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Life history of the blackspotted whipray *Himantura astra*

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Features of the life history of *Himantura astra* from north-east Australia were examined including its age and growth, reproduction and diet. Centrum edge and marginal increment ratio analyses were used to validate annual band formations with the Gompertz growth function providing the best fit to male ($W_{D\infty} = 722.7$ mm, $k = 0.104$) and female ($W_{D\infty} = 821.8$ mm, $k = 0.073$) disc width (W_D)-at-age data. At 29 years, the maximum age of females was higher than males (18 years). Sizes at 50% sexual maturity (W_{D50}) for males and females were 469.3 and 462.3 mm, respectively. Ages at sexual maturity (A_{M50}) were reported at 7.32 (males) and 8.67 (females) years. An index of relative importance (I_{RI}) revealed carid shrimps (77.9%), brachyurans (12.1%) and stomatopods (4.9%) as the most important prey groups, with prey diversity increasing with W_D from 0.92 to 1.63 (Shannon–Weiner index). This study provides significant insights into the biology of *H. astra* and contributes to the ongoing development of fisheries-based risk assessments for this species.

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Key words: by-catch; Dasyatidae; diet; reproduction; von Bertalanffy.

INTRODUCTION

The family Dasyatidae (stingrays) contains *c.* 70 living species, about a third of which are whiptail rays belonging to the genus *Himantura*. A diverse group of stingrays, members of this genus range from the small dwarf whipray *Himantura walga* (Müller & Henle 1841) (200 mm disc width, W_D) to the large freshwater stingray *Himantura polylepis* (Bleeker 1852) (up to 2400 mm W_D) (Monkolprasit & Roberts, 1990; Last & Stevens, 2009). When compared with other elasmobranch genera, the biology of *Himantura* species has received very little attention. White & Dharmadi (2007) provided some insight into the reproductive biology of Indonesian *Himantura*, as did Chatchavalvanich *et al.* (2005a, b) for the white-edge freshwater Whipray *Himantura signifer* Compagno & Roberts 1982. Limited information on the diet of the blackspotted whipray *Himantura astra* Last, Manjaji-Matsumoto & Pogonoski 2008 (identified by its synonym *Himantura toshi* Whitley 1939; Last *et al.*, 2008) and the reticulate ray *Himantura uarnak* (Gmelin 1789) has also been presented in broader multispecies studies (Salini *et al.*, 1994; Raje, 2003).

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Himantura astra is a medium-sized batoid inhabiting tropical and subtropical waters of north-east Australia. While not retained for sale in Australian waters, *H. astra* is caught as by-catch in a number of prawn trawl fisheries (Salini *et al.*, 2007; Dell *et al.*, 2009). As a consequence, *H. astra* has been the subject of a number of fisheries-based risk assessments (Stobutzki *et al.*, 2002; Salini *et al.*, 2007; Zhou & Griffiths, 2008). These assessments indicate that *H. astra* (identified by its synonym *H. toshi*) has a low level of susceptibility to both capture- and trawl-induced mortality when compared to other elasmobranchs (Stobutzki *et al.*, 2002; Salini *et al.*, 2007; Zhou & Griffiths, 2008). A deficiency in biological data has, however, restricted the scope and accuracy of these assessments with some model parameters needing to be based on preliminary estimates, conservative estimates or excluded from the analysis altogether (Stobutzki *et al.*, 2002; Salini *et al.*, 2007; Zhou & Griffiths, 2008).

The following is an examination of *H. astra* life-history variables including its diet, age and growth development and reproduction. It provides important information on growth rates, longevity, fecundity, habitat usage, dietary shifts, and age and size at sexual maturity. It is the first study to validate *Himantura* age and growth and contributes to the ongoing management of this species throughout its range including in the Indo-west Pacific.

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.*, 2007a, b; Queensland Department of Primary Industries & Fisheries, 2006a, b) between November 2003 and April 2007 (Fig. 1). Disc length (L_D) and 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 approval.

AGE AND GROWTH

A full description of the age and growth methodology is provided in Jacobsen & Bennett (2010). Ten consecutive thoracic vertebrae were removed from specimens and cleaned through manual and chemical measures (Cailliet *et al.*, 1983; McFarlane & King, 2006). 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 (Jacobsen & Bennett, 2010). All vertebrae were sectioned using a diamond wafering-saw (Leco VC-50; www.leco.com) with band clarity found to be greatest in sagittal sections of 200–300 μm .

Vertebrae were viewed and photographed (Nikon Coolpix 995; www.nikon.com.au/index.php) using a dissection microscope (WILD-Heerberg M3Z-type S; www.wild-heerbrugg.com). Centrum diameter (D_C ; mm) was measured using an eyepiece micrometer and plotted against W_D . The birth band 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). Specimen photographs were 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 (Jacobsen & Bennett, 2010).

Age estimates were based on three counts (Smith *et al.*, 2007; Kume *et al.*, 2008) and each section assigned a clarity and readability grade of 1 to 5 (Officer *et al.*, 1996; Smith *et al.*, 2007). 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). All counts were made with no prior knowledge of 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,

