

## Reproductive biology of the Magellan skate, *Bathyraja magellanica* (Chondrichthyes, Rajidae), in the south-western Atlantic

Lorena B. Scenna<sup>A,B,D</sup> and Juan M. Díaz de Astarloa<sup>B,C</sup>

<sup>A</sup>Laboratorio de Ictiología, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Funes 3350, B7602AYL, Mar del Plata, Argentina.

<sup>B</sup>Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Avenida Rivadavia 1917, C1033AAJ, Ciudad Autónoma de Buenos Aires, Argentina.

<sup>C</sup>Laboratorio de Biotaxonomía Morfológica y Molecular de Peces, Instituto de Investigaciones Marinas y Costeras, Universidad Nacional de Mar del Plata, Funes 3350, B7602AYL, Mar del Plata, Argentina.

<sup>D</sup>Corresponding author. Email: lscenna@mdp.edu.ar

**Abstract.** The knowledge of reproductive parameters is essential to develop effective management and conservation plans. The present study provides the first information on the reproductive biology of an abundant and important trawl by-catch skate, *Bathyraja magellanica*, along its geographic range in the south-western Atlantic (43–55°S). In total, 81 males (205–738 mm total length, TL) and 104 females (157–768 mm TL) were analysed. Length–frequency distributions were significantly different between sexes, with females being larger than males. However, no sexual dimorphism was observed in TL–total body weight relationship and liver size. Length at maturity was similar between males (638 mm TL) and females (653 mm TL), ~85% of maximum observed size. The mean number of vitellogenic oocytes per skate was 14.37 ( $\pm 4.43$ ), increasing with female TL. Egg cases of *B. magellanica* had striated surface, broad lateral keels, extremely long posterior horns, and its wall consisted of three layers. An important area for the reproduction of *B. magellanica* was found between 48°50'S and 50°30'S. The present results indicated that this species has a low reproductive efficiency, suggesting that the *B. magellanica* population should be monitored closely to avoid large-scale changes in skate community structure of the south-western Atlantic.

**Additional keywords:** egg cases, egg-laying area, elasmobranchs, maturity, Patagonian Shelf, vitellogenic oocytes.

Received 8 June 2013, accepted 13 November 2013, published online 16 June 2014

### Introduction

Chondrichthyans play an important role in the functioning of marine ecosystems (Stevens *et al.* 2000). The life-history characteristics of this group of fishes, such as large adult size, late sexual maturity and the reduced number of well developed offspring, make them extremely susceptible to overfishing and habitat loss (Hoenig and Gruber 1990; Camhi *et al.* 1998). For these reasons, effective conservation management of chondrichthyans needs to be achieved. The knowledge of reproductive parameters is crucial to assess the status of the populations and develop effective fisheries management plans (Walker 2005; Serra-Pereira *et al.* 2011). Particularly, length at sexual maturity is widely used as an indicator of minimum permissible size at capture (Lucifora *et al.* 1999).

Skates are traditionally caught as by catch in Argentinean bottom-trawl fisheries and commercial interest on these fishes has considerably increased over the past two decades (Cousseau *et al.* 2007). Landings reached a peak in 2007, with an increase

of 131% compared with 1997 (Sánchez *et al.* 2011). Catches consist of mixed species; however, skates are not identified to species level in the catch reports (Massa *et al.* 2004). This situation and the lack of biological information on several skate species on the Argentinean Continental Shelf (South-west Atlantic Shelf between 35° and 55°S) make it difficult to develop adequate management and conservation programs for skates.

The Patagonian Shelf (South-west Atlantic Shelf between 41° and 55°S) is among the few places in the world's oceans with a high diversity of skates (Arkhipkin *et al.* 2012). In total, 16 species belonging to six genera inhabit this area (Cousseau *et al.* 2007; Díaz de Astarloa *et al.* 2008). The Magellan skate, *Bathyraja magellanica* (Philippi, 1902), is a medium-sized and wide-ranging species (maximum total length recorded 750 mm) occurring from 47°S in the south-western Atlantic off Argentina to 42°40'S in the south-eastern Pacific off Chile (Pequeño and Lamilla 1985; Sánchez and Mabrugaña 2002; Cousseau *et al.* 2007). In the south-western Atlantic, this species

inhabits depths of 51–554 m within a bottom-temperature range of 3.5–11°C, and feeds mainly on teleosts (Menni and Stehmann 2000; Barbini *et al.* 2010). *B. magellanica* is one of the most common skate species on the Patagonian Shelf, it is a regular by-catch in bottom-trawl fisheries for bony fishes, and is occasionally captured in the multispecies skate fishery of the Falkland/Malvinas Islands (Agnew *et al.* 2000; Cousseau *et al.* 2007; McCormack *et al.* 2007). Most previous studies on this species have dealt with taxonomy and distribution (Stehmann 1978; Bellisio *et al.* 1979; Menni and Gonztonyi 1982; Menni and López 1984; Pequeño and Lamilla 1993; Menni and Stehmann 2000; Cousseau *et al.* 2007; Mabrugaña *et al.* 2011), whereas the reproductive features of *B. magellanica* remain unknown.

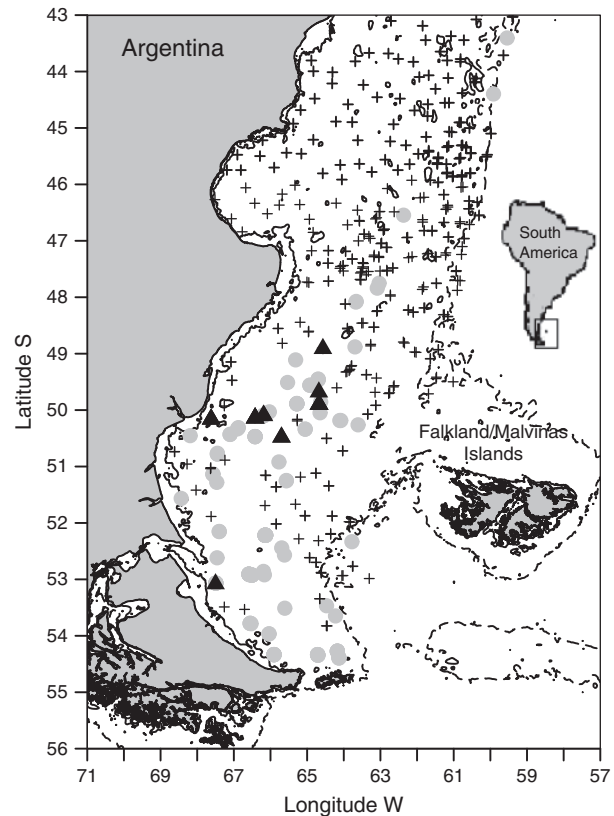
Recently, a National Plan of Action (PAN–Tiburones) was developed in Argentina for the conservation and management of chondrichthyans, according to the United Nations Food and Agriculture Organisation (FAO) guidelines (Consejo Federal Pesquero 2009). However, biological knowledge of several species remains fragmentary or unknown, preventing a full assessment of species conservation status. This is the case of *B. magellanica*; its biological data and information on its distribution and catch trends are scarce to make an assessment of its risk of extinction, according to the International Union for Conservation of Nature (IUCN) (McCormack *et al.* 2007). Therefore, in the present paper, we analyse the reproductive biology of *B. magellanica* in the south-western Atlantic. We assess sexual dimorphism, estimate the length at sexual maturity in each sex, quantify the number of vitellogenic oocytes, describe egg cases and identify egg-laying areas of this species. The present work is the first report regarding the reproductive characteristics of this species and will provide life-history information needed for effective species conservation.

