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Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the Southwest Atlantic

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Size at maturity, sexual dimorphism, gonad development, and abundance of white-dotted skate, *Bathyraja albomaculata*, were assessed along its geographic range in the Southwest Atlantic, from Uruguay to Tierra del Fuego (Argentina). In all, 291 specimens from eight research cruises conducted between 1998 and 2003 were examined. Length–mass relationships were sexually dimorphic, adult females being significantly heavier than males of the same length. The largest female observed was 762 mm total length (L_T), and 50% maturity (L_{T50}) was attained at 653 mm L_T. The largest male was 732 mm L_T, and male L_{T50} was 628 mm L_T. Female and male L_{T50} were not significantly different and were about 86% of observed maximum size, similar to other *Bathyraja* species. The lack of sexual dimorphism in size at maturity and the slight difference in maximum size between sexes support the hypothesis of relaxation of selection for large female size in oviparous elasmobranchs. Liver size was not sexually dimorphic. Mature female gonads were symmetrical in terms of mass, and similar in ovarian follicle number and size. Females carried egg cases in April, September, and October, consistent with previous observations around the Islas Malvinas and suggesting year-round egg laying. *Bathyraja albomaculata* was most abundant on the outer continental shelf and slope between 36°30′S and 45°S (northern area). In contrast, it was generally absent between 48°S and 52°S (southern area), a region where it was formerly reported as abundant. These differences are coincident with the development of a fishery targeting skates in the southern area, whereas in the north *B. albomaculata* taken as bycatch are mostly discarded alive.

Keywords: Argentina, elasmobranch, life history, oviparity.

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Introduction

Skates (Rajidae) are the most diverse elasmobranch fish, with a total of more than 200 species worldwide (McEachran and Dunn, 1998). They inhabit depths from the coast to at least 3000 m (McEachran and Miyake, 1990) and may be found along open coasts, in bays, estuaries, and even the intertidal zone at higher latitudes (Ebert *et al.*, 1991). However, skates are absent over the inner shelves of tropical and subtropical waters (McEachran and Miyake, 1990).

The genus *Bathyraja* is the most diverse of the Rajidae (Ishihara and Ishiyama, 1986). Stehmann (1986) listed ten species for the Southwest Atlantic, seven of which are endemic on the Argentine continental shelf (Menni and Stehmann, 2000); since that listing, a new species of *Bathyraja* has been described from the area (Díaz de Astarloa and Mabragaña, 2004). Among species of this genus, the white-dotted skate *Bathyraja albomaculata* is medium sized and wide ranging, from Uruguay in the Atlantic to central Chile in the Pacific, and from 72 to 945 m deep (Cousseau *et al.*, 2000; Menni and Stehmann, 2000).

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Most previous studies on *Bathyraja albomaculata* focused on taxonomy (Stehmann, 1978; Menni *et al.*, 1984; Herman *et al.*, 1995; Sáez and Lamilla, 2004) and feeding (Brickle *et al.*, 2003), or were limited to observations and comments on distribution (Bellisio *et al.*, 1979; Menni and López, 1984; Lloris and Rucabado, 1991; Pequeño and Lamilla, 1993). The only studies on the life history of *B. albomaculata* were either restricted to the waters around the Islas Malvinas (Henderson *et al.*, 2004), representing only a small portion of the species' range (Menni and Stehmann, 2000), or focused on the egg-case stage (Lucifora and García, 2004).

Skates are becoming increasingly important to the fisheries of the Southwest Atlantic (Agnew *et al.*, 1999; Paesch and Meneses, 1999). Catches of all skates combined increased from 300 t in 1991 to 14 856 t in 1998 (Cousseau *et al.*, 2000), and skates have become the sixth most economically important fish resource (among a total of 46 commercial fish species) landed by commercial bottom-trawl fisheries in Argentina (García de la Rosa *et al.*, in press). *Bathyraja* spp. are increasingly targeted as traditional commercial fisheries for bony fish are depleted (Díaz de Astarloa and Mabragaña, 2004). They are also caught as bycatch (Cedrola *et al.*, 2005). *Bathyraja albomaculata* is one of the most valuable bycatch species caught by finfish trawlers targeting southern blue whiting *Micromesistius australis*, hoki *Macruronus magellanicus*, hake *Merluccius hubbsi* and *M. australis*, and Patagonian cod *Salilota australis* around the Islas Malvinas (Brickle *et al.*, 2003). Little is known about the reproductive biology of *Bathyraja*, and the only information currently available on aspects of reproduction was obtained in the northern hemisphere (Teshima and Tomonaga, 1986; Cailliet *et al.*, 1999; Stehmann and Merrett, 2001; Ebert, 2005). Biological data (especially on reproduction) of skates are needed to improve management of their fisheries.

In this paper we analyse the reproductive biology (size at maturity, gonad development, and egg-case description) and abundance (spatial variability and density) of *B. albomaculata* caught in the Southwest Atlantic.

Material and methods

The catch data and samples of skates used in this paper were obtained from eight research cruises conducted in the Southwest Atlantic between 34°S and 55°S, over a depth range of 43–440 m, by the RVs "Capitán Oca Balda" and "Dr Eduardo Holmberg" of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) between 1998 and 2003 (Figure 1). The main objective of these cruises was to collect biological data on *M. hubbsi*, *M. magellanicus*, Argentine squid *Illex argentinus*, and other demersal fish resources in the area. A 59-m Engel-type bottom trawlnet, with a stretched mesh size of 200 mm in the wings and 103 mm in the codend, vertical height of 4 m, and horizontal opening of 15 m was used. Haul duration was 30 min at a trawling speed of 3.6 knots.

