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THE BIOLOGY OF THE SKATES *RAJA WALLACEI* AND *R. PULLOPUNCTATA* (BATOIDEA: RAJIDAE) ON THE AGULHAS BANK, SOUTH AFRICA

S. A. WALMSLEY-HART, W. H. H. SAUER* and C. D. BUXTON†*

Aspects of the biology of *Raja wallacei* and *R. pullopunctata* were investigated using data collected in 1995 and 1996 from research and commercial trawls on the Agulhas Bank, South Africa. Age and growth parameters were investigated by examination of bands on the vertebral centrum. Estimates of Von Bertalanffy parameters for *R. wallacei* were L_∞ = 405.40 mm disc width (*DW*), K = 0.27 and t_0 = −0.08 years for males and L_∞ = 435.23 mm *DW*, K = 0.26 and t_0 = −0.21 years for females. For *R. pullopunctata*, the estimates were L_∞ = 770.50 mm *DW*, K = 0.10 and t_0 = −2.37 years for males and L_∞ = 1 326.75 mm *DW*, K = 0.05 and t_0 = −2.20 years for females. Growth was significantly different between sexes for both species. The oldest aged *R. wallacei* and *R. pullopunctata* were 15 and 18 years respectively. The length at first maturity was approximately 350 mm *DW* or 7 years of age for *R. wallacei* and 600 mm *DW* or 9 years of age for *R. pullopunctata*. The length-at-50% maturity for *R. wallacei* was 395 mm *DW* for males and 400 mm *DW* for females. *R. wallacei* fed primarily on benthic teleosts and crustaceans. There were significant differences ($p < 0.05$) in the diet between research- and commercially caught fish, in terms of percentage frequency of occurrence and volume of prey.

Skates (Rajidae) are common members of the South African demersal fish community. In research trawls on the Agulhas Bank, skates contribute 4.2% by mass to the total catch (Japp *et al*. 1994), and they occur in 88% of commercial trawl landings at Mossel Bay (South African Network for Coastal and Oceanographic Research, unpublished data). However, studies on South African rajids have concentrated mostly on their taxonomy and distribution. Wallace (1967) reviewed the skates of the South African east coast, Hulley (1970, 1972) studied those on the South and West coasts and Compagno *et al.* (1991) described the distribution of the skates on the West Coast. Although there is some understanding of the biology of South African skates, for example, their diet (Ebert *et al*. 1991, Smale and Cowley 1992), there is little information on their age and growth or reproductive biology. This is particularly so for the yellowspot skate *Raja wallacei* and the slime skate *R. pullopunctata*, both of which are commonly caught by the hake-directed trawlers operating on the Agulhas Bank (Walmsley 1996). *R. wallacei* is found over soft substrata at depths of between 95 and 430 m, from Lüderitz in Namibia to southern Moçambique. *R. pullopunctata* occurs at depths of between 50 and 460 m, from Lüderitz to Port Elizabeth on the south-east coast of South Africa (Compagno *et al*. 1989).

The limited information on age and growth in skates (e.g. Ishiyama 1951, Nottage and Perkins 1983) and the few validation studies (Holden 1972, Holden and Vince 1973, Natanson 1993) are likely a reflection of the limited methods available to assess age in elasmobranchs. In the absence of hard structures such as otoliths, scales or operculae, which are used to determine age in teleosts, the most common method of determining age in elasmobranchs is counting concentric bands or zones in the vertebral centrum (Cailliet *et al*. 1986). The vertebral centrum bands are seen as alternating patterns of translucent and opaque zones. Many techniques have been used to enhance these bands, including alizarin red S and crystal violet staining, and metal substitution reactions (Cailliet *et al*. 1983, 1986). Usually, the number of bands increases with body size or vertebral diameter, and it has generally been assumed that bands are laid down annually with one opaque and one translucent zone constituting one year (Smith and Merriner 1987, Abdel-Aziz 1992). However, for some species of elasmobranchs, more than one band may be laid down annually (Branstetter and Musick, 1994). Validation of band deposition is important (Beamish and McFarlane 1983), but few studies have provided such information for elasmobranchs (Smith 1984, Branstetter 1987, Brown and Gruber 1988).

Studies on rajid reproduction have centred largely on their copulatory behaviour (Price 1967, Luer and Gilbert 1985), egg laying and gestation (Luer and Gilbert 1985, Berestovskii 1994, Ellis and Shackley 1995), and egg case structure (McEachran 1970) and its use in taxonomy (Ishiyama 1958). The structure

* Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown 6140, South Africa. E-mail: walmsley@botzoo.uct.ac.za
† Tasmanian Aquaculture and Fisheries Institute, Nubeena Cresent, Taroona, Hobart, TAS 7053, Australia. E-mail: colin.buxton.@dppif.taz.gov.au

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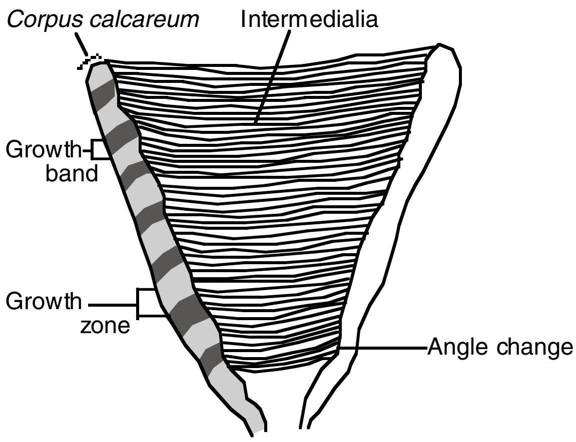

Fig. 1: A diagrammatic representation of a sectioned vertebral centrum of *R. wallacei*, showing the terminology referred to in the text

of the testis was described by Pratt (1988) and the ovarian cycle of the cuckoo ray *Raja naevus* was described by Du Buit (1976).

This study aims to increase knowledge of the age and growth and reproductive biology of *R wallacei* and *R. pullopunctata*. Although their diet has been described (Smale and Cowley 1992), this study attempts to assess possible differences in diet between the heavily fished commercial trawling grounds and the less fished research trawling grounds on the Agulhas Bank.

MATERIAL AND METHODS

Sample collection

Samples were collected from routine biomass surveys aboard the F. R. S. *Africana* between Cape Agulhas (34°50´S, 20°00´E) and Port Alfred (33°26´S, 26°54´E) during winter (April/May) and spring (September/October) of 1995 and 1996. Samples were also taken from the commercial trawlers F. V. *Midhavid* and F. V. *Zuiderzee* operating out of Port Elizabeth (34°00´S, 26°40´E). All research surveys used a 180-ft German bottom trawl with a cod-end liner of 35-mm mesh. When possible, trawling lasted for 30 minutes at each sampling site, during daylight on a semi-random, depth-stratified basis from inshore to a depth of around 500 m. The survey area and sampling procedures are described by Badenhorst and Smale (1991).

Disc width (*DW*, mm), total length (*TL*, mm), from the tip of the snout to the end of the tail, total mass (*TM*, g), gonad mass (*GM*, g), and inner clasper length (*ICL*, mm) for males, were recorded for each individual. Seven or eight vertebrae were removed from the abdominal cavity of each individual and frozen for later analysis. Maturity stages were determined visually and gonadal tissue was removed for subsequent histological analysis. Tissues were fixed in 4% buffered formalin for a maximum period of 4 days and transferred to 70% propanol. Stomach contents were removed on capture and stored in 4% buffered formalin for further analysis.