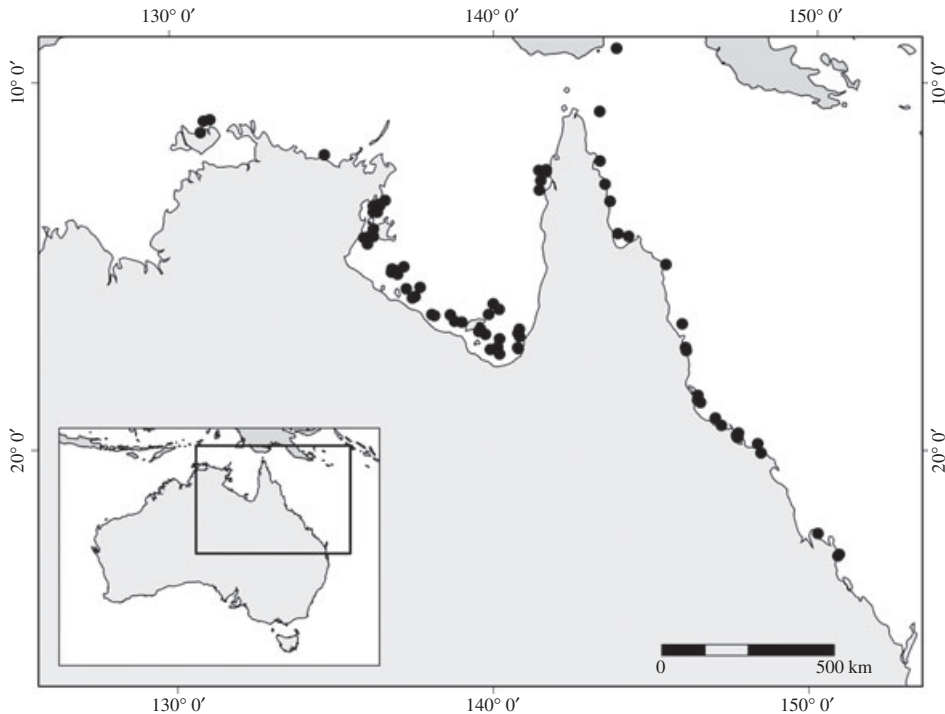


FIG. 1. Sample collection sites for *Himantura astra* from north-east Australia. Inset: sample area circumscribed by square.

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} ; Beamish & Fournier, 1981; Chang, 1982; Campana, 2001) and the mean c.v. (Bishop *et al.*, 2006; Francis *et al.*, 2007).

The periodicity and temporal deposition of bands were analysed using centrum edge analysis (CEA) and mean monthly marginal increment ratios (R_{MI}) (Cailliet *et al.*, 2006). The centrum edge of a vertebra was classified as narrow opaque (OP1), broad opaque (OP2), narrow translucent (T1) or broad translucent (T2) after Smith *et al.* (2007). Marginal increment ratios were calculated following protocols outlined by Conrath *et al.* (2002). A non-parametric Kruskal–Wallis test by ranks was employed to compare potential R_{MI} differences (Cailliet *et al.*, 2006). Pair-wise comparisons using the Dunn (1964) comparison of group rank sums for unequal sample sizes was applied to assess which months provided the greatest degree of variance. The R_{MI} of immature and mature fish was also compared for intraspecific variability, with specimens divided into immature (includes sub-adult) and mature fish.

Three growth models were fitted to W_D -at-age data: a three-parameter von Bertalanffy growth function (VBGF; von Bertalanffy, 1938), a modified two-parameter VBGF (2VBGF; Fabens, 1965; Braccini *et al.*, 2007) and the Gompertz growth function (GGF; Ricker, 1975). Model parameters were estimated using the least-squares non-linear regression function of the SPSS statistical programme (SPSS Inc; www.spss.com). AIC was used to determine a model's goodness-of-fit with the lowest value providing the best fit for W_D -at-age data (Buckland *et al.*, 1997; Burnham & Anderson, 2002; Braccini *et al.*, 2007). The probability of choosing the correct model was determined using Akaike weight (ω_i) (Braccini *et al.*, 2007). 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). Ages at which 50% of males and females attained sexual maturity (A_{M50}) were estimated using a modified logistic model and in accordance with methods outlined in Pierce & Bennett (2009).

REPRODUCTION

Males were assigned to one of three maturity stages based on testis and clasper development: (1) immature, (2) sub-adult and (3) mature. Females were assigned a maturity stage of 1 to 5 based on ovary and uterine 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 (Bass *et al.*, 1973; White *et al.*, 2001). 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). A full description of the reproductive methods has been provided in Jacobsen *et al.* (2009).

DIET

The stomach of each individual was excised, prepared and examined in accordance with methods outlined in Jacobsen *et al.* (2009). An index of relative importance (I_{RI}) was used to analyse dietary data where $I_{RI} = (N_c + V_c) F_o$ and F_o is the percentage of stomachs containing a specific prey category, N_c is the number of items of a specific prey category expressed as a percentage of the total number of prey items and V_c is the volume of a specific prey category expressed as a percentage of the total prey volume (Cortés, 1997). Prey categories used to calculate the I_{RI} included: Penaeidea, Caridea, Brachyura, Palinura, Amphipoda, Isopoda, Stomatopoda, Polychaeta, Oligochaeta, Echinodermata, Mollusca, Osteichthyes (teleosts) and Cephalochordata. A cumulative prey curve was constructed by randomizing the stomach order 15 times and plotting the mean number of prey groups against the number of stomachs analysed (Ferry *et al.*, 1997). If the plot reached an asymptote, the number of stomachs analysed was considered sufficient to fully characterize the diet.

Volumetric dietary data of I_{RI} prey categories were also examined using non-metric multi-dimensional scaling (nMDS) ordination (PRIMER v5.0; Clarke & Gorley, 2001). Volumetric dietary data were randomly allocated into groups of five (minimum) and the mean values for each prey category calculated (Platell *et al.*, 1998; White *et al.*, 2004; Marshall *et al.*, 2007). Prior to nMDS ordination, the mean volumetric contribution of each prey category was square-root transformed and a similarity matrix constructed using the Bray–Curtis similarity coefficient and nMDS (Clarke & Warwick, 2001; White *et al.*, 2004). Analysis of similarities (ANOSIM) showed that the volumetric dietary data of males and females were statistically similar (global R -statistic = 0.041, $P > 0.05$) allowing dietary samples to be combined and analysed as a single entity. Ontogenetic shifts in volumetric dietary data were compared using nMDS with specimens divided into three size categories, which effectively mapped to sexual development: ≤ 300 mm W_D (immature); 301–450 mm W_D (sub-adults) and > 450 mm W_D (mature specimens).

The diversity of prey species within each size class was evaluated using the Shannon–Wiener index (Pielou, 1966). Prey size comparisons were made between size classes using total length (L_T) for stomatopods, penaeid prawns and carid shrimps, and carapace width (W_C) for brachyurans.