## Materials and methods

### Source of samples and study site

Individuals of *B. magellanica* were collected from eight summer (February and March) scientific trawl surveys carried out on board the RV ‘Dr Eduardo L. Holmberg’ of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Mar del Plata, Argentina) between 2004 and 2007. Sampling was randomly stratified and designed for assessment of hoki, *Macruronus magellanicus*, Argentine squid, *Illex argentinus*, and other species of commercial value on the Patagonian Shelf. The fishing gear used during the cruises was an Engel-type bottom-trawl net, with a mesh size of 200 mm in the wings and 103 mm in the cod-end. Specimens of *B. magellanica* were immediately examined after capture or were frozen on board, for subsequent examination in the laboratory.

The study area was located in the south-western Atlantic between 43°S and 55°S and extended from 50-m depth to the continental shelf slope (Fig. 1). In this region, water masses are of Subantarctic origin (Guerrero and Piola 1997). They are produced by mixing of Subantarctic waters flowing from the northern Drake Passage and the Falkland/Malvinas Current, which are diluted by small continental discharges and the low-salinity water outflowing from the Magellan Strait



**Fig. 1.** Map of study area, showing the location of trawl stations where specimens of *Bathyraja magellanica* were (grey dots) or were not (crosses) collected in the south-western Atlantic. Black triangles indicate sites where females with egg cases in uteri were caught. Continuous and dashed lines are 50-m and 200-m isobaths, respectively. The rectangle in the inset represents the study area in South America.

(Bianchi *et al.* 1982; Guerrero and Piola 1997; Palma *et al.* 2008). The gravel is the predominant bottom type (Parker *et al.* 1997) and summer bottom temperature ranges from 4°C to 12°C.

### Size composition and morphometric relationships

Total length (TL, mm), disc width (DW, mm), total body weight (TW, g), liver weight (LW, g) and sex of each individual were recorded. Total length and DW were measured from the tip of the snout to the end of the caudal fin and the maximum distance between the edges of pectoral fins, respectively. The relationship between DW and TL, with TL as the dependent variable, was estimated for each sex, so as to estimate TL for any skate with damaged tail. Furthermore, the TL–TW and TL–LW relationships were calculated for each sex. Residual plots were used to determine whether the errors follow the assumptions of normality and homogeneity of variances. The null hypothesis of no differences between slopes of males and females in each relationship was evaluated using ANCOVA on log-transformed data (Crawley 2005). Length–frequency distributions between males and females were compared with a two-sample Kolmogorov–Smirnov test (Crawley 2005).

**Table 1. Criteria used to determine maturity stages of male and female *Bathyraja magellanica* (adapted from Stehmann 2002)**

Maturity stage	Males	Females
Immature	Flexible non-calcified claspers with length shorter than pelvic fin length; alar thorn patch not yet developed; small and not lobated testes; straight and filiform sperm ducts.	Small ovaries with undifferentiated oocytes or all uniformly small; hardly recognisable oviducal glands; narrow and thread-like uteri.
Maturing	Calcifying claspers as long as or a bit longer than pelvic fins; developing alar thorn patch; enlarged testes starting to lobate; sperm ducts beginning to coil.	Enlarged ovaries with differentiated oocytes of several sizes; oviducal glands in development; uteri caudally enlarging.
Mature	Rigid calcified and elongated claspers; developed alar thorn patch; fully lobated testes; highly coiled sperm ducts.	Enlarged ovaries with vitellogenic oocytes (yellow); wide, large and heart-shaped oviducal glands; wide uteri over their entire length, with and without egg cases.

**Table 2. Morphometric (mm) and gravimetric (g) data for males and females of *Bathyraja magellanica***  
DW, disc width; LW, liver weight; TL, total length; TW, total body weight

Morphometric and gravimetric parameter	Males	Females
DW range (mean $\pm$ s.d.)	138–482 (418.83 $\pm$ 62.35)	112–540 (426.87 $\pm$ 84.26)
TL range (mean $\pm$ s.d.)	205–738 (621.21 $\pm$ 91.76)	157–768 (631.95 $\pm$ 121.43)
TW range (mean $\pm$ s.d.)	56–3465 (2099 $\pm$ 713)	30–4100 (2403 $\pm$ 1064)
LW range (mean $\pm$ s.d.)	1.32–309.99 (111 $\pm$ 61.7)	0.75–303.8 (124 $\pm$ 72.8)
Mean weight of right gonad $\pm$ s.d.	23.09 $\pm$ 5.62	57.04 $\pm$ 21.39
Mean weight of left gonad $\pm$ s.d.	22.37 $\pm$ 5.21	46.86 $\pm$ 20.84

### Reproductive analyses

For males, the clasper length (CL, mm) was measured from the point of insertion to the distal end *sensu* Compagno (1984) and the number of rows in the alar thorn patch was recorded. For females, maximum uterus width (UW, mm) and maximum oviducal gland width (OGW, mm) were recorded. Maturity stage of each individual was determined by visual examination of reproductive organs. Males and females were classified as immature, maturing, and mature (Table 1), using the criteria modified from the maturity scale proposed by Stehmann (2002). Presence of egg cases in the uteri of mature females was recorded.

The onset of maturity for males and females was assessed from changes in reproductive organs (CL, UW and OGW) relative to TL. For each sex, the proportion of mature individuals in 20-mm TL intervals was calculated. A logistic model ( $P = 1/(1 + \exp(\alpha + (\beta \times TL)))$ ), where P is the estimated proportion of mature individuals at a given length class, and  $\alpha$  and  $\beta$  are model parameters) was fitted to binomial maturity data (immature or maturing, mature) so as to estimate the length at which 50% of individuals ( $TL_{50}$ ) were sexually mature (Crawley 2007).

The testes and ovaries (with the epigonal organ) were weighed ( $M_G$ , g) in each mature individual to analyse symmetry of gonads. Furthermore, the number and maximum diameter (in mm) of the largest vitellogenic oocytes in each ovary were recorded in females. Data were tested for the assumption of normality using the one-sample Kolmogorov–Smirnov test. Differences between mean weight of right and left gonads in each sex were assessed by paired *t*-test (Crawley 2005). In females, this statistical procedure was also used to analyse differences in the number of oocytes and the largest-oocyte diameter between right and left ovaries. The number of

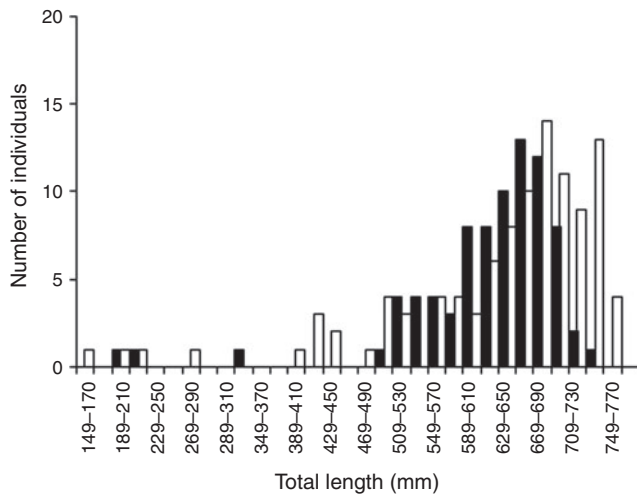
vitellogenic oocytes in both ovaries was plotted against female TL. Statistical analyses were performed using the R statistical software, version 2.13.0 (R Development Core Team 2011).

The presence of females carrying egg cases in uterus was mapped using Surfer 8 (Golden Software, Inc., CO) to identify egg-laying areas of *B. magellanica*. Furthermore, fully formed egg cases were collected from the uteri of females and described following Ishiyama and Ishihara (1977). Variables measured from each egg case (in mm) were as follows: egg-case length without horns, the longitudinal distance between the anterior and posterior borders; maximum width, the transversal distance at its widest part of the case; anterior and posterior horn length, the distance from the horn base to the tips; and lateral keel width, the distance from the case keel junction to the keel edge. Coloration and surface microscopical configuration of the egg-case wall were recorded. To measure the thickness of the egg-case wall (in mm), transverse sections of  $\sim 0.5$  mm were taken from the surface of egg cases, using a scalpel. The sections were placed on histological slides, covered with water, and observed and measured under microscope.