Growth

PREPARATION AND PROCESSING OF VERTEBRAE

The centra were removed from the thawed vertebral segment using a scalpel and the neural arches were removed. All connective tissue was dissolved in a 3% solution of sodium hypochlorite and clean centra were rinsed in freshwater and stored in 60% propyl alcohol for subsequent analysis.

A preliminary study was undertaken to determine the best method of viewing the growth bands on the centra. Whole centra were viewed unstained or stained with cobalt nitrate (Hoenig and Brown 1988), crystal violet (Johnson 1979), and alizarin red S (Brown and Gruber 1988). Unstained centra were embedded in a clear casting resin and sectioned through the nucleus using a double-bladed diamond-edged saw. The section (approximately 3μm thick) was stained and mounted in DPX on a microscope slide and viewed under transmitted light with a binocular microscope at 20× magnification. Growth bands were most distinct on centra that were immersed in 0.01% crystal violet for 20 minutes.

Vertebrae were processed from 244 *R. wallacei* (124 males and 120 females) and 180 *R. pullopunctata* (93 males and 87 females). Male and female *R. wallacei* ranged in size between 135 and 512 mm *DW* and from 119 to 571 mm *DW* respectively and between 177 and 696 mm *DW* and from 130 to 747 mm *DW* for male and female *R. pullopunctata* respectively.

The term "band" in this study refers to a wide opaque zone (dark purple when stained) and a narrow translucent zone (light purple when stained). The first band was found at an angle change of the centrum and was taken to be the birth band (Fig. 1). Bands were fairly distinct in the corpus calcareum region and were occasionally observed in the intermedialia.

Bands were counted twice for each centrum without any reference to fish size or previous counts. If there

Table I: Description of maturity stages for male and female *R. wallacei* and *R. pullopunctata*

Stage	Description
	Males
2	Testis composed of undifferentiated, white tissue. Vas deferens is a thin white line along the dorsal surface of the abdominal cavity. Clasper small and soft
2.5	Testis highly vascularized. No development in the seminal vesicle and clasper
3	Dorsal surface of the testis becomes lobular. Vas deferens begins to thicken. Coiling may be seen within the tissue. Clasper begins to elongate but not calcify
3.5	Dorsal surface of the testis is fully lobular. Seminal vesicle and vas deferens are highly coiled and developed. Clasper protrudes beyond the trailing edge of the pelvic fin and starts to become calcified
4	Fully mature. Clasper fully calcified and hard. Testis, vas deferens and seminal vesicle are fully developed. Sperm may be present
	Female
2	Ovary consists of white, undifferentiated tissue. Oviduct is a thin, white line on the dorsal surface of the abdominal cavity. Nidamental gland is a small swelling on the oviduct
2.5	Ovary becomes highly vascularized and takes on a granular appearance. Slight swelling apparent in the nidamental gland
3	Small, immature, opaque eggs apparent within the ovary. Nidamental gland is heart-shaped and the oviduct wall begins to thicken
3.5	Eggs are white. Two distinct tissue zones apparent within the nidamental gland. Uterus wall continues to thicken
4	Fully mature. Ovary is full of yellow eggs. Eggs range in size from 40 mm diameter and smaller. Nidamental gland is fully developed and uterus wall is thick and muscular
4.5	Pregnant. A fully or partially formed egg case is found within one or both uteri
5	Post parturition. The uterus wall is extremely stretched and flaccid, indicating that eggs have recently been laid

was disagreement, a third count was taken. If this third count corresponded to either of the first two, that count was accepted. If all three counts were different but consecutive (e.g. 2, 3 and 4 rings), the middle reading was taken. If all three counts disagreed, the centrum was rejected. A single reader did the counting, and the reproducibility of the counts was measured using the average percentage error (*APE*) method of Beamish and Fournier (1981).

Growth parameters were calculated and modelled by PC-Yield 2.2 (Punt 1992). A non-parametric, one-sample runs test (Draper and Smith 1966) was used to test for randomness of the residuals, and a Bartlett's test was used for homoscedacity. Variance estimates were calculated using (conditioned) parametric bootstrap sampling (Efron 1981), with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984). The results were fitted to a relative error model using the Von Bertalanffy equation

$$L_t = L_\infty\,(1 - e^{-K(t-t_0)}) \quad ,$$

where L_t is the disc width at time t, L_∞ is the theoretical maximum disc width, K is the growth constant and t_0 is the theoretical length at zero age which, according to Holden (1972), is the hatching time.

CENTRUM EDGE ANALYSIS

The periodicity of band formation was investigated using the marginal increment ratio (*MIR*)

$$MIR = (CD - R_n) / (R_n - R_{n-1}) \quad ,$$

where CD is the centrum diameter, R_n is the width of the last complete band and R_{n-1} is the width of the penultimate band.

Disc width-at-age values were back-calculated using ratios based on the linear relationship between centrum radius and disc width (Langler 1956), and were compared to the values obtained using the growth parameters.

Reproduction

Gonads were assessed visually and a clarification of developmental stages was constructed (Table I). Changes in clasper length and gonad mass relative to disc width were used as indicators of the onset of maturity. Length-at-maturity was modelled using a two-parameter logistic ogive, according to King (1995):

$$P_l = \frac{1}{1 + \exp^{-(l-l_{50})/\delta}} \quad ,$$

where P_l is the percentage of mature fish at length l, l_{50} is the length at which 50% of the fish are sexually mature and δ is the width of the ogive.

