

Aspects of the reproductive biology of skates (Chondrichthyes: Rajiformes: Rajoidei) from southern Africa

David A. Ebert, Leonard J. V. Compagno, and Paul D. Cowley

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New information is presented on the reproductive biology of 22 southern African skate species. Sex ratios for most species were relatively even. Sexual dimorphic differences in disc shape were evident in all species, but the total length (L_T) to disc width (D) relationship was significantly different in only three species, and the L_T to weight (W) relationship significant in just five species. Sexual dimorphism relative to maximum total length (L_{Tmax}) was absent in all but the two largest species. Males and females of the same species grow to a similar L_{Tmax} except those whose L_{Tmax} is > 1.5 m L_T . Size at first and 50% (L_{T50}) sexual maturity was approximately the same for both sexes in all but the two largest species. First maturity occurred at $> 60\%$ of L_{Tmax} for all species for which sufficient data were available, and most ($n = 18$) matured at $> 75\%$ L_{Tmax} . The large size at maturity relative to L_{Tmax} suggests that growth slows or is partially suspended following sexual maturity. The egg cases of 15 species are described, and a key to their identification is presented. Egg cases *in utero* were observed throughout the year suggesting that most species reproduce year-round.

Keywords: egg cases, maturity, oviparity, Rajiformes, sexual dimorphism.

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D. A. Ebert: Pacific Shark Research Center, Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA. L. J. V. Compagno: Shark Research Centre, Iziko—South African Museum, PO Box 91, Cape Town 8000, South Africa. P. D. Cowley: South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa. Correspondence to D. A. Ebert: tel: +1 831 7714427; fax +1 831 6324403; e-mail: debert@mlml.calstate.edu

Introduction

Skates, like other chondrichthyans, exhibit life history characteristics, such as slow growth, late attainment of sexual maturity, long lifespan, and low fecundity (Holden, 1973, 1974, 1977; Walker and Heessen, 1996), that may make them vulnerable to over-exploitation (Dulvy *et al.*, 2000; Stevens *et al.*, 2000; Dulvy and Reynolds, 2002). However, this diverse batoid group has received very little research relative to the shark-like fish that are the target of major fisheries worldwide (Bonfil, 1994; FAO FishStat, 2006). Skates have become a concern because of the regularity and volume with which they are taken as bycatch in groundfish fisheries or as a directed fishery (Walker and Heessen, 1996; Walker, 1998; Walker and Hislop, 1998; Zorzi *et al.*, 2001; Gaichas *et al.*, 2003; Matta *et al.*, 2006). They are especially vulnerable to groundfish fisheries because of their generally large size and demersal existence. Although information from southern Africa is limited, Walmsley-Hart *et al.* (1999) reported that skates were present in 88% of all commercial trawl landings.

Southern Africa has one of the most diverse chondrichthyan faunas in the world, comprising some 46 families, 106 genera, and 210 species (Compagno *et al.*, 1989; Compagno, 1999). Of this total, skate species (Chondrichthyes: Rajiformes: Rajoidei) constitute ~ 12.3 – 12.6% ($n = 28$), including at least 15 species endemic to southern Africa (Compagno and Ebert, 2007). Moreover, some 11.4% of all skate species are found in southern African waters (Ebert and Compagno, 2007).

Despite their abundance and diversity (Compagno and Ebert, 2007), the skates of this region are poorly known biologically although they are a common and important component of the demersal fish community (Macpherson and Roel, 1987; Roel, 1987; Macpherson and Gordo, 1992; Ebert and Bizzarro, 2007). Information on critical life history parameters such as age and growth or reproduction is limited, although Walmsley-Hart *et al.* (1999) studied the age, growth, and reproductive biology of two skates, *Dipturus pullopunctata* and *Leucoraja wallacei*, commonly caught by hake-directed trawlers operating on the Agulhas Bank. However, most studies have concentrated on distribution, taxonomy (Wallace, 1967; Hulley, 1970, 1972; Compagno *et al.*, 1991; Stehmann, 1995; Compagno, 1999; Compagno and Ebert, 2007), and to a limited extent diet (Ebert *et al.*, 1991; Smale and Cowley, 1992; Walmsley-Hart *et al.*, 1999).

Given the paucity of published information, increasing bycatch concerns, and the life history characteristics that skates exhibit, data were collected during groundfish surveys and at beach-angling competitions along the southern African coast. This paper is part of a series on the biology of cartilaginous fish found around the coastal and offshore waters of southern Africa. Here, we report on aspects of the reproductive biology of 22 skate species. In addition, the egg cases of 15 species encountered either *in situ* or *in utero* during the study are described and were used to develop a taxonomic key for identifying individual species.

Material and methods

Field sampling

The survey area extended from central Namibia to southern Mozambique (Figure 1) and was subdivided into three regions, referred to as the west coast, the south coast, and the east coast. Most sampling within these regions was concentrated on the west and south coasts, with occasional surveys to the east coast, in conjunction with the annual hake surveys conducted by the South African Department of Environment Affairs and Tourism's Marine and Coastal Management (MCM) section, with the FRS "Africana".

The west coast survey area between 1985 and 1990 extended from Walvis Bay, Namibia (23°S 14°E) to Cape Agulhas, South Africa (36°S 20°E) between 50 and 1016 m deep, with most trawls being conducted shallower than 500 m. During those six years, an annual summer and a winter survey cruise were conducted. Starting in 1991 only a summer cruise was conducted and the survey area ranged from the international border with Namibia and South Africa (ca. 29°S) to Cape Agulhas.

The south coast survey area extended from Cape Agulhas to about Port Elizabeth (ca. 26°E) out to 200 m. For some surveys the upper continental slope between 200 and 500 m was included. The south coast surveys were conducted in autumn and/or spring, with generally one or two surveys per year.

A random stratified sampling design of the west and south coasts was made by means of at least 2800 pre-determined bottom trawl stations, of which at least 2280 stations had skate station records. The gear used was a 60-m German bottom trawl. Payne *et al.* (1984, 1985) provide a detailed description of the gear deployment and the basic methodology for station selection. Additional skates were collected on 14 longline stations set from RV "Sardinops" on the south coast and by commercial

bottom trawlers including FV "Iris" and FV "Boulonnais" off the west coast (37 skate stations).

East coast skate data were provided by RV "Benguela" off KwaZulu-Natal (12 skate stations), and by RV "Algoa" off Mozambique (40 skate stations). Several nearshore species were opportunistically collected at beach-angling competitions, and where possible biological data were collected from them. Furthermore, museum specimens for several of the less common species were examined for reproductive status. Data from both these sources were intended to augment reproductive data collected from the survey cruises. In all, 3534 skates belonging to 22 species were examined during the study.

Biological data

The sex, maturity, total length (L_T), and disc width (D) were recorded. The number and proportion of adults, adolescents, and juveniles of each sex were analysed using a χ^2 test with Yates correction to determine whether the observed sex ratios deviated significantly within species from the expected ratio of 1:1 (Zar, 1996). Measurements for L_T and D were made in a straight line with the skate lying in its natural position. The relationship between L_T and D are described (Table 1) by the equation $D = aL_T^b$, where D is the disc width, L_T the total length, and a and b are fitted constants (Ricker, 1973). To evaluate differences in $L_T - D$ relationships between males and females, linear regression coefficients were calculated and compared by ANCOVA to determine if there were any differences (Ricker, 1973). The $L_T - D$ relationships between males and between females for four species (*Cruriraja parcomaculata*, *D. pullopunctata*, *L. wallacei*, and *Raja straeleni*) commonly found on both the west and south coasts were also compared to determine whether there were any differences between specimens of each species in these two

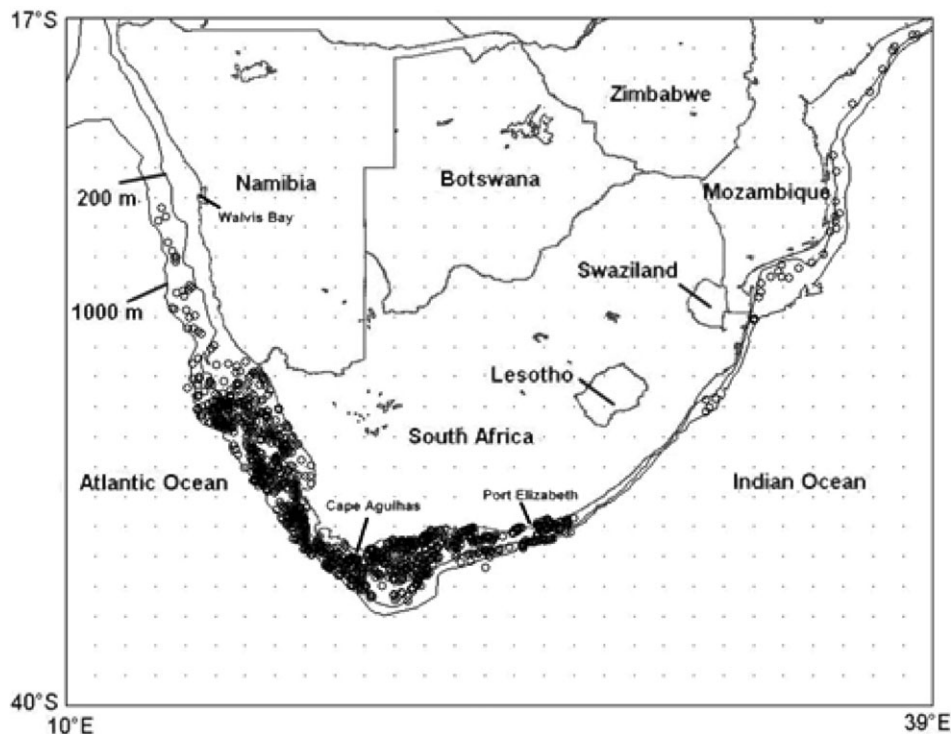


Figure 1. Map of the southern African survey area.

Table 1. The L_T – D and L_T – W equations for 22 species of southern African skates.

Common name	Species	n	L_T to D equation	r^2	L_T to W equation	r^2	
African softnose skate	<i>Bathyraja smithii</i>	Male	82	$D = 0.6988(L_T) + 0.334$	0.99	$W = (0.0024) L_T^{1.6548}$	0.75
		Female	118	$D = 0.7186(L_T) - 0.476$	0.99	$W = (0.0003) L_T^{1.132}$	0.73
Roughnose skate	<i>Cruriraja 'parcomaculata'</i> west coast	Male	92	$D = 0.5788(L_T) - 0.0358$	0.97	$W = (9 \times 10^{-06}) L_T^{2.755}$	0.87
		Female	61	$D = 0.5888(L_T) - 0.4935$	0.99	$W = (4 \times 10^{-05}) L_T^{2.3891}$	0.65
	<i>C. 'parcomaculata'</i> south coast	Male	44	$D = 0.566(L_T) + 0.0919$	0.93	$W = (1 \times 10^{-05}) L_T^{2.733}$	0.98
		Female	59	$D = 0.5862(L_T) - 0.2501$	0.99	$W = (6 \times 10^{-06}) L_T^{2.9447}$	0.80
Triangular skate	<i>C. 'triangularis'</i>	Male	48	$D = 0.6057(L_T) - 1.2764$	0.99	$W = (4 \times 10^{-06}) L_T^{2.8906}$	0.96
		Female	35	$D = 0.604(L_T) - 0.8482$	0.94	$W = (3 \times 10^{-06}) L_T^{3.008}$	0.95
Slime skate	<i>Dipturus pullopunctata</i> west coast	Male	120	$D = 0.6704(L_T) + 3.47$	0.99	$W = (2 \times 10^{-06}) L_T^{3.3005}$	0.98
		Female	89	$D = 0.6876(L_T) + 3.12$	0.99	$W = (2 \times 10^{-06}) L_T^{3.2829}$	0.98
	<i>D. pullopunctata</i> south coast	Male	54	$D = 0.675(L_T) + 2.5085$	0.99	$W = (9 \times 10^{-06}) L_T^{2.9428}$	0.97
		Female	69	$D = 0.6937(L_T) + 2.4824$	0.87	$W = (1 \times 10^{-05}) L_T^{2.8042}$	0.85
Roughbelly skate	<i>D. springeri</i>	Male	24	$D = 0.7711(L_T) + 1.661$	0.99	$W = (4 \times 10^{-06}) L_T^{3.0551}$	0.99
		Female	21	$D = 0.7637(L_T) + 1.5536$	0.99	$W = (2 \times 10^{-06}) L_T^{3.1665}$	0.99
Prownose skate	<i>D. stenorhynchus</i>	Male	22	$D = 0.687(L_T) - 1.3356$	0.99	–	–
		Female	9	$D = 0.7179(L_T) - 2.0151$	0.96	–	–
Yellowspot skate	<i>Leucoraja wallacei</i> west coast	Male	61	$D = 0.6418(L_T) - 2.7275$	0.98	$W = (1 \times 10^{-06}) L_T^{3.3999}$	0.98
		Female	96	$D = 0.6325(L_T) - 2.1132$	0.98	$W = (1 \times 10^{-06}) L_T^{3.4266}$	0.97
	<i>L. wallacei</i> south coast	Male	137	$D = 0.6164(L_T) - 1.0763$	0.99	$W = (2 \times 10^{-05}) L_T^{2.6986}$	0.93
		Female	110	$D = 0.6349(L_T) - 1.961$	0.99	$W = (2 \times 10^{-06}) L_T^{3.3323}$	0.99
Roughskin skate	<i>Malacoraja spinacidermis</i>	Male	16	$D = 0.678(L_T) - 0.3087$	0.96	–	–
		Female	14	$D = 0.7147(L_T) - 1.7024$	0.99	–	–
African dwarf skate	<i>Neoraja stehmanni</i>	Male	58	$D = 0.5107(L_T) + 2.0543$	0.78	$W = (4 \times 10^{-5}) L_T^{2.9691}$	0.92
		Female	63	$D = 0.2422(L_T) + 9.8429$	0.16	$W = (2 \times 10^{-7}) L_T^{4.5066}$	0.96
Twineyed skate	<i>Raja miraletus</i>	Male	55	$D = 0.601(L_T) + 2.7229$	0.96	$W = (3 \times 10^{-7}) L_T^{3.8094}$	0.89
		Female	63	$D = 0.6765(L_T) + .3632$	0.96	$W = (7 \times 10^{-7}) L_T^{3.5555}$	0.96
Biscuit skate	<i>R. straeleni</i> west coast	Male	238	$D = 0.6606(L_T) + 3.0839$	0.96	$W = (9 \times 10^{-06}) L_T^{2.9433}$	0.85
		Female	401	$D = 0.7503(L_T) - 0.109$	0.98	$W = (7 \times 10^{07}) L_T^{3.6023}$	0.96
	<i>R. straeleni</i> south coast	Male	261	$D = 0.6696(L_T) + 2.0204$	0.98	$W = (3 \times 10^{-06}) L_T^{3.1826}$	0.98
		Female	237	$D = 0.7482(L_T) - 0.5422$	0.98	$W = (5 \times 10^{-06}) L_T^{3.0531}$	0.96
Bigthorn skate	<i>Rajella barnardi</i>	Male	80	$D = 0.6791(L_T) - 4.234$	0.93	$W = (2 \times 10^{-06}) L_T^{3.2848}$	0.95
		Female	78	$D = 0.619(L_T) - 1.5935$	0.97	$W = (6 \times 10^{-06}) L_T^{2.9534}$	0.9
Munchkin skate	<i>R. caudaspinosa</i>	Male	54	$D = 0.6251(L_T) - 2.786$	0.86	$W = (0.0004) L_T^{1.8976}$	0.84
		Female	40	$D = 0.5984(L_T) - 2.0073$	0.94	$W = (2 \times 10^{-06}) L_T^{3.2252}$	0.97
Ghost skate	<i>R. dissimilis</i>	Male	50	$D = 0.6224(L_T) - 1.8955$	0.96	$W = (1 \times 10^{-06}) L_T^{3.3693}$	0.96
		Female	35	$D = 0.6205(L_T) - 2.8235$	0.96	$W = (7 \times 10^{-07}) L_T^{3.4447}$	0.98
Leopard skate	<i>R. leopardus</i>	Male	104	$D = 0.7009(L_T) - 3.3393$	0.98	$W = (1 \times 10^{-06}) L_T^{3.3772}$	0.97
		Female	116	$D = 0.6907(L_T) - 3.963$	0.97	$W = (4 \times 10^{-07}) L_T^{3.6298}$	0.98
Spearnose skate	<i>Rostroraja alba</i>	Male	92	$D = 0.7785(L_T) + 0.1811$	0.99	$W = (4 \times 10^{-06}) L_T^{3.0883}$	0.97
		Female	75	$D = 0.7828(L_T) - 0.74$	0.98	$W = (4 \times 10^{-06}) L_T^{3.0971}$	0.96

regions. These were the only species found on at least two coasts in sufficient number for such comparisons. Fish were weighed (W) on a calibrated spring balance, to the nearest 0.1 g. The relationships between L_T and W are described (Table 1) by the equation $W = aL_T^b$, where W is the weight in kg, L_T the total length, and a and b are fitted constants (Ricker, 1973). To determine whether any differences exist between males and females, L_T and W data were log-transformed, and linear regressions were fitted to pairs of observations by sex. ANCOVA was used to test for differences between regression coefficients for L_T and W relationships between males and females (Ricker, 1973), and between regions for each sex.