RESULTS

AGE AND GROWTH

A total of 177 *H. astra* specimens were collected from north-east Australia (Fig. 1), which had a male-to-female ratio of 0.82:1 (Z-test, $Z = 1.00$, $P > 0.05$). Males ranged from 171 to 660 mm W_D and 96.5 to 8200 g M . Females ranged from 171

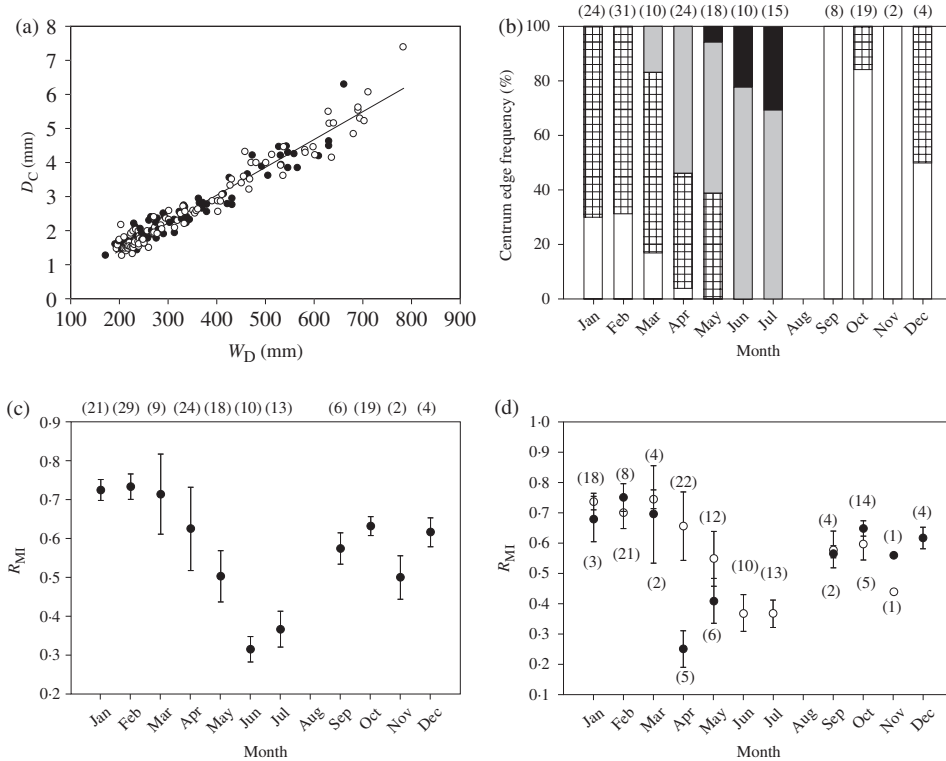


FIG. 2. Centrum characteristics of *Himantura astra*: (a) relationship between disc width (W_D) and centrum diameter (D_C), males (●), females (○), (b) centrum edge analysis (CEA), narrow translucent (T1) band (□), broad translucent (T2) band (▨), narrow opaque (OP1) band (▤), broad opaque (OP2) band (■), (c) variations in mean \pm S.E. monthly marginal ring increment ratios (R_{MI}) determined from pooled sexes and size classes, and (d) mean \pm S.E. R_{MI} comparisons between juvenile (○) and mature (●) specimens. Numbers in parentheses represent numbers for each category.

to 782 mm W_D and 196.8 to 12 000 g M . No significant difference was detected between regressions representing male and female M to W_D (ANCOVA, $F_{1,174} = 0.950$, $P > 0.05$) or W_D to D_C relationships (ANCOVA; $F_{1,174} = 0.220$, $P > 0.05$). Combining male and female data resulted in the following power equation $M = 1.827E-05(W_D)^{3.058}$ and the W_D to D_C relationship represented in Fig. 2(a).

Sixty-eight per cent of vertebrae were assigned a clarity grade of 3. Percentages for the remaining grades were: grade 1 (1.2%), grade 2 (9.6%) and grade 4 (8.8%). Twelve vertebrae (6.8%) were omitted due to poor band clarity and a further 10 (5.6%) omitted due to inconsistent band counts. Overall I_{APE} for the study was calculated at 7.8%, which equates to a c.v. of 11.0%. CEA indicated translucent band completion occurred in March to May and opaque band completion in June to August [Fig. 2(b)]. Marginal increment ratios (R_{MI} , $n = 155$) increased progressively from June through to February [Fig. 2(c)], with monthly values differing significantly ($H = 35.67$, d.f. = 10, $P < 0.001$). Pair-wise comparisons (Dunn's method) identified February and June as contributing the greatest amount of variation to the sample ($Q = 4.215$, $P < 0.05$). When separated, juvenile ($n = 110$) and mature ($n = 45$)

R_{MI} plots showed similar trends to the overall sample [Fig. 2(d)]. Centrum edge and R_{MI} analyses indicate that band pair deposition in *H. astra* is singular and annual [Fig. 2(b), (c)].

Band pair counts for *H. astra* ranged from 1 to 18 years for males and 1 to 29 years for females [Fig. 3(a)–(c)]. Measures of model performance indicated that the GGF provided the best fit for both males ($\omega_i = 0.87$) and females ($\omega_i = 0.57$) [Table I and