Oceanographic conditions in the study area

Water masses on the Argentine continental shelf consist of a mixture of several water types: coastal, Subantarctic, subtropical, and mixed waters (Bisbal, 1995). In the south, the low salinity, coastal Patagonian Current, of Subantarctic origin, flows north along the coast, from the Strait of Magellan (52°30′S) to 40–42°S, where it veers offshore and flows northwards over the outer shelf and slope. In the north, the circulation is influenced by the warm, more saline, south-flowing Brazil Current, which runs along the continental margin of South America and moves offshore at about 36–38°S (Olson *et al.*, 1988). These systems correspond to two biogeographic provinces: the Magellanic Province in the south, which also includes southern Chile, and the Argentine Province in the north, extending up to Rio de Janeiro, Brazil (Menni and López, 1984). *Bathyraja albomaculata* is considered typical of the Magellanic fauna (Menni and Stehmann, 2000).

Sexual dimorphism

In all, 146 female and 145 male *B. albomaculata* were collected and frozen on board ship for subsequent examination in the laboratory. Upon capture, each specimen was sexed and weighed. Total length (L_T) and disc width (D) were measured to the nearest mm, according to Hubbs and Ishiyama (1968). The relationship between D and L_T, with L_T as the dependent variable, was estimated separately for each sex in order to estimate L_T for any skate with a damaged tail. The null hypothesis of no difference between slopes of the regressions of males and females was tested with a Student's t-test (Zar, 1984).

Total mass (M_T) was recorded to the nearest 0.1 g for each specimen. L_T and M_T relationships were calculated separately for each sex with ln-transformed data, and the null hypothesis of no difference between slopes was tested with a Student's t-test (Zar, 1984).

Reproductive analysis

To determine the onset of sexual maturity in males, clasper length (L_C), the degree of calcification of the claspers, the number of rows in the alar thorn patch, and the condition of efferent ducts were recorded. Males were sorted into three categories: immature (short, non-calcified claspers; alar thorn patch not yet developed; straight efferent ducts), maturing (long calcifying claspers; developing alar thorn patch; efferent ducts beginning to coil), and mature (long, fully calcified claspers; alar thorn patch fully developed; highly coiled efferent ducts; Mabragaña *et al.*, 2002; Mabragaña and Cousseau, 2004).

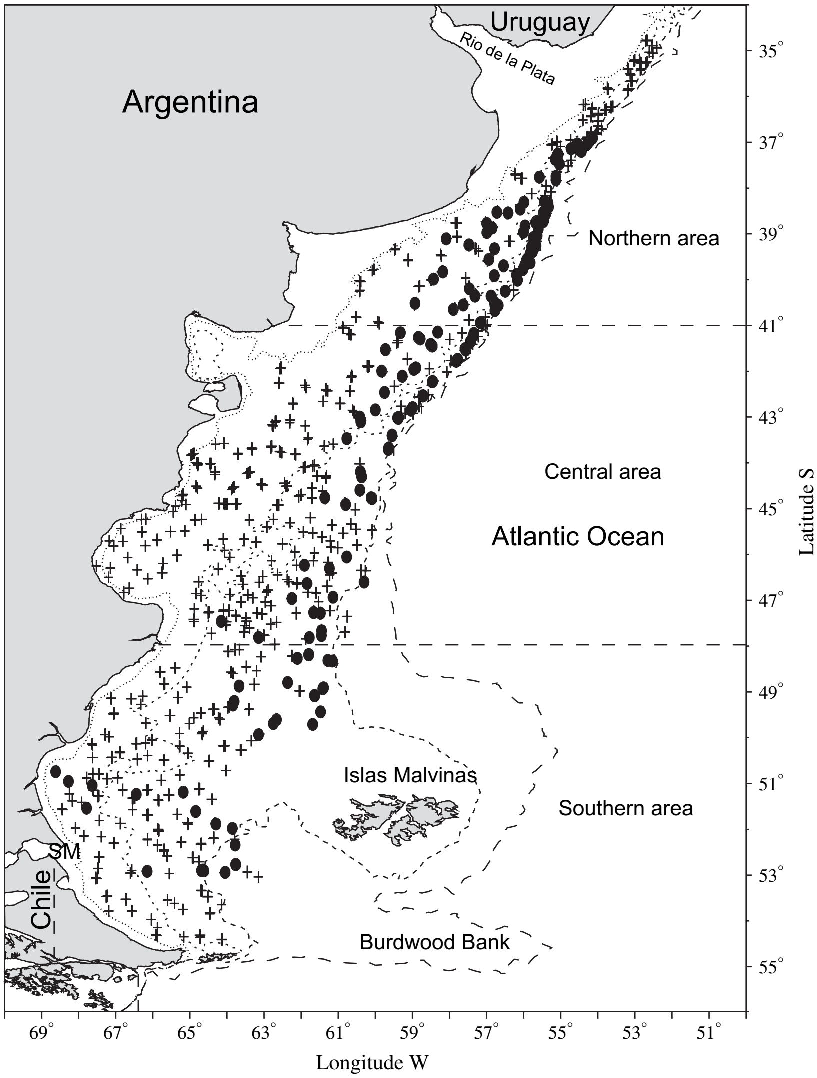

Figure 1. Map of the study area showing the location of trawl stations. Black dots show the positions of trawls that caught *Bathyraja albomaculata* during eight research cruises carried out between 1998 and 2003; plus signs show the positions of trawls that made no catch of *B. albomaculata*. SM, Strait of Magellan. Isobaths shown are are 50, 100, 200, and 1000 m.