Maturity was assessed primarily by visual inspection of the reproductive organs, following Ebert (2005). Males were considered to be mature when the claspers were elongated and calcified. Adolescent skates are those whose claspers extend beyond the posterior edge of the pelvic fins, but lack calcification. Juveniles had short, flexible claspers that did not extend beyond the posterior edge of the pelvic fins. The inner clasper length, measured from the point of insertion of the clasper shaft to the clasper tip, was recorded and plotted as a ratio against L_T . An abrupt change in the ratio between clasper length and L_T was considered to indicate maturity. Internally, coiling of the epididymides and development of the testes were also good indicators

of maturation. Mature females were determined by the presence of large, mature oocytes, an oviducal gland that was distinctly differentiated from the uterus, and pendulous posterior portions of the uteri. Adolescent skates had smaller ovaries, with some differentiation, but lacked mature oocytes, the oviducal gland was undeveloped, and the uteri were narrow and constricted. Juveniles lacked differentiation of the ovaries, and the oviducal gland was not differentiated from the uterus (Ebert, 2005). Oviducal gland width was measured and plotted as a ratio against L_T . An abrupt change in the ratio between oviducal gland width and L_T was considered to indicate maturity. Length at 50% (L_{T50}) maturity was calculated for each sex by means of a logistic regression (Roa *et al.*, 1999). For the same four species listed above as common to both coasts, the reproductive parameters size at first and L_{T50} maturity, and maximum size (L_{Tmax}), were calculated separately for each region and compared qualitatively.

Skate egg cases encountered either *in situ* or *in utero* were saved in 10% buffered formaldehyde, and subsequently returned to the laboratory. Following the method described by Ebert and Davis (2007), the egg cases were measured, described, and used to develop a key to the egg cases of southern African skates. The egg cases used in the key were those removed *in utero*, or if collected *in situ* the embryonic development was such that the species could be identified with certainty. If egg cases were trawled and lacked sufficient embryonic development to determine the species, or if the egg case could not be identified to a known species, they were retained but not included in the key.

Results

Amblyraja robertsi (Hulley, 1970)

Only two specimens, both males, were examined during the study; one measured 91.5 cm L_T and was determined to be an adult, the other an adolescent measuring 83.0 L_T . Both were caught during summer at depths of 1150 and 1200 m.

Four egg cases, each with near-term embryos, were trawled during a single haul from 1150 m (Figure 2a). A small external yolk sac was visible on all of them. The egg cases are very large, >130 mm long excluding horns, with a striated surface, posterior and anterior apron widths similar in size, and with broad lateral keels, ca. 12% of maximum egg case width. Horns taper towards tips, and the posterior horns are ca. $1.5 \times$ the length of the anterior horns (Figure 3a).

Bathyrāja smithii (Müller and Henle, 1841)

A total of 200 *B. smithii* was sampled with an overall female:male (F:M) sex ratio of 1:0.69, significantly different from the expected 1:1 ratio ($\chi^2 = 6.13$, d.f. = 1, $p < 0.05$). Comparison by maturity status showed a significant difference between ratios of adults, 1:0.44 ($\chi^2 = 6.94$, d.f. = 1, $p < 0.05$) and juveniles 1:0.63 ($\chi^2 = 6.23$, d.f. = 1, $p < 0.05$). There were 14 adolescent males, but no adolescent females were caught during the study. There was no significant difference between males and females in terms of either L_T-D ($p > 0.05$) or L_T-W ($p > 0.05$) relationships (Table 1).

Males ranged from 12.7 cm to 109.7 cm L_T , and 16 (19.5%) were determined to be mature. Clasper length increased rapidly between 90.0 and 100.0 cm L_T (Figure 4a). The smallest mature individual measured 97.0 cm L_T and the largest immature 95.2 cm L_T . First maturity was at 88.4% of maximum length (L_{Tmax}), and L_{T50} was estimated to be 96.0 cm. Females ranged from 22.5 to 108.6 cm L_T and 36 (30.5%) of those examined

were mature. Oviducal gland width increased between 80 and 90 cm L_T (Figure 4b). The size at first maturity was 87.5 cm L_T or $\sim 80.6\%$ of L_{Tmax} . The largest maturing skate was in the juvenile stage of development and measured 87.5 cm L_T . None of those caught were determined to be in an adolescent phase of development. The length at L_{T50} was estimated to be 87.4 cm.

Partially developing egg cases, one from each uterus, were collected from a 108.0 cm L_T specimen caught on a summer cruise at a depth of 520 m (Figure 2a). One adult male was also caught during the same trawl. This is the only known record of egg cases for this species. As the egg cases were developing, only the posterior halves are described. Egg cases are probably very large, ca. one-third developed (70–79 mm long excluding horns), surface striated, covered with dense fibres, and lateral keels broad and ca. 12% of maximum egg case width. The horns are very long, thin, 160–170 mm long, and taper to a filamentous tip (Figure 3a).

Cruriraja 'parcomaculata' (not von Bonde and Swart, 1924, but *sensu* Smith, 1964, and most subsequent authors); see Compagno and Ebert (2007) for the nomenclature of this apparently undescribed species

In all, 256 *C. 'parcomaculata'* were sampled, 153 from the west coast and 103 from the south coast (Table 1). West coast specimens had an overall sex ratio (F:M) of 1:1.51 that differed significantly from unity ($\chi^2 = 5.88$, d.f. = 1, $p < 0.05$). Comparison of the ratios of adults, adolescents, and juveniles did not show a significant difference ($p > 0.05$) for any one of these groups. The sex ratio of south coast *C. 'parcomaculata'* was not significantly different from the expected 1:1 ratio ($p > 0.05$), and there was no significant difference between the sexes for any of the maturity groups compared.

There was no significant difference ($p > 0.05$) in the L_T-D or L_T-W relationships between males and females for west coast or for south coast specimens (Table 1), nor between west and south coast males or females ($p > 0.05$).

West coast males ranged from 13.6 to 58.0 cm L_T . The smallest mature male measured 46.5 cm L_T and the largest immature male was 47.0 cm L_T . Clasper length increased between 45.0 and 50.0 cm L_T (Figure 5a). In total, 40 (43.5%) mature males were captured, first maturity was at 80.2% of L_{Tmax} , and L_{T50} was estimated at 45.1 cm. South coast males ranged from 9.6 to 53.6 cm L_T , with the smallest mature male measuring 46.5 cm L_T and the largest immature one measuring 47.0 cm L_T . In total, 19 males (43.2%) were determined to be mature, with first maturity relative to L_{Tmax} and L_{T50} estimated at 86.8% and 45.0 cm L_T , respectively. Clasper length for south coast *C. 'parcomaculata'* increased between 45.0 and 50.0 cm L_T (Figure 5b).

West coast females ranged from 12.0 to 59.4 cm L_T , and 25 (41.0%) were determined to be mature. The smallest mature female measured 48.0 cm L_T and the largest immature female measured 49.2 cm L_T . Oviducal gland width increased between 45 and 50 cm L_T (Figure 5c). Except for four individuals, all females >48.0 cm L_T were mature. First maturity was at 80.8% of L_{Tmax} , and L_{T50} was estimated at 48.0 cm. South coast females ranged from 16.5 to 51.9 cm L_T , with the smallest mature female measuring 46.7 cm L_T . In all, 29 (49.2%) individuals were determined to be mature, with first maturity at 90.0% of L_{Tmax} and L_{T50} estimated at 46.1 cm L_T .

Three of 25 west coast adult females (12%) contained a single egg case in each uterus (Figure 2a). Two were caught on

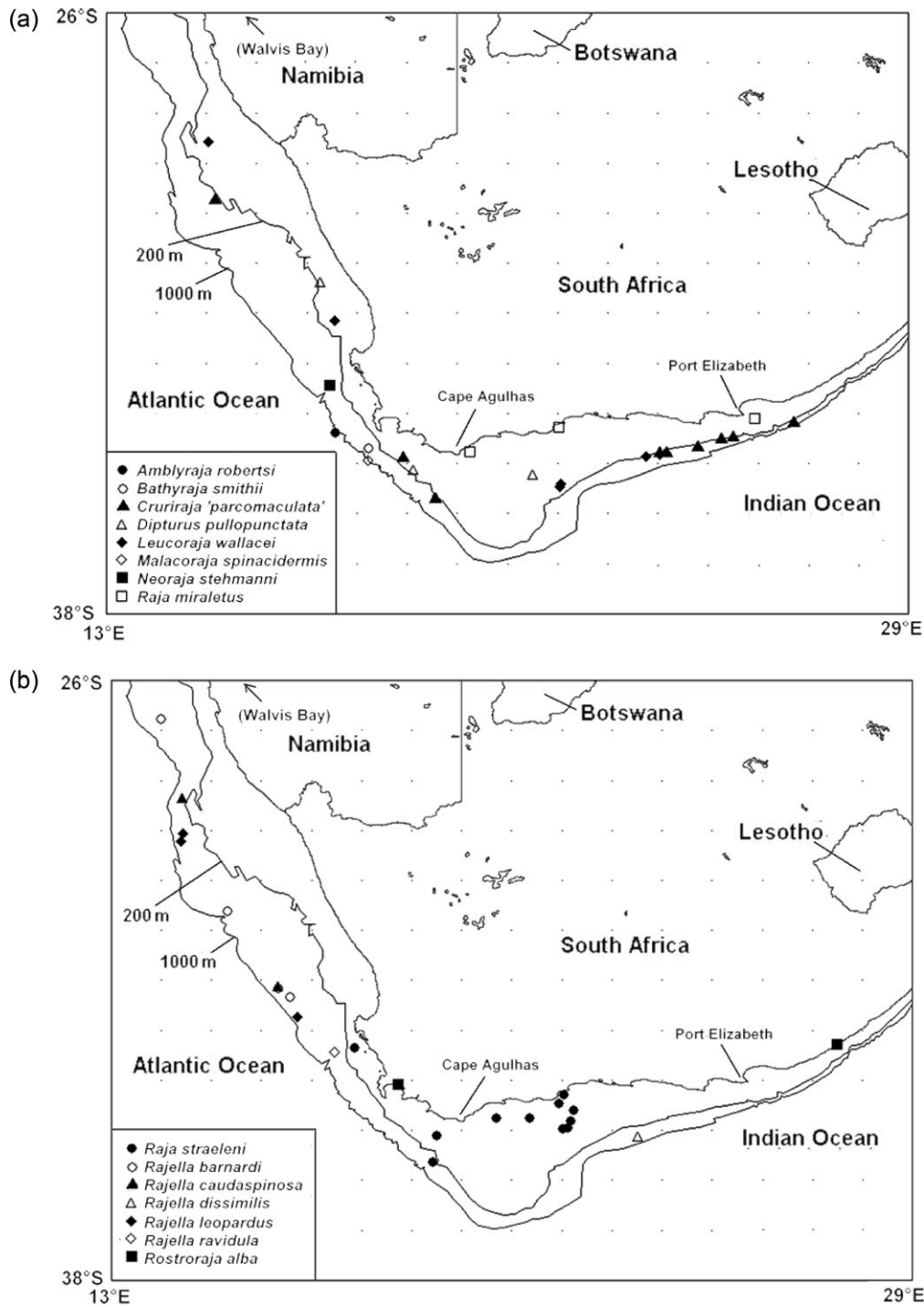


Figure 2. Distribution of skate egg cases for (a) *Amblyraja robertsi*, *Bathyraja smithii*, *Cruriraja 'parcomaculata'*, *Dipturus pullopunctata*, *Leucoraja wallacei*, *Malacoraja spinacidermis*, *Neoraja stehmanni*, and *Raja miraletus*, and (b) *R. straeleni*, *Rajella barnardi*, *R. caudaspinosa*, *R. dissimilis*, *R. leopardus*, *R. ravidula*, and *Rostroraja alba*.

summer cruises and one in winter. The depth at which these gravid skates were caught ranged from 172 to 270 m. Six of 29 adult south coast *C. 'parcomaculata'* (21.7%) were found to contain egg cases *in utero*. Five of them were caught during spring cruises and one on an autumn cruise. The depth at which these egg-bearing skates were caught ranged from 194 to 450 m. In all instances, never more than one gravid skate was caught per trawl on either the west or the south coast.

The egg cases are small, vase-like, measuring <50 mm long excluding horns, the surface coarsely striated, and with very narrow lateral keels, <1% of maximum egg case width. The posterior horns are ca. 45% longer than the anterior horns, tapering to thin tips, curving inwards and with fine attachment fibres; the anterior horns are hook-shaped, with acute tips (Figure 3a). There did not appear to be any visible difference between egg cases from the south and the west coast.