Histological assessment of testes collected during

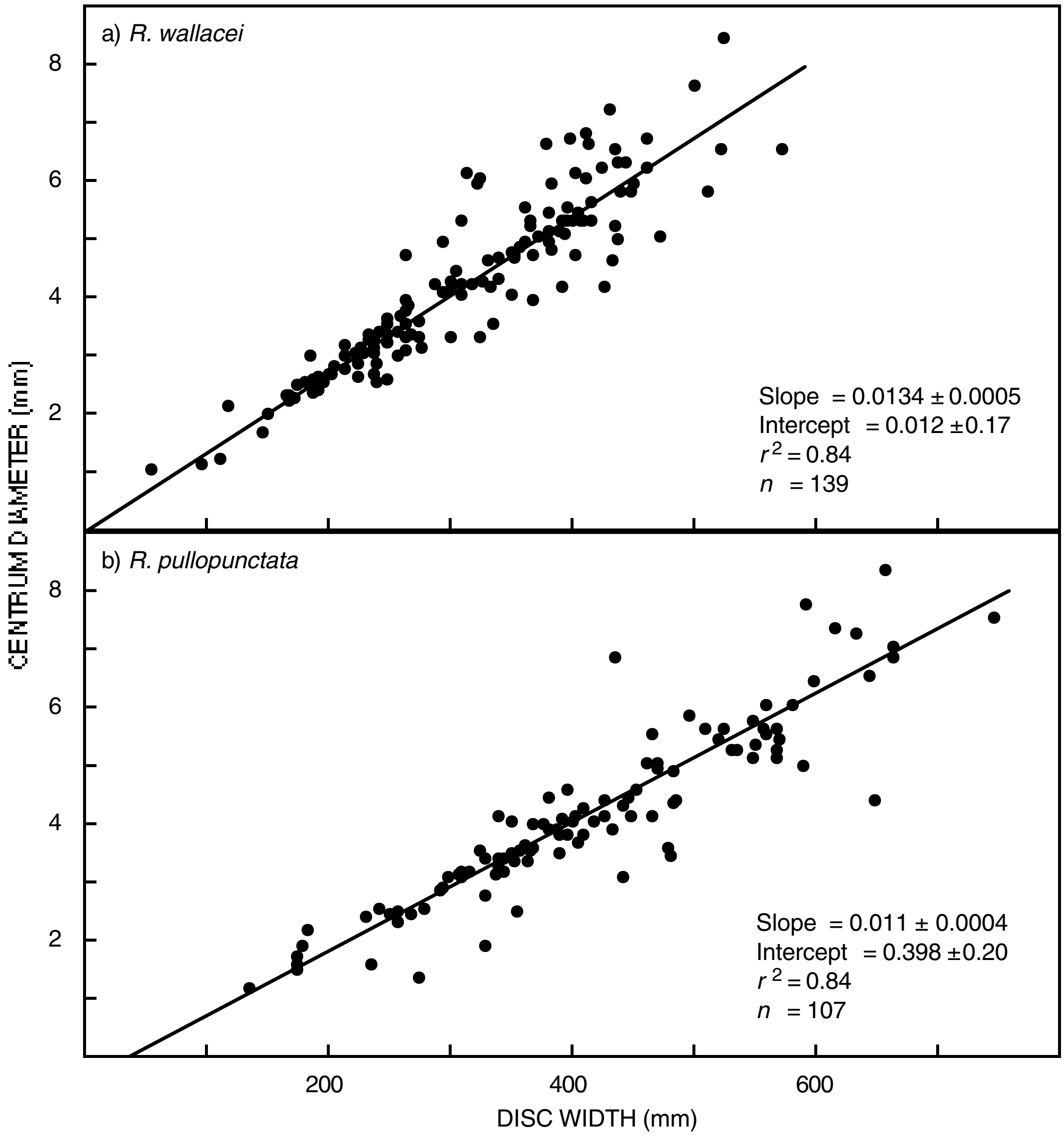

Fig. 2: Relationships between vertebral centrum diameter and disc width for (a) *R. wallacei* and (b) *R. pullopunctata*

research cruises was used to verify the maturity stages that were classified visually, and mature nidamental glands were examined for evidence of sperm storage. Testes and nidamental glands were dehydrated through a series of alcohol and xylene immersions, embedded in wax and sectioned for histological examination. Sections were stained with Gill's haematoxylin and Papanicolaou eosin A. Five random counts of seminal follicles were taken to determine the percentage of follicles containing sperm at each maturity stage.

Feeding

Prey items were identified to the lowest possible taxon and grouped into 13 main categories. The percentage volume contributed by each prey group was

Table II: Relationship between disc width (*DW*) and mass and total length for male and female *R. wallacei* and *R. pullopunctata*. Differences in the slope and intercept were compared using log-transformed data

Regression	Intercept	Slope	r^2	*n*	Range (*DW* mm)	Mean (*DW*)
			Log DW v. log mass			
R. wallacei (combined)	0.02 ± 0.01	1.20 ± 0.01	0.98	1 000	88 – 657	337.56 ± 2.64
R. pullopunctata (males)	−4.70 ± 0.17	2.97 ± 0.06	0.90	243	138 – 790	452.67 ± 8.18
R. pullopunctata (females)	−5.35 ± 0.12	3.23 ± 0.04	0.96	199	130 – 747	441.08 ± 9.20
			Log DW v. log total length			
R. wallacei (combined)	0.39 ± 0.02	0.93 ± 0.01	0.89	1 212	88 – 657	337.02 ± 2.45
R. pullopunctata (males)	0.26 ± 0.07	0.95 ± 0.03	0.85	261	138 – 790	459.46 ± 7.93
R. pullopunctata (females)	0.10 ± 0.03	1.02 ± 0.11	0.98	217	130 – 742	443.99 ± 8.79

determined visually (Hyslop 1980). A randomly chosen prey group was designated a volume of zero and the ratio of that volume was assigned to all other groups. The ratios were summed and calculated as a percentage. The contents were dried to constant mass at 60°C and each prey group weighed to the nearest 0.0001g.

No one method of assessing prey importance is wholly unbiased (Hynes 1950, Windell and Bowen 1979, Hyslop 1980). Numerical methods over-emphasize the importance of small prey items and gravimetric measurements are biased towards large prey items that take longer to digest. Prey importance was assessed by percentage frequency of occurrence (*%F*), which provided an indication of how often a particular prey item is selected, by percentage volume (*%V*) and mass (*%M*), which each give a measure of the energy contribution of the prey item. Contingency table analysis was used to test for differences between the diets of research- and commercially caught fish (Cortèz *et al*. 1996).

RESULTS

Age and growth

The disc width and mass and total length relationships between male, female and all *R. wallacei* and *R. pullopunctata* are shown in Table II. The relationships did not differ significantly ($p > 0.05$) for *R. wallacei*, but there were significant differences between sexes for *R. pullopunctata*. The relationship between centrum diameter and disc width was linear (Fig. 2), with no significant difference ($p > 0.05$) between males and females for both species.

The precision estimates (*APE*) calculated for *R. wallacei* were 14.1 and 10.4% for males and for females respectively. Estimates for *R. pullopunctata* were 10.7 and 11.4% for males and females respectively. The overall sample mean was 11.7%.

Band counts were obtained from 74 male and 65 female *R. wallacei* and 53 male and 54 female *R. pullopunctata*. The parameters of the Von Bertalanffy model are given in Table III. A likelihood ratio test (Draper and Smith 1966), using size-at-age data, showed

Table III: Calculated Von Bertalanffy growth parameters, *SE*s and 95% confidence intervals (*CI*) for *R. wallacei* and *R. pullopunctata*

Parameter	Value			
	Estimate	*SE*	Left 95% *CI*	Right 95% *CI*
R. wallacei, males (*n* = 65)				
t_0	−0.08	0.82	−2.33	0.90
K	0.27	0.12	0.07	0.57
L_∞	405.40	6 009.86	339.82	722.41
R. wallacei, females (*n* = 74)				
t_0	−0.21	0.95	−2.79	0.85
K	0.26	0.12	0.08	0.53
L_∞	435.23	13 699.84	363.01	738.15
R. wallacei, males and females combined (*n* = 139)				
t_0	−0.17	0.52	−1.46	0.60
K	0.26	0.08	0.13	0.44
L_∞	421.90	42.92	369.37	543.92
R. pullopunctata, males (*n* = 56)				
t_0	−2.37	1.56	−6.82	−0.62
K	0.10	0.06	0.00	0.25
L_∞	770.50	43 534.33	539.97	1 773 227.74
R. pullopunctata, females (*n*=51)				
t_0	−2.20	0.47	−3.23	−1.47
K	0.05	0.03	0.00	0.11
L_∞	1 326.75	89 500.39	759.76	443 181.77
R. pullopunctata, males and females combined (*n* = 107)				
t_0	−1.95	0.61	−3.79	−1.32
K	0.08	0.03	0.00	0.14
L_∞	873.24	59 693.12	673.62	212 472.26