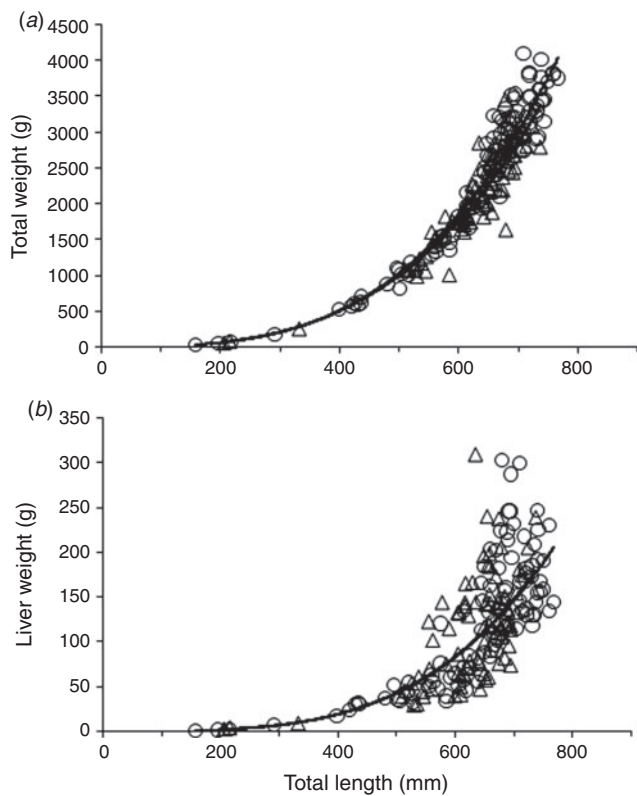
### Results

#### Size composition and morphometric relationships

In total, 185 *B. magellanica* (81 males and 104 females) were collected between 43°24'S and 54°24'S and from 50–245-m depth, with the bulk of them (97.30%) caught between 48°S and 54°24'S and 50–150-m depth (Fig. 1). Morphometric data for males and females are shown in Table 2. The DW–TL relationship did not differ significantly between the sexes (ANCOVA:  $F = 0.008$ , d.f. = 176,  $P = 0.928$ ). Therefore, males and females were pooled and a DW–TL relationship was



**Fig. 2.** Length–frequency distribution for 20-mm size classes of *Bathyraja magellanica* males (solid bars) and females (open bars) analysed.



**Fig. 3.** Relationships between total length and (a) total weight and (b) liver weight for *Bathyraja magellanica* males (triangles) and females (circles) from the south-western Atlantic.

estimated for both sexes combined ( $TL = 1.438(DW) + 16.736$ ,  $r^2 = 0.974$ ). Length–frequency distributions were significantly different between the sexes (Kolmogorov–Smirnov test:  $D = 0.239$ ,  $n = 185$ ,  $P = 0.011$ ), with females being larger than males (Mann–Whitney:  $U = 3339.5$ ,  $n = 185$ ,  $P = 0.016$ ) (Fig. 2). However, there was no sexual dimorphism in either

TL–TW (ANCOVA:  $F = 0.449$ , d.f. = 179,  $P = 0.504$ ) or TL–LW relationships (ANCOVA:  $F = 0.069$ , d.f. = 173,  $P = 0.792$ ) (Fig. 3, Table 2).

#### Reproductive characteristics

Of the total male sample, 21% were immature, 35% maturing and 44% mature. All males <550-mm TL (CL < 63 mm) were immature. Immature males had no alar thorns, except one individual of 556-mm TL that had one developing row of alar thorns on each pectoral fin. The smallest mature male measured 615 mm in TL (129.2 mm in CL), whereas the largest immature one was 617 mm in TL (106.3 mm in CL). Clasper length increased sharply between 560- and 670-mm TL. Maturing males had one to five and mature males had three to seven fully formed rows of alar thorns per fin. The  $TL_{50}$  for males was estimated at 638.32 mm, representing 86.5% TL of the largest male sampled (Fig. 4a–c).

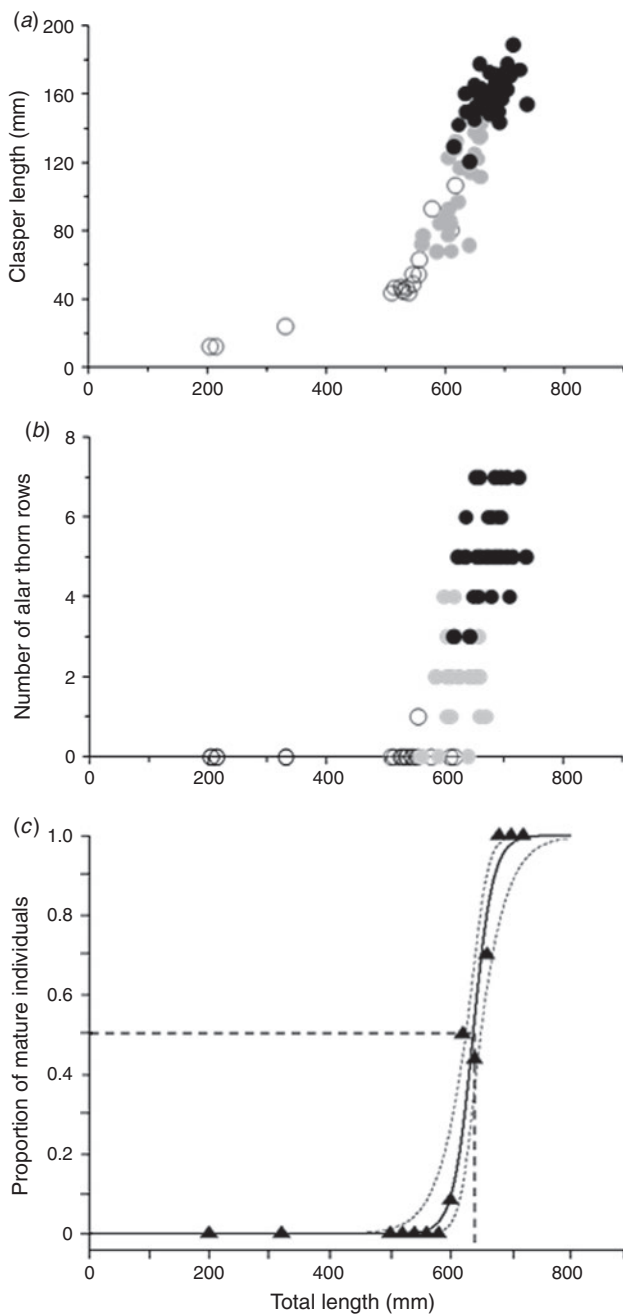
Of the total female sample, 27% were immature, 20% maturing and 55% mature. The relationship between TL–UW and TL–OGW was exponential during maturation, indicative of rapid growth in uterus and oviducal gland during that period (Fig. 5a, b). All females <570-mm TL (UW < 10 mm, OGW < 19 mm) were immature. The range between the smallest mature and the largest immature female was from 645- (13.72-mm UW, 43.52-mm OGW) to 618-mm TL (6.52-mm UW, 19.4-mm OGW). A rapid increase in the width of oviducal gland and uterus occurred between 575- and 694-mm TL. The fitted logistic curve produced an estimated  $TL_{50}$  of 652.88 mm, which corresponded to 85% TL of the largest female sampled (Fig. 5c).