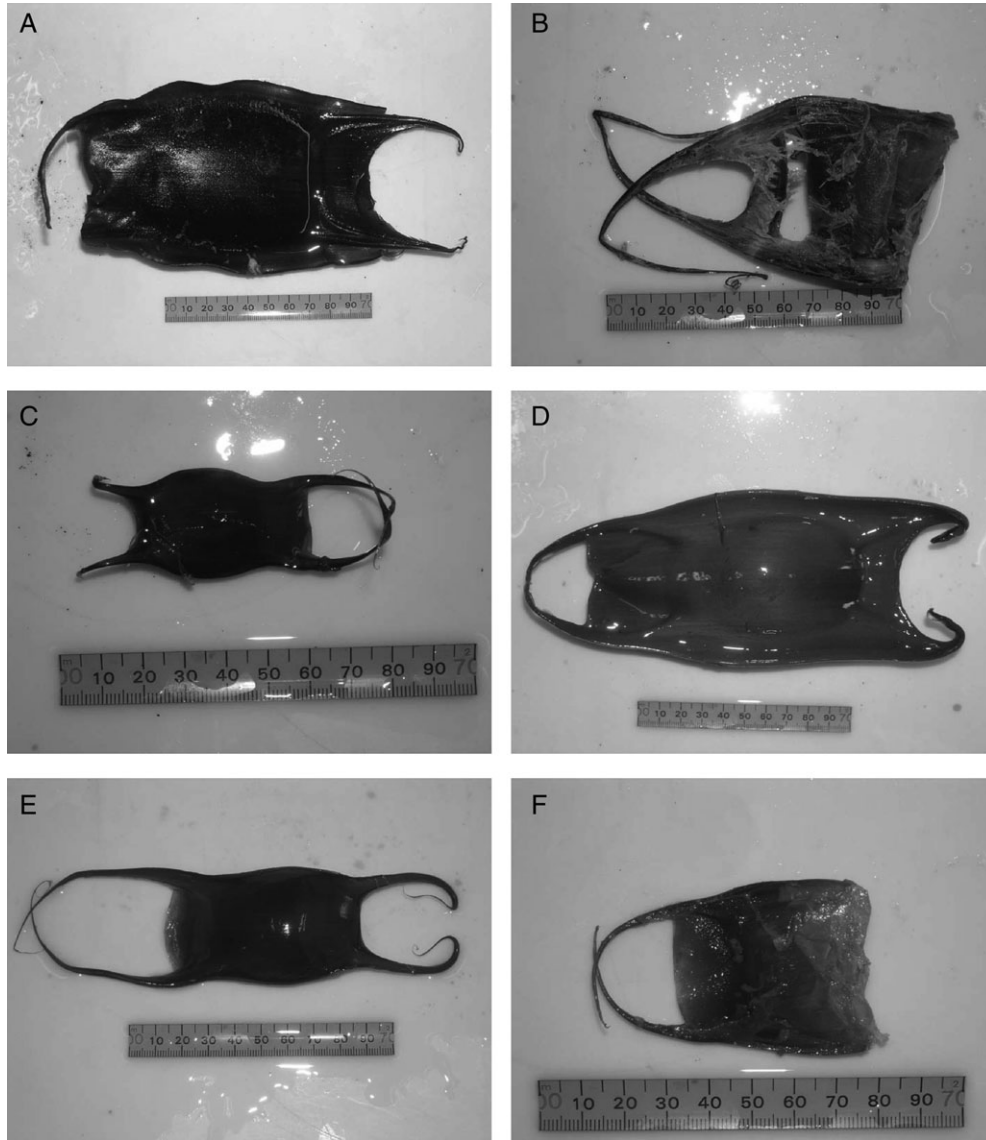


Figure 3a. Egg cases of A *Amblyraja robertsi*, B *Bathyraja smithii*, C *Cruriraja* 'parcomaculata', D *Dipturus pullopunctata*, E *Leucoraja wallacei*, and F *Malacoraja spinacidermis*.

***Cruriraja* 'triangularis' Smith, 1964, =
C. 'parcomaculata' (von Bonde and Swart, 1923);
see Compagno and Ebert (2007)**

A total of 83 *C. 'triangularis'* was sampled with no significant difference from the expected 1:1 sex ratio ($p > 0.05$) for any of the groups compared except adolescents. No adolescent females were collected during the study. Comparison of the L_T - D and L_T - W relationships between the sexes revealed no significant differences ($p > 0.05$) (Table 1).

Males ranged from 9.2 to 39.2 cm L_T . The smallest mature male measured 36.9 cm L_T and the largest immature male was 35.2 cm L_T . Clasper length increased in those individuals >35.0 cm L_T (Figure 6a), and all individuals >36.0 cm L_T were mature. In total, 14 mature males were collected, first maturity was at 94.1% of L_{Tmax} , and L_{T50} was estimated at 35.5 cm L_T .

Females ranged from 18.8 to 42.9 cm L_T . The smallest mature female measured 37.8 cm L_T and the largest immature female

was 32.2 cm L_T . Oviducal gland width increased between 30 and 40 cm L_T (Figure 6b). All females measuring >37.0 cm L_T were mature. In all, 10 (28.6%) mature females were examined, with first maturity at 88.1% of L_{Tmax} , and L_{T50} estimated at 34.5 cm L_T . Egg cases have not been described for this species, and none were found during this study.

***Dipturus campbelli* (Wallace, 1967)**

A total of 13 *D. campbelli* was sampled. Males ranged from 18.2 to 59.5 cm L_T . Eight of ten males examined were mature with the smallest measuring 56.5 cm L_T (Figure 7). The two immature animals measured 18.2 and 20.0 cm L_T . First maturity was at 95.0% L_{Tmax} . Two of three females examined, both measuring 63.5 cm L_T , were mature, and a third, measuring 35.6 cm L_T , was immature. Size at L_{T50} could not be estimated for either sex because of the small sample size. Egg cases are unknown for this species and none were found in either of the two adults examined.

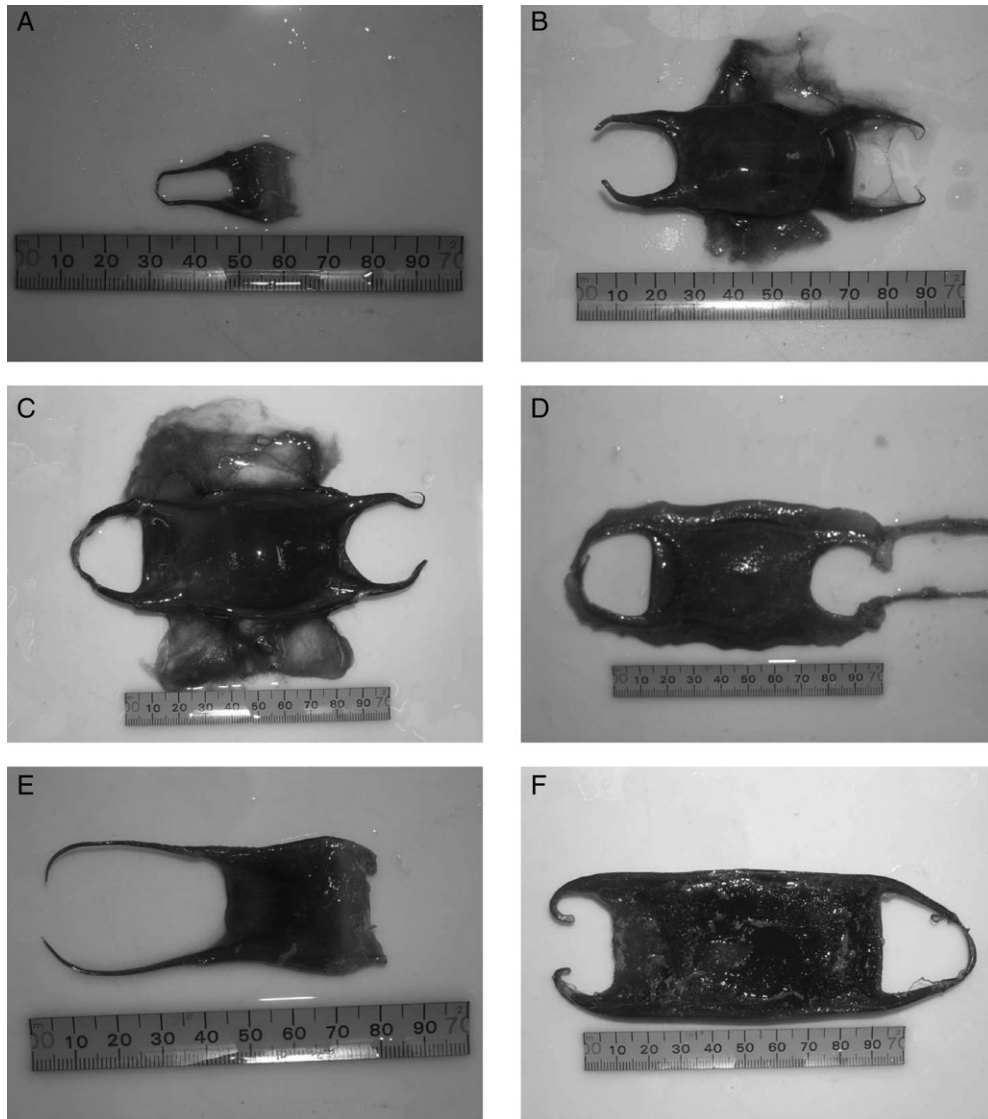


Figure 3b. Egg cases of A *Neoraja stehmanni*, B *Raja miraletus*, C *Raja straeleni*, D *Rajella barnardi*, E *Rajella caudaspinosa*, and F *Rajella dissimilis*.

***Dipturus doutrei* (Cadenat, 1960)**

Only a single individual of this rare species was collected. It was an adult male measuring 100.6 cm L_T . Egg cases are unknown for this species.

***Dipturus pullopunctata* (Smith, 1964)**

In all, 209 *D. pullopunctata* were sampled from the west coast and 123 from the south coast (Table 1). Overall, the west coast sex ratio (F:M) of 1:1.4 was significantly different from the expected 1:1 ratio ($\chi^2 = 4.31$, d.f. = 1, $p < 0.05$). A significant difference was found in the F:M ratio for adults 1:2.3 ($\chi^2 = 4.36$, d.f. = 1, $p < 0.05$), but the sex ratios of adolescents and juveniles were not significantly different from 1:1 ($p > 0.05$). The south coast overall sex ratio (F:M) of 1:0.8 was not significantly different from the expected 1:1 ratio ($p > 0.05$). Analysis by maturity status also failed to reveal a significant difference in sex ratio for adults, adolescents, or juveniles ($p > 0.05$).

Comparison of male and female relationships for $L_T - D$ and $L_T - W$ revealed no significant difference for either the west coast or the south coast ($p > 0.05$) (Table 1). A comparison of $L_T - D$ between males and females from the west and south coasts did not reveal any significant differences ($p > 0.05$). Likewise, the $L_T - W$ relationships between west and south coast males and females were not significantly different ($p < 0.05$).

West coast males ranged from 28.2 to 113.0 cm L_T . The smallest mature male measured 96.6 cm L_T and the largest immature male 95.0 cm L_T . Clasper length increased between 85.0 and 95.0 cm L_T (Figure 8a). In all, 23 (19.2%) mature males were captured, first maturity was at 85.5% L_{Tmax} , and L_{T50} was estimated at 91.4 cm L_T . South coast males ranged from 26.0 to 100.8 cm L_T . The smallest mature male on the south coast was 87.9 cm L_T and the largest immature male was 91.9 cm L_T . Clasper length increased between 80.0 and 90.0 cm L_T (Figure 8b). In all, 16 (29.6%) mature males were examined, first maturity was at 87.2% of L_{Tmax} , and L_{T50} was estimated at 86.5 cm L_T .

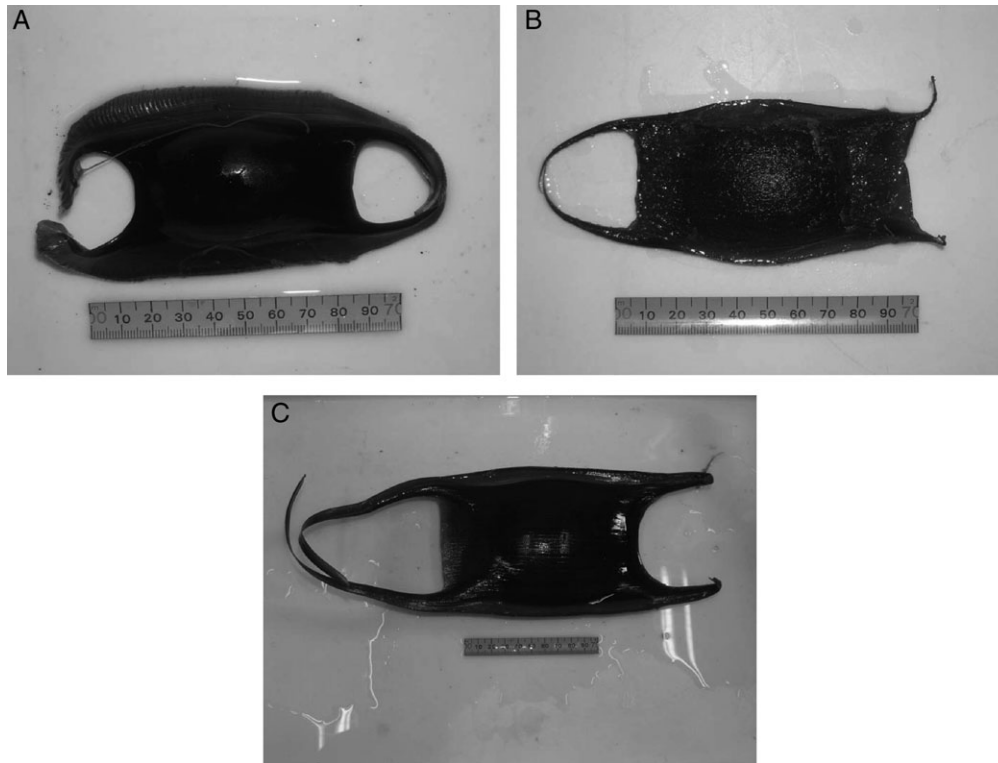


Figure 3c. Egg cases of A *Rajella leopardus* B *Rajella ravidula*, and C *Rostroraja alba*

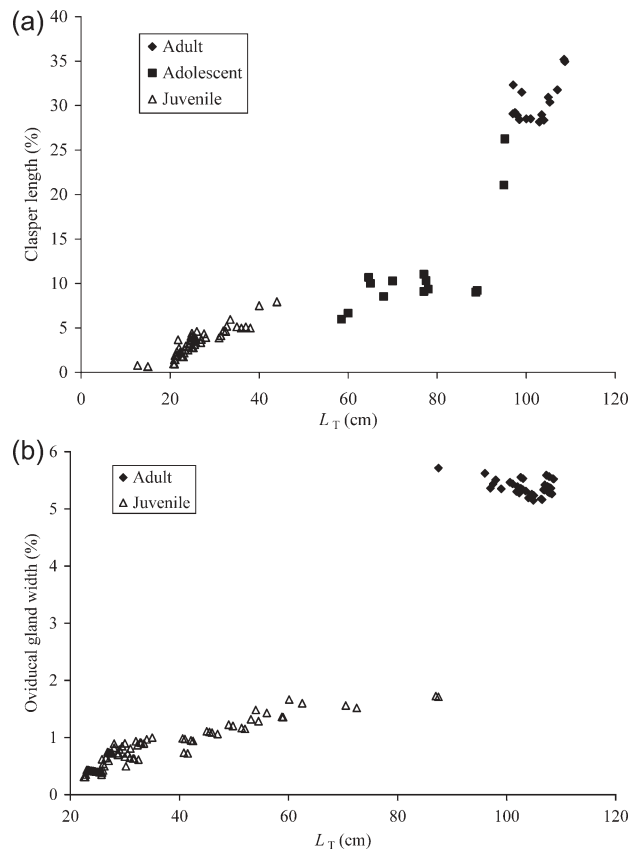


Figure 4. Relationships for *B. smithii* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

West coast females ranged from 23.2 to 124.5 cm L_T . The smallest mature female measured 100.6 cm L_T and the largest immature female 111.0 cm L_T . Oviducal gland width increased at ~ 100 cm L_T (Figure 8c). All females > 112.0 cm L_T were mature. Ten (11.2%) mature females were examined, first maturity was at 80.8% relative to L_{Tmax} , and L_{T50} was estimated to be 104.1 cm L_T . South coast females ranged from 19.2 to 103.0 cm L_T . The smallest mature female was 78.5 cm L_T and the largest immature female 82.3 cm L_T . Ten (14.5%) mature females were examined, first maturity was at 77.7% L_{Tmax} , and L_{T50} was estimated at 81.2 cm L_T .

