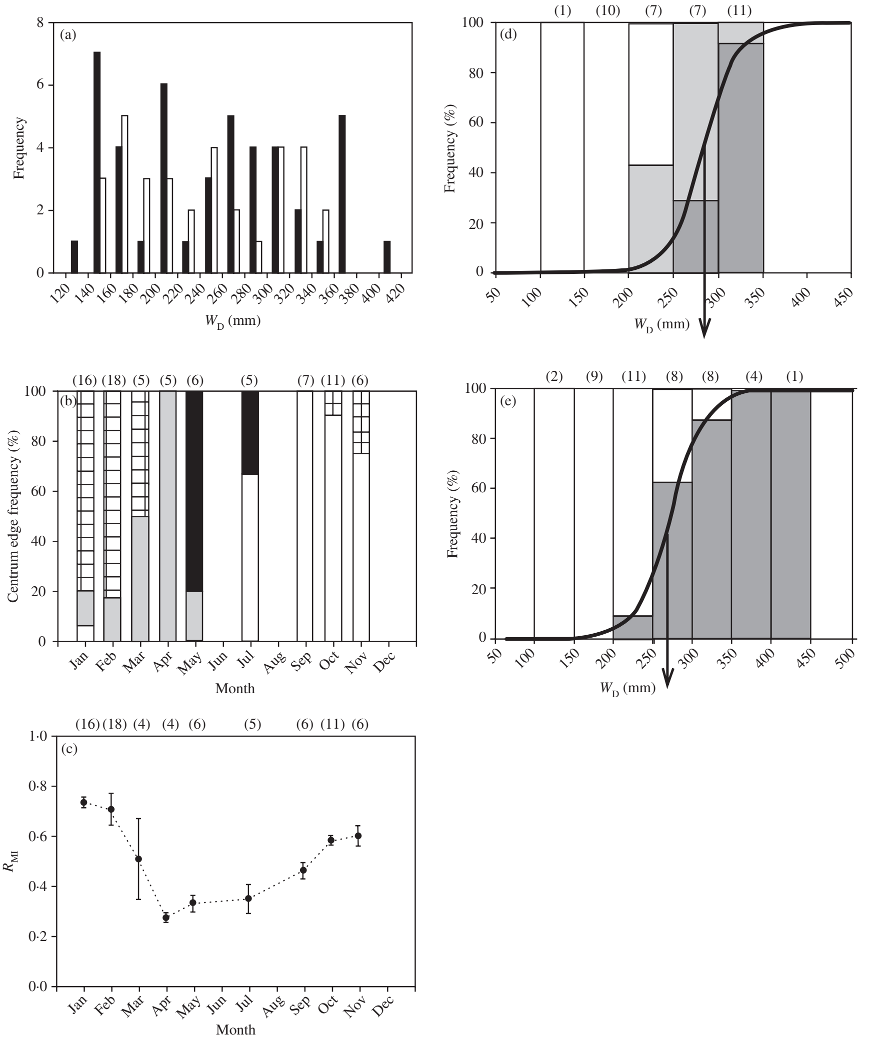

FIG. 5. Age, growth and reproductive summary for *Neotrygon kuhlii:* (a) male and female sample frequency, (b) centrum edge analysis, (c) $R_{MI} \pm$ S.E., (d) male per cent frequency of occurrence and (e) female per cent frequency of occurrence (Figure descriptions as for Fig. 2).

in *N. kuhlii* between February and March with opaque band completion occurring between June and August [Fig. 5(b)]. When compared, R_{MI} values increased progressively from April through to December [Fig. 5(c)]. These differences in R_{MI} values were statistically significant ($H = 40{\cdot}12$, d.f. $= 8$, $P < 0{\cdot}001$), with February and April (Dunn's method, $Q = 4{\cdot}46$, $P < 0{\cdot}05$) identified as the major sources of variance. Centrum edge analysis and R_{MI} analyses indicated that band pair deposition in *N. kuhlii* was singular and annual.