In females, uterus width (W_U), oviducal gland width (W_O), and the number and diameter (in mm) of ovarian follicles were recorded. Females were categorized as immature when they had non-developed, thread-like uteri firmly attached to the dorsal wall of the body cavity, ovaries with indistinguishable ovarian follicles, and hardly recognizable oviducal glands. Maturing females had enlarged ovaries, ovarian follicles of several sizes, oviducal glands recognizable as an oval widening in the anterior part of the oviduct, and uteri caudally enlarging. Mature females had wide, pendulous uteri, vitellogenic ovarian follicles, and large, wide, heart-shaped oviducal glands. The masses of right and left ovaries were recorded separately in mature females (Mabragaña *et al.*, 2002).

Male size at maturity was estimated from the pattern of growth of claspers relative to L_T. Female size at maturity was estimated from the relationship between oviducal gland and uteri widths with L_T. For both sexes, the proportion of mature individuals in 10 mm L_T intervals was calculated. A logistic ogive was fitted to the data using a maximum-likelihood approach, in order to estimate the size at which 50% of individuals (L_{T50}) were sexually mature (Roa *et al.*, 1999). The null hypothesis of no difference between males and females was tested with a χ^2 test (Aubone and Wöhler, 2000).

Liver mass (M_L) and gonad mass (M_G) of each fish were recorded to the nearest 0.1 g. Sexual dimorphism in M_L was assessed by performing a Student's t-test, the null hypothesis of no difference in slopes of the linear regressions between L_T and M_L being estimated from ln-transformed data (Zar, 1984).

The null hypothesis of no difference between mean masses of right and left ovaries in mature females was tested with a paired-sample t-test (Zar, 1984). This statistical process was also carried out to check differences in the diameter and number of ovarian follicles between right and left ovaries of mature females. The gonadosomatic index (I_G) was calculated as $I_G = 100\ M_G\ M_T^{-1}$. The null hypothesis of no difference between the I_G of juvenile and mature females was tested through a t-test for independent samples (Zar, 1984).

Egg cases of *Bathyraja albomaculata* are described. Egg-case length without horns (L_{EC}) and maximum width (W_{EC}) were measured according to Hubbs and Ishiyama (1968). The date and the geographic position of all females carrying egg cases in the uteri were recorded to identify egg-laying seasons and areas.

Spatial distribution and abundance

Distribution (by latitude and depth) of *B. albomaculata* was deduced over eight research cruises. The study area was divided into three areas (Figure 1): northern (off Uruguay and the Argentine Province of Buenos Aires, 34−41° S), central (north Patagonia, 41−48° S), and southern (southern Patagonia, 48−55° S). The northern area is a region of submergence of the Magellanic fauna (Menni and López, 1984), whereas in the central and southern areas the Magellanic fauna dominate though the two areas experience distinct oceanographic conditions driven by differences in climate (Guerrero and Piola, 1997).

Data from three research cruises carried out in 1998 were used to estimate densities of *B. albomaculata* throughout the survey area. The cruises were conducted during the periods 4−28 March in the northern area (n = 87 hauls), 19 July−3 August in the central area (n = 77 hauls), and 10−30 August in the southern area (n = 85 hauls), with the same vessel (RV "Dr Eduardo Holmberg") and fishing gear. Densities (d) were calculated according to the swept-area method described by Alverson and Pereyra (1969), as follows:

$$d = C \times a^{-1} \times q$$

where C is the catch in tonnes, a is the swept area in square nautical miles (a is the distance trawled × distance between the net wings), and q is the catch coefficient, which was assumed to be 1 because the net was designed to catch demersal and benthic fish.

To describe the distribution of *B. albomaculata*, all mean densities were averaged over 1° latitude intervals, using all hauls irrespective of whether the species was caught. Frequency of occurrence by degree of latitude was calculated as the number of times *B. albomaculata* was present in each haul, related to the total number of trawl stations including trawls with no *B. albomaculata* (García de la Rosa, 1998). Mean densities and percentage *B. albomaculata* presence by 30-m depth intervals were also calculated.

Results

Sexual dimorphism

Females ranged from 455 to 762 mm L_T (mean 597 mm), and males from 379 to 732 mm L_T (mean 579 mm). There was no significant difference in the relationships between D and L_T between sexes (t = 0.724; d.f. = 287; p > 0.469), so a D−L_T relationship was estimated for both sexes combined ($L_T = 1.377D + 21.259$; $r^2 = 0.975$; s.e. = 19.04). A typical dimorphism in disc shape between adult males and females was observed, adult males having an indented, almost heart-shaped disc.

Length−mass relationships of females ($M_T = 5e^{-0.6} L_T^{3.08}$; $r^2 = 0.976$, n = 139) and males ($M_T = 2e^{-0.6} L_T^{3.20}$; $r^2 = 0.932$, n = 133) were significantly different (t = 2.42; d.f. = 268; p < 0.016); for skates >548 mm L_T, females were heavier than males at similar length (Figure 2). Liver size at a given mass was not sexually dimorphic (t = 0.414; d.f. = 70; p = 0.68; Figure 3).