In males and females of *B. magellanica*, both gonads were functional. Mature males had symmetric testes (paired  $t$ -test:  $t = 1.574$ , d.f. = 32,  $P = 0.125$ ) (Table 2). However, significant differences were found between the weights of right and left ovaries in mature females ( $t = 2.33$ , d.f. = 32,  $P = 0.026$ ) (Table 2). No differences between right and left oocyte numbers (mean  $\pm$  s.d. right and left:  $6.89 \pm 2.58$  and  $7.21 \pm 3.41$ , respectively;  $t = 0.665$ , d.f. = 32,  $P = 0.511$ ) and diameters (mean  $\pm$  s.d. right and left:  $29.52 \pm 5.56$  mm and  $28.95 \pm 5.35$  mm, respectively;  $t = 0.584$ , d.f. = 32,  $P = 0.563$ ) were found. The number of vitellogenic oocytes ranged from 7 to 25 and from 2 to 22 in non-egg-bearing and egg-bearing mature females, respectively. The mean number of vitellogenic oocytes was 14.37 (s.d. = 4.43,  $n = 33$ ) and the correlation coefficient of the number of vitellogenic oocytes with female TL was significantly different from 0 (Pearson's product–moment correlation:  $r = 0.610$ ,  $t = 4.217$ , d.f. = 30,  $P = 0.0002$ ), with an increasing number of oocytes with increasing TL (Fig. 6).

In total, 18 females with egg cases in different stages of formation were observed (34% of mature females). All females contained a single egg case in each uterus and they ranged between 645- and 760-mm TL. Mature females were found between 48°50'S and 54°10'S, at 52–139-m depth. However, females with egg cases were found between 48°50'S and 50°30'S, and at depth range between 94 and 117 m, only one female was caught at 53°S and 67°30'W, and 66-m depth (Fig. 1).

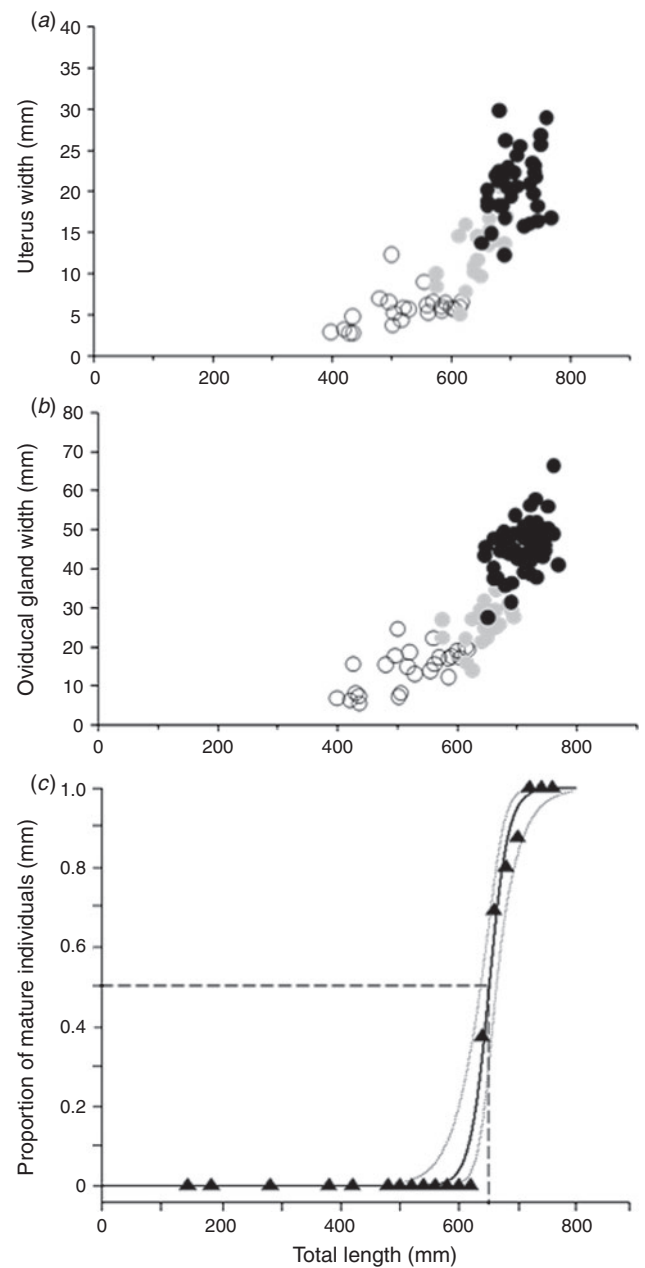
In total, 20 fully formed egg cases were collected from the uteri of female *B. magellanica*. All egg-case surfaces, including





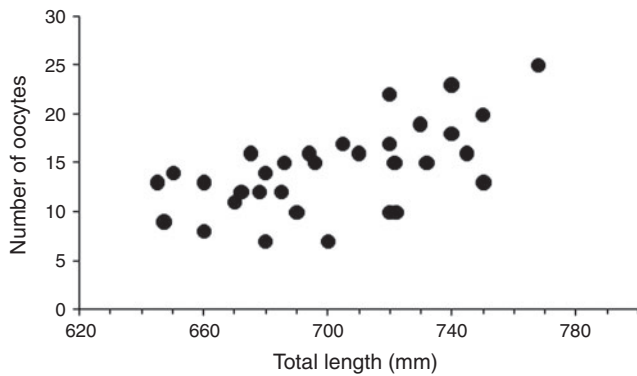
**Fig. 4.** Relationships between total length and (a) clasper length and (b) number of alar thorn rows in *Bathyraja magellanica* male specimens according to maturity stages (immature individuals, open circles; maturing individuals, grey circles; mature individuals, black circles). (c) Proportion of mature males in 20-mm total-length intervals, showing the logistic ogive fitted (solid line) to the observed values (black triangles) and the 95% confidence intervals (short-dashed lines). Long-dashed lines represent the size at 50% maturity.

horns, were covered by a layer of sticky yellow fibrils. Colour of fresh egg cases was light brown, becoming lighter along broad lateral keels. The dorsal and ventral surfaces were convex in lateral view and longitudinally striated with microscopic prickles (Fig. 7), making the texture rough to the touch. The

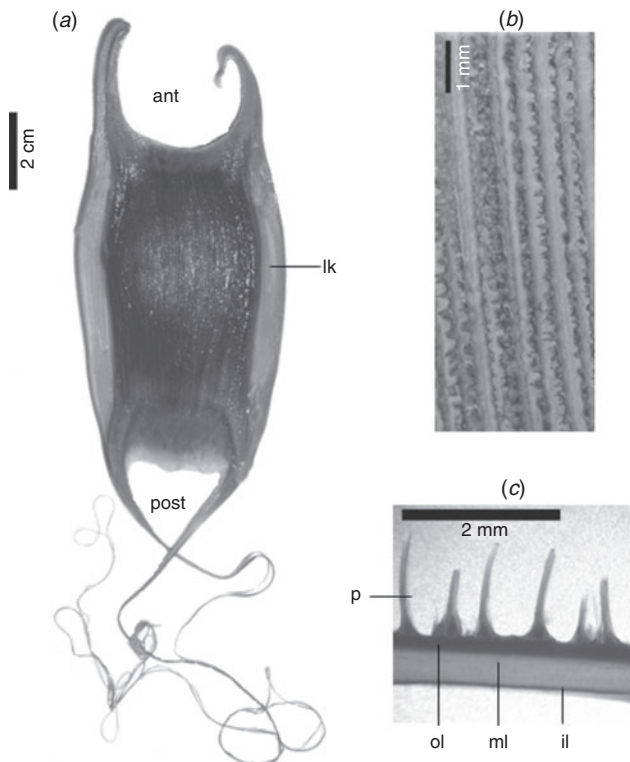


**Fig. 5.** Relationships between total length and (a) uterus width, and (b) oviducal gland width in females of *Bathyraja magellanica* according to maturity stages (immature individuals, open circles; maturing individuals, grey circles; mature individuals, black circles). (c) Proportion of mature females in different size classes, showing the logistic ogive fitted (solid line) to the observed values (black triangles) and the 95% confidence intervals (short-dashed lines). Long-dashed lines represent the size at 50% maturity.

wall of the egg case had a mean thickness of 0.77 mm (s.d. = 0.13 mm,  $n = 15$ ) and the prickles had a mean height of 2.74 mm (s.d. = 0.39 mm,  $n = 15$ ). The wall of the egg case consisted of three layers, including a dark outer layer, a laminar middle layer, lighter than the rest, and a thin dark inner layer (Fig. 7). Posterior horns were extremely long (~4 or 6 times the length of the case), curved inward, and becoming thread-like



**Fig. 6.** Relationship between total length and the number of vitellogenic oocytes for mature females of *Bathyraja magellanica* from the south-western Atlantic.