Band pair counts for *N. kuhlii* ranged from one to 15 (male) and one to 17 (female). The sample I_{APE} was 7·5% or a C.V. of 10·6%. On the basis of the model performance criteria, the traditional VBGF ($\omega_i = 0{\cdot}65$) and 2VBGF ($\omega_i = 0{\cdot}84$)

provided the best fit for male and female W_D-at-age data, respectively [Table I and Fig. 3(g)–(i)]. Likelihood ratio tests comparing male and female 2VBGFs indicated that growth curves did not differ significantly (χ^2, d.f. = 3, $P > 0{\cdot}05$); VBGF curves were significantly different (χ^2, d.f. = 3, $P < 0{\cdot}01$).

REPRODUCTION

Internally, the reproductive anatomy of mature *Neotrygon* spp. showed little interspecific variability. Mature males possessed two functional compound testes, with sperm recorded from both the left and the right epididymis. Mature females possessed a single functional ovary and uterus on the left side of the body.

Male and female sample populations for all three species comprised a high proportion of mature animals (Table II). Of the three, *N. picta* ($n = 336$) recorded the smallest size at first sexual maturity, smallest gravid female (172 mm W_D) and the lowest W_{D50} values: male, 172 mm (95% CI: 167·4–184·1 mm) and female, 180·7 mm (95% CI: 177·4–184·1 mm) [Fig. 2(e), (f)]. In comparison, the smallest gravid *N. annotata* was 201 mm W_D with the species recording a male and female W_{D50} of 204·4 mm ($n = 52$, 95% CI: 199·8–209·0 mm) and of 190·8 mm ($n = 42$, 95% CI: 182·3–200·3 mm), respectively [Fig. 4(e), (f)]. One gravid *N. kuhlii* of 291 mm W_D was obtained from the study with males recording a W_{D50} of 285·4 mm ($n = 37$, 95% CI: 262·2–314·9 mm) and females a W_{D50} of 266·8 mm ($n = 42$, 95% CI: 247·5–287·0 mm) [Fig. 5(d), (e)]. Maximum uterine fecundity for *N. picta* ($n = 25$, mean ± S.E. $1{\cdot}4 \pm 0{\cdot}1$) and *N. annotata* ($n = 5$, mean ± S.E. $1{\cdot}2 \pm 0{\cdot}3$) was three and two, respectively. Two *in situ* embryos were observed in a single *N. kuhlii*.

DISCUSSION

The primary objective of the present study was to contribute to an understanding of age, growth and reproduction of these *Neotrygon* species, thus improving the

TABLE II. *Neotrygon picta*, *Neotrygon annotata* and *Neotrygon kuhlii* reproductive samples; numbers in parentheses represent proportion of the total male or female sample population

Maturity stage	*Neotrygon picta*	*Neotrygon annotata*	*Neotrygon kuhlii*
Male	$n = 175$	$n = 52$	$n = 37$
1–Immature	105–141 (18·3%)	137–173 (7·7%)	144–230 (41·7%)
2–Sub-adult	137–191 (25·7%)	168–212 (48·1%)	236–310 (25·0%)
3–Mature	164–249 (56·0%)	192–240 (44·2%)	263–350 (33·3%)
W_{D50} (mm)	172	204·4	285·4
Female	$n = 161$	$n = 42$	$n = 42$
1–Immature	97–152 (28·6%)	141–164 (11·9%)	127–220 (30·2%)
2–Sub-adult	144–200 (23·6%)	168–211 (16·7%)	178–313 (27·9%)
3–5, Mature	167–322 (47·8%)	184–278 (71·4%)	249–402 (41·9%)
W_{D50} (mm)	180·7	190·8	266·8
Total range	97–322	137–278	127–402

n, number of specimens examined; W_{D50}, disc width (W_D) at which 50% of males and females attained maturity.

accuracy of risk assessments. Results obtained also enable previously outdated variables to be updated including maximum size, size at sexual maturity and size at birth. This is particularly relevant to *N. picta* and *N. annotata* whose life-history variables remain poorly documented. The level of information on *N. kuhlii* has increased in recent years with at least two studies examining the biology of the species in Indonesia (identified as *Dasyatis cf. kuhlii*, White, 2003; White & Dharmadi, 2007) and Moreton Bay in south-east Queensland (Pierce & Bennett, 2009; Pierce *et al.*, 2009). Information on north Australian *N. kuhlii* populations though remains somewhat limited. On a broader scale, this study provides important information on ageing batoid species caught as by-catch in tropical north-east Australia using vertebral band formation analysis.