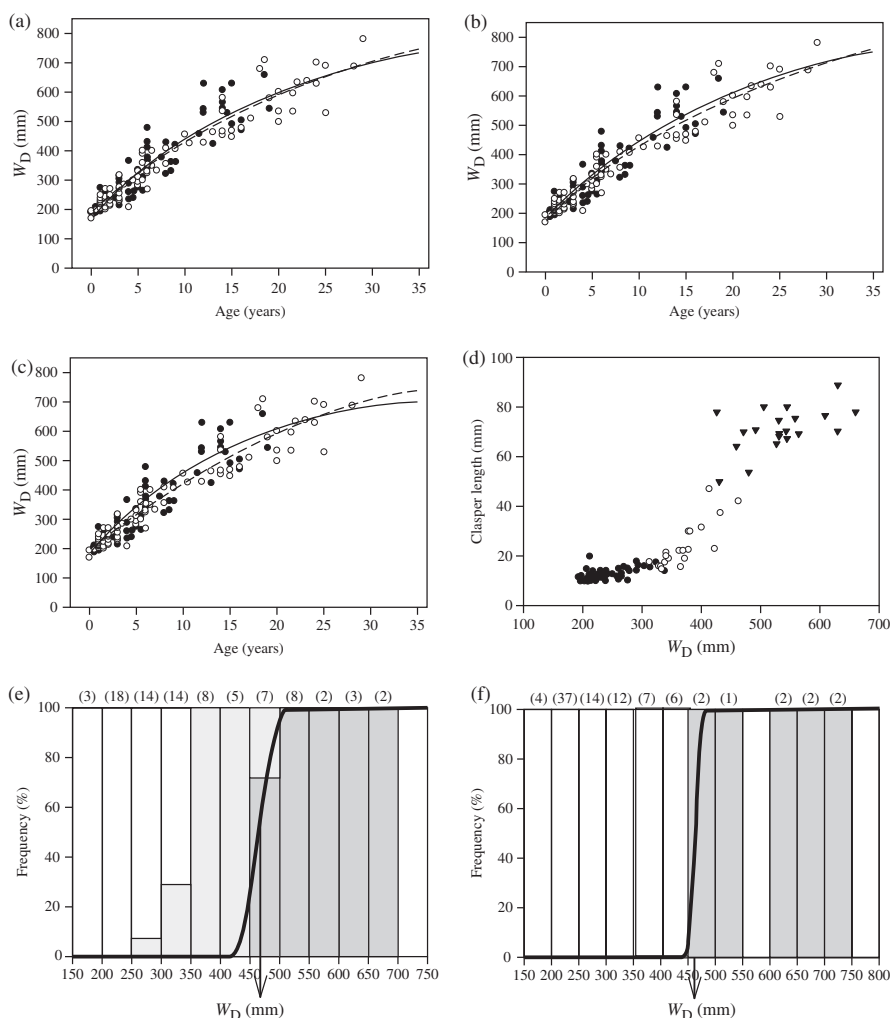


FIG. 3. Growth curves and reproductive summary for *Himantura astra*: (a) von Bertalanffy growth function (VBGF), (b) two-parameter VBGF (2VBGF), (c) Gompertz growth function (GGF), male (●), female (○), male model regression (—), female model regression (-----); (d) relationship between clasper length and W_D, immature (●), sub-adult (○), mature (▼); (e) and (f) frequency of occurrence for males and females, respectively, immature (□), sub-adult, males only (□) and mature (□). Logistic curves fitted to (e) and (f); arrow denotes W_{D50}. Numbers in parenthesis represent numbers for each category. The curves were fitted by: (e) $y = 1 + \{1 + e^{[-\ln 19(x-469.3)(490.7-469.3)^{-1}]}\}^{-1}$ and (f) $y = 1 + \{1 + e^{[-\ln 19(x-462.7)(487.7-462.7)^{-1}]}\}^{-1}$.

TABLE I. Growth estimates and model selection criteria for male and female *Himantura astra* collected from north-east Australia

Model	Parameter	Females ($n = 80$)					Males ($n = 75$)				
		Estimate	r^2	AIC	Δ AIC	ω_i	Estimate	r^2	AIC	Δ AIC	ω_i
VBGF	$W_{D\infty}$	933.0	0.90	1451.0	2.9	0.14	1064.0	0.90	1211.11	12.5	0.0
	W_{D0}	192.4					190.1				
	k (year^{-1})	0.03					0.03				
	t_0 (years)	-5.8					-5.9				
2VBGF	$W_{D\infty}$	933.0	0.90	1449.5	1.4	0.29	737.1	0.83	1202.4	3.8	0.13
	k (year^{-1})	0.04					0.07				
	b	0.8					0.8				
GGF	$W_{D\infty}$	763.8	0.90	1448.1	0.0	0.57	639.9	0.83	1198.6	0.0	0.87
	W_{D0}	202.0					180.4				
	k (year^{-1})	0.09					0.13				
	t_0 (years)	-3.4					-1.9				

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

Fig. 3(a)–(c)]. Likelihood ratio tests indicated differences in male and female GGF curves were significant (χ^2 , d.f. = 3, $P < 0.01$). The youngest estimated ages at sexual maturity were 7 and 8 years for males and females, respectively. The A_{M50} ($\pm 95\%$ C.I.) was 7.32 (6.22–8.45) years for males and 8.67 (7.26–9.75) years for females.

REPRODUCTION

Immature specimens were common in both male ($n = 84$) and female ($n = 89$) sub-samples (Table II). Males had a size at first sexual maturity of 460 mm W_D [Table II and Fig. 3(d)–(e)] and a W_{D50} of 469.3 mm (95% C.I.: 437.0–490.7 mm)

TABLE II. *Himantura astra* reproductive sample from north-east Australia; per cent total male or female sample population in parentheses

	Males	Females	Combined
Size range (mm)			
Immature	171–337 (46.4%)	194–357 (71.9%)	171–357 (59.5%)
Sub-adult	312–426 (29.8%)	301–429 (18.0%)	301–429 (23.7%)
Mature	460–660 (23.8%)	457–780 (10.1%)	457–780 (16.8%)
W_{D50} (mm)	469.3	462.7	—
Total range	171–660	194–780	171–780

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

[Fig. 3(e)]. All males ≤ 450 mm W_D had non-calcified or partially calcified claspers. Female size at first sexual maturity was recorded at 457 mm W_D with the smallest gravid female and W_{D50} reported at 536 mm W_D and 462.7 mm (95% C.I.: 430.9–478.7 mm), respectively [Table II and Fig. 3(f)]. Two gravid females collected in February (1536 mm W_D) and December (1710 mm W_D) contained three and two embryos, respectively, ranging in size from 63.1 to 101 mm W_D and 11.0 g to 68.1 g M . Internally, the reproductive anatomy of mature male *H. astra* included two compound testes. Mature females had one functional ovary and one functional uterus located on the left side of the body.