**Fig. 7.** (a) Upper view, (b) detail of cases surface ( $\times 250$ ) and (c) transverse section of the egg case ( $\times 100$ ) of *Bathyraja magellanica*. Ant, anterior end of egg case; post, posterior end of egg case; lk, lateral keel; ol, outer layer; ml, middle layer; il, inner layer; and p, prickles.

**Table 3.** Measurements (mm) recorded for egg cases ( $n = 20$ ) of *Bathyraja magellanica*

Measurement	Range	Mean $\pm$ s.d.
Egg case length without horns	81.86–94.96	87.55 $\pm$ 3.58
Egg case maximum width	49.84–65.22	57.50 $\pm$ 3.74
Anterior horn length	35.98–60.72	45.54 $\pm$ 5.83
Posterior horn length	362.00–576.16	477.32 $\pm$ 70.08
Lateral keel width	5.10–8.84	7.19 $\pm$ 1.03

at their tips (Fig. 7). Measurements are presented in Table 3. A pair of egg cases was fixed in 4% buffered formaldehyde, subsequently preserved in 70% ethanol and deposited in the ichthyological collection of the Instituto Nacional de Investigación y Desarrollo Pesquero under the Catalogue number INIDEP822.

## Discussion

Our results showed that females of *B. magellanica* attain a larger size than males, but no sexual dimorphism was observed in DW–TL and TL–TW relationships and TL<sub>50</sub>. Females of viviparous shark species generally reach a larger size and tend to mature later than males (Cortés 2000; Capapé *et al.* 2004; Graham and Daley 2011). The need of females to attain larger size to carry pups, thus causing a delayed onset of sexual maturity, may explain this pattern (Cortés 2000). However, sexual dimorphism in maturity size appears to be variable among skate species. It has been reported in several skate species that females mature later than males (Ebert 2005; Estalles *et al.* 2009; Ainsley *et al.* 2011; Bustamante *et al.* 2012). In other skate species, both sexes mature at similar sizes (Mabragaña *et al.* 2002; Ebert 2005; Ruocco *et al.* 2006; Ebert *et al.* 2008) or males reach sexual maturity at larger size than do females (Braccini and Chiamonte 2002; Mabragaña and Cousseau 2004; San Martín *et al.* 2005). In oviparous elasmobranch females, eggs develop outside the body, which implies that body size of females has little effect on the size of hatchlings. Thus, selection pressure for a larger size at maturity (and possible greater maximum size) in females is not as strong among oviparous as among viviparous elasmobranchs (Klimley 1987; Lucifora and García 2004).

Specimens of *B. magellanica* attained sexual maturity at  $\sim 85\%$  of the maximum observed TL, suggesting that females and males seem to undergo a relatively extended immature phase before full maturity, being a general pattern observed in elasmobranchs (Cortés 2000; Ebert 2005). The delay in size at maturity in this group of fishes indicates that they are particularly sensitive to fishing pressure and once they are overfished, populations would take several decades to recover and long-term shifts in community structure may also be observed (Walker and Hislop 1998; Stevens *et al.* 2000). In Argentina, skate landings have been increasing considerably because of international demand. Before 1994, skate captures were less than 1000 t; since then, skate landings considerably increased, reaching values higher than 25 000 t in 2008 (Sánchez *et al.* 2011). However, not all species are equally sensitive to the impact of fisheries, with species that attain larger lengths and have later sexual maturity being more vulnerable to fishing pressure (Dulvy *et al.* 2000). Therefore, the abundance of smaller species increases after fishing removes larger ones, leading to shifts in community structure (Dulvy *et al.* 2000; Ruocco *et al.* 2012). Among sympatric *Bathyraja* species that inhabit between 48°S and 55°S in the south-western Atlantic, the smallest size at maturity was found for *B. macloviana*, followed by *B. albomaculata*, *B. magellanica*, *B. brachyurops* and *B. griseocauda* (Henderson *et al.* 2005; Ruocco *et al.* 2006; Arkhipkin *et al.* 2008; Paesch and Oddone 2009; Scenna 2011). So far, a change in species composition over the 10-year course

of fishery was observed in the skate community around Falkland/Malvinas Islands. Here, one of the largest skate species with delayed sexual maturity, *B. griseocauda*, is being replaced by smaller skates with earlier sexual maturity, namely *B. albomaculata* and *B. brachyurops* (Agnew *et al.* 2000). Thus, knowledge of reproductive parameters of each skate species is an important step for designing management and conservation programs attempting to avoid changes in community structure, as was observed in this skate community of the south-western Atlantic. In turn, fishery management is mostly geared to the target species, but fisheries affect several species simultaneously. Species caught extensively as by-catch may be even more vulnerable than are target species taken in fisheries, because discards and landings are generally poorly monitored and signs of declining catches and collapsing stocks may thus be overlooked (Camhi *et al.* 1998). Therefore, it is necessary to assess not just the conservation status of target species but also the status of the by-catch, as was the case of *B. magellanica*.

Weight difference between ovaries of mature females of *B. magellanica* is not due to differences either in the number or size of oocytes. Differences in weight between ovaries may be related to different development of the epigonal organ that surrounds each ovary. Determining fecundity for oviparous species is a difficult task. One method may be keeping animals in captivity (Holden 1975). In the present work, the fecundity could be estimated only by counting the number of vitellogenic oocytes in both ovaries, considering vitellogenic oocytes those that were yellow-coloured. *B. magellanica* displayed a low fecundity, with values similar to those found in other *Bathyraja* species in the south-western Atlantic (Henderson *et al.* 2005) and North Pacific (Ebert 2005), which were calculated using the same method as in our work. *B. magellanica* possibly has a protracted breeding season, with eggs continuing to develop throughout the year, as was suggested for *B. albomaculata*, *B. brachyurops* and *B. griseocauda* in the south-western Atlantic and other oviparous elasmobranchs around the world (Ruocco *et al.* 2006; Arkhipkin *et al.* 2008; Griffiths *et al.* 2012). Therefore, our approach may lead to an underestimation of fecundity. However, it has also been observed that oocyte maturation size is species-specific in skates. The yolk begins to deposit in *Sympterygia acuta*, *Atlantoraja castelnaui* and *A. cyclophora* when oocytes reach 1 mm, 10 mm and 9 mm, respectively (Oddone and Vooren 2005; Oddone *et al.* 2008; Díaz-Andrade *et al.* 2009). Díaz-Andrade *et al.* (2009) microscopically determined that, in *S. acuta*, ~60% of oocytes that were catalogued as pre-vitellogenic following the macroscopic criteria, were already committed to its reproductive function. This is particularly important to avoid misinterpretations of the reproductive potentialities and species-recovery rates. Therefore, histological analysis of skate ovaries should be considered in future studies. Finally, the total number of vitellogenic oocytes increased with female size in *B. magellanica*, which indicates that larger females potentially have higher fecundity.