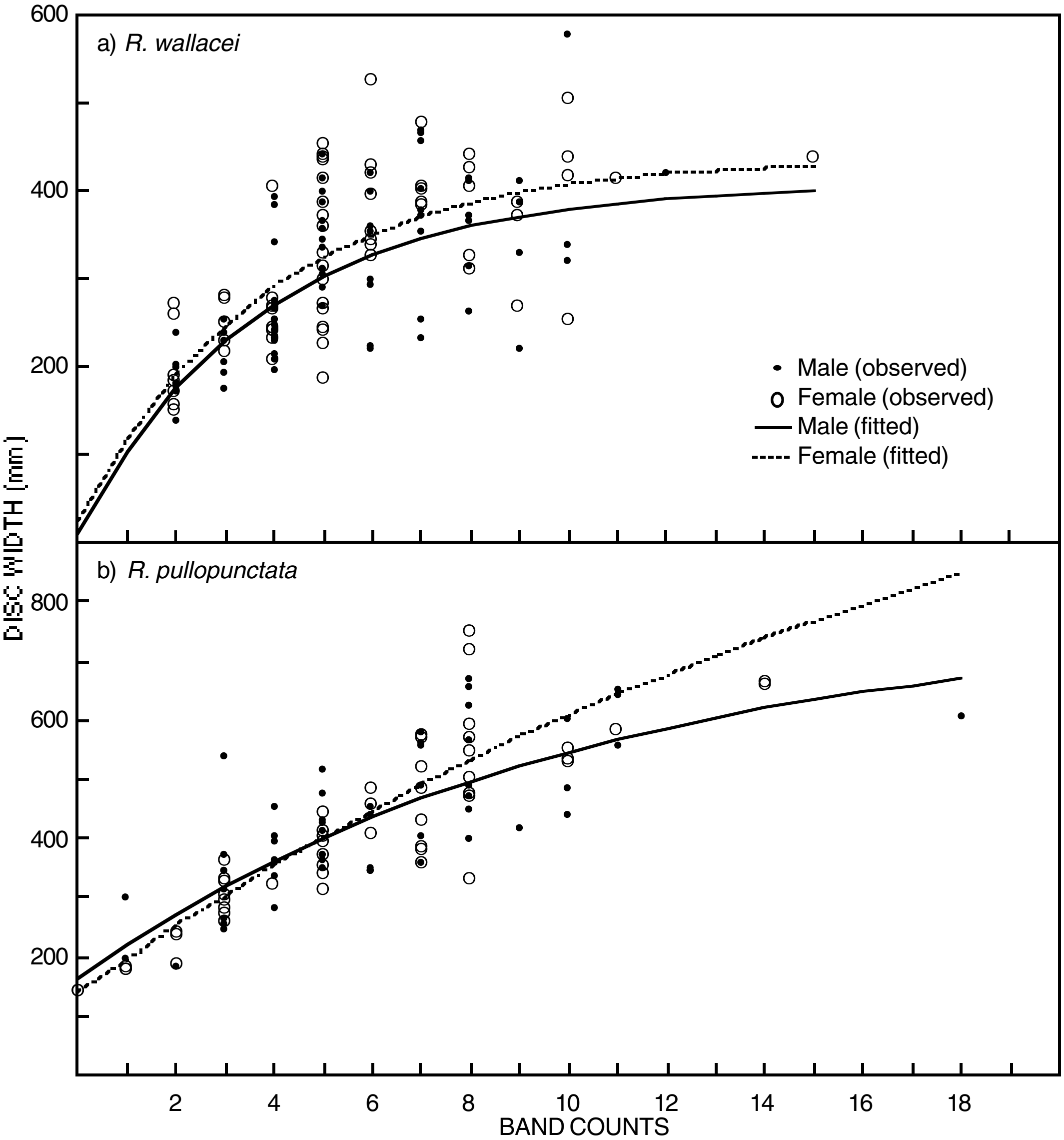

Fig. 3: Fitted and observed growth curves for male and female (a) *R. wallacei* and (b) *R. pullopunctata*

significant differences ($p < 0.05$) between sexes of both species. The observed data and fitted curves are illustrated in Figure 3.

The scarcity of marginal increment data for all months of the year prohibits an accurate determination of the annual band formation (Fig. 4). The ratio was high for both species in February/March and low in April/May. The ratio for October was also low, indicating little growth in that month. Results of back-calculated disc-widths-at-age are shown in Table IV.

Reproduction

The reproductive systems of *R. wallacei* and *R. pullopunctata* consisted of paired testes, efferent ducts,

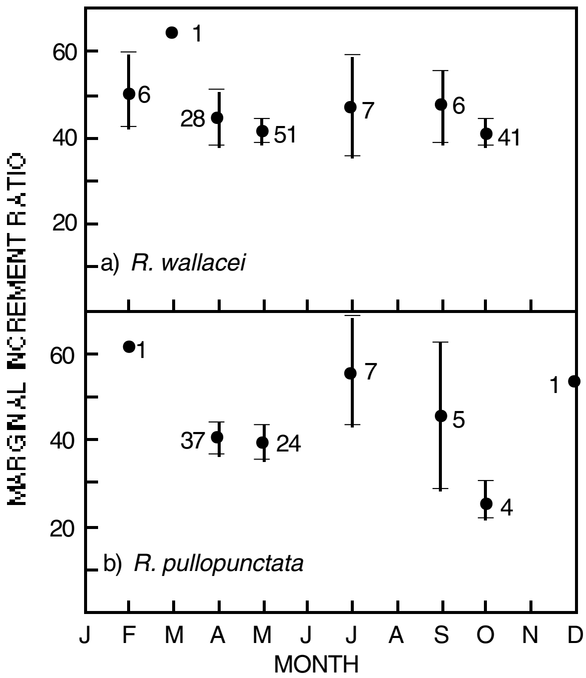

Fig. 4: Mean monthly marginal increment ratios (± SD) for (a) *R. wallacei* and (b) *R. pullopunctata*

vasa deferentia, seminal vesicles and claspers in males, and paired ovaries, nidamental glands and uteri in females, similar to those reported for other oviparous elasmobranchs (Luer and Gilbert 1991).

The relationship between disc width and inner clasper length and gonad mass was linear in immature males, but exponential during maturation, indicative of rapid growth in clasper length and gonad mass during that period (Fig. 5). Elongation in the claspers began at approximately 350 mm *DW* for *R. wallacei* and 600 mm *DW* for *R. pullopunctata*, accompanied by rapid gonad growth. Claspers began to calcify once they protruded beyond the trailing edge of the pelvic fin and were fully calcified in mature males. A Scheffe multiple comparison test revealed a significant increase in mean disc width with maturity stage for both *R. wallacei* (F = 413.97, df = 4.602, p < 0.001) and *R. pullopunctata* (F = 81.5, df = 5.261, p < 0.001, Fig. 6). The smallest mature male of *R. wallacei* and *R. pullopunctata* measured 338 and 584 mm *DW* respectively. Length-at-50% maturity for male *R. wallacei* was 395 mm *DW* (Fig. 7), at around 9 years of age. As a result of too few male *R. pullopunctata* being caught, the percentage of mature animals was grouped by 20-cm *DW* classes (Fig. 7). The length-at-50% maturity was estimated to be 641–660 mm *DW*.