Reproductive analysis

The smallest mature male was 590 mm L_T (185 mm L_C), and the largest immature male was 694 mm L_T (139 mm L_C). Most immature males, however, were <580 mm L_T, with claspers <130 mm long (Figure 4). The number of rows in the alar thorn patch of immature and mature individuals ranged from zero to six. Most immature males had no alar thorns, except two fish of 535 and 694 mm L_T that had one and two alar thorn rows, respectively. Maturing males had one to two and mature males had two to six rows of alar thorns (Figure 5). The fitted logistic curve produced an estimated L_{T50} of 628 mm (Figure 6), which is

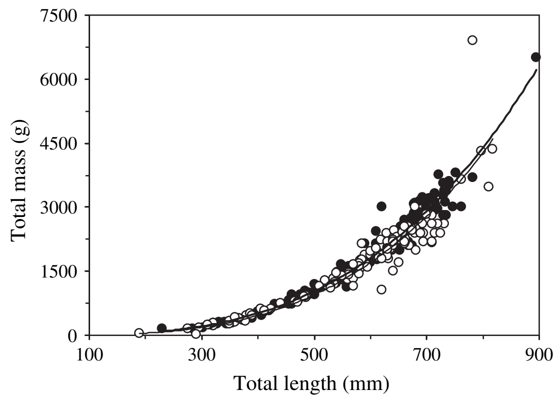

Figure 2. Relationship between total length and total mass of *Bathyraja albomaculata* from the Southwest Atlantic. Open circles and lower line, males (n = 145); black dots and upper line, females (n = 146); differences between sexes were statistically significant.

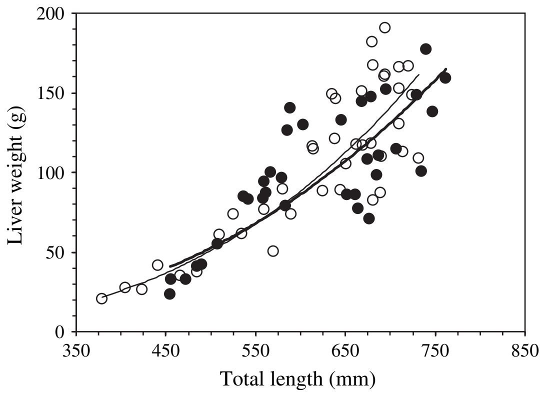

Figure 3. Relationship between total length and liver mass for *Bathyraja albomaculata* from the Southwest Atlantic. Open circles and thin line, males (n = 40); black dots and bold line, females (n = 34).

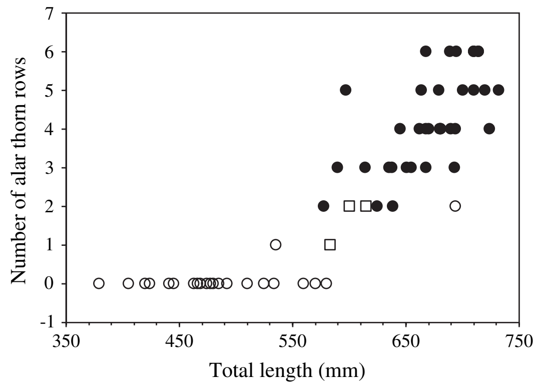

Figure 5. Relationship between the number of rows in the alar thorn patch and total length for male *Bathyraja albomaculata* from the Southwest Atlantic. Open circles, immature males; open squares, maturing males; black dots, mature males; n = 60.

85.9% of the maximum L_T observed for males (732 mm). There were no significant differences between right and left M_G of males (mean ± s.d. right testis, 25.59 ± 3.52 g; left, 25.63 ± 3.71 g; t = 0.076; d.f. = 10; p > 0.94).

The smallest mature female was 652 mm L_T (W_O = 41 mm; W_U = 20 mm) and the largest immature female was 579 mm L_T (W_O = 18 mm; W_U = 13 mm; Figure 7). Maturing females were between 583 and 603 mm L_T. Both W_O and W_U increased rapidly with increasing length. The estimate of female L_{T50} from the logistic curve was 653 mm, 85.7% of the maximum L_T observed (Figure 6). Size at 50% maturity was not significantly different between sexes (χ^2 = 2.08; p > 0.14).

Mature females had symmetrical gonads, as shown by the lack of significant differences in mass between right (mean ± s.d. 32.54 ± 25.39 g) and left (34.92 ± 15.39 g) ovaries (t = 0.338; d.f. = 9; p = 0.742). No differences between right (mean 4.28) and left (6.4) ovarian follicle numbers (t = 1.698; d.f. = 6; p = 0.14) and diameters (mean right and left: 28.73 and 32.56 mm, respectively; t = 1.253; d.f. = 7, p > 0.25) were found. The I_G was significantly different between juvenile and mature females (t = 4.676; d.f. = 22; p < 0.0001).

Females were observed with egg cases in April, September, and October, but only four were found in all. A

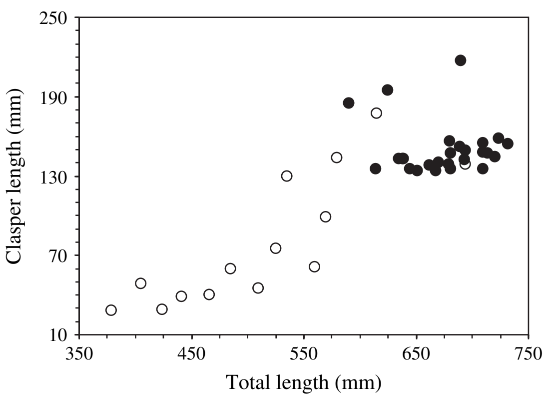

Figure 4. Relationship between clasper length and total length for *Bathyraja albomaculata* from the Southwest Atlantic. Black dots, mature males; open circles immature males; n = 40.