Results obtained from the R_{MI} and CEA are consistent with previous myliobatoid age and growth analyses (Cailliet & Goldman, 2004; Smith *et al.*, 2007) and support the default hypothesis that band pair deposition in batoids is (generally) singular and annual (Cailliet & Goldman, 2004). These results are also consistent with age and growth studies from south-east Queensland where band formation in *N. kuhlii* was validated through chemical tag and release methods (Pierce & Bennett, 2009). Notably, inter-study comparisons revealed that the timing of band completion of south-east Queensland *N. kuhlii* (Pierce & Bennett, 2009: opaque, March to June; translucent, November to December) varies from the present study [Fig. 5(b)]. Reduced seasonality in northern Australia was a probable contributor to this variance, as was the respective geographical sample areas with Pierce & Bennett (2009) focusing on a more defined location (Moreton Bay). Nevertheless, the temporal range of band deposition in north-eastern *N. kuhlii* (this study) may increase with a larger sample size. Results obtained from both the present study and the study of Pierce & Bennett (2009) indicate that annual band deposition is likely to be a uniform occurrence for all *Neotrygon* species including the Western Australian species the painted maskray *Neotrygon leylandi* (Last).

By anchoring the curve with a known size of birth, the 2VBGF aims to reduce the influence sample size, $W_{D\infty}$ and t_0 has on the final growth curve (Sulikowski *et al.*, 2005, 2007; Braccini *et al.*, 2007). These factors appeared to have little influence on the present study, with the VBGF and 2VBGF producing relatively close parameter estimates (Table I and Fig. 3). Notably, predicted $W_{D\infty}$s for the GGF were lower than both the VBGF and the 2VBGF, but closest to the sample maximum (Fig. 3). This suggests that the GGF represented upper size limits with the greatest degree of accuracy. This, however, does not necessarily equate to an accurate representation of a species' overall growth characteristics, as the GGF probably underestimated $W_{D\infty}$ in samples where larger fishes were underrepresented. This in itself may explain why the *N. annotata* $W_{D\infty}$ was lower than expected; it is reported to grow to 450 mm W_D (Stobutzki *et al.*, 2002). Directly correlated to $W_{D\infty}$ (Sulikowski *et al.*, 2007), this factor may have also contributed to the species having a higher k-value (Table I).

Maximum age estimates and growth coefficients (k-values) were similar to previous batoid age and growth analyses. With respect to *N. picta*, a preliminary study (Barratt, 2003) (identified by its synonym *Dasyatis leylandi*) reported non-validated age estimates of 7 and 12 years for males and females, respectively. Consequently, maximum age estimates for the present study (11 and 18 years) represent a considerable extension to the empirically derived life span estimates for this species. This was also the case in *N. kuhlii*, in which maximum age estimates have previously been reported as 10 years and 13–15 years for males and females, respectively (White, 2003; Pierce & Bennett, 2009). Outside the *Neotrygon* species complex, maximum age estimates obtained in the present study were comparable to similar-sized batoids, *i.e*. 9–17 years for a variety of urolophid and dasyatid species (Edwards, 1980; Cowley, 1997; White *et al*., 2001, 2002; Mollet *et al*., 2002; Ismen, 2003; Hale & Lowe, 2008), but below that reported for larger species *e.g*. 28 years for the diamond stingray *Dasyatis dipterura* (Jordan & Gilbert) (Smith *et al*., 2007) and 23 years for the bat ray *Myliobatis californica* Gill (Martin & Cailliet, 1988).