DIET

Of the 173 stomachs analysed, 136 (78.6%) contained 2075 prey items, which the cumulative prey curve indicated was sufficient to describe the dietary composition of the species [Fig. 4(a)]. On the basis of % I_{RI} , the most important prey categories in the diet of *H. astra* were carids (77.9%), brachyurans (12.1%), stomatopods (4.9%) and penaeids (3.9%) (Table III). This was invariably reflected within individual indices where carid shrimps were the most important prey category based on F_o (93.1%), N_c (73.5%) and V_c (47.0%). Almost two thirds (62.7%) of all identifiable carid shrimps ($n = 1144$) belonged to one of two families; Pasiphaeidae (35.5%) or Ogyrididae (29.2%). Brachyuran crabs, penaeid prawns, stomatopods and amphipods were the only other prey categories with representatives from more than one family (Table III). Digestion, maceration and broken assemblages restricted the number of prey items that could be identified beyond the level of order.

Ontogenetic comparisons revealed carid shrimps to be the most important prey item based on % I_{RI} in all three size classes (Table IV). Carid shrimps I_{RI} declined by >50% from the smallest size class (≤ 300 mm W_D) to the largest (>450 mm W_D) with both stomatopods and brachyurans I_{RI} increasing progressively (Table IV). When compared using nMDS ordination [Fig. 4(b)], size class volumetric (V_c) dietary data were significantly different (ANOSIM, global R -statistic = 0.368, $P < 0.001$). Additional pair-wise comparisons revealed significant differences between V_c dietary data of the ≤ 300 mm W_D size class and both the 301–450 mm W_D (R -statistic = 0.275, $P < 0.01$) and the >450 mm W_D (R -statistic = 0.275, $P < 0.01$) size classes. Percentage similarity (SIMPER) analysis identified changes in carid shrimps V_c as being most responsible for the ontogenetic variance (Table IV). In three of the four major prey categories, median prey size increased with increasing W_D [Fig. 4(c)–(f)], as too did prey diversity with the >300 mm W_D (0.92) size class recording the smallest Shannon–Weiner index followed by 300–450 mm W_D (1.46) and >450 mm W_D (1.63).

DISCUSSION

The introduction of by-catch reduction devices has reduced the number of large *H. astra* caught as prawn-trawl by-catch in north-east Australia (Brewer *et al.*, 2007). Despite this, *H. astra* still comprises a considerable proportion of the elasmobranch by-catch (Tonks *et al.*, 2008; Zhou & Griffiths, 2008; Dell *et al.*, 2009) and therefore will need to be included in future sustainability-based risk assessments. As age and

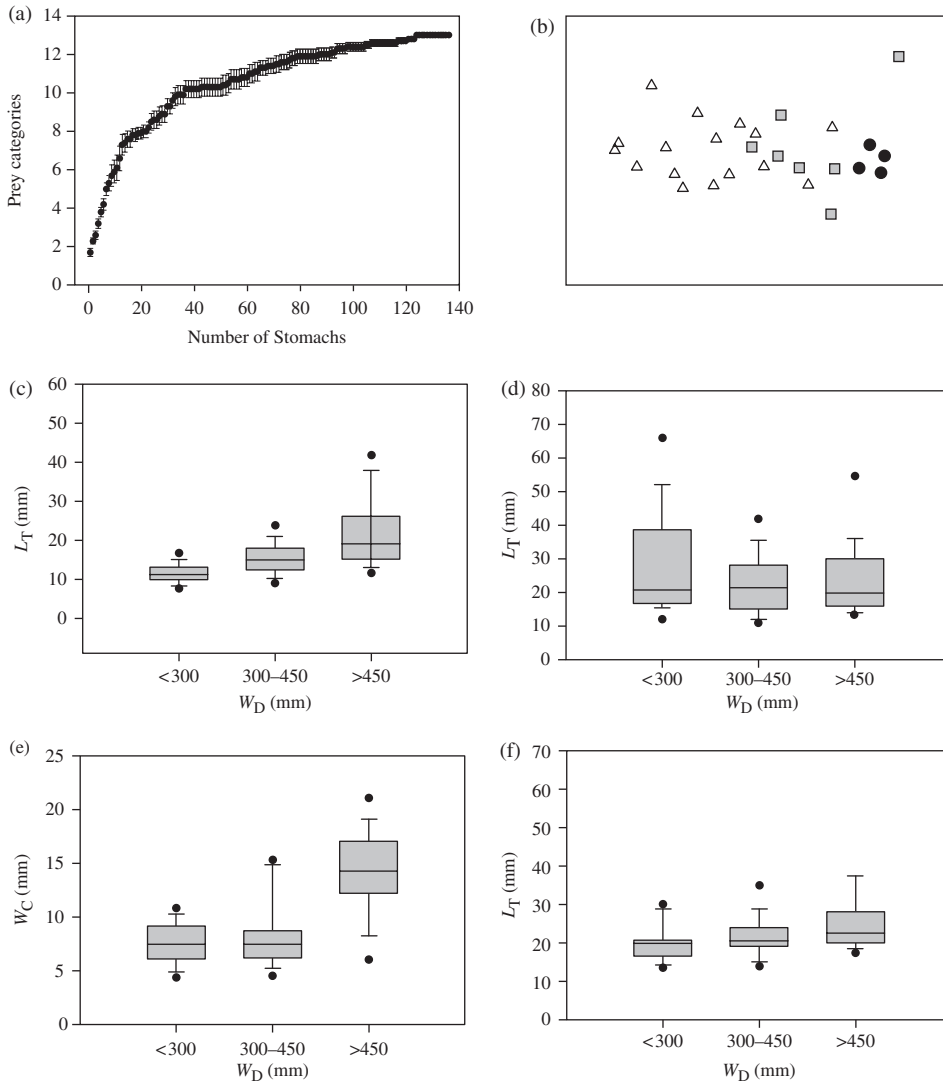


FIG. 4. Diet summary of *Himantura astra*: (a) cumulative prey curve representing mean \pm S.E. number of prey groups, (b) multidimensional scaling (nMDS) ordination of the mean volumetric dietary data, Stress = 0.14, ≤ 300 mm disc width, W_D (Δ); 301–450 mm W_D (\square) and >450 mm W_D (\bullet) and box photo for prey size of (c) carid (total length, L_T), (d) penaeid (L_T), (e) brachyuran (carapace width, W_C) and (f) stomatopod (L_T) prey items for sequential size classes [median (—), 25th and 75th percentiles (\square), 10th and 90th percentiles (I) and 5th and 95th percentiles (\bullet)].

growth variables were not included in previous assessments, these components of the present study will contribute significantly to their ongoing development. This study also updates a number of key variables, including size at maturity and fecundity. In addition, the dietary analysis provides greater insight into how this species utilizes its immediate habitat and its propensity to interact with trawl fisheries. All of which

will enable a substantive risk assessment to be prepared for the species, rather than a comparative risk index as presented to date.