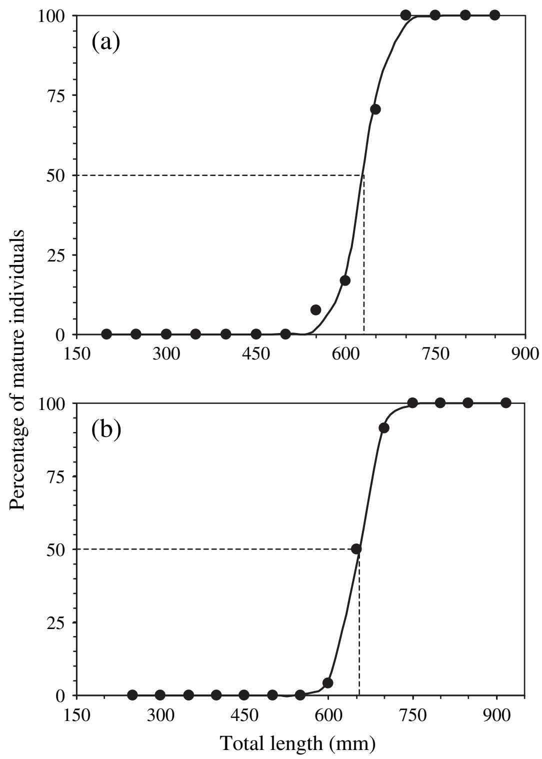

Figure 6. Percentage mature (a) males and (b) females in different length classes of *Bathyraja albomaculata* from the Southwest Atlantic. The lines are logistical ogives fitted by maximum-likelihood techniques, and the dots are observed values.

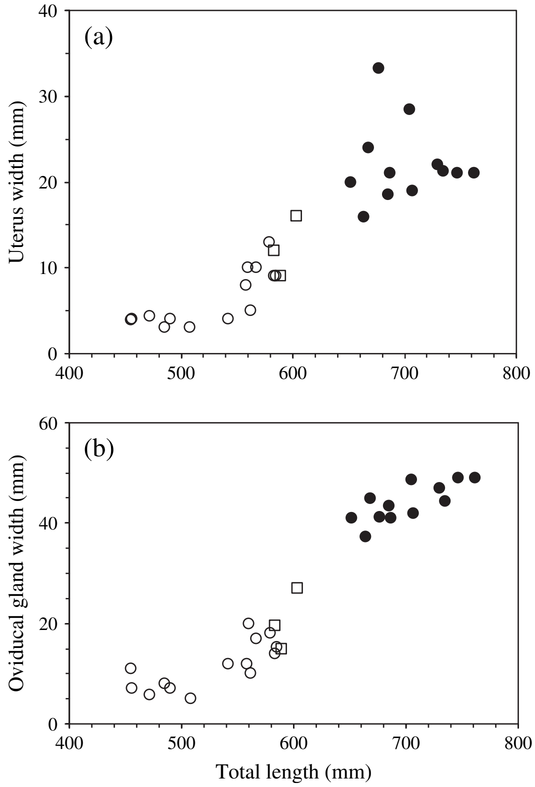

Figure 7. Relationship between total length and (a) uterus and (b) oviducal gland width for *Bathyraja albomaculata* from the Southwest Atlantic. Open circles, immature females; open squares, maturing females; black dots, mature females; n = 35.

679 mm L_T female had an egg case (approximately one-quarter developed) in each uterus (caught in October 2002 at 44°47′S 60°05′W), another of 758 mm L_T possessed a three-quarters formed egg case (caught in September 2003 at 44°12′S, 60°24′W), and two females of 740 and 675 mm L_T had fully formed egg cases. These two females were caught in October 2002 at 44°47′S 60°05′W and in April 2003 at 37°06′S 54°38′W, respectively. Mean (±s.d.) L_{EC} was 97.33 ± 1.03 mm, and W_{EC} was 62.38 ± 1.58 (n = 4).

Egg cases of *B. albomaculata* (Figure 8) were barrel-shaped, yellow-brown when recently laid, but changing to dark brown during development. The surface of the case was relatively smooth, but with an apparent longitudinal striation, that was more obvious under magnification. The posterior horns appeared first and were longer, thinner, and more convoluted than the anterior ones. The anterior edge was concave, the posterior end straight. The lateral keels were narrow (<6% of egg-case width).

Spatial distribution and abundance

Bathyraja albomaculata were found along the entire outer continental shelf between 36°S and 53°S, from 65 m to

Figure 8. Egg case of a 675 mm L_T female *Bathyraja albomaculata* from the Southwest Atlantic.

the upper slope, at 310 m. They were absent between 34°S and 36°S and between 53°30′S and 55°S (Figure 1). During 1998, two major concentrations of *B. albomaculata* were found (Figure 9), one in the northern and central areas between 36°30′S and 45°S, with densities of >0.6 t nautical mile^{-2} (ca. 80% of species occurrence), and the other in the southern area, between 50°S and 53°30′°S, with densities of up to 0.5 t nautical mile^{-2} (ca. 18% of the species occurrence).

Depth distribution of *B. albomaculata* over the continental shelf was different in the three areas. In the northern area, *B. albomaculata* was found at a depth range of 65−310 m, with high densities of up to 0.35 t nautical mile^{-2} between 250 and 310 m (Figure 10). In the central area, *B. albomaculata* was concentrated in shallower water between 70 and 140 m, with the highest densities of 0.24 t nautical mile^{-2} at a depth range of 100−130 m (Figure 10). In the southern area, *B. albomaculata* was distributed over a broader depth range (70−310 m), but abundance peaked between 160 and 190 m at a maximum density of 0.7 t nautical mile^{-2} (Figure 10).

Discussion

Rajids commonly differ in the relative size of several body parts, and these differences are often sexually specific (Hubbs and Ishiyama, 1968). In *Bathyraja albomaculata*, however, there were no significant differences between sexes in the relationship between D and L_T. However, L_T and M_T relationships were significantly different between the sexes, with adult females heavier at a given length than males, a difference also observed in other skates, such as the zipper sand skate, *Psammobatis extenta* (Braccini and Chiaramonte, 2002a), the smallnose fanskate, *Sympterygia bonapartii* (Mabragaña *et al.*, 2002), and the shortfin sand skate, *Psammobatis normani* (Mabragaña and Cousseau, 2004). These differences may be related to the production of eggs.