Testes were examined histologically to determine whether the onset of spermatogenesis corresponded to

Table IV: The fitted and back-calculated disc width-at-age for *R. wallacei* and *R. pullopunctata* (one band = 1 year)

Band counts	Size-at-age (mm disc width): *R. wallacei*, Fitted, Male, Mean	Fitted, Female, Mean	Back-calculated, Male, Mean	Male, *SD*	Male, *n*	Back-calculated, Female, Mean	Female, *SD*	Female, *n*	*R. pullopunctata*, Fitted, Male, Mean	Fitted, Female, Mean	Back-calculated, Male, Mean	Male, *SD*	Male, *n*	Back-calculated, Female, Mean	Female, *SD*	Female, *n*
1	89.0	115.2	90.1	16.7	65	92.7	32.6	74	214.7	185.1	123.6	26.3	53	120.4	25.4	52
2	173.6	187.2	140.7	27.1	65	142.5	45.2	65	266.1	237.5	189.8	35.1	51	190.1	38.4	50
3	228.2	243.5	182.3	33.1	52	189.7	62.6	54	312.7	287.5	247.0	44.6	59	249.4	40.2	49
4	270.1	286.3	222.2	38.0	48	226.9	56.0	49	355.0	335.3	291.9	60.0	42	304.2	46.7	36
5	302.0	319.8	258.9	41.4	39	269.1	64.8	42	393.4	380.8	335.8	59.5	33	352.7	58.0	35
6	326.4	345.8	294.0	45.3	28	315.2	76.5	26	428.2	424.2	379.1	65.2	25	396.1	64.1	28
7	345.0	365.9	328.8	46.2	22	344.6	82.3	19	459.9	465.6	426.8	74.0	20	433.5	48.6	22
8	359.3	381.5	356.6	48.1	14	377.2	97.2	14	488.6	505.2	469.0	88.8	16	483.4	47.1	14
9	367.1	395.6	386.6	49.1	9	403.3	32.2	9	514.7	542.9	501.0	87.4	8	540.4	47.6	6
10	378.5	403.0	395.2	45.9	5	409.7	25.7	6	538.3	578.9	523.9	105.9	7	583.6	56.3	6
11	384.8	410.2	383.5	–	1	439.7	34.5	2	559.8	613.2	490.5	112.7	4	635.8	78.3	3
12	389.7	415.8	401.1	–	1	405.6	–	1	579.3	646.0	486.7	–	1	735.0	1.8	2
13		420.2				409.0	–	1	597.0	677.3	477.8	–	1	651.7	23.6	2
14		423.6				418.4	–	1	613.0	707.1	502.3	–	1	680.8	44.9	2
15		426.2				427.6	–	1	627.6		520.7	–	1			
16									640.8		557.4	–	1			
17									652.8		594.4	–	1			
18									663.7		630.2	–	1			

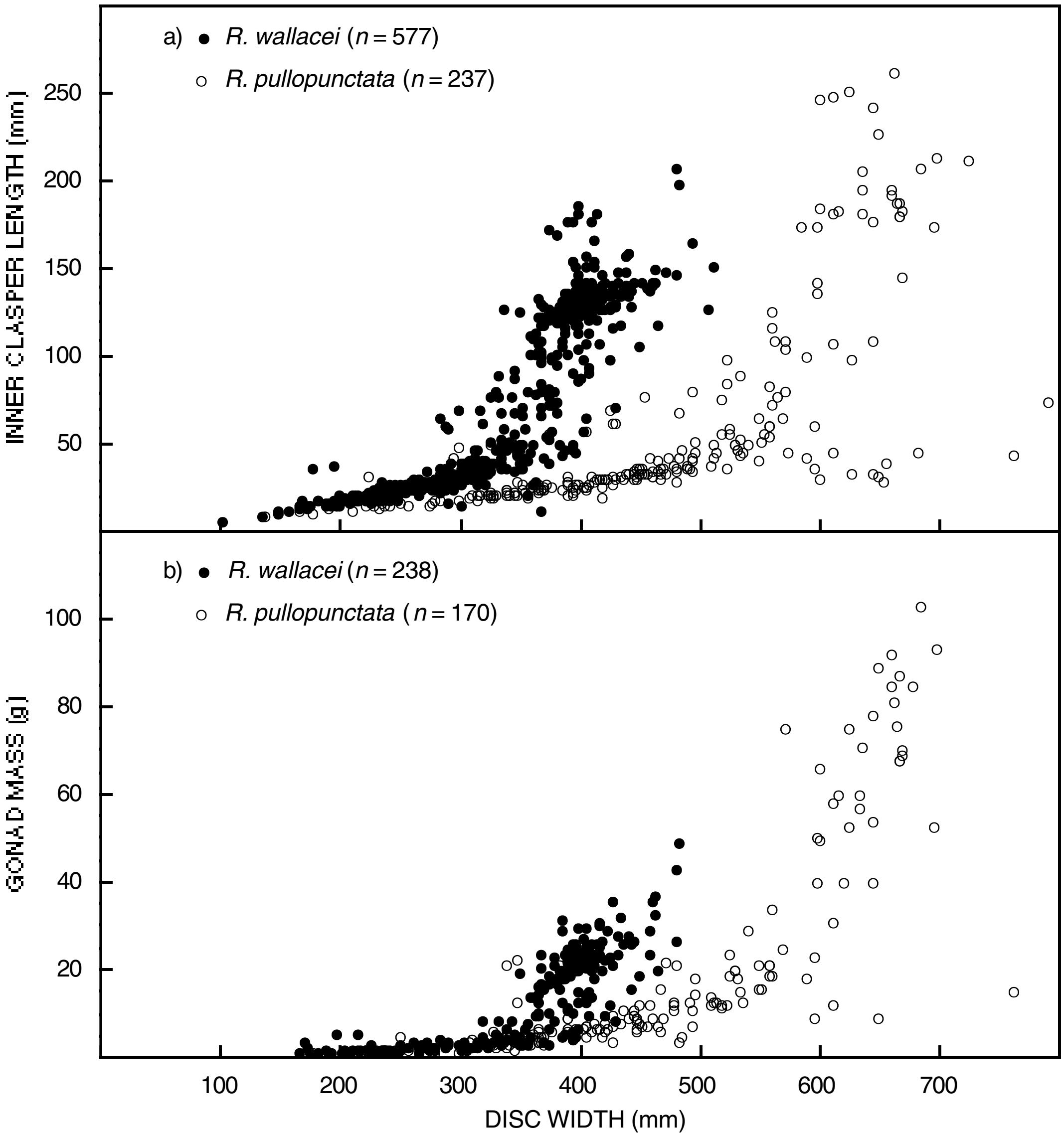

Fig. 5: Relationship between (a) inner clasper length and (b) gonad mass and disc width for male *R. wallacei* and *R. pullopunctata*

the visual maturity stages (Table I). Sperm was found in all maturity stages. Because of problems with the histological sections, the presence of a functional efferent duct could not be discerned. During the embedding process, the wax did not fully penetrate the gonad tissue, despite the process taking place in a vacuum. As a result, the xylene evaporated during sectioning and the remaining tissue became hard and crumbled. For both species, the proportion of follicles containing sperm markedly increased with increasing maturity stage (Fig. 8). Sperm was present in only 9% of follicles in immature *R. wallacei*, compared with 60% in mature animals. A similar trend was found for *R. pullopunctata*.