While the maximum age estimate for *H. astra* (29 years) was the highest recorded for a dasyatid species, the diamond stingray *Dasyatis dipterura* (Jordan & Gilbert 1880) and the bat ray *Myliobatis californica* Gill 1865 both recorded comparable age estimates (Table V). Maximum age estimates for the common stingray *Dasyatis pastinaca* (L. 1758) and the blue stingray *Dasyatis chrysonota* (Smith 1828), which are of similar size to *H. astra* and *D. dipterura*, were however, notably lower (Table V). This would indicate that dasyatid age and growth may not conform to the general hypothesis that larger species live longer and grow more slowly when compared to smaller species (Camhi *et al.*, 1998; Frisk *et al.*, 2001).

In a review of age and growth studies, Cailliet *et al.* (2006) argued that consideration must be given to both a model's fit to W_D -at-age data and its ability to produce reasonable biological coefficients. While the GGF provided the best fit for W_D -at-age data, $W_{D\infty}$ estimates for the VBGF and 2VBGF were more consistent with previous reports (Stobutzki *et al.*, 2002; Salini *et al.*, 2007; White & Dharmadi, 2007); although reports on *H. astra* reaching $W_D > 1000$ mm may be the result of misidentifications (Last & Stevens, 2009). A more probable maximum W_D for the species would be 850 to 1000 mm, which indicates that the GGF (Table I) slightly underestimated the $W_{D\infty}$ (White & Dharmadi, 2007; Last & Stevens, 2009). The most probable contributor to this was an under-representation of larger animals that can often occur in elasmobranch age and growth analyses (Braccini *et al.*, 2007; Jacobsen & Bennett, 2010).

Growth coefficients derived from the VBGF and 2VBGF were marginally higher than for *D. pastinaca*, which has the lowest recorded k -value for a dasyatid (Table V). While slightly higher, GGF values were also at the lower end of the scale when compared to previous studies (Table V). All three growth models, however, produced results similar to those obtained for *D. dipterura*, which attains a similar size and age to *H. astra* (Smith *et al.*, 2007). It should be noted though that comparing age and growth studies is considered problematic given the variance in sample sizes, size range distributions, validation or verification techniques, specimen sources (captivity or free living) and model constraints (Cailliet & Goldman, 2004). In addition, Smith *et al.* (2007) indicated that growth coefficient comparisons only provide a generalized characterization of fundamental life-history traits. Given this, k -value comparisons are arguably more useful when species are analysed in relative groupings, *e.g.* $<0.1 \text{ year}^{-1}$, $0.1\text{--}0.2 \text{ year}^{-1}$ and $>0.2 \text{ year}^{-1}$ (Branstetter, 1990).

Ultimately, all three models indicated that *H. astra* was a long-lived species with a comparatively slow growth rate (Table I). When both the goodness-of-fit criteria and the biological coefficients were taken into consideration, the GGF was considered to be the best descriptor for *H. astra* age and growth development [Fig. 3(c)]. While not as prominent as the VBGF, the GGF has also been found to produce the best explanations of age and growth development in the cownose ray *Rhinoptera bonasus* (Mitchill 1815) and the pelagic stingray *Pteroplatytrygon violacea* (Bonaparte 1832) (Mollet *et al.*, 2002; Neer & Thompson, 2005) (Table V).

At 457 mm W_D , the size at first sexual maturity for females was considerably smaller than that previously reported, 660 mm W_D (Stobutzki *et al.*, 2002). Size at first sexual maturity for males, however, was slightly larger at 460 mm W_D (400 mm W_D ; Stobutzki *et al.*, 2002). On the basis of these results, the onset of

TABLE III. Dietary composition of *Himantura astra* displayed as percentage frequency of occurrence (% F_o), percentage numerical composition (% N_c), percentage volumetric contribution (% V_c) and index of relative importance (I_{RI}) and % I_{RI}

Prey	F_o (%)	N_c (%)	V_c (%)	I_{RI}	% I_{RI}
CRUSTACEA	99.3	96.9	91.5	18701.4	
Penaeidea	22.1	7.5	13.7	465.6	3.9
Unknown	14.7	3.4	5.6	133.3	
<i>Penaeus</i> spp.	8.8	1.4	3.6	44.2	
<i>Penaeus esculentus</i>	1.5	0.2	1.4	2.3	
Metapenaeus	2.9	2.3	2.6	14.2	
Metapenaeopsis	0.7	<0.1	0.1	0.1	
Atypopenaeus	0.7	0.1	0.4	0.4	
Caridea	91.9	69.6	32.6	9393.2	77.9
Unknown	53.7	12.4	3.9	876.5	
Alpheidae					
Unknown	18.4	4.9	2.8	142.8	
<i>Batellia</i> spp.	0.7	<0.1	<0.1	<0.1	
Processidae	0.7	0.6	0.2	0.5	
Hyppolytidae	0.7	<0.1	1.7	1.3	
Ogyrididae					
<i>Ogyrides delli</i>	30.1	15.7	2.6	552.2	
Palaemonidae	5.9	4.0	1.6	33.3	
Pasiphaeidae					
Unknown	3.7	1.0	0.2	4.4	
<i>Leptochela</i> spp.	39.7	15.8	4.9	822.2	
Crangonidae	11.0	9.0	11.4	224.9	
Pandaloidae	14.0	6.1	3.2	95.6	
Brachyura	36.0	9.6	30.8	1454.1	12.1
Unknown	27.9	6.5	24.7	872.5	
Cyclodoripidae	0.7	0.1	0.1	0.2	
Leucosiidae	0.7	0.1	0.6	0.5	
Majidae	0.7	0.1	0.8	0.6	
Xanthidae	2.2	0.2	0.2	0.9	
Parthenopidae	0.7	<0.1	<0.1	0.1	
Portunidae	5.1	0.6	2.4	15.6	
<i>Portunus triberealatus</i>	0.7	0.4	0.7	0.8	
Eriphiidae	0.7	0.5	0.1	0.5	
Belliidae	0.7	0.5	0.4	0.6	
Ocypodidae	1.5	0.5	0.6	1.7	
Raninidae	0.7	<0.1	0.1	0.1	
Palinura	0.7	0.1	0.2	0.2	<0.1
Scyllaridae	0.7	0.1	0.2	0.2	
Amphipoda	11.0	2.0	0.5	27.2	0.2
Gammaridea	9.6	0.8	0.1	8.8	
Unknown	6.6	0.6	0.1	4.3	
Lysianassidae	2.2	0.2	<0.1	0.5	
Dexaminidae	0.7	<0.1	<0.1	<0.1	
Caprellidea	1.5	1.2	0.3	2.3	
Unknown	1.5	1.2	0.3	2.3	
Isopoda	1.5	0.3	0.1	0.5	<0.1