The occurrence of large vitellogenic oocytes in females carrying egg cases indicates that the development of oocytes occurs simultaneously with egg-case development in the uteri of *B. magellanica*. In turn, females need to store great amounts of lipids in their livers to produce vitellogenin, the yolk-precursor proteins (Hamlett and Koob 1999). Therefore, females often

have larger livers than do males. However, the TL–LW relationship did not differ between sexes in *B. magellanica*, which is consistent with results described in other skate species (Bustamante *et al.* 2012).

Skate females lay their egg cases on the sea floor where they attach to marine debris, which includes pieces of dead mollusk shells, loose algal fronds, sand and gravel (Hamlett and Koob 1999). The egg case protects the embryo during its development from natural dangers and predators. Thus, egg cases might have undergone successive changes in their characteristics, to adapt to their environment (Ishiyama 1958). Microscopically, the egg-case wall of *B. magellanica* is thicker than that of *Rioraja agassizi* but both have similar layer patterns (Oddone *et al.* 2006). In turn, egg-case surfaces of *B. magellanica* have longitudinal striations, as has also been observed in egg cases of other *Bathyraja* species (Ishiyama and Ishihara 1977; Ishihara and Ishiyama 1985; Stehmann and Merrett 2001; Ebert and Davis 2007; Mabrugaña *et al.* 2011), whereas egg-case surfaces of *R. agassizi* are smooth to the touch (Oddone *et al.* 2006). Ishiyama (1958) determined that there is a close relationship between the structure of egg case and the geographical distribution of the species. *B. magellanica* inhabits cold waters of the south-western Atlantic and is commonly restricted to depths of 60–130 m (Cousseau *et al.* 2007). In contrast, *R. agassizi* prefers shallower waters up to 50 m deep in the south-western Atlantic (Oddone *et al.* 2006). On one hand, the presence of striations on external surfaces and a thick wall in *B. magellanica* egg cases are likely to serve mechanically or physiologically, or both, for protection of the embryo throughout the development from the exposure to colder waters than for species inhabiting shallower waters with a higher temperature. On the other hand, egg-case morphology is species-specific and is commonly used as a taxonomic tool for species identification (Hubbs and Ishiyama 1968). The egg cases of *B. magellanica* have long tendril-like posterior horns, not mentioned in a previous documented description (Mabrugaña *et al.* 2011). This is a very relevant characteristic because it allows, along with lateral keel width, to distinguish egg cases of *B. magellanica* from those of other species of *Bathyraja* genus occurring in the south-western Atlantic (Scenna 2011). The elongation of the tendril-like posterior horns of *B. magellanica* would be an efficient tool for fixing egg case to debris, as was suggested for *S. acuta* in the south-western Atlantic (Oddone and Vooren 2002). This would happen mainly in sandy and gravel bottoms, as is the case of Patagonian Shelf where *B. magellanica* females with egg cases were found.

Female skates generally select oviposition sites (Hamlett and Koob 1999). Our results revealed that the Patagonian Shelf between 48°50'S and 50°30'S is an important egg-laying area for *B. magellanica*. Increased fisheries exploitation during the past two decades and increasing habitat deterioration threatens skate population on the Argentinean Continental Shelf. *B. magellanica* is commonly caught as by-catch in bottom-trawl fisheries for bony fishes in the south-western Atlantic (McCormack *et al.* 2007). The relative abundance of this species on the continental shelf between 45°S and 54°S began to decline from 1997, coinciding with an increased fishing pressure applied on the hoki, *Macruronus magellanicus*, in that area since 1998 (Hansen and Wöhler 2002; Mari 2005). Thus, a detailed



monitoring of this zone and appropriate conservation measures would be necessary because of the continued expansion of the fisheries.

Skates are a common and important component of demersal fish community on the south-western Atlantic shelves. Fishery survey data collected during the past years have revealed a general decrease in the relative biomass of some skate species in Argentinean waters (Massa *et al.* 2004). Knowledge of reproductive processes in elasmobranchs is priority work, providing an approach to the species exploitation status and the subsequent implementation of conservation procedures (Quiroz *et al.* 2009). The results of the present study will contribute to the knowledge on the basic biological parameters necessary to build a scenario of how overexploitation affects the skate community and, so, to develop effective management of fishery and species conservation to avoid large-scale changes in ecosystem functioning.

### Acknowledgements

We thank the Instituto Nacional de Investigación y Desarrollo Pesquero for specimens collected from research cruises. We are also grateful to F. Lo Nostro, D. Thomas, P. Martos and three anonymous referees for their valuable suggestions and corrections to English grammar that greatly improved the manuscript. This research was supported by the ECORAYA program funded by the Volkswagen Stiftung (Project number 03F0383A) and Universidad Nacional de Mar del Plata (EXA 342/06). L. B. Scenna was supported by a scholarship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