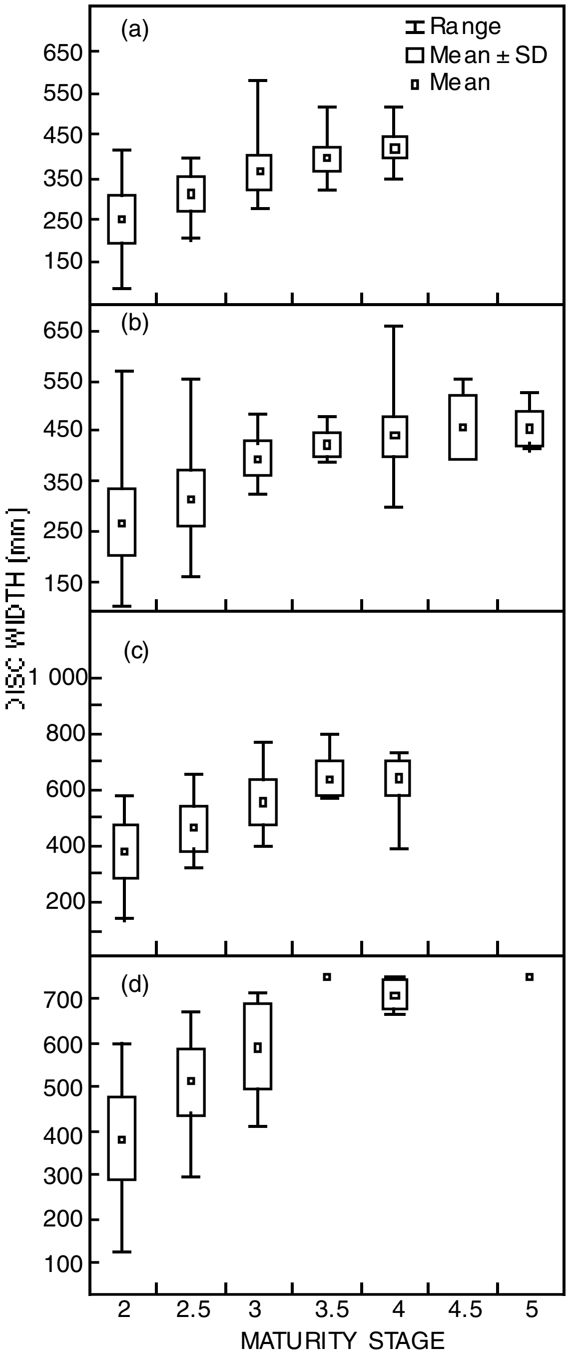

Fig. 6: Box and whisker plot of the relationship between disc width and maturity stage for (a) male and (b) female *R. wallacei* and (c) male and (d) female *R. pullopunctata*

There was rapid gonad growth at the onset of maturity in females (Fig. 9), at around 350 mm *DW* for *R. wallacei* and 650 mm *DW* for *R. pullopunctata*. The smallest mature female was 297 mm *DW* for *R. wallacei* and 658 mm *DW* for *R. pullopunctata*, both smaller than their male counterparts. The onset and rate of *R. wallacei* maturity was not significantly different between sexes ($p > 0.05$). Female *R. wallacei* reach 50% maturity at 400 mm *DW*, at approximately 9 years of age. Length-at-50% maturity for female *R. pullopunctata* was estimated to be between 681 and 700 mm *DW*.

Egg cases were not found in *R. pullopunctata*. However, 25 cases were found in *R. wallacei*, five in March, seven in April and 13 in May, suggesting that they lay their eggs in autumn. Pregnant *R. wallacei* were found on the Agulhas Bank in water 50–200 m deep. Examination of the egg cases within the uterus indicated that the anterior end of the egg case forms first. A single egg was found in all egg cases examined. There was no evidence of sperm storage in the histological sections of mature female *R. wallacei*.

Feeding

Stomachs from 137 *R. wallacei* (119–574 mm DW) were examined (81 and 56 from research and commercial trawls respectively). The food composition from the stomachs of research- and commercially caught fish is shown in Table V. The contribution of the 13 prey groups to the research-caught skate differed significantly ($p < 0.05$) from that of the commercially caught fish, in terms of percentage frequency of occurrence ($\chi^2 = 41.67$, $df = 12$) and percentage volume of prey ($\chi^2 = 91.42$, $df = 12$), but not in terms of percentage mass ($\chi^2 = 30.14$, $df = 12$).

The anomuran *Upogebia capensis* was prominent in the diet of commercially caught fish, being present in the stomachs of 21% of fish examined and contributing 3.3% by mass to the diet. However, it was absent in the stomach of research-caught fish. Also, mysids were frequent prey items in research-caught fish (occurring in 27.2% of stomachs), but virtually absent in commercial samples (occurring in only 1.8% of stomachs). The crab *Mursia cristimanus* was more frequent in research-caught samples than in those caught commercially, but their dietary importance was similar in terms of percentage mass and volume. The conger *Gnathophis* sp. dominated the diet by mass and volume in both research- and commercially caught animals. The importance of such smaller teleosts as the dragonet *Paracallionymus costatus* and the codlet *Bregmatoceros macclellandii* was greatest in the diet of research-caught fish.

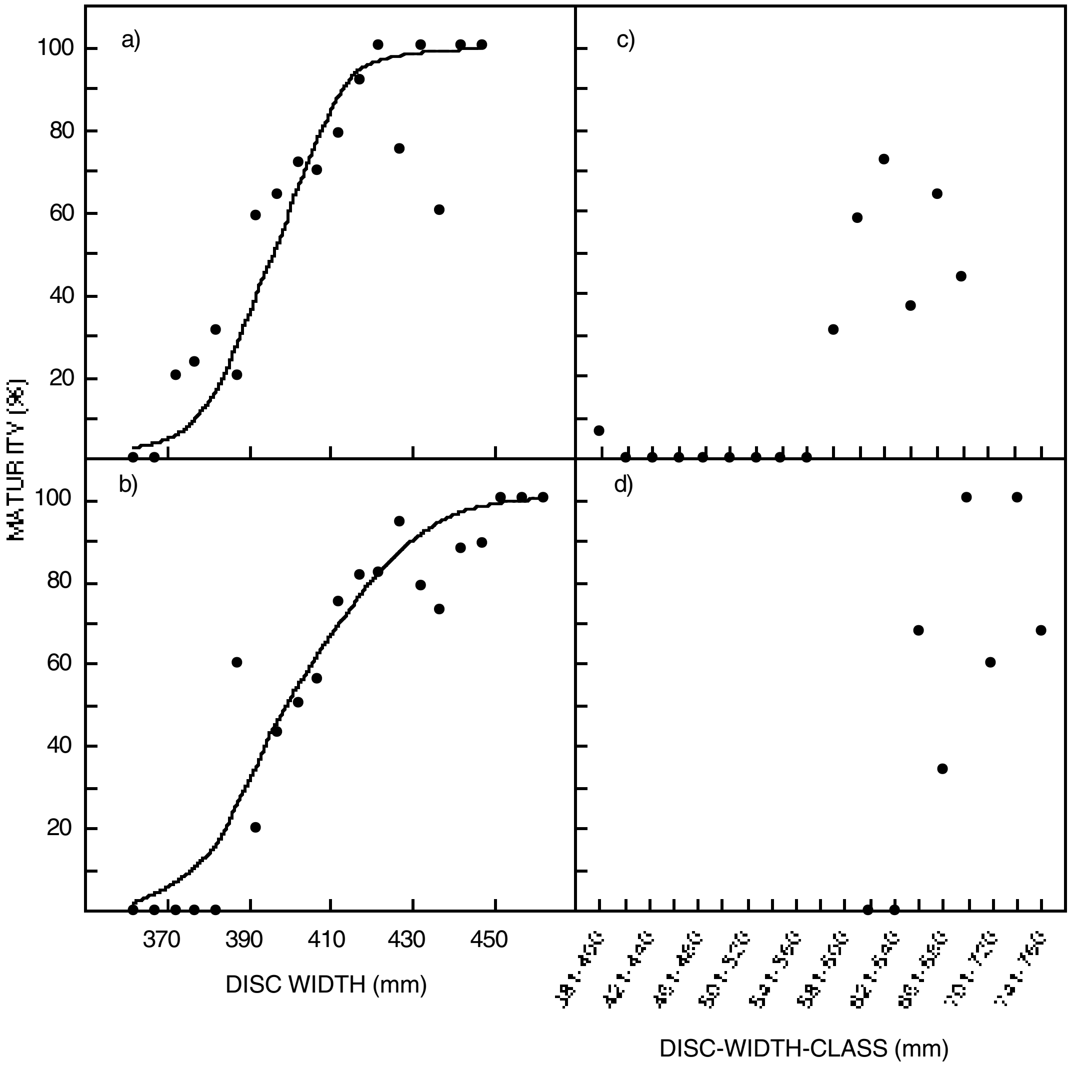

Fig. 7: Length-at-maturity ogives for (a) male and (b) female *R. wallacei*, and the relationship between disc-width-class and percentage maturity for (c) male and (d) female *R. pullopunctata*