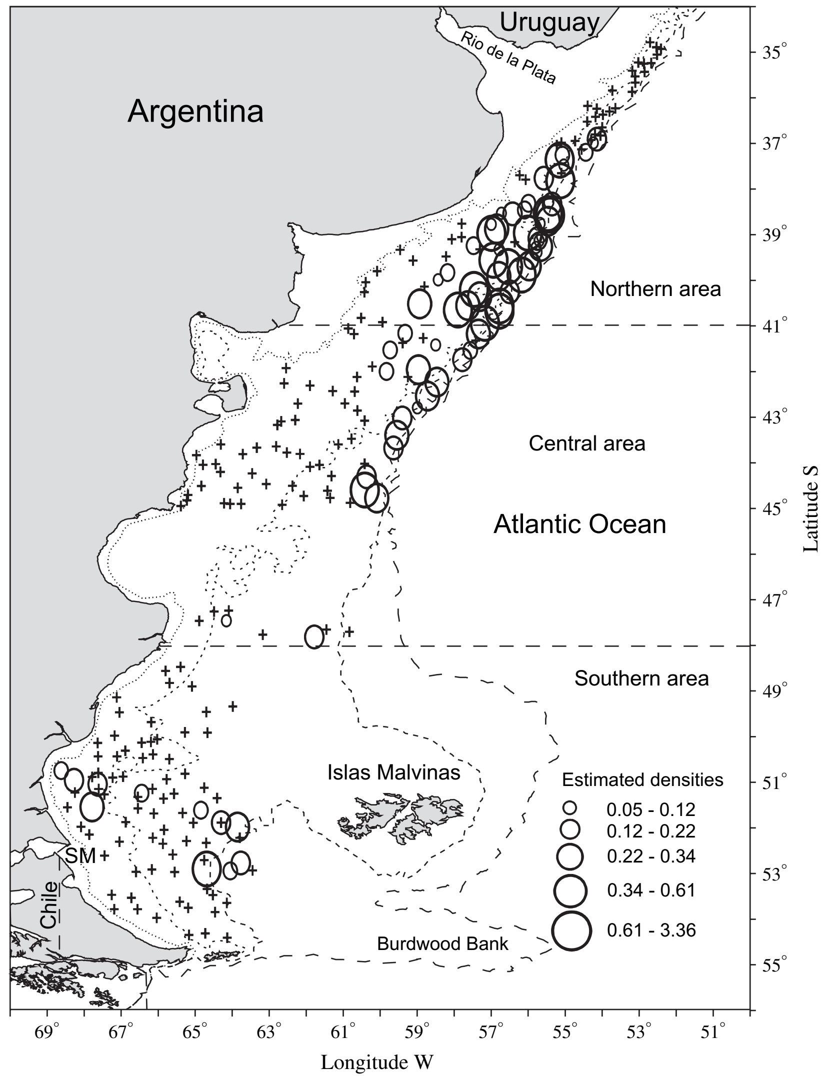

Figure 9. Map of the study area showing estimated densities (t nautical mile^{-2}) of *Bathyraja albomaculata* from three research cruises in 1998. Plus signs represent trawls with no catch. SM, Strait of Magellan. Isobaths shown are 50, 100, 200, and 1000 m.

Female *Leucoraja wallacei* and *Dipturus pullopunctatus* commonly attain greater lengths than males, although females grow more slowly (Walmsley-Hart *et al.*, 1999). The same trend has been observed in *Raja binoculata* and *R. rhina* by Zeiner and Wolf (1993). Within the genus *Bathyraja*, male maximum L_T can be larger than (e.g. *B. interrupta*, *B. minispinosa* and *B. parmifera*), smaller than (*B. aleutica* and *B. taranetzi*), or the same size as (e.g. *B. lindbergi*, *B. maculata* and *B. trachura*) that of females (Ebert, 2005). In our samples, the largest female *B. albomaculata* (762 mm L_T) was 30 mm larger than the largest male (732 mm L_T). Cousseau *et al.* (2000), who took samples from the entire Argentine shelf, also found that females were larger than males, although the lengths they recorded were substantially greater (960 and 818 mm L_T for females and males, respectively).

We found no sexual differences in size at maturity, although the estimate of L_{T50} from the logistic curve was slightly greater in females (654 mm) than in males (629 mm). It is common among elasmobranchs that females mature larger than males. However, sexual dimorphism in size at maturity is quite variable among skate species. Braccini and Chiaramonte (2002a) reported that female *P. extenta* matured at a smaller size than males. The same is true for *P. rudis* and *P. normani* (Mabragaña and Cousseau, 2004). Jardas (1973) and Nottage and Perkins (1983) showed that females *Raja clavata* attain sexual maturity at a larger size than males, a trend also reported for *R. pulchra* (Yeon *et al.*, 1997), *Dipturus chilensis*, and *Atlantoraja castelnaui* (Oddone *et al.*, 2005). In contrast, no significant differences in the size at maturity of male and female *L. wallacei* (Walmsley-Hart *et al.*, 1999),