Three adult females carried egg cases *in utero*; two from the west coast and one from the south (Figure 2a). Each of these had a single egg case in each uterus. The west coast specimens were both caught in summer, at depths of 176 and 213 m, and the single pregnant south coast female was taken in autumn at a depth of 110 m. The egg cases are very large, > 130 mm excluding horns, striated, covered with dense fibres, and with broad lateral keels, ca. 19% of maximum width. The horns taper, with the anterior horns hook-like, slightly longer than posterior horns that curve inwards, but not hook-like (Figure 3a). Egg cases from the south and west coasts appear to be similar in morphology.

Dipturus springeri (Wallace, 1967)

A total of 45 *D. springeri* was sampled with no significant difference from the expected 1:1 sex ratio ($p > 0.05$), and the sex ratios of maturity groups (adults, adolescents, or juveniles) were also not significantly different ($p > 0.05$). The relationships for $L_T - D$ and $L_T - W$ between sexes revealed no significant difference ($p > 0.05$) (Table 1).

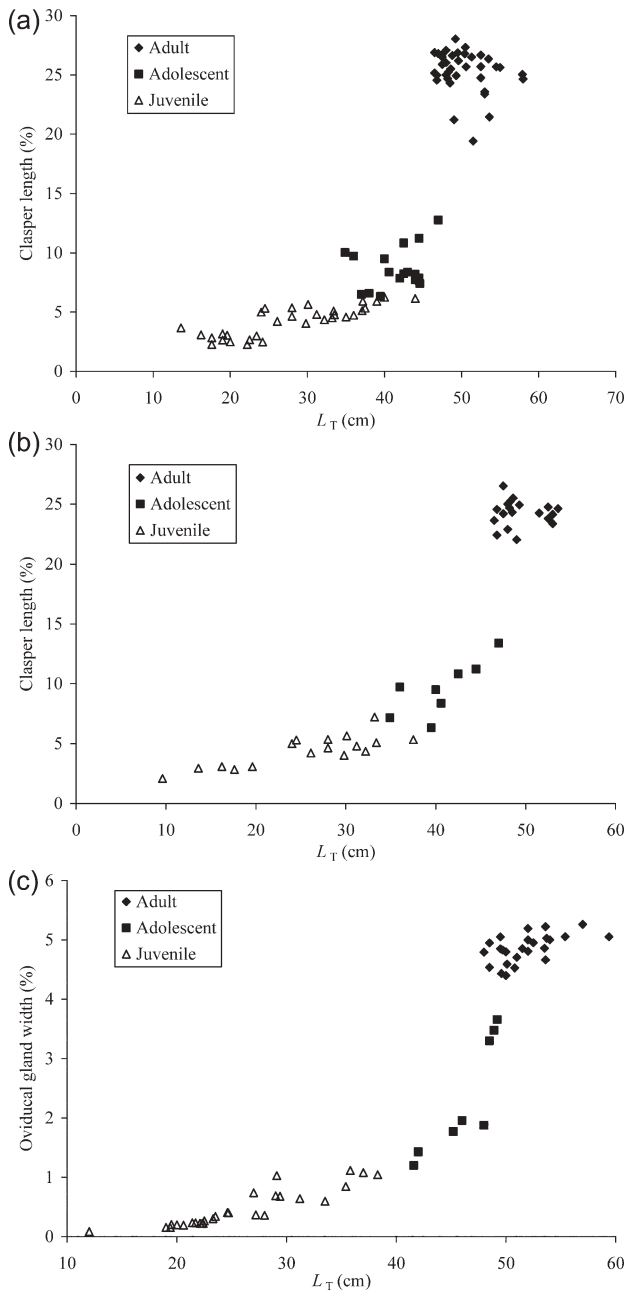


Figure 5. Relationships for *C. parcomaculata* between (a) clasper length (% L_T) and L_T for the west coast, (b) clasper length (% L_T) and L_T for the south coast, and (c) oviducal gland width (% L_T) and L_T for west coast females.

Males ranged from 34.0 to 154.5 cm L_T . The smallest mature male measured 134.8 cm L_T and the largest immature male 125.2 cm L_T . Clasper length increased rapidly between 120.0 and 135.0 cm L_T (Figure 9a). The three largest males were all mature, with first maturity at 87.2% of L_{Tmax} . An insufficient number of animals was collected to determine L_{T50} .

Females ranged from 27.0 to 192.0 cm L_T . Oviducal gland width increased between 170.0 and 190.0 cm L_T (Figure 9b). The smallest mature female measured 190.0 cm L_T and the largest immature female 171.2 cm L_T . The 27.0 cm L_T specimen, caught at 194 m on the south coast in winter, still had an internal yolk sac. All three females ≥ 190.0 cm L_T were mature, with first maturity at

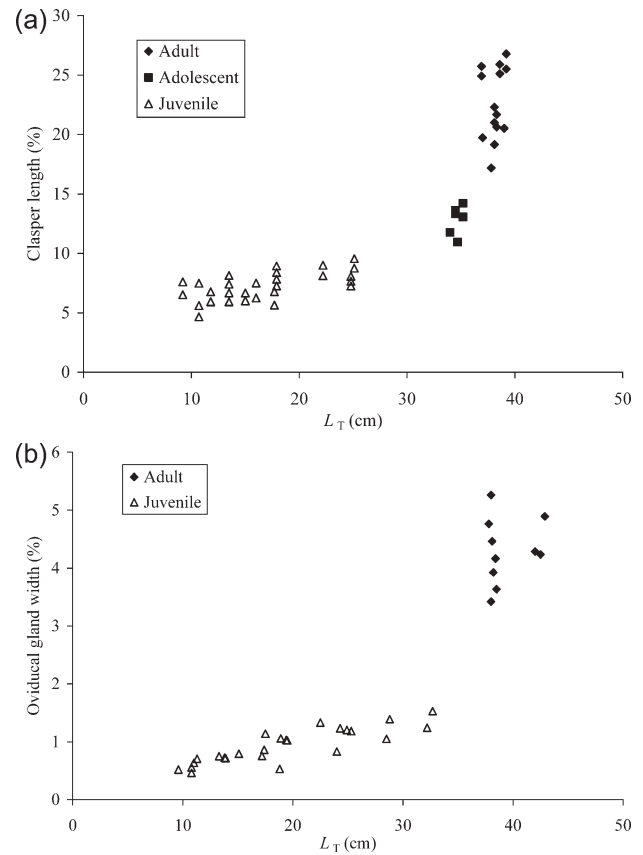


Figure 6. Relationships for *C. triangularis* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

99.0% of L_{Tmax} . L_{T50} could not be estimated because of the small sample size. Egg cases are unknown for this species and none were found during the study.

***Dipturus stenorhynchus* (Wallace, 1967)**

A total of 31 *D. stenorhynchus* was sampled. The $L_T - D$ relationship between males and females showed no significant difference ($p > 0.05$) (Table 1). The $L_T - W$ relationship between males and females was not estimated because of the small sample size.

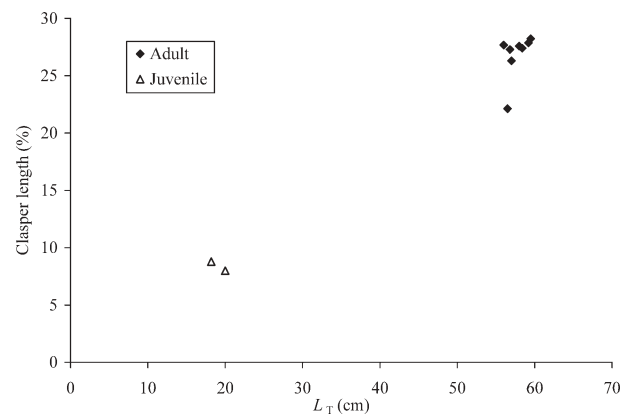


Figure 7. Relationship for *D. campbelli* between clasper length (% L_T) and L_T .

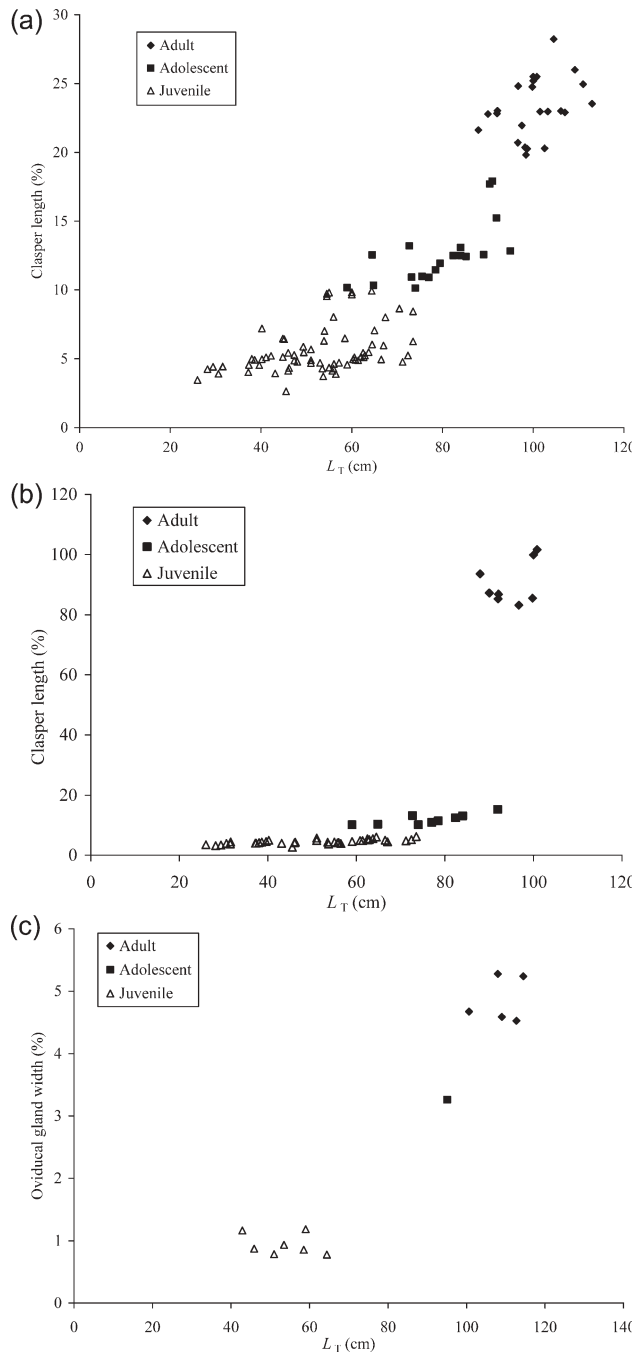


Figure 8. Relationships for *D. pullopunctata* between (a) clasper length (% L_T) and L_T for the west coast, (b) clasper length (% L_T) and L_T for the south coast, and (c) oviducal gland width (% L_T) and L_T for west coast females.

Males ranged from 24.0 to 101.2 cm L_T , with the smallest mature male measuring 98.0 cm L_T and the largest immature male 83.0 cm L_T . Clasper length increased between 83.0 and 98.0 cm L_T (Figure 10). Two males were determined to be mature, with first maturity at 96.8% of L_{Tmax} . The small sample size precluded estimation of L_{T50} .

Females ranged from 23.5 to 50.1 cm L_T , and none were mature. The smallest female, a neonate, had a small external yolk sac and a

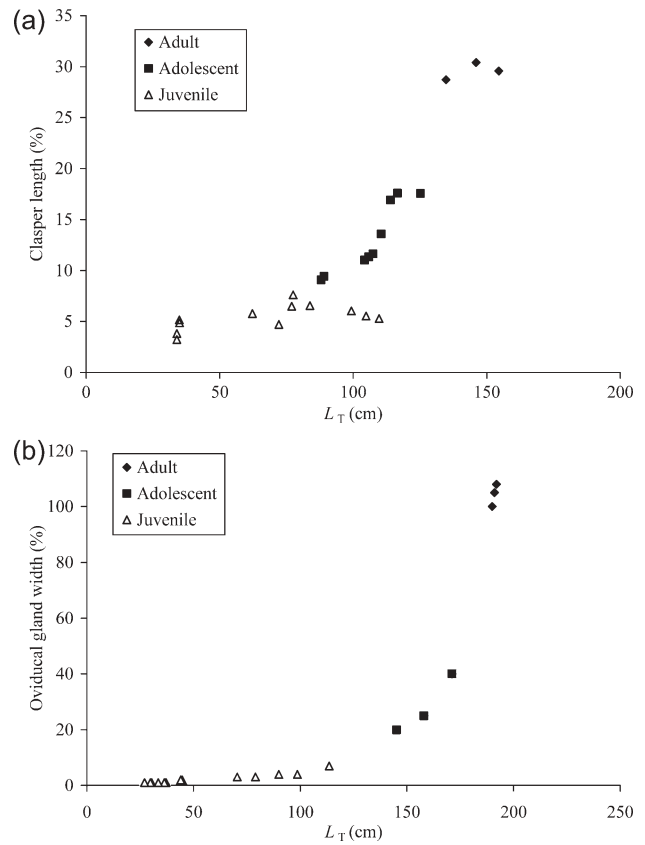


Figure 9. Relationships for *D. springeri* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

filamentous tail, indicating that it had recently birthed. Egg cases are unknown for this species and none were collected.

***Leucoraja compagno* (Stehmann, 1995)**

A total of 10 *L. compagno* was caught (7 males and 3 females). Males ranged from 13.6 to 51.7 cm L_T . The largest male was an adolescent measuring 51.7 cm L_T , and the largest female an immature measuring 28.5 cm L_T . Egg cases have not been found for this species.

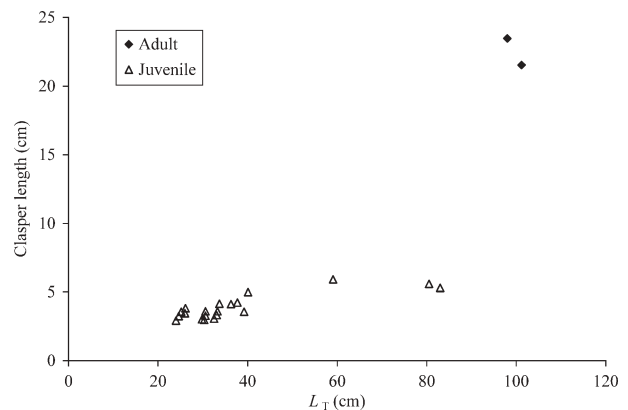


Figure 10. Relationship for *D. stenorhynchus* between clasper length (% L_T) and L_T .