DISCUSSION

Reading bands within the vertebral centra is the only effective method available for ageing skates. However, precision is dependent on the ease with which the bands can be read accurately. The success of enhancement techniques is highly species specific. Abdel-Aziz (1992) reported that 1% silver nitrate enhanced the rings on unsectioned vertebrae of *R. miraletus*, whereas Holden and Vince (1973) used reflected light on whole *R. clavata* centra to aid reading bands. Natanson (1993) used haematoxylin to stain sectioned vertebrae of *R. erinacea* and Waring (1984) used paraffin wax, calcium oxide powder and decolouring carbon to enhance bands in sectioned centra of that

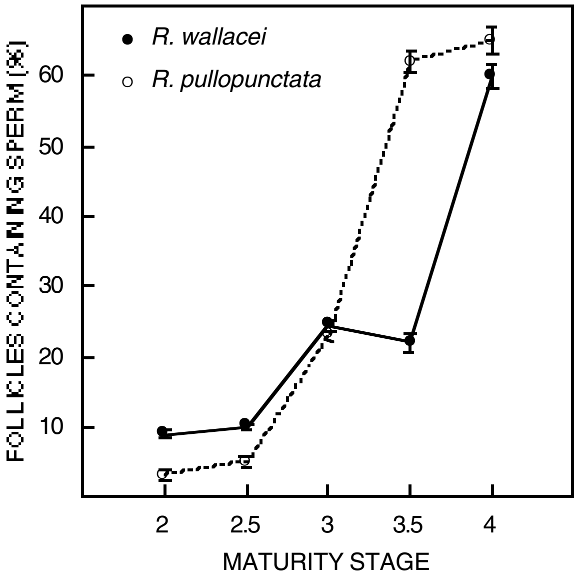

Fig. 8: Percentage of seminal follicles containing sperm at different stages of maturity for male *R. wallacei* and *R. pullopunctata*. Vertical bars indicate standard errors

species.

It was not possible to validate the periodicity of growth bands for *R. wallacei* and *R. pullopunctata* because of the paucity of marginal increment data for all months of the year. Studies on other temperate skate species indicate that one opaque and translucent band is laid down per year (Holden and Vince 1973, Waring 1984, Natanson 1993, Abdel-Aziz 1992).

Growth rate in *R. wallacei* and *R. pullopunctata* differed between sexes, a common feature in *Raja* species (Table VI). Females typically attain a larger size than males, but they grow more slowly. This is likely a consequence of their different reproductive strategies; females grow larger to hold the egg cases within the body cavity and males grow faster to reach sexual maturity. This study showed that male *R. wallacei* obtain sexual maturity earlier than females.

The L_∞ value of 1 326.75 mm *DW* (1 903.4 mm *TL*) for female *R. pullopunctata* was large compared to those calculated for other skate species (Table VI). The L_∞ value obtained was also higher than the maximum disc width recorded in this study and that reported for *R. pullopunctata* by Compagno *et al*. (1989). It is likely that the small sample size and the rareness of large individuals examined in this study resulted in an overestimation of L_∞ The combined L_∞ value

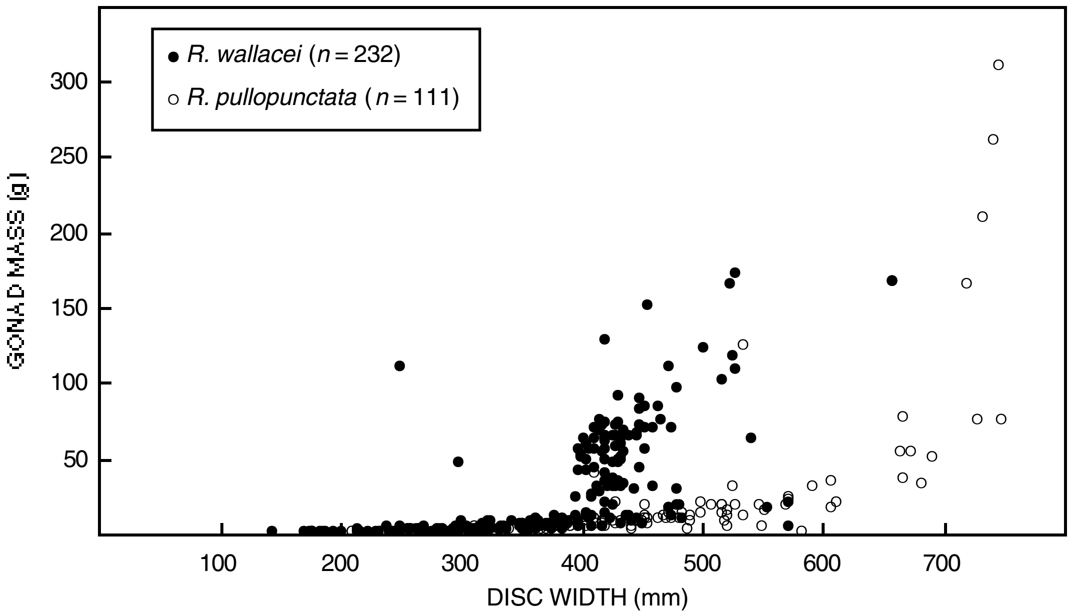

Fig. 9: Relationship between gonad mass and disc width for female *R. wallacei* and *R. pullopunctata*

Table V: Stomach contents of research- and commercially caught *R wallacei* from the Agulhas Bank, expressed as percentage frequency of occurrence (%*FO*), percentage volume (%*V*) and percentage mass of prey (%*M*)