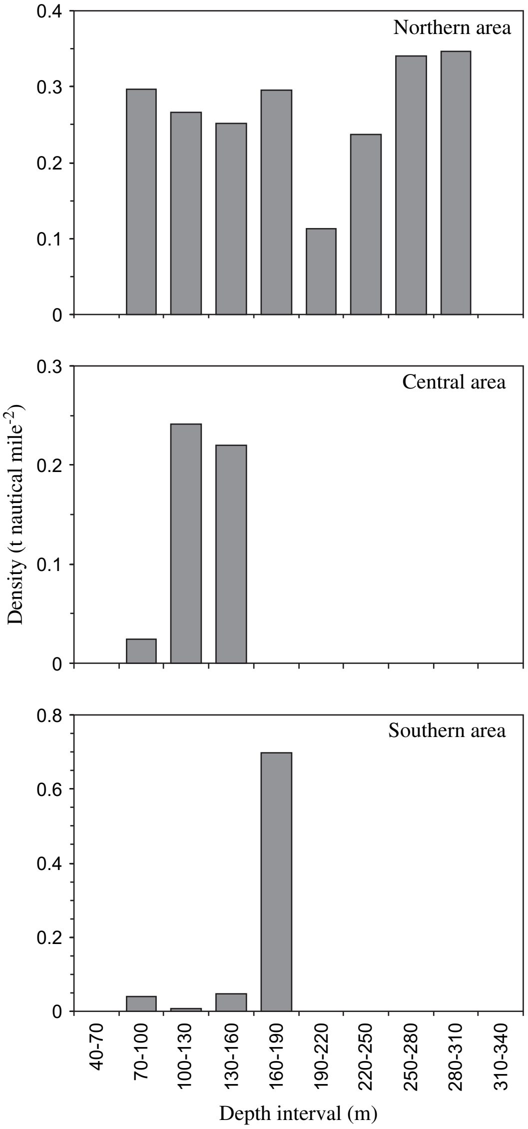

Figure 10. Densities per depth strata of *Bathyraja albomaculata* in the northern (35−41°S), central (41−48°S), and southern areas (48−55°S) of the Southwest Atlantic continental shelf.

L. naevus, *L. melitensis* (Capapé, 1975), and *S. bonapartii* (Mabragaña *et al.*, 2002) have been documented. Seven out of eight North Pacific species of *Bathyraja* exhibit no significant differences in size at maturity (Ebert, 2005). This mosaic pattern, in which some species are sexually dimorphic in size at maturity and maximum size while others are not, indicates that selection pressure for larger size at maturity (and possibly greater maximum size) is not as strong in skates as among viviparous elasmobranchs (Klimley, 1987; Ebert, 2005). Oviparity releases skates from the constraint of holding embryos within their bodies, which limits fecundity, and allows them to have higher fecundities than most viviparous elasmobranchs (Lucifora and García, 2004).

Size at maturity is one characteristic that allows fish populations to be distinguished, and to establish a baseline for monitoring changes in a population caused by fishing (Templeman, 1987). For *Bathyraja albomaculata* around the Islas Malvinas, 50% of fish were mature at 400 and 416 mm D in males and females, respectively (Henderson *et al.*, 2004). This corresponds to 572 and 594 ± 21 mm (95% confidence interval) mm L_T for males and females, respectively. These values are smaller than those reported in this study, but it is unlikely that the difference is attributable to differences in the methods for assessing maturity, because our criteria for determining maturity were the same as those used by Henderson *et al.* (2004). Also, the conversion from D to L_T is not likely to introduce bias in our estimates because of the good fit of the relationship between the two parameters. As *B. albomaculata* is a wide-ranging species in the Southwest Atlantic, different populations with different size at maturity might occur, as found for *Amblyraja radiata* (Templeman, 1987). Further research on larger sample sizes for different areas of the Southwest Atlantic is required to test this hypothesis.

In several skates from southern Patagonia (48−54°30′S), L_{T50} was achieved at >70% of the maximum L_T observed (Sánchez and Mabragaña, 2002). In *P. normani* L_{T50} corresponded to 76.3% and 74.2% of the maximum L_T observed for males and females, respectively (Mabragaña and Cousseau, 2004). Male and female *P. extenta* attain maturity at about 79% and 89% of their maximum size, respectively (Braccini and Chiaramonte, 2002b). In *B. albomaculata*, L_{T50} corresponds to ca. 86% of the maximum L_T observed for males and females, a value well within the range observed for other species of *Bathyraja*, which usually mature at >80% of maximum L_T (Ebert, 2005). This indicates that *B. albomaculata* could be particularly sensitive to fishing pressure and overexploitation, a conclusion also supported by the late age at which females mature (10 years, Henderson *et al.*, 2004).

In skates, male maturation can be determined by analysis of alar thorns (Mabragaña *et al.*, 2002). Alar thorns are used by male skates to hold on to females during copulation (Luer and Gilbert, 1985). In *B. albomaculata*, the number of alar thorn rows increases concomitantly with size at maturity. Alar thorns in adult male *Bathyraja hubbsi* are arranged in five to eight rows, whereas in *B. interrupta*, *B. pseudoisotrachys*, and *B. trachura*, alar thorns are arranged in four to five, six to seven, and four to eight rows, respectively (Ishihara and Ishiyama, 1985). Norman (1937) mentioned the presence of three or four rows of alar thorns in a mature male *B. albomaculata*. Young male *B. caeluronigricans* appear to have no alar thorns whereas fully developed males have six to seven alar thorn rows (Ishihara and Ishiyama, 1985). The number of alar thorns in the mature male *B. albomaculata* we observed was similar to that in other *Bathyraja* species.

Many elasmobranchs have asymmetrical ovaries of different size and, in certain cases, one ovary may become atrophied or be completely absent (Hamlett and Koob, 1999). The present data show that both male and female *B. albomaculata* have symmetrical gonads, and we found no difference in the number and the size of ovarian follicles between left and right ovaries. This symmetry is also seen in other species of *Bathyraja* (Ebert, 2005), and other skates (Braccini and Chiaramonte, 2002a; Mabragaña *et al.*, 2002).