Leucoraja wallacei (Hulley, 1970)

A sample of 157 *L. wallacei* from the west coast and 247 from the south coast was available (Table 1). The overall sex ratio (F:M) of 1:0.64 for the west coast was significantly different from the expected 1:1 ratio ($\chi^2 = 7.36$, d.f. = 1, $p < 0.05$). A significant difference was also found in the F:M ratio for juveniles, 1:0.36 ($\chi^2 = 19.38$, d.f. = 1, $p < 0.05$), but the sex ratios for adults and adolescents were not significantly different from unity ($p > 0.05$). The overall F:M ratio of 1:1.25 from the south coast was not significant from the expected unity ($p > 0.05$), nor was the sex ratio for adults and juveniles ($p > 0.05$), but the sex ratio for adolescents was significantly different ($\chi^2 = 9.13$, d.f. = 1, $p < 0.05$).

Comparison of the L_T-D and L_T-W relationships between males and females from the west coast was not significant ($p > 0.05$) (Table 1). The L_T-D relationship between females and males from the south coast was not significantly different, but the L_T-W relationship between sexes was significantly different ($p < 0.05$) (Table 1). Moreover, both the L_T-D and L_T-W relationships were significantly different between west and south coast males ($p < 0.05$), but not females ($p > 0.05$).

West coast males ranged from 31.0 to 87.0 cm L_T , with the smallest mature male measuring 77.0 cm L_T and the largest immature male measuring 77.7 cm L_T . Clasper length increased between 65.0 and 80.0 cm L_T (Figure 11a). In all, 11 (18.0%) mature males were captured, first maturity was at 88.5% L_{Tmax} , and L_{T50} was an estimated 77.1 cm L_T . South coast males ranged from 15.5 to 78.5 cm L_T . The smallest mature male was 64.0 cm L_T and the largest immature male was 71.0 cm L_T . Clasper length increased between 60.0 and 65.0 cm L_T (Figure 11b). In all, 40 mature males (29.2%) were examined, first maturity was at 81.5% of L_{Tmax} , and L_{T50} was an estimated 65.9 cm L_T .

West coast females ranged from 30.7 to 96.3 cm L_T . The smallest mature female measured 72.8 cm L_T and the largest immature female 81.4 cm L_T . Oviducal gland width increased between 80 and 90 cm L_T (Figure 11c). A total of 16 (16.7%) mature females was captured, first maturity was at 75.6% L_{Tmax} , and L_{T50} was estimated to be 80.1 cm L_T . South coast females ranged from 18.5 to 84.4 cm L_T . The smallest mature female was 64.5 cm L_T and the largest immature female 69.8 cm L_T . In all, 26 mature females (23.6%) were examined, first maturity was at 76.4% of L_{Tmax} , and L_{T50} was estimated to be 67.3 cm L_T .

One of 16 adult females (6.3%) collected on the west coast contained a single egg case in each uterus (Figure 2a). This fish was caught during summer at a depth of 170 m. Four of 24 adult females (16.7%) examined from the south coast had egg cases *in utero*, all four caught in spring between 144 and 225 m.

A medium-sized egg case measuring 80–83 mm, excluding horns, had a surface with very fine striations, smooth, no fibres or lateral keels, and a posterior apron ca. 50% wider than the anterior apron (Figure 3a). Horns tapered to a filamentous tip, and posterior horn length was nearly twice that of the anterior horns. Comparison of egg cases from the south and west coasts revealed no morphological differences.

Malacoraja spinacidermis (Barnard, 1923)

A total of 30 *M. spinacidermis* was caught. Overall, there was no significant difference in the F:M ratio ($p > 0.05$). Comparison of adults and juveniles showed no significant difference from the

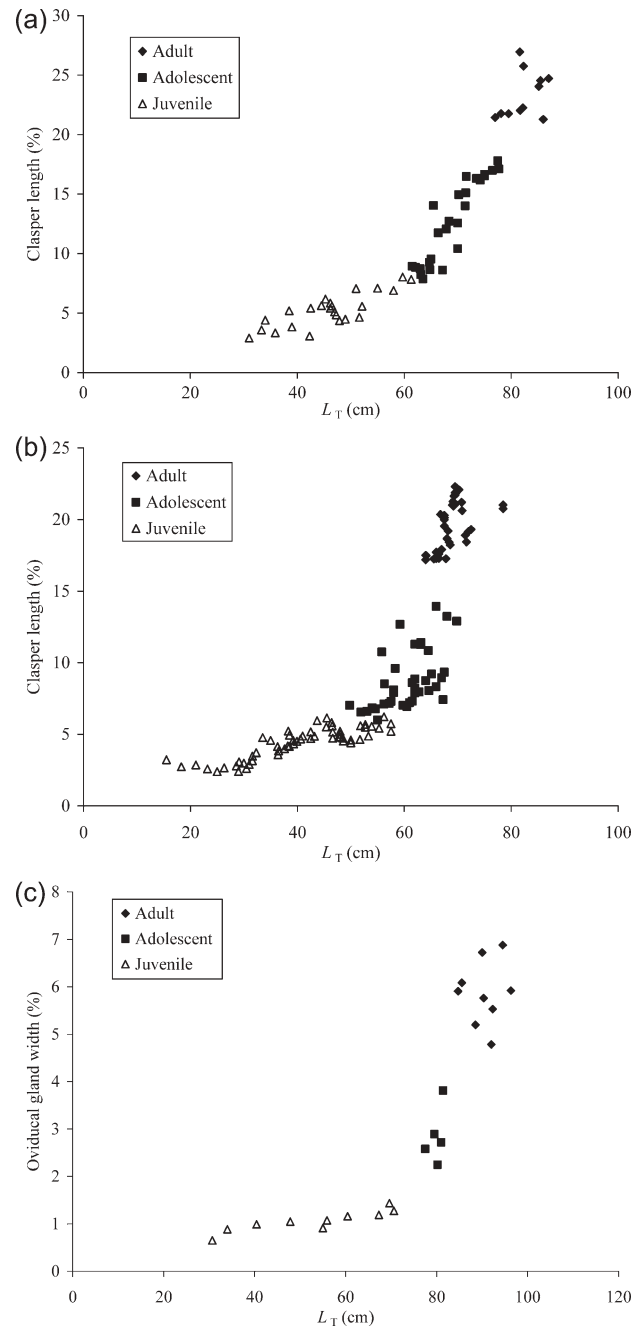


Figure 11. Relationships for *L. wallacei* between clasper length (% L_T) and L_T for (a) the west coast and (b) the south coast, and (c) oviducal gland width (% L_T) and L_T for west coast females.

expected 1:1 sex ratio ($p > 0.05$). No adolescents of either sex were found.

The L_T-D relationship between males and females showed no significant difference (Table 1), and the L_T-W relationship could not be statistically compared because of the small sample size.

Males ranged from 12.7 to 70.5 cm L_T . The smallest mature male was 58.0 cm L_T and the largest immature 38.0 cm L_T . Clasper length increased between 50.0 and 60.0 cm L_T (Figure 12a). In total, 11 mature males (68.8%) were captured, first maturity was at 82.3% of L_{Tmax} , and L_{T50} was estimated to be 48.0 cm L_T .

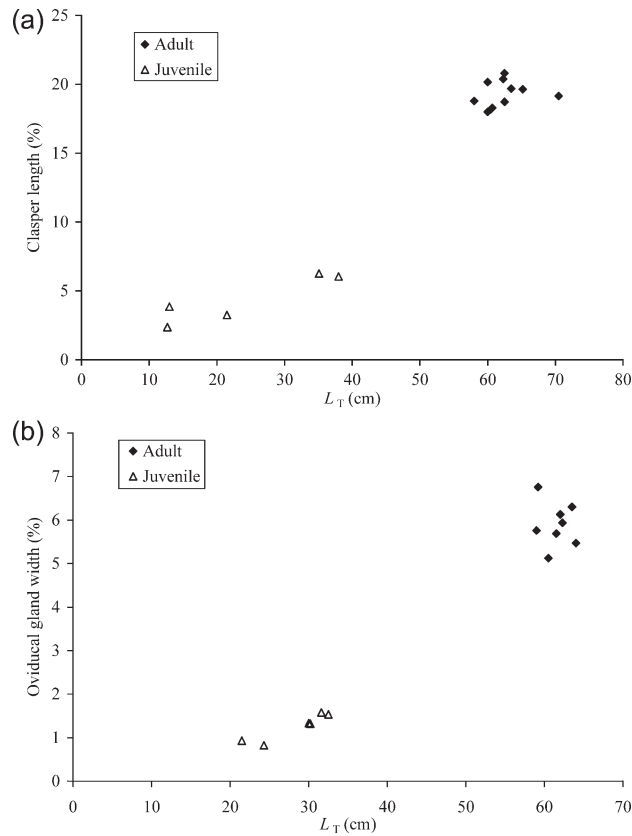


Figure 12. Relationships for *M. spinacidermis* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

Females ranged from 21.5 to 64.0 cm L_T . Oviducal gland width increased at ~ 60 cm L_T (Figure 12b). The smallest mature female measured 59.0 cm L_T . A total of eight mature females (57.1%) was examined, first maturity was at 92.2% of L_{Tmax} , and L_{T50} was an estimated 45.4 cm L_T .

One of eight adult females (12.5%) contained a single developing egg case in each uterus (Figure 2a). This fish was caught on a summer cruise at 894 m. Egg cases ca. 50% developed (43–45 mm), probably <100 mm long fully developed, had very fine striations, were smooth, the lateral keels broad, ca. 11.6% maximum width, and with horns tapering to tips (Figure 3a).

Neoraja stehmanni (Hulley, 1972)

In all, 121 *N. stehmanni* were available for analysis. The overall sex ratio of 1:0.92 (F:M) was not significantly different from unity ($p > 0.05$), and there was no significant difference in the sex ratios of adults, adolescents, or juveniles ($p > 0.05$). The L_T – W relationship between females and males was not significantly different ($p > 0.05$), but the L_T – D relationship was ($p < 0.05$) (Table 1).

Males ranged from 24.0 to 37.6 cm L_T , the smallest mature male measured 30.9 cm L_T , and the largest immature male was 31.5 cm L_T . Clasper length increased rapidly at ~ 28.0 cm L_T (Figure 13a). All males > 32.0 cm L_T were mature. For the 19 mature males captured, first maturity was at 82.2% of L_{Tmax} , and L_{T50} was estimated to be 30.3 cm L_T .

Females ranged from 15.3 to 36.8 cm L_T , with 17 (27%) determined to be mature. The smallest adult female measured 29.5 cm

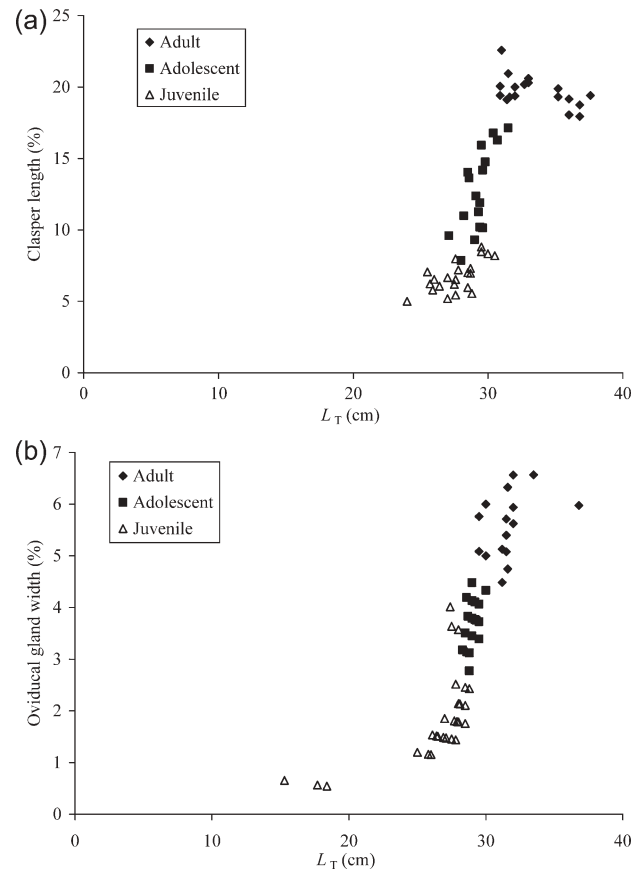


Figure 13. Relationships for *N. stehmanni* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

L_T and the largest immature female was 30.0 cm L_T . Oviducal gland width increased between 25 and 30 cm L_T (Figure 13b). All females > 30.0 cm L_T were mature, first maturity was at 80.2% of L_{Tmax} , and L_{T50} was an estimated 29.6 cm L_T .

One of 17 adult females (5.9%), collected during summer at 680 m, had a single developing egg case passing into each uterus (Figure 2a). These egg cases were ca. 25% developed. The egg cases were very small with a smooth surface, without fibres, and with broad lateral keels. The posterior horns narrow to acute tips and are pointed inwards towards each other (Figure 3b).

Okamejei heemstrai (McEachran and Fechhelm, 1982)

Two *O. heemstrai*, both adult females measuring 60.0 and 60.5 cm L_T , were collected, the first records of mature fish of this species. Egg cases are unknown.

Raja miraletus (Linnaeus, 1758)

A total of 118 *R. miraletus* was caught and sampled, with no significant difference from the expected 1:1 ratio ($p > 0.05$) between the sexes for any of the maturity groups compared. There was, however, a significant difference ($p < 0.05$) in the L_T – D relationship between males and females, but no difference ($p > 0.05$) in the L_T – W relationship (Table 1).

Males ranged from 27.5 to 52.3 cm L_T . The smallest mature male measured 37.6 cm L_T and the largest immature 42.5 cm L_T . Clasper length increased in specimens > 35.0 cm L_T (Figure

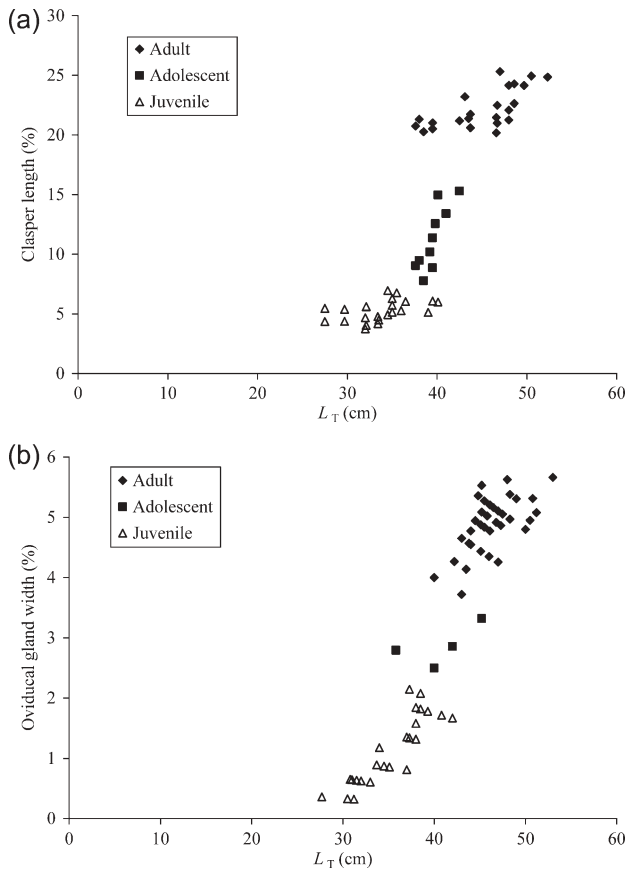


Figure 14. Relationships for *R. miraletus* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

14a). In all, 23 mature males (41.8%) were captured, first maturity was at 71.9% of L_{Tmax} , and L_{T50} was estimated to be 42.5 cm L_T .