### References

- Agnew, D. J., Nolan, C. P., Beddington, J. R., and Baranowski, R. (2000). Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 429–440. doi:10.1139/F99-264
- Ainsley, S. M., Ebert, D. A., and Cailliet, G. M. (2011). A comparison of reproductive parameters of the Bering skate, *Bathyraja interrupta*, from two Alaskan large marine ecosystems. *Marine and Freshwater Research* **62**, 557–566. doi:10.1071/MF10140
- Arkipkin, A. I., Baumgartner, N., Brickle, P., Laptikhovskiy, V. V., Pompert, J. H. W., and Shcherbich, Z. N. (2008). Biology of the skates *Bathyraja brachyurops* and *B. griseocauda* in waters around the Falkland Islands, southwest Atlantic. *ICES Journal of Marine Science* **65**, 560–570. doi:10.1093/ICESJMS/FSN015
- Arkipkin, A., Brickle, P., Laptikhovskiy, V., Pompert, J., and Winter, A. (2012). Skate assemblage on the eastern Patagonian shelf and slope: structure, diversity and abundance. *Journal of Fish Biology* **80**, 1704–1726. doi:10.1111/J.1095-8649.2012.03260.X
- Barbini, S. A., Scenna, L. B., Figueroa, D. E., Cousseau, M. B., and Díaz de Astarloa, J. M. (2010). Feeding habits of the Magellan skate: effects of sex, maturity skate, and body size on diet. *Hydrobiologia* **641**, 275–286. doi:10.1007/S10750-010-0090-5
- Bellisio, N. B., López, R. B., and Torno, A. (1979). 'Peces Marinos Patagónicos.' (Editorial Códex: Buenos Aires.)
- Bianchi, A., Massonneau, M., and Olivera, R. M. (1982). Análisis estadístico de las características T–S del sector austral de la plataforma continental Argentina. *Acta Oceanográfica Argentina* **3**, 93–118.
- Braccini, J. M., and Chiamonte, E. (2002). Reproductive biology of *Psammodon extenta*. *Journal of Fish Biology* **61**, 272–288. doi:10.1111/J.1095-8649.2002.TB01752.X
- Bustamante, C., Vargas-Caro, C., Oddone, M. C., Concha, F., Flores, H., Lamilla, J., and Bennett, M. B. (2012). Reproductive biology of *Zearaja chilensis* (Chondrichthyes: Rajidae) in the south-east Pacific Ocean. *Journal of Fish Biology* **80**, 1213–1226. doi:10.1111/J.1095-8649.2011.03164.X
- Camhi, M., Fowler, S., Musick, J., Brautigam, A., and Fordham, S. (1998). 'Sharks and Their Relatives: Ecology and Conservation.' (IUCN/SSC Shark Specialist Group – IUCN: Gland, Switzerland.)
- Capapé, C., Seck, A. A., Diatta, Y., Reynaud, C., Hemida, F., and Zaouali, J. (2004). Reproductive biology of the blacktip shark, *Carcharhinus limbatus* (Chondrichthyes: Carcharhinidae) off west and north African coasts. *Cybio* **28**, 275–284.
- Compagno, L. J. V. (1984). FAO Species Catalogue. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Part I Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis* **125**, 1–249.
- Consejo Federal Pesquero (2009). 'Plan de Acción Nacional para la Conservación y el Manejo de Condrictios (Tiburones, Rayas y Quimeras) en la República Argentina.' (Subsecretaría de Pesca y Acuicultura, Secretaría de Ambiente y Desarrollo Sustentable y Ministerio de Relaciones Exteriores, Comercio Internacional y Culto: Buenos Aires, Argentina.)
- Cortés, E. (2000). Life-history patterns and correlations in sharks. *Reviews in Fisheries Science* **8**, 299–344. doi:10.1080/10641260008951115
- Cousseau, M. B., Figueroa, D. E., Díaz de Astarloa, J. M., Mabrugaña, E., and Lucifora, L. O. (2007). 'Rayas, Chuchos y otros Batoideos del Atlántico Sudoccidental (34°S–55°S).' (Instituto Nacional de Investigación y Desarrollo Pesquero: Mar del Plata, Argentina.)
- Crawley, M. J. (2005). 'Statistics: an Introduction Using R.' (Wiley: Chichester, UK.)
- Crawley, M. J. (2007). 'The R Book.' (Wiley: Chichester, UK.)
- Díaz-Andrade, M. C., Galíndez, E., and Estecondo, S. (2009). The ovary of the bignose fanshake *Sympterygia acuta* Garman, 1877 (Chondrichthyes, Rajidae) in the Bahía Blanca Estuary, Argentina: morphology and reproductive features. *Brazilian Journal of Biology* **69**, 405–413. doi:10.1590/S1519-69842009000200025
- Díaz de Astarloa, J. M., Mabrugaña, E., Hanner, R., and Figueroa, D. E. (2008). Morphological and molecular evidence for a new species of longnose skate (Rajiformes: Rajidae) from Argentinean waters based on DNA barcoding. *Zootaxa* **1921**, 35–46.
- Dulvy, N. K., Metcalfe, J. D., Glanville, J., Pawson, M. G., and Reynolds, J. D. (2000). Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology* **14**, 283–293. doi:10.1046/J.1523-1739.2000.98540.X
- Ebert, D. A. (2005). Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology* **66**, 618–649. doi:10.1111/J.0022-1112.2005.00628.X
- Ebert, D. A., and Davis, C. D. (2007). Description of skate egg cases (Chondrichthyes: Rajiformes: Rajoidei) from the eastern North Pacific. *Zootaxa* **1393**, 1–18.
- Ebert, D. A., Compagno, J. V., and Cowley, P. D. (2008). Aspects of the reproductive biology of skates (Chondrichthyes: Rajiformes: Rajoidei) from southern Africa. *ICES Journal of Marine Science* **65**, 81–102. doi:10.1093/ICESJMS/FSM169
- Estalles, M., Perez Comesaña, J. E., Tamini, L. L., and Chiamonte, G. E. (2009). Reproductive biology of the skate, *Rioraja agassizi* (Müller and Henle, 1841), off Puerto Quequén, Argentina. *Journal of Applied Ichthyology* **25**, 60–65. doi:10.1111/J.1439-0426.2008.01103.X
- Graham, K. J., and Daley, R. K. (2011). Distribution, reproduction and population structure of three gulper sharks (*Centrophorus*, Centrophoridae) in south-east Australian waters. *Marine and Freshwater Research* **62**, 583–595. doi:10.1071/MF10158
- Griffiths, A. M., Jacoby, D. M. P., Casane, D., McHugh, M., Croft, D. P., Genner, M. J., and Sims, D. W. (2012). First analysis of multiple paternity in an oviparous shark, the small-spotted catshark (*Scyliorhinus canicula* L.). *The Journal of Heredity* **103**, 166–173. doi:10.1093/JHERED/ESR112
- Guerrero, R. A., and Piola, A. R. (1997). Masas de agua en la plataforma continental. In 'El Mar Argentino y sus Recursos Pesqueros. Tomo 1.