Females carrying egg cases were found in the same area (44–60°W) in two consecutive years. High numbers of *B. albomaculata* egg cases have been found near this area (43–60°W) in benthic samples (Lucifora and García, 2004), coinciding with the greatest abundance of *B. albomaculata* in the central area of this study, suggesting that it is an important area for the reproduction of the species. The present data indicate that egg cases are deposited at least by autumn in the northern area, and during winter and spring in the central area, suggesting either a long egg-laying season, or the existence of geographical differences in the timing of egg-case deposition. Though our data on females with egg cases are limited, Henderson et al. (2004) state that females bearing egg cases are common year round near the Islas Malvinas (which gives some support to the first suggestion above). Year-round egg deposition appears to be common in skates, e.g. in *Leucoraja garmani* (McEachran, 1970) and *R. clavata* (Cannizaro *et al.*, 1995). Skates with well-defined egg-laying seasons in spring or summer tend to be coastal species that inhabit very shallow water, such as *S. bonapartii* (Mabragaña *et al.*, 2002) and *P. extenta* (Braccini and Chiaramonte, 2002a). Skates that inhabit deeper water may experience less environmental variability, and their life history strategy may reflect this lack of seasonality.

Elasmobranchs lack adipose tissue and store fat in the liver (García-Garrido *et al.*, 1990). While some of the hepatic reserves can be used in producing gametes in female oviparous elasmobranchs (Craik, 1978), the role of the liver in reproduction in male elasmobranchs is still not completely understood (García-Garrido *et al.*, 1990). It has been suggested for another batoid, the guitarfish *Rhinobatos annulatus*, that liver reserves can be used to support migration by males (Rossouw, 1987). No sexual dimorphism in the relationship between L_T and M_L was observed in *Bathyraja albomaculata*, suggesting a similar importance of liver as an energy source for adult males and females.

Bathyraja albomaculata is widely distributed in the Magellanic Zoogeographic Province in the Southwest Atlantic (Menni and Gosztonyi, 1982; Menni and López, 1984; Menni and Stehmann, 2000). Norman (1937) reported the species from an area between 51°44′–53°30′S and 58°27′–64°19′W at a depth of 137–403 m. The distribution of the species covers the southern Patagonian shelf between 52°S and 54°S, around the Islas Malvinas and the Burdwood Bank (Menni and Stehmann, 2000). North of 52°S, it occurs on the outer shelf and upper slope as far north as 41°S (Bellisio *et al.*, 1979), with its northernmost record off Uruguay (Nion *et al.*, 2002). Although *B. albomaculata* is present both in shallower shelf areas and in deeper water in the south, in the north it is restricted to deeper water, following the cold-temperate, north-flowing Malvinas Current. It is therefore likely that the northern limit of its distribution is determined by water temperature (Figueroa *et al.*, 1999).

Several species of *Bathyraja* (*B. albomaculata*, *B. griseocauda*, *B. magellanica*, *B. multispinis*, and *B. scaphiops*) are relatively more abundant in the southern area (García de la Rosa *et al.*, 2000), and in deep and cold water in the northern area (Menni and Stehmann, 2000). However, our results indicate that *Bathyraja albomaculata* is considerably more abundant in the northern area. This could be related to the recent higher fishing pressure in the southern area. The high level of fishing in the early 1990s was associated with the discovery of a "ray hotspot" south of the Islas Malvinas, where a large part of the catch was concentrated (Agnew *et al.*, 1999). The rajid fishery around Islas Malvinas exploits several skate species, but *B. albomaculata* is the second most common skate caught over the continental shelf and along the shelf edge to the northeast of the islands, contributing ca. 28% of the estimated total rajid catch (Agnew *et al.*, 1999). The biomass (estimated by bottom-trawl research surveys) of *B. albomaculata* south of 45°S has diminished drastically from 32 179 t in 1998 to 5448 t in 1999, a decline of 83% (García de la Rosa *et al.*, 2000).

In contrast, in the northern area, directed skate fishing on the outer continental shelf is limited. About 80% of the skate landings into Argentine ports are made in Mar del Plata (38°S), where most of the landings consist of coastal species (Massa and Hozbor, 2003). *Bathyraja albomaculata* constitutes $<2\%$ of the skate landings in Mar del Plata, only *B. griseocauda*, at $<1\%$ of the skate landings, being less common than *B. albomaculata* (Massa and Hozbor, 2003). Skates are also caught as bycatch in groundfish trawl fisheries in the northern area (Massa and Hozbor, 2003), but the survival of discarded skates is believed to be high (Laptikhovsky, 2004). Differences in fishing mortality may explain the differences in abundance between the northern and the southern areas.

Rajids are highly susceptible to fishing pressure and overexploitation (Walker and Hislop, 1998; Dulvy and Reynolds, 2002). However, many aspects of the life history of *B. albomaculata* that may be important from a fisheries management perspective (reproductive grounds, nursery areas, fecundity and mortality) remain unknown. Moreover, in order to understand fully the impact of fisheries on the species, it is necessary to identify the spatial distribution of the different stages of the life cycle of *B. albomaculata*, and to make reliable estimates of fishing and discard mortality at all of these stages. Detailed landing and effort statistics, and a better knowledge of population structure and possible latitudinal clines in life history and population parameters, are necessary if sustainable management of the species is to be attained.

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(*Amblyraja*), *Raja* (*Dipturus*), *Raja* (*Leucoraja*) *Raja* (*Raja*), *Raja* (*Rajella*) (with two morphotypes), *Raja* (*Rioraja*), *Raja* (*Rostroraja*), *Raja lintea*, and *Sympterygia*. Bulletin de L'Institut Royal des Sciences Naturelles de Belgique (Biologie), 65: 237−307.

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