Females ranged from 31.2 to 53.0 cm L_T , the smallest mature female measuring 40.0 cm L_T and the largest immature female 45.2 cm L_T . Oviducal gland width increased at ~ 40 cm L_T (Figure 14b). Of the 35 mature females (55.6%) examined, first maturity was at 75.0% of L_{Tmax} and L_{T50} was an estimated 42.0 cm L_T .

Three of 35 adult females examined (8.6%) had egg cases *in utero*. All three were caught during spring between 28 and 44 m deep (Figure 2a). A very small egg case, measuring < 50 mm long excluding horns, had a surface densely covered in fibres, though beneath the fibrous surface were fine striations and a texture smooth to the touch. There was no lateral keel, and the posterior apron was ca. 1.3 times that of the anterior apron. The horns are robust and of even length; posteriors tapering to filamentous tips, anterior horns tapering and hook-like, but with acute tips (Figure 3b).

Raja straeleni (Poll, 1951)

A total of 639 *R. straeleni* was sampled from the west coast, yielding a F:M sex ratio of 1:0.59, significantly different from unity ($\chi^2 = 41.1$, d.f. = 1, $p < 0.05$). Similarly, adults, adolescents, and juveniles all showed significant differences in F:M sex ratios, 1:0.43 ($\chi^2 = 29.3$, d.f. = 1, $p < 0.05$), 1:0.6 ($\chi^2 = 5.39$, d.f. = 1, $p < 0.05$), and 1:0.7 ($\chi^2 = 10.88$, d.f. = 1, $p < 0.05$), respectively. Of the 498 *R. straeleni* examined from the south coast, the overall

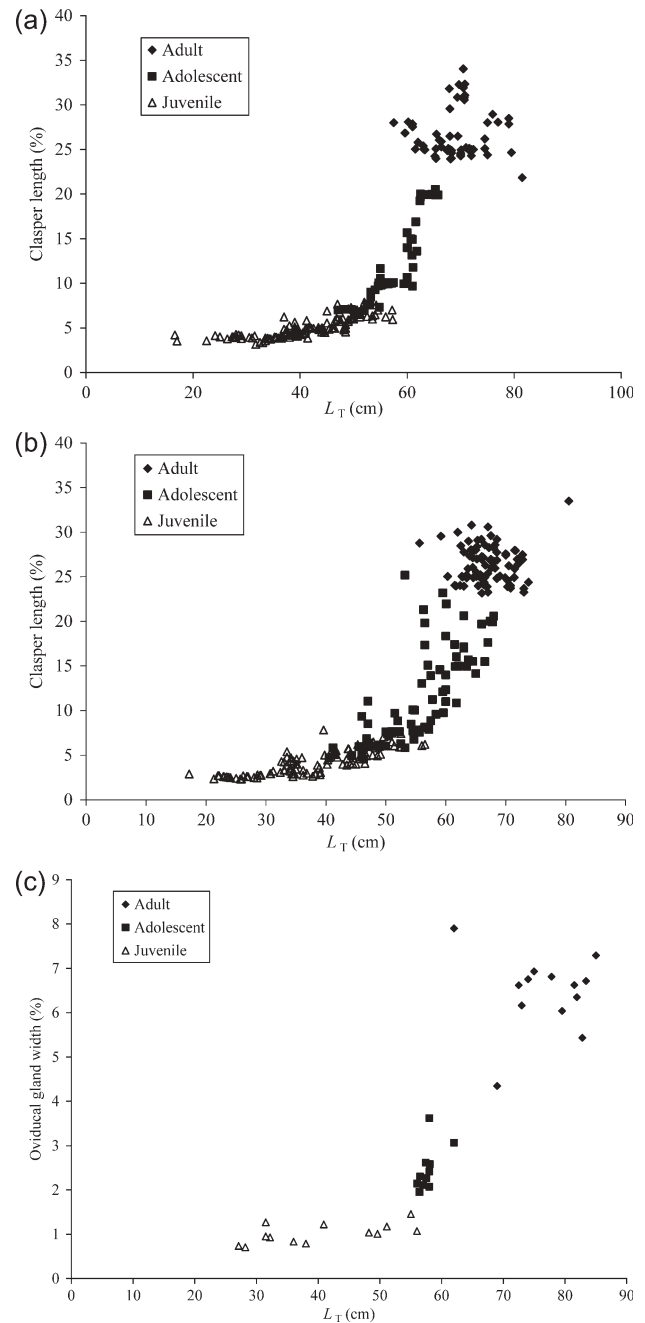


Figure 15. Relationships for *R. straeleni* between clasper length (% L_T) and L_T for (a) the west coast, and (b) the south coast, and (c) oviducal gland width (% L_T) and L_T for west coast females.

F:M ratio revealed no significant difference ($p > 0.05$), adults and juveniles failing to show a significant difference in F:M ratio ($p > 0.05$), but adolescents showing one, a ratio of 1:1.54 ($\chi^2 = 5.52$, d.f. = 1, $p < 0.05$).

A comparison of the L_T-D and L_T-W relationships between females and males from the west coast showed significant differences ($p < 0.05$) (Table 1). Likewise, the L_T-D and L_T-W relationships between females and males from the south coast were significantly different ($p < 0.05$) (Table 1). The L_T-D relationships between west and south coast males and females was not significant ($p > 0.05$), but the L_T-W relationships

between west and south coast males and females were significantly different ($p < 0.05$).

West coast males ranged from 16.6 to 79.5 cm L_T . The smallest mature male was 57.5 cm L_T and the largest immature male 65.8 cm L_T . Clasper length increased in males >55.0 cm L_T (Figure 15a). In all, 58 mature males (24.4%) were captured, first maturity was at 72.3% of L_{Tmax} , and L_{T50} was an estimated 63.2 cm L_T . South coast males ranged from 17.2 to 80.5 cm L_T . The smallest mature male was 55.6 cm L_T and the largest immature male 68.0 cm L_T . Clasper length increased between 55.0 and 60.0 cm L_T (Figure 15b). A total of 84 mature males (32.2%) was examined, first maturity was at 69.1% of L_{Tmax} , and L_{T50} was estimated to be 61.6 cm L_T .

West coast females ranged from 23.7 to 85.9 cm L_T . The smallest mature female measured 55.0 cm L_T and the largest immature one 70.9 cm L_T . Oviducal gland width increased between 60 and 70 cm L_T (Figure 15c). All females >71.0 cm L_T were mature. Of the 134 mature females (33.4%) captured, first maturity was at 64.0% L_{Tmax} , and L_{T50} was an estimated 65.8 cm L_T . South coast females ranged from 21.7 to 84.0 cm L_T . The smallest mature female was 65.2 cm L_T and the largest immature 69.4 cm L_T . In all, 64 mature females (27.0%) were examined, first maturity was at 77.6% of L_{Tmax} , and L_{T50} was an estimated 65.1 cm L_T .

Of 198 adult females, 13 (6.6%) contained a single egg case in each uterus (Figure 2b). Three of them were caught on the west coast, two in winter and one in summer, at depths between 148 and 234 m. Ten fish had egg cases *in utero* from the south coast, eight caught in spring and two in autumn, all captured at depths of 42–110 m.

A medium-sized egg case measuring ca. 75 mm long, excluding horns, had a surface densely covered in fibres, though beneath the fibres the surface was smooth. The case had a broad lateral keel ca. 8% of maximum egg case width, and a posterior apron ca. 1.3 times the length of the anterior apron. Horns tapered and became filamentous at their tips, the posterior horns ca. 1.2 times the length of anterior horns (Figure 3b). Egg cases from south and west coasts were morphologically similar.

Rajella barnardi (Norman, 1935)

A total of 158 *R. barnardi* was sampled, with the F:M sex ratio showing no significant difference from the expected unity for any of the maturity groups compared ($p > 0.05$). The L_T – D relationship between males and females was not significantly different ($p > 0.05$), but the L_T – W relationship was significantly different ($p < 0.05$) (Table 1).

Males ranged from 10.7 to 75.0 cm L_T . The smallest mature male was 60.5 cm L_T and the largest immature 61.9 cm L_T . Clasper length increased at ~ 60.0 cm L_T (Figure 16a). In total, 18 mature males (22.5%) were captured, first maturity was at 80.7% of L_{Tmax} , and L_{T50} was an estimated 62.5 cm L_T .

Females ranged from 14.9 to 70.5 cm L_T . The smallest mature female was 59.4 cm L_T and the largest immature 64.5 cm L_T . Oviducal gland width increased in fish >60 cm L_T (Figure 16b). All females >65.0 cm L_T were mature. Of the 19 mature females (24.4%) examined, first maturity was at 84.3% of L_{Tmax} and L_{T50} 62.7 cm L_T .

Four of 19 adults (21.1%) had egg cases *in utero* (Figure 2b), two taken during summer and two during winter, at depths between 395 and 491 m. Egg cases were rather small, some ca. 55 mm long excluding horns, with a smooth surface and very fine striations. The posterior apron width was ca. 1.5 times that

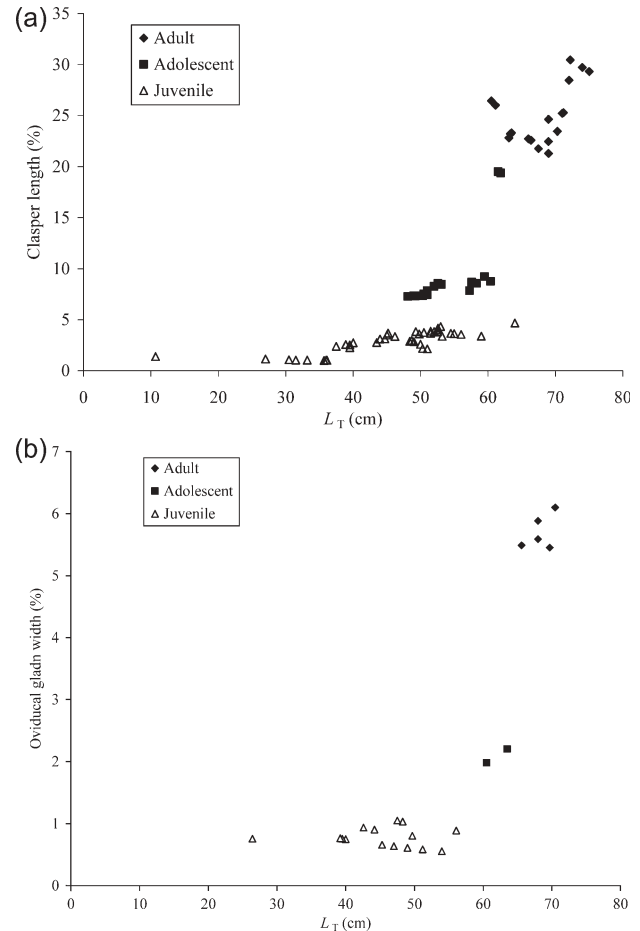


Figure 16. Relationships for *Rajella barnardi* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

of the anterior apron width, the lateral keels were broad and feathery in appearance, ca. 18.6% of maximum egg case width, and extended the entire length of the egg case, including the horns. The horns were robust and tapered, with the posterior horns ca. 1.7 times the length of the anterior horns, though the latter had attachment fibres near the tips of the horns (Figure 3b).

Rajella caudaspinosa (von Bonde and Swart, 1923)

A total of 94 *R. caudaspinosa* was caught and sampled. The overall F:M sex ratio was not significantly different from unity ($p > 0.05$), but adults were significantly different from 1:1, at 1:2.1 ($\chi^2 = 4.6$, d.f. = 1, $p < 0.05$). Adolescents and juveniles, however, showed no significant difference ($p > 0.05$). The L_T – D relationship between males and females was not significantly different ($p > 0.05$), but the L_T – W relationship was ($p < 0.05$) (Table 1).

Males ranged from 10.0 to 64.8 cm L_T . The smallest mature male was 53.3 cm L_T and the largest immature male 59.3 cm L_T . Clasper length increased between 50.0 and 60.0 cm L_T (Figure 17a). All males >60.0 cm L_T were mature. In all, 29 mature males (53.7%) were collected, first maturity was at 82.3% of L_{Tmax} and L_{T50} an estimated 51.1 cm L_T .

Females ranged from 24.2 to 65.1 cm L_T . The smallest mature female was 50.0 cm L_T and the largest immature 57.1 cm L_T . Oviducal gland width increased rapidly in fish >50 cm L_T

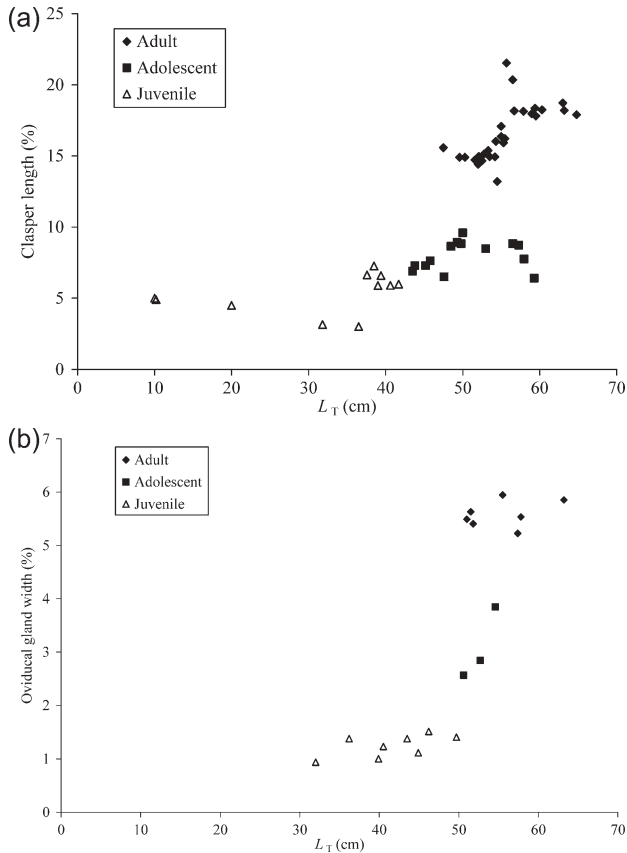


Figure 17. Relationships for *Rajella caudaspinosa* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

(Figure 17b). Of the 14 mature females (35.0%) examined, first maturity was at 76.8% of L_{Tmax} and L_{T50} at 55.2 cm L_T .