While growth coefficients for *N. picta* and *N. kuhlii* were lower than for *N. annotata*, k-values of 0·08 and 0·12 (VBGF) are not without precedent. Hale & Lowe (2008) for example recorded k-values of $<0{\cdot}15$ year^{-1} for the round stingray *Urobatis halleri* (Cooper), as did Smith *et al*. (2007) for *D. dipterura*. It should be noted though that k-value comparisons should be treated with a level of caution, as they provide only a generalized characterization of a species fundamental life-history traits (Smith *et al*., 2007). Furthermore, the outputs of individual age and growth studies are inherently limited by their sample size, size range distribution, validation or verification techniques and model constraints (Branstetter, 1990; Cailliet & Goldman, 2004; Smith *et al*., 2007). As a consequence, k-value estimates can exhibit considerable variation not only between studies but between species of the same family, *e.g*. urolophids (0·09–0·514 year^{-1}) (Edwards, 1980; White *et al*., 2001, 2002; Hale & Lowe, 2008). With respect to the current study, the largest *N. picta* female (322 mm W_D) was initially perceived as an outlier contributing to the low VBGF k-estimate [Table I and Fig. 2(a)]. Removing this specimen from the sample reduced the k-estimate to 0·04 year^{-1} with $W_{D\infty}$ increasing to an improbably large 514·1 mm. This suggests that estimates derived from the complete sample provided a more realistic account of growth in female *N. picta*. An indirect benefit of the specimen's exclusion was that it clearly showed the influence larger fishes have on the VBGF curve.

Intraspecific comparisons between the three *N. kuhlii* age and growth studies showed considerable variation in growth coefficients. For example, k-values (VBGF) for the south-east Queensland population were 0·20 year^{-1} for males and 0·13 year^{-1} for females (Pierce & Bennett, 2009), with Indonesian *N. cf. kuhlii* recording 0·311 (males) and 0·831 (females) (White, 2003). The observed variance is likely to come from a variety of sources, including sample size, sample configuration and geographical distributions. For instance, *N. kuhlii* from south-east Queensland are likely to experience greater seasonality, therefore would experience more pronounced periods of slow growth. In contrast, *N. cf. kuhlii* is likely to experience more consistent growth throughout the year. It is also important to note that the Indonesian *N. cf. kuhlii* is believed to be taxonomically distinct from Australian *N. kuhlii* (White & Dharmadi, 2007; W. White, pers. comm.) and therefore the observed differences may be interspecific.

Sizes at first maturity were generally lower than that reported in previous studies (Stobutzki *et al*., 2002; Salini *et al*., 2007; Last & Stevens, 2009; Pierce & Bennett, 2009; P. J. Barratt, unpubl. data). The high degree of overlap between sub-adult and mature specimens indicates that the onset of sexual maturity occurs over a broad size range in these species. On the basis of the results obtained, the onset of sexual maturity for *N. picta* probably occurs between 160 and 190 mm W_D, with *N. annotata* (180–210 mm W_D) and *N. kuhlii* (250–300 mm W_D) maturing at a larger body size. These differences were also reflected in the age at first sexual maturity, which when based on the VBGF was 2–3 years for *N. picta* and *N. annotata* and 5–7 years for *N. kuhlii*. Ages at W_{D50} were slightly higher at 3–4 years (*N. picta*), 4 years (*N. annotata*) and 6–7 years (*N. kuhlii*) (Table II).

Late-term *N. picta* and *N. kuhlii* embryos provided a good indication of size at birth with the largest *N. picta* embryo (99 mm W_D) marginally larger than the smallest neonate (97 mm W_D). This suggests that size at birth occurs very close to 100 mm W_D. *Neotrygon kuhlii* neonates were slightly larger, with size at birth estimated to be between 140 and 170 mm W_D. In comparison, size at birth estimates for the GGF and VBGF were 123–128 mm W_D for *N. picta* and 119–147 mm W_D for *N. kuhlii* (Table I). These estimates conform well to previous studies which place size at birth for *N. picta* and *N. kuhlii* at 110 mm W_D (P. J. Barratt, unpubl. data) and 115–170 mm W_D (Pierce *et al.*, 2009), respectively. Size at birth for *N. annotata* based on the smallest free-living specimen is expected to be between 120 and 140 mm W_D.

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