TABLE III. Continued

Prey	F_o (%)	N_c (%)	V_c (%)	I_{RI}	% I_{RI}
Unknown	1.5	0.3	0.1	0.5	
Stomatopoda	27.2	7.8	13.8	589.1	4.9
Unknown	4.4	0.5	0.5	4.3	
Squillidae					
Unknown	20.6	3.9	8.1	247.1	
<i>Cloridina</i> spp.	2.9	0.7	0.8	4.6	
<i>Clordea</i> spp.	0.7	<0.1	0.1	0.1	
<i>Anchisquilloides</i>	3.7	2.5	3.2	20.7	
Eurysquillidae					
<i>Erugosquilla woodmason</i>	0.7	<0.1	0.4	0.4	
Tetrasquillidae	0.7	0.1	0.7	0.6	
ANNELIDA	14.0	2.0	6.0	112.5	
Polychaeta	14.0	2.0	6.0	111.8	0.9
Unknown	6.6	0.8	2.3	20.3	
Idoteidae	0.7	0.1	<0.1	0.1	
Glyceridae	2.9	0.2	0.5	2.2	
Goniadidae	2.2	0.2	0.2	0.9	
Cossuridae	4.4	0.3	1.0	5.5	
Nereidae	0.7	<0.1	0.1	0.1	
Pectinariidae	0.7	0.3	2.0	1.7	
Oligochaeta	0.7	<0.1	<0.1	<0.1	<0.1
Unknown	0.7	<0.1	<0.1	<0.1	
ECHINODERMATA	1.5	0.1	0.4	0.8	<0.1
Echinoidea	0.7	<0.1	<0.1	<0.1	
Unknown	0.7	<0.1	<0.1	<0.1	
Holothuroidea	0.7	0.1	0.4	0.4	
Unknown	0.7	0.1	0.4	0.4	
MOLLUSCA	2.2	0.1	0.4	1.1	<0.1
Bivalvia	1.5	0.1	0.4	0.7	
Unknown	1.5	0.1	0.4	0.7	
Gastropoda	0.7	<0.1	<0.1	<0.1	
Unknown	0.7	<0.1	<0.1	<0.1	
OSTEICHTHYES	5.9	0.4	1.6	12.2	0.1
Perciformes	4.4	0.3	1.5	8.1	
Unknown	4.4	0.3	1.5	8.1	
Unknown order	1.5	0.1	0.1	0.3	
CEPHALOCHORDATA	1.5	0.4	<0.1	0.7	<0.1
Amphioxus	1.5	0.4	<0.1	0.7	
TOTAL				12056.4	100.0

sexual maturity in *H. astra* is likely to occur over a relatively broad size range, *i.e.* 400–480 and 450–500 mm W_D for males and females, respectively (Table II). This relates to an estimated age at sexual maturity based on the GGF of 8–10 years. Notably, both the size at first sexual maturity and W_{D50} (Table II) were lower than that used in the most recent risk assessment (660 mm W_D ; Salini *et al.*, 2007).

TABLE IV. Dietary contributions of the four major crustacean prey categories in the diet of *Himantura astra* collected from north-east Australia

Size class (W_D , mm)	Contribution to dietary index (% I_{RI} , % F_o , % N_c , % V_c)		
	≤ 300	301–450	> 450
% I_{RI}			
Carid shrimps	93.9	78.3	27.7
Penaeid prawns	1.8	6.6	6.8
Brachyuran crabs	3.6	8.4	39.3
Stomatopods	0.2	6.2	20.8
% F_o			
Carid shrimps	96.2	91.9	75.0
Penaeid prawns	15.2	29.7	35.0
Brachyuran crabs	20.3	40.5	90.0
Stomatopods	8.9	43.2	70.0
% N_c			
Carid shrimps	85.4	72.8	29.5
Penaeid prawns	2.6	8.53	16.7
Brachyuran crabs	5.9	7.6	20.9
Stomatopods	1.0	8.1	22.5
% V_c			
Carid shrimps	58.3	41.7	21.0
Penaeid prawns	13.9	21.3	10.0
Brachyuran crabs	20.0	20.3	38.8
Stomatopods	2.8	11.3	18.2

% F_o , percentage frequency of occurrence; % I_{RI} , index of relative importance; % N_c , percentage numerical composition; % V_c , percentage volumetric contribution; W_D , disc width.

The maximum litter size (three), while within that previously reported for *Himantura* species (White & Dharmadi, 2007), was also higher than that used by both Stobutzki *et al.* (2002) and Salini *et al.* (2007). This suggests the size at sexual maturity and fecundity levels may not be as conservative as previously thought.