Of the 14 adult females examined, one (7.1%) had a single developing egg case passing through each oviducal gland (Figure 2b). This fish measured 50.0 cm L_T and was caught 241 m deep during winter on the west coast. The egg cases were ca. 50% developed, each 32 mm long excluding horns, the finely striated surface beneath the fibrous covering was smooth, and there was a narrow lateral keel ca. 6.3% of maximum egg case width (Figure 3b). The posterior horns tapered to an acute tip.

***Rajella dissimilis* (Hulley, 1970)**

A total of 85 *R. dissimilis* was sampled. There was no significant difference in the sex ratio for any of the groups compared ($p > 0.05$), nor for the $L_T - D$ and $L_T - W$ relationships between males and females ($p > 0.05$) (Table 1).

Males ranged from 13.0 to 79.0 cm L_T . The smallest mature male was 52.0 cm L_T and the largest immature 65.0 cm L_T . Clasper length increased between 50.0 and 60.0 cm L_T (Figure 18a). Of the 19 mature males (38.0%) examined, first maturity was at 65.8% L_{Tmax} and L_{T50} 58.3 cm L_T .

Females ranged from 22.0 to 82.3 cm L_T . The smallest mature female was 60.6 cm L_T and the largest immature one 53.8 cm L_T . Oviducal gland width increased between 55 and 60 cm L_T (Figure 18b). A total of 10 mature females (28.6%) was examined, first maturity was at 72.8% of L_{Tmax} , and L_{T50} was an estimated 60.0 cm L_T .

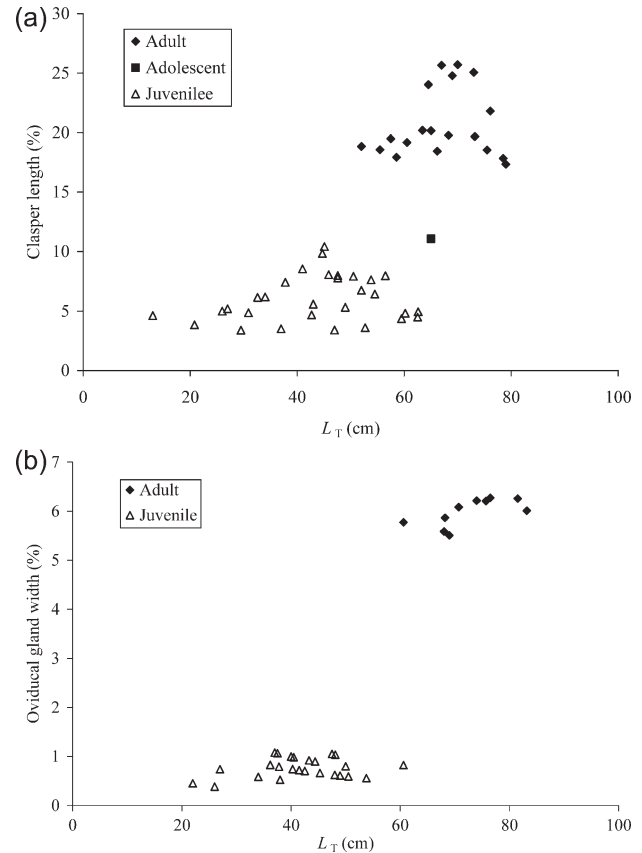


Figure 18. Relationships for *Rajella dissimilis* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

One fish of 69.0 cm L_T , caught in summer at 680 m, had a single egg case in each uterus (Figure 2b). The egg cases measured ca. 80 mm long excluding horns, had a smooth surface with no striations, anterior and posterior aprons similar in size, and a very narrow lateral keel. Horns tapered, becoming filamentous, the posterior ones nearly twice the length of the anterior horns (Figure 3b).

***Rajella leopardus* (von Bonde and Swart, 1923)**

In all, 220 *R. leopardus* were sampled, and there was no significant difference in the sex ratios for any of the groups compared ($p > 0.05$). The $L_T - D$ relationship between males and females was not significantly different ($p > 0.05$), but the $L_T - W$ relationship between sexes was significantly different ($p < 0.05$) (Table 1).

Males ranged from 15.3 to 87.5 cm L_T . The smallest mature male was 61.6 cm L_T and the largest immature male 73.0 cm L_T . Clasper length increased between 60.0 and 70.0 cm L_T (Figure 19a). All males >73.0 cm L_T were mature. In total, 27 mature males (26.0%) were captured, first maturity was at 70.4% of L_{Tmax} , and L_{T50} was estimated to be 71.8 cm L_T .

Females ranged from 28.5 to 93.0 cm L_T . The smallest mature female measured 61.0 cm L_T and the largest immature one 69.7 cm L_T . Oviducal gland width increased between 60 and 70 cm L_T (Figure 19b). All females >70.0 cm L_T were mature. A total of 33 mature females (28.4%) was examined, first maturity was at 65.6% of L_{Tmax} , and L_{T50} was an estimated 64.8 cm L_T .

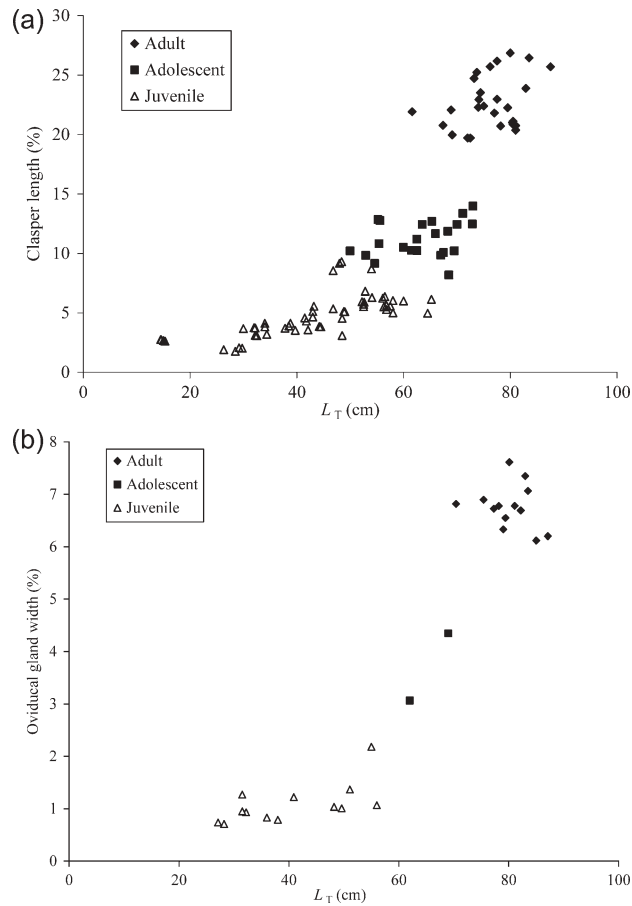


Figure 19. Relationships for *Rajella leopardus* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

Egg cases were found in four (12%) of 33 adult females, all caught during summer (Figure 2b). All four were caught between 457 and 467 m, two in one trawl. The egg cases were small, ca. 55 mm long excluding horns, with a smooth surface, and with broad feathery lateral keels extending the length of the entire egg case from horn tip to tip. The posterior horns were ca. 1.2 times the length of the anterior horns; the latter had a fibrous tendril attachment (Figure 3c).

Rajella ravidula (Hulley, 1970)

A total of 19 *R. ravidula* was caught during the surveys, with a F:M sex ratio of 1:1.4 that did not differ significantly from unity ($p > 0.05$). Similarly, the ratio of all other maturity groups did not differ significantly ($p > 0.05$). There was an insufficient sample size to compare the L_T -D and L_T -W relationships between males and females.

Of the 11 males, the length range was 38.5–73.7 cm L_T , the smallest mature male was 70.5 cm L_T , and the largest immature male 71.8 cm L_T . Clasper length increased at ~ 70.0 cm L_T (Figure 20a). Three mature males were captured, with first maturity at 95.7% L_{Tmax} . L_{T50} was not estimated because of the small sample size.

Eight females ranged from 42.0 to 79.2 cm L_T . The smallest mature female was 72.7 cm L_T . Oviducal gland width increased in those > 65 cm L_T (Figure 20b). Four mature females were

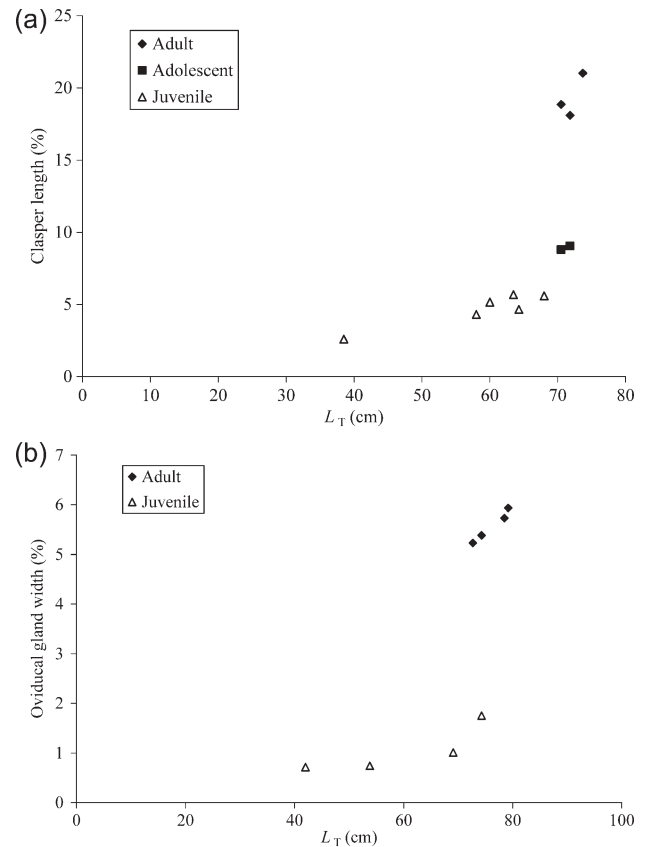


Figure 20. Relationships for *Rajella ravidula* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

examined and first maturity was at 94.6% of L_{Tmax} , but because of the small sample size, L_{T50} could not be estimated.

One female, 78.5 cm L_T , with egg cases was caught during summer at a depth of 680 m (Figure 2b). A moderately large egg case measured ca. 90 mm excluding horns, the surface was finely striated and rough to the touch, both aprons were similar in width, and the lateral keels were broad, ca. 13% of the maximum length of the egg cases (Figure 3c). The posterior horns were more than twice the length of the anterior horns.

Rostroraja alba (Lacépède, 1803)

A total of 173 *R. alba* was sampled, with an overall sex ratio (F:M) of 1:1.3, not significantly different from unity ($p > 0.05$). Analysis by maturity status failed to reveal significant differences in the sex ratios of adults and juveniles ($p > 0.05$), but did show a significant difference in sex ratio for adolescents 1:5 ($\chi^2 = 9.38$, d.f. = 1, $p < 0.05$). Comparison of the L_T -D and L_T -W relationships between sexes showed no significant difference ($p > 0.05$) (Table 1).

Males ranged from 39.5 to 198.5 cm L_T . The smallest mature male was 154.0 cm L_T and the largest immature male 166.0 cm L_T . Clasper length increased at ~ 150.0 cm L_T (Figure 21a). Of the 16 mature males captured (16.3%), first maturity was at 77.6% of L_{Tmax} and L_{T50} an estimated 167.2 cm L_T .

Females ranged from 44.0 to 240.0 cm L_T . The smallest mature female was 195.0 cm L_T and the largest immature female 197.6 cm L_T . Oviducal gland width increased between 150 and 200 cm L_T (Figure 21b). Of the 13 mature females examined

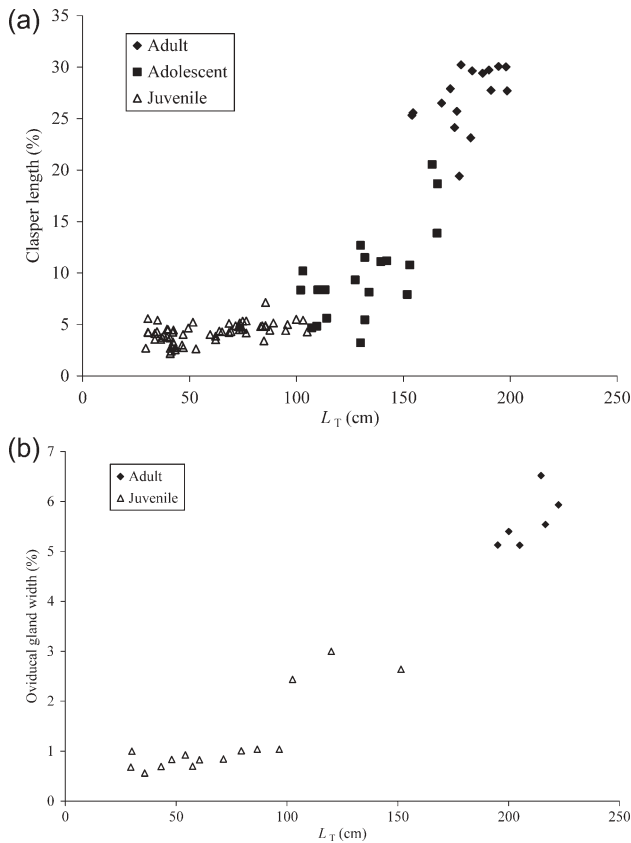


Figure 21. Relationships for *Rostroraja alba* between (a) clasper length (% L_T) and L_T , and (b) oviducal gland width (% L_T) and L_T .

(17.3%), first maturity was at 81.3% of L_{Tmax} and L_{T50} at an estimated 195.0 cm L_T .

Egg cases *in utero* were found in two specimens, one caught during summer and one in autumn (Figure 2b). Both were caught off beaches at angling competitions. Egg cases were very large, measuring ca. 150 mm excluding horns, had coarsely striated surfaces, rough to the touch, and broad lateral keels ca. 11.5% of maximum egg case width. The posterior horns were very long, three times the length of the anterior horns. The posterior horns tapered and flattened towards their tips, whereas the anterior horns were short, tapered, and with attachment fibres (Figure 3c).

Discussion

The sex ratios of most species in this study were relatively even, suggesting that southern African skates display limited sexual segregation. Five species (*B. smithii*, *C. 'parcomaculata'*, *D. pullopunctata*, *L. wallacei*, and *R. straeleni*) were caught on the west coast at sex ratios different from unity, but except for *B. smithii*, the sex ratios for the south coast were not significantly different. Females dominated catches of three species (*B. smithii*, *L. wallacei*, and *R. straeleni*) and males of two species (*C. 'parcomaculata'* and *D. pullopunctata*). The differences in skate sex ratios may be a consequence of behaviour, because many species segregate by sex, size, and maturity (Fitz and Daiber, 1963; Richards *et al.*, 1963; Holden, 1975; Braccini and Chiamonte, 2002).