	Research-caught (n = 81)			Commercially caught (n = 56)		
	%*FO*	%*V*	%*M*	%*FO*	%*V*	%*M*
Nematoda	1.23	0.35	0.01	3.57	0.03	0.00
Annelida						
Polychaeta	22.22	3.86	0.80	26.79	4.09	0.21
Arthropoda						
Crustacea						
Crustacean remains	20.99	3.44	0.37	8.93	1.19	0.97
Stomatopoda						
Pterygosquilla armata capensis	0.62	0.62	0.05	1.79	0.45	0.08
Anomura						
Upogebia capensis				21.40	12.30	3.26
Amphipoda						
Amphipod remains	7.41	0.44	0.04	2.12	0.17	0.00
Ampelisca capensis	9.88	0.33	0.02	1.80	1.70	0.10
Unidentified white amphipod	3.70	0.18	0.12			
Gammaridae				1.80	0.20	0.04
Paramoera capensis	2.47	0.02	0.01			
Isopoda						
Isopod remains	4.93	0.41	0.08	5.36	0.57	0.10
Eurydice longicornis	3.70	0.52	0.07			
Mysidacea						
Unidentified mysids	27.16	13.68	1.21	1.78	0.40	0.00
Caridae						
Shrimp remains	6.19	0.68	0.07	5.36	0.31	0.04
Unidentified shrimp	9.88	2.55	0.57	3.57	1.87	0.70
Leptochela robustus	3.70	1.36	0.09			
Pandalina brevirostris	1.23	0.81	0.73			
Pontophilus sculptus	9.88	2.85	0.27	1.79	1.79	0.51
Brachyuridae						
Decapod remains	6.17	1.66	0.36	5.36	2.61	0.18
Mursia cristimanus	16.05	3.39	0.63	5.36	2.92	0.77
Scyllarides elizabethae	1.23	0.40	0.14			
Goneplax angulata	2.47	0.21	0.30			
Megalopa	6.17	0.54	0.03			
Mollusca						
Ostracoda				1.79	0.00	0.00
Bivalvia	2.47	0.10	0.02	1.79	0.26	0.57
Gastropoda	2.47	0.30	0.11			
Cephalopoda	3.70	0.91	1.49	3.57	0.43	0.00
Chordata						
Chondrichthyes						
Squalus sp.				3.57	0.94	4.63
Raja pullopunctata				1.79	1.12	0.75
Egg case				1.79	0.49	0.03
Teleostei						
Teleost remains	25.93	11.01	8.25	50.00	23.26	9.53
Paracallionymus costatus	25.93	11.02	9.72	1.79	1.43	0.35
Gnathophis sp.	28.40	17.00	55.16	39.29	32.42	52.57
Bregmatoceros macclellandii	14.82	2.09	0.12			
Pleuronectiformes	6.17	3.01	3.67	5.36	2.69	4.40
Anguilliformes				1.79	0.85	4.54
Cynoglossus zanzibarensis	1.23	1.21	8.36			
Sardinops sagax head	1.23	0.91	2.02	10.71	1.15	14.77
Sardinops sagax tail	1.23	0.63	1.67			
Amorphous material	35.81	12.96	2.63	30.58	3.91	1.61

Table VI: Comparison of the Von Bertalanffy growth function parameters for various *Raja* species from different studies

Species	Source	Region	Sex	L_∞	K	t_0	ϕ'	t_{max}
R. brachyura	Clarke (1922)	Plymouth, English Channel	M	138.90	0.12	−1.52	3.36	23.45
			F	118.40	0.19	−0.80	3.43	14.99
R. clavata			M	85.60	0.21	−0.60	3.19	15.23
			F	128.10	0.09	−1.32	3.17	31.97
R. montagui			M	68.70	0.19	−0.56	2.95	13.69
			F	72.80	0.18	−0.37	2.98	22.48
R. brachyura	Holden (1972)	Bristol Channel, Irish Sea	M	115.00	0.19	−0.80	3.40	14.99
			F	118.40	0.19	−0.80	3.43	14.99
R. clavata			M	85.60	0.21	−0.60	3.19	15.23
			F	107.00	0.13	−0.60	3.17	16.30
R. montagui			M	68.70	0.19	−0.56	2.95	13.69
			F	72.80	0.18	−0.37	2.98	22.48
R. batis	Du Buit (1977)	Celtic Sea		253.70	0.06	−1.63	3.56	51.00
R. naevus				91.64	0.09	−0.47	2.85	27.18
R. clavata	Ryland and Ajayi (1984)	Carmarthen Bay		139.77	0.09	−2.63	3.25	22.90
R. microocellata				137.00	0.09	−3.01	3.21	23.92
R. montagui				98.70	0.16	−1.72	3.18	13.61
R. erinacea	Waring (1984)	US North-East Coast		52.73	0.35	−0.45	2.99	8.06
R. clavata	Brander and Palmer (1985)	North-East Irish Sea		105.00	0.22	−0.45	3.37	14.40
R. miraletus	Abdel-Aziz (1992)	Mediterranean Sea	M	87.87	0.19	−0.50	3.17	15.00
			F	91.92	0.17	−0.25	3.16	17.20
R. wallacei	This study	Agulhas Bank	M	66.78	0.27	−0.08	3.08	11.10
			F	70.68	0.26	−0.21	3.11	11.54
R. pullopunctata			M	102.66	0.10	−2.37	3.01	28.52
			F	190.34	0.05	−2.20	3.23	61.55

t_{max} = The theoretical maximum age
ϕ' = LogK + 2 Log L_∞

of 873.24 mm *DW* (1 334.30 mm *TL*) for male and female *R. pullopunctata* is lower and a more realistic estimate.

Back-calculated values of disc-width-at-age compare favourably with those obtained using growth parameters, although the back-calculated values underestimated disc width for younger individuals and overestimated disc width for older individuals. This concurs with the belief that the t_{max} values typically show that larger species have a longer lifespan than smaller species and that females live longer than males (Holden 1972, Du Buit 1977).

All skates are oviparous, showing similar patterns of gonad development, spawning behaviour and embryonic development to other skates worldwide (Luer and Gilbert 1991). That sperm production was found in immature males of both *R. wallacei* and *R. pullopunctata* before the secondary sexual characteristics were developed is puzzling. It is unclear whether sperm produced by immature skates degenerates or is stored in the seminal vesicles until maturity. Given that visual examination of immature seminal vesicles showed no evidence of sperm storage before the development of secondary sexual characteristics, and that no functional efferent ducts were found, it is likely that sperm was reabsorbed. However, there was no evidence to support this assumption in the animals under study.

Skates are capable of reproducing all year round (Clemens and Wilby 1961, McEachran 1970, Du Buit 1976). For *R. wallacei*, mature ova were noted throughout the year, but egg cases were found only between March and May. No uterine wounds were noted for either species. The scarcity of data for all months of the year prohibited an accurate determination of the spawning period of *R. wallacei*.

Ovulation in *R. wallacei* occurs when the egg case is one-third formed. This is similar to the ovulation in little skate *R. erinacea* (Richards *et al*. 1963), but contrasts with that of the thorny skate *R. radiata*, in which ovulation occurs when the egg case is fully formed (Templeman 1982). Egg case formation in *R. wallacei* begins at the anterior end, as in *R. erinacea* and *R. eglanteria* (Fitz and Daiber 1963), whereas development of the egg case in *Bathyraja aleutica* begins at the posterior end (Teshima and Tomonaga 1986). The egg cases of *R. wallacei* contained a single egg, which is common in most other skate species (Richards *et al*.

1963, Du Buit 1976, Teshima and Tomonaga 1986), except for *R. binoculata*, whose egg cases contain more than one egg (Hitz 1964, cited in Teshima and Tomonaga 1986). Richards *et al*. (1963) reported that, in the rare instances of an egg case containing two eggs, its twin was empty.

The dorso-ventrally flattened body and ventrally situated mouth of skates are characteristic of bottom-dwelling fish. *R. wallacei* fed primarily on benthic teleosts and crustaceans, shifting their diet to larger species with increasing size, a feeding pattern found in other skate species, both in South African waters (Ebert *et al*. 1991) and elsewhere (McEachran *et al*. 1976, Macpherson 1986, Berestovskii 1990, Pedersen 1995).

The present result showed significant differences in the diet between research- and commercially caught *R. wallacei* on the Agulhas Bank. The dietary difference could be a result of a number of factors, such as different substrata or modification of the benthos as a result of commercial trawling (Jones 1992). However, inadequate knowledge of these factors precludes further speculation. It is probable that a combination of several factors is responsible for the differences observed.

Elasmobranchs are characteristically long-lived and exhibit slow growth (Beamish and McFarlane 1985), and skates are no exception. Slow growth, especially when combined with reproductive strategies in which few well-developed young are produced, are important considerations when evaluating the potential impact that a fishery might have on local skate populations.

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