The dietary analysis indicates that *H. astra* were feeding in environments with predominantly sandy or soft substrata (Table III). The results obtained also showed strong similarities with those of Salini *et al.* (1994) where 'other' crustaceans (18.8%), penaeid prawns (20.3%), brachyuran crabs (14.1%) and stomatopods (7.3%) were reported as the most important prey groups by mass (identified as *H. toshi*). These similarities were to be expected, given that the geographic region sampled in the present study partially overlapped with that of Salini *et al.* (1994). In contrast, the most important prey items in the diet of *H. uarnak* (Raje, 2003) were teleosts (55.6%) and molluscs (14.1%), both of which had a combined contribution of just 0.1 and 2.0% to the I_{RI} and V_c of *H. astra*, respectively. While the frequency of ingestion of teleosts shows some variability between studies (this study and Salini *et al.*, 1994), the consistency of crustacean prey between the studies indicates it is the primary prey group ingested by *H. astra*. One other preliminary study ($n = 7$) examining the

TABLE V. Comparison of selected age and growth variables among myliobatiform stingrays

Species	Maximum age (years)	VBGF (k)		GGF (k)		Source
		Female	Male	Female	Male	
<i>Himantura astra</i>	29	0.03	0.03	0.09	0.13	This study
<i>Dasyatis chrysonata</i>	14	0.07	0.175	—	—	Cowley (1997)
<i>D. dipterura</i>	28	0.05	0.1	0.09	0.14	Smith <i>et al.</i> (2007)
<i>D. pastinaca</i>	10	0.089*		—	—	Ismen (2003)
	12	0.039	0.041	—	—	Yeldan <i>et al.</i> (2009)
<i>D. americana</i>	13	0.11	0.44	0.26	0.68	Henningsen & Leaf (2010)
<i>Pteroplatytrygon violacea</i>	9	0.20	0.35	0.41	0.58	Mollet <i>et al.</i> (2002)
<i>Neotrygon picta</i>	18	0.08	0.12	0.13	0.18	Jacobsen & Bennett (2010)
<i>N. annotata</i>	13	0.2	0.31	0.25	0.37	Jacobsen & Bennett (2010)
<i>N. kuhlii</i>	17	0.08	0.08	0.15	0.15	Jacobsen & Bennett (2010)
	13	0.13	0.2	0.2	0.27	Pierce & Bennett (2009)
<i>N. cf. kuhlii</i>	15	0.311	0.831	—	—	White (2003)
<i>Rhinoptera bonasus</i>	18	0.074*		0.133*		Neer & Thompson (2005)
<i>Myliobatis californica</i>	23	0.10	0.229	—	—	Martin & Cailliet (1988)
<i>Trygonoptera mucosa</i>	17	0.241	0.493	—	—	White <i>et al.</i> (2002)
<i>T. personata</i>	16	0.143	0.203	—	—	White <i>et al.</i> (2002)
<i>Urolophus lobatus</i>	14	0.369	0.514	—	—	White <i>et al.</i> (2001)
<i>U. paucimaculatus</i>	10	0.21	0.45	—	—	Edwards (1980)
<i>Urobatus halleri</i>	14	0.09	0.15	—	—	Hale & Lowe (2008)

GGF, Gompertz growth function; k , growth coefficient estimate; VBGF, von Bertalanffy growth function; 2VBGF, two-parameter von Bertalanffy growth function.

*Combined sexes.

food habits of the mangrove whipray *Himantura granulata* (Macleay 1883) identified teleosts, sipunculids and cephalopods in the stomach contents (Ishihara *et al.*, 1993).

While the diet of *H. astra* undergoes a size-based shift, this difference is driven by changing prey percentages rather than a change in prey composition (Table IV). These changes were reflected in the nMDS ordination [Fig. 4(b)] and the Shannon–Wiener index, which indicated the diet of *H. astra* diversified with increasing W_D . The consistency of prey groups between size classes, however, indicates that feeding grounds for *H. astra* (sandy and soft sediments) coincide with environments preferred by prawn trawl fisheries (Stobutzki *et al.*, 2002) throughout its development.

One explanation for the size-based dietary shift is that larger fish have an increased ability to handle and ingest larger prey items. Evidently, three of the four major prey categories showed a corresponding increase in prey size with increasing W_D [Fig. 4(c)–(f)]. Other factors including the need to meet higher energy demands (White *et al.*, 2004; Kyne *et al.*, 2008), increased swimming speeds (Farias *et al.*, 2006) and a greater potential to forage deeper into the substratum (Gray *et al.*, 1997) would, however, more than likely have contributed to the observed differences. Similarly, increased morphological variables including body mass and mouth size may help larger fishes negate the effectiveness of prey defensive mechanisms (Gray *et al.*, 1997). For example, dietary studies involving *R. bonasus* identified elevated crushing capabilities as a factor contributing to the increased presences of bivalves in the diet of larger fishes (Peterson *et al.*, 2001; Collins *et al.*, 2007). This increase in crushing capabilities effectively provided larger *R. bonasus* with greater access to prey not available to smaller fishes (Ebert & Cowley, 2003). This ability to overcome both direct (defensive chelipeds) and indirect (burrowing) defensive mechanisms may partially explain why brachyuran and stomatopod prey items were more prevalent in the diet of larger *H. astra* (Table IV).

The life history of *H. astra* conforms well to the broader generalization of elasmobranchs being relatively long-lived animals, with delayed maturity and low fecundity. Results obtained from the present study indicate that the reproductive biology of *H. astra* may not be as conservative as previously thought. For instance, the downward revised sizes at maturity and increased fecundity estimates would theoretically make this species less susceptible to the negative effects of trawl-induced mortality. The time taken for this species to reach sexual maturity (7–9 years) as well as its overall longevity may, however, counteract these benefits. As a consequence, the ability of *H. astra* to replace themselves prior to their capture is considered to be relatively low, a problem compounded by the fact that smaller elasmobranchs caught as prawn-trawl by-catch have a comparatively high mortality rate, *e.g.* 53% in Stobutzki *et al.* (2002). The dietary results also indicate that the feeding grounds of *H. astra* overlap with environments conducive to trawl fishing throughout its development. As a consequence, the capture of this species as prawn-trawl by-catch is likely to continue.

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