The relationship between L_T and D for males and females was linear and not significantly different for all but three species, *R.*

straeleni from the west and south coasts, and *N. stehmanni* and *R. miraletus*. Contrary to these findings in southern Africa, the relationship between L_T and D was not significant for *R. miraletus* in the Adriatic Sea (Ungaro, 2004). McEachran *et al.* (1989) compared *R. miraletus* specimens from throughout its range in the Mediterranean with those off southern Africa and concluded that the species consisted of several morphologically similar species. However, they did not compare morphological differences between the sexes to determine whether there was sexual dimorphism elsewhere within the range of the species. Species exhibiting a significantly different relationship between L_T and D between sexes show sexual dimorphism in disc shape. Male skates are sexually dimorphic, with the disc becoming bell-shaped as they mature. For *Atlantoraja cyclophora*, Oddone and Vooren (2004) found a significant difference in disc shape between the sexes, females exhibiting a broader D than males >35 cm. Significant differences in the same relationship between sexes has also been reported for *R. clavata* (Nottage and Perkins, 1983). However, what, if any, behavioural or ecological implications this may have is unknown and worth further investigation.

Comparison of the relationship between L_T and D for male *L. wallacei* revealed a significant difference between the species on South Africa's west and south coasts, but reasons for this apparent gender difference in disc shape between the two coasts is unknown. There was no significant difference between males of the other three species compared: *C. 'parcomaculata'*, *D. pullopunctata*, or *R. straeleni*. Moreover, there was no significant difference in disc shape between females of these species on the two coasts.

L_T is used by most researchers and fishery biologists for skates. Hubbs and Ishiyama (1968) preferred the use of D as the independent variable, whereas others have argued that D can be highly variable when used as a reference measurement (Hulley, 1970; Stehmann, 1970; Templeman, 1973, 1987a). Disc length can be even more variable, because most researchers do not define this measurement adequately (Francis *et al.*, 2001; Francis, 2007).

Comparisons of the relationship between L_T and W between sexes revealed a significant difference for five species, including *L. wallacei* (south coast), *R. straeleni* (west and south coasts), *R. barnardi*, *R. caudaspinosa*, and *R. leopardus*. The size at first maturity and L_{Tmax} was similar between sexes, but the female weight for each of these species was heavier. Braccini and Chiamonte (2002) found for *Psammobatis extenta* that, although males reach L_{T50} at a significantly larger size than females, females weighed more at a given L_T . Growth curves of the two largest species, *D. springeri* and *R. alba*, did not significantly differ, even though the maximum weight attained by females was greater than males. The slope of the curve, and the weight for a given L_T , was similar between the sexes for these species up to L_{Tmax} for males.

The relationship between L_T and W between west and south coast males was significantly different for *L. wallacei* and *R. straeleni*. The difference was significant also between west and south coast *R. straeleni* females. It appears that male *L. wallacei* and *R. straeleni* on the west coast attain a larger size than south coast males of the same species. Likewise, west coast *R. straeleni* females appear to attain a larger size than south coast females. These differences suggest discrete west and south coast populations of these two skate species. Templeman (1987a) found that *A. radiata* differed in size at maturity and weight between different geographic locations, and Richards *et al.* (1963) found differences in size at maturity and maximum L_T between two

populations of *L. erinacea*. Differences in size at maturity and other life history parameters, such as age at maturity and fecundity, may have profound implications in the way these skates should be managed if the differences represent clearly different stocks (McEachran and Martin, 1977; Dulvy and Reynolds, 2002; Frisk, 2004; Frisk and Miller, 2006).

In five instances, males attained a slightly larger $L_{T_{max}}$ than females. Overall, the $L_{T_{max}}$ size differential between males and females (for 15 species) was slight, most being ≤ 12 cm L_T . There were insufficient data to determine the $L_{T_{max}}$ of males relative to females for five species, but female *D. springeri* and *R. alba*, the two largest species in the study, attained a much greater length (> 40 cm) than males of the same species. Along with the results of other studies (Templeman, 1987a; Braccini and Chiaramonte, 2002; Mabragna and Cousseau, 2004; Ebert, 2005), these results confirm that, for medium and small skates at least, $L_{T_{max}}$ is similar between males and females. However, for those species that attain large size (≥ 150 cm L_T), the size differences between sexes can be substantial. Other large skates that show substantial size difference between sexes include *B. richardsoni*, *D. batis*, *D. innominatus*, and *R. binoculata* (Templeman, 1973; Zeiner and Wolf, 1993; Francis et al., 2001; McFarlane and King, 2006).

Males and females of three species, *C. 'parcomaculata'*, *D. pullopunctata*, and *L. wallacei*, attained a larger $L_{T_{max}}$ on the west coast than their conspecifics on the south coast. These differences were relatively small (< 12 cm L_T) for *C. 'parcomaculata'* and *L. wallacei*, though larger for *D. pullopunctata* males and females, 13 and 21 cm L_T , respectively. In contrast, *R. straeleni* showed no difference in $L_{T_{max}}$ between coasts. *R. miraletus* in Mediterranean waters appears to exhibit regional differences, those from the Egyptian coast attaining an $L_{T_{max}} > 20$ cm greater than those in the Adriatic Sea (Abdel-Aziz, 1992; Ungaro, 2004). Southern African *R. miraletus* attained a similar $L_{T_{max}}$ to those found in the Adriatic. Templeman (1982, 1987b) found regional differences for several life history parameters, including $L_{T_{max}}$ for *A. radiata*, and although he did not imply that the differences represented separate stocks, he did not dismiss the possibility.

The size at first maturity was approximately the same for males and females, both maturing within 10 cm or less of each other, for 15 of 17 species for which sufficient information was available to determine maturity. Of the 15 species in which males and females matured within 10 cm of each other, males matured at a slightly larger size than females for eight species. The size difference at first maturity (with females bigger than males) for the two largest species, *D. springeri* and *R. alba*, were 56 and 45 cm L_T , respectively. It is widely believed that female elasmobranchs mature at a larger size than males. In a survey of shark life history patterns, Cortés (2000) found that females matured at a larger size than males in $> 85\%$ of 162 species studied. However, of the oviparous shark species in his survey, 9 out of 17 (53%) reported males maturing at a size equal to or greater than females. Although Cortés (2000) did not include batoids in his survey, there is a growing body of evidence that oviparous elasmobranchs, specifically those of the families Rajidae, Heterodontidae, and Scyliorhinidae, show very little difference in size at maturity between males and females (Lucifora and Garcia, 2004; Ebert, 2005; Ebert et al., 2006). This conclusion is plausible because there are no advantages for oviparous females to attain a larger size to produce larger young.

Size at maturity of west and south coast *C. 'parcomaculata'*, *D. pullopunctata*, *L. wallacei*, and *R. straeleni* did not differ

between sexes. However, there was a difference in size at maturity between west and south coast populations of *D. pullopunctata* and *L. wallacei*. The sizes at maturity for both male and female *D. pullopunctata* and *L. wallacei* were larger on the west coast. Reasons for these differences are uncertain, but it might be that there are discrete populations of these species or perhaps latitudinal variation in size at maturity (Templeman, 1987b; Frisk, 2004; Ruocco et al., 2006). Previously, Walmsley-Hart et al. (1999) studied the biology of *D. pullopunctata* and *L. wallacei* on the south coast. Results from the field-sampled portion of that study, conducted subsequent to the present study, found that *L. wallacei* matured smaller than we found. Differences in size at maturity of some exploited skate populations in the North Sea and the Southwest Atlantic have been attributed to long-term changes in abundance, growth, and maturation as a consequence of overexploitation (Walker, 1998; Oddone et al., 2005). The size at maturity of west coast *D. pullopunctata* reported by Walmsley-Hart et al. (1999) was comparable with our findings. Comparison of the size at maturity for male and female *C. 'parcomaculata'* and *R. straeleni* showed that both matured at about the same size throughout their range.

The size at first maturity was slightly higher than estimates of L_{T50} for males and females of some species. However, the differences were all relatively small and most likely related to the small sample sizes. Other studies with larger sample sizes showed size at first maturity and L_{T50} to be similar (Braccini and Chiaramonte, 2002; Ruocco et al., 2006). Sampling bias may be another reason for possible differences observed in size at first and L_{T50} maturity. Similar to other elasmobranchs (Springer, 1967; Sims, 2005), skates tend to segregate by sex and size (Steven, 1933; Fitz and Daiber, 1963; Richards et al., 1963; Holden, 1975; Ebert, 2005). Therefore, the behaviour of these fish might bias sampling depending on how the population of a particular species is distributed within, or outside, the study area. Another possibility for the differences may be changes in growth and size at maturation. Oddone et al. (2005) stated that the size at first maturity was greater than L_{T50} for two southwestern Atlantic skate species and concluded that fishing pressure in that region may have contributed to the changes. The same authors speculated that loss of reproducing females may have caused a shift over time in the minimum size at maturity, a result observed elsewhere (Walker and Hislop, 1998).

First maturity was at a length $> 60\%$ of $L_{T_{max}}$ for all species for which sufficient data were available. On closer examination, 18 of 21 matured at $> 75\%$ of $L_{T_{max}}$, and seven at $> 90\%$ of $L_{T_{max}}$. L_{T50} was between 75 and 90% of $L_{T_{max}}$ for 15 of 18 species, and the remaining three were between 69 and 72.5% of $L_{T_{max}}$. These findings generally conform to Holden's (1973, 1974, 1977) observation that most elasmobranchs mature within 60–90% of their $L_{T_{max}}$. Skates, like other oviparous elasmobranchs, tend to undergo a prolonged juvenile stage followed by a short adolescent phase prior to attaining full maturity (Zeiner and Wolf, 1993; Walker and Hislop, 1998; Dulvy et al., 2000; Ebert, 2005; Ebert et al., 2006). The relatively large size at maturity relative to $L_{T_{max}}$ suggests that once skates, and perhaps other oviparous elasmobranchs, mature, they tend to grow very little (Ebert, 2005; Ebert et al., 2006). It has been suggested that the relatively large size at which skates mature relative to their $L_{T_{max}}$ makes them particularly sensitive to fishing pressure and overexploitation (Henderson et al., 2004; Ruocco et al., 2006). However, although they may be vulnerable to overexploitation, the biological and physiological requirements of oviparous elasmobranchs may be

different from those of viviparous species, such that egg layers do not need to grow after attaining sexual maturity.

The taxonomic use of egg cases has been well documented (Ishiyama, 1958; Hubbs and Ishiyama, 1968; Ishiyama and Ishihara, 1977; Ishihara and Ishiyama, 1985; Ebert, 2005; Ebert and Davis, 2007). Of the 22 species examined, the egg cases of just four (*Anacanthobatis marmoratus*, *R. miraletus*, *R. barnardi*, *R. alba*) have been illustrated before (Wallace, 1967; Smith and Griffiths, 1997). The provisional key developed here for the skate egg cases of southern Africa (Table 2) includes all skate species known to occur within our study area. Although the morphology of egg cases may vary slightly between different geographic locations (McEachran, 1970; Templeman, 1982), species whose egg cases were found on both west and south coasts appeared to be morphologically similar.

Reproductive seasonality was difficult to determine given the scarcity with which we caught gravid females. Egg cases *in utero* were observed for 15 of the species studied, and were collected in all seasons of the year. Egg cases from *C. 'parcomaculata'* and *R. straeleni* were found in five and six months, respectively, and from all seasons. Egg cases *in utero* from *L. wallacei* were found during spring, summer, and winter, for *D. pullopunctata* and *R. barnardi* during summer and winter, and for *R. alba* during summer and autumn. The lack of a defined season for southern African skates is consistent with the findings from other studies (McEachran, 1970; Holden *et al.*, 1971; Holden, 1975; Ishihara *et al.*, 2002; Henderson *et al.*, 2004; Koop, 2005). However, it has been suggested that some shallow-water skate species may exhibit a defined egg-laying season (Braccini and Chiramonte, 2002; Mabragna *et al.*, 2002; Ruocco *et al.*, 2006).

Estimates of “gestation periods” (egg case time *in utero*) could not be made from our data, but captive studies have revealed that the time for which an egg case is held until deposition may range from 1 to 6 days. Holden *et al.* (1971), in a captive study of three skate species, reported an average of one egg case per day during the height of the spawning season, but found that this average slowed to one egg case every five days towards the end of the spawning season. Ishihara *et al.* (2002) found that *Okamejei kenojei* deposited egg cases every 3–6 days. Koop (2005) observed five skate species held in captivity over a nine-year period to exhibit distinct seasonal patterns in egg case deposition, with peaks at certain times throughout the year.

Given the intense fishing pressure in southern African waters it is important to understand the life history of these potentially vulnerable fish. Critical life history information (e.g. age and growth, reproductive cycles, fecundity, nursery grounds, and habitat) is required to develop and implement effective sustainable management practices. Although limited, this study has provided new information on aspects of the reproductive biology of 22 species of southern African skate, 15 of which are endemic and or possibly have a limited distributional range. Prior to this study, information on the reproductive biology of southern African skates was largely unknown or limited to anecdotal accounts. However, much still remains unknown about the life history of southern African skates, so much research still needs to be done if management is to improve.

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Table 2. Provisional key to the skate egg cases of southern Africa. The descriptions of egg cases (*Bathyraja smithii*, *Rajella caudaspinosa*, *Malacoraja spinacidermis*, *Neoraja stehmanni*) that were not fully developed have a question mark because the characters used to distinguish them here may change as better data, e.g. more fully developed egg cases, become available.

1a. Egg cases very large, > 120 mm L_T excluding horns.	2
1b. Egg cases smaller, < 100 mm L_T excluding horns.	5
2a. Posterior horns very long > twice the length of anterior horns.	3
2b. Posterior horns short < twice the length of anterior horns.	4
3a. Posterior horns flattened toward tips, surface coarsely striated, rough to the touch.	<i>Rostroraja alba</i>
3b. Posterior horns filamentous towards tips, surface striated, densely covered with fibres?.	<i>Bathyraja smithii</i>
4a. Egg case striated, densely covered with fibres, keels broad, ca. 20% maximum egg-case width.	<i>Dipturus pullopunctata</i>
4b. Egg case striated, without fibre covering, keels broad, ca. 12% maximum egg-case width.	<i>Amblyraja robertsi</i>
5a. Eggs cases large, > 50 mm L_T , excluding horns.	6
5b. Egg cases very small, < 50 mm L_T excluding horns.	13
6a. Egg case surface covered by dense fibres.	7
6b. Egg case surface without dense fibres.	8
7a. Lateral keels narrow, posterior horns tapering to an acute tip?.	<i>Rajella caudaspinosa</i>
7b. Lateral keels broad, horns tapering to a filamentous tip.	<i>Raja straeleni</i>
8a. Egg case surface texture rough to the touch.	<i>Rajella ravidula</i>
8b. Egg case surface texture smooth to the touch.	9
9a. Lateral keels absent.	<i>Leucoraja wallacei</i>
9b. Lateral keels present.	10
10a. Lateral keels very narrow.	<i>Rajella dissimilis</i>
10b. Lateral keels broad.	11
11a. Lateral keels not extending length of horns?.	<i>Malacoraja spinacidermis</i>
11b. Lateral keels extending length of horns.	12
12a. Egg case surface finely striated.	<i>Rajella barnardi</i>
12b. Egg case surface without striations.	<i>Rajella leopardus</i>
13a. Egg case with lateral keels absent.	<i>Raja miraletus</i>
13b. Egg case with lateral keels present.	14
14a. Egg case surface coarsely striated, lateral keels very narrow.	<i>Cruiriraja 'parcomaculata'</i>
14b. Egg case surface smooth to the touch, lateral keels broad?.	<i>Neoraja stehmanni</i>

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