- Antecedentes Históricos de las Exploraciones en el Mar y las Características Ambientales'. (Ed. E. E. Boschi.) pp 107–118. (INIDEP: Mar del Plata, Argentina.)
- Hamlett, W. C., and Koob, T. J. (1999). Female reproductive system. In 'Sharks, Skates, and Rays: the Biology of Elasmobranch Fishes'. (Ed. W. C. Hamlett.) pp. 398–443. (Johns Hopkins University Press: Baltimore, MD.)
- Hansen, J., and Wöhler, O. (2002). Aspectos generales de la pesquería argentina de merluza de cola (*Macruronus magellanicus*) durante el período 1995–2001 y estimación de índices de abundancia derivados de la flota comercial argentina. Informe Técnico INIDEP N°12. (Instituto de Investigación y Desarrollo Pesquero: Mar del Plata, Argentina.)
- Henderson, A. C., Arkhipkin, A. I., and Chtcherbich, J. N. (2005). Distribution, growth and reproduction of the white-spotted skate *Bathyraja albomaculata* (Norman, 1937) around the Falkland Islands. *Journal of Northwest Atlantic Fishery Science* **35**, 79–87.
- Hoenig, J. M., and Gruber, S. H. (1990). Life-history patterns in the elasmobranchs: implications for fisheries management. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries'. NOAA Technical Report NMFS. (Eds H. L. Pratt, S. H. Gruber and T. Taniuchi.) pp. 1–16. (National Oceanic and Atmospheric Administration: Honolulu, HI.)
- Holden, M. J. (1975). The fecundity of *Raja clavata* in British waters. *Journal du Conseil international pour l'Exploration de la Mer* **36**, 110–118. doi:10.1093/ICESJMS/36.2.110
- Hubbs, C. L., and Ishiyama, R. (1968). Methods for the taxonomic study and description of skates (Rajidae). *Copeia* **1968**, 483–491. doi:10.2307/1442016
- Ishihara, H., and Ishiyama, R. (1985). Two new North Pacific skates (Rajidae) and a revised key to *Bathyraja* in the area. *Japanese Journal of Ichthyology* **32**, 143–179.
- Ishiyama, R. (1958). Observations on the egg-capsules of skates of the family Rajidae, found in Japan and its adjacent waters. *Bulletin of the Museum of Comparative Zoology at Harvard College* **118**, 1–24.
- Ishiyama, R., and Ishihara, H. (1977). Five new species of skates in the Genus *Bathyraja* from the western North Pacific, with reference to their interspecific relationships. *Japanese Journal of Ichthyology* **24**, 71–90.
- Klimley, A. P. (1987). The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* **18**, 27–40. doi:10.1007/BF00002325
- Lucifora, L. O., and García, V. B. (2004). Gastropod predation on egg cases of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: quantification and life history implications. *Marine Biology* **145**, 917–922. doi:10.1007/S00227-004-1377-8
- Lucifora, L. O., Valero, J. L., and García, V. B. (1999). Length at maturity of the greeneye spurdog shark, *Squalus mitsukurii* (Elasmobranchii: Squalidae), from the SW Atlantic, with comparisons with other regions. *Marine and Freshwater Research* **50**, 629–632. doi:10.1071/MF98167
- Mabragaña, E., and Cousseau, M. B. (2004). Reproductive biology of two sympatric skates in the south-west Atlantic: *Psammobatis rudis* and *Psammobatis normani*. *Journal of Fish Biology* **65**, 559–573. doi:10.1111/J.0022-1112.2004.00473.X
- Mabragaña, E., Lucifora, L. O., and Massa, A. M. (2002). The reproductive ecology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic. *Journal of Fish Biology* **60**, 951–967.
- Mabragaña, E., Figueroa, D. E., Scenna, L. B., Díaz de Astarloa, J. M., Colonello, J. H., and Delpiani, G. (2011). Chondrichthyan egg cases from the south-west Atlantic Ocean. *Journal of Fish Biology* **79**, 1261–1290. doi:10.1111/J.1095-8649.2011.03111.X
- Marí, N. (2005). Síntesis de la información derivada de las Campañas de Evaluación Estival de Especies Demersales Australes, desarrolladas en el Mar Argentino, entre los 45° y 54°S, por los buques del INIDEP, durante el período 1992 al 2001. Peces cartilagosos. Informe Técnico INIDEP N°93. (INIDEP: Mar del Plata, Argentina.)
- Massa, A. M., Lucifora, L. O., and Hozbor, N. M. (2004). Condrictios de la región costera bonaerense y uruguaya. In 'El Mar Argentino y sus Recursos Pesqueros. Tomo 4. Los Peces Marinos de Interés Pesquero. Características Biológicas y Evaluación del Estado de Explotación'. (Eds R. P. Sánchez and S. I. Bezzi.) pp 85–99. (INIDEP: Mar del Plata, Argentina.)
- McCormack, C., Lamilla, J., San Martín, M. J., and Stehmann, M. (2007). '*Rhinoraja magellanica*. In 'IUCN 2012. IUCN Red List of Threatened Species (Version 2012.2)'. Available at <http://www.iucnredlist.org/details/63143/0> [accessed 25 August 2012].
- Menni, R. C., and Gonztanyi, A. E. (1982). Benthic and semidemersal fish associations in the Argentine Sea. *Studies on Neotropical Fauna and Environment* **17**, 1–29. doi:10.1080/01650528209360599
- Menni, R. C., and López, H. L. (1984). Distributional patterns of Argentine marine fishes. *Physis (Rio de Janeiro, Brazil)* **42**, 71–85.
- Menni, R. C., and Stehmann, M. F. W. (2000). Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. *Revista del Museo Argentino de Ciencias Naturales n. s.* **2**, 69–109.
- Oddone, M. C., and Vooren, C. M. (2002). Egg-cases and size at hatching of *Sympterygia acuta* in the south-western Atlantic. *Journal of Fish Biology* **61**, 858–861. doi:10.1111/J.1095-8649.2002.TB00919.X
- Oddone, M. C., and Vooren, C. M. (2005). Reproductive biology of *Atlantoraja cyclophora* (Regan 1903) (Elasmobranchii: Rajidae) off southern Brazil. *ICES Journal of Marine Science* **62**, 1095–1103. doi:10.1016/J.ICESJMS.2005.05.002
- Oddone, M. C., Mesa, A., and Ferreira de Amorim, A. (2006). The egg capsule of *Rioraja agassizi* (Müller & Henle) (Elasmobranchii, Rajidae), endemic to the SW Atlantic. *Pan-American Journal of Aquatic Sciences* **1**, 43–48.
- Oddone, M. C., Amorim, A. F., and Mancini, P. L. (2008). Reproductive biology of the spotback skate, *Atlantoraja castelnaui* (Ribeiro, 1907) (Chondrichthyes, Rajidae), in southeastern Brazilian waters. *Revista de Biología Marina y Oceanografía* **43**, 327–334.
- Paesch, L., and Oddone, M. C. (2009). Size at maturity and egg capsules of the softnose skates *Bathyraja brachyurrops* (Fowler, 1910) and *Bathyraja macloviana* (Norman, 1937) (Elasmobranchii: Rajidae) in the SW Atlantic (37°00'–39°30'S). *Journal of Applied Ichthyology* **25**, 66–71. doi:10.1111/J.1439-0426.2008.01114.X
- Palma, E. D., Matano, R. P., and Piola, A. R. (2008). A numerical study of the southwestern Atlantic Shelf circulation: stratified ocean response to local and offshore forcing. *Journal of Geophysical Research* **113**, C11010. doi:10.1029/2007JC004720
- Parker, G., Paterlini, M. C., and Violante, R. A. (1997). El fondo marino. In 'El Mar Argentino y sus Recursos Pesqueros. Tomo 1. Antecedentes Históricos de las Exploraciones en el Mar y las Características Ambientales'. (Ed. E. E. Boschi.) pp. 65–87. (INIDEP: Mar del Plata, Argentina.)
- Pequeño, R. G., and Lamilla, J. G. (1985). Estudio sobre una colección de rayas del sur de Chile (Chondrichthyes, Rajidae). *Revista de Biología Marina* **21**, 255–271.
- Pequeño, R. G., and Lamilla, J. G. (1993). Batoideos comunes a las costas de Chile y Argentina–Uruguay (Pisces: Chondrichthyes). *Revista de Biología Marina* **28**, 203–217.
- Quiroz, J. C., Wiff, R., and Céspedes, R. (2009). Reproduction and population aspects of the yellownose skate, *Dipturus chilensis* (Pisces, Elasmobranchii: Rajidae), from southern Chile. *Journal of Applied Ichthyology* **25**, 72–77. doi:10.1111/J.1439-0426.2007.00914.X
- R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org> [Accessed 20 February 2012]
- Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., and Wöhler, O. (2006). Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the southwest Atlantic. *ICES Journal of Marine Science* **63**, 105–116. doi:10.1016/J.ICESJMS.2005.08.007

- Ruocco, N. L., Lucifora, L. O., Díaz de Astarloa, J. M., Menni, R. C., Mabragna, E., and Giberto, D. A. (2012). From coexistence to competitive exclusion: can overfishing change the outcome of competition in skate (Chondrichthyes, Rajidae)? *Latin American Journal of Aquatic Research* **40**, 102–112. doi:10.3856/VOL40-ISSUE1-FULLTEXT-10
- San Martín, M. J., Perez, J. E., and Chiaramonte, G. E. (2005). Reproductive biology of the south west Atlantic marbled sand skate *Psammodontus obsoletus* Marini, 1932 (Elasmobranchii, Rajidae). *Journal of Applied Ichthyology* **21**, 504–510. doi:10.1111/J.1439-0426.2005.00667.X
- Sánchez, M. F., and Mabragna, E. (2002). Características biológicas de algunas rayas de la región sudpatagónica. Informe Técnico INIDEP N°48. (INIDEP: Mar del Plata, Argentina.)
- Sánchez, R. P., Navarro, G., Calvo, E., and del Castillo, F. (2011). La pesca y comercialización de condriactios en la Argentina: aportes de la Dirección Nacional de Planificación Pesquera para la elaboración del Plan de Acción Nacional. In 'Contribución Sobre Biología, Pesca y Comercialización de Tiburones en la Argentina: Aportes para la Elaboración del Plan de Acción Nacional'. (Eds O. C. Wöhler, P. Cedrola and M. B. Cousseau.) pp. 151–184. (Consejo Federal Pesquero: Buenos Aires, Argentina.)
- Scenna, L. B. (2011). Biología y ecología reproductiva de las especies del Género *Bathyrhaja* (Elasmobranchii, Rajidae) en la plataforma continental argentina. Ph.D. Thesis, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.
- Serra-Pereira, B., Figueiredo, I., and Serrano Gordo, L. (2011). Maturation, fecundity, and spawning strategy of the thornback ray, *Raja clavata*: do reproductive characteristics vary regionally? *Marine Biology* **158**, 2187–2197. doi:10.1007/S00227-011-1723-6
- Stehmann, M. (1978). 'Illustrated Field Guide to Abundant Marine Fish Species in Argentine Waters.' (Mitteilungen Institute Sea Fischerei: Hamburg, Germany.)
- Stehmann, M. F. W. (2002). Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Archiv fuer Fischerei und Meeresforschung* **50**, 23–48.
- Stehmann, M. F. W., and Merrett, N. R. (2001). First record of advanced embryos and egg capsules of *Bathyrhaja* skates from the deep north-eastern Atlantic. *Journal of Fish Biology* **59**, 338–349. doi:10.1111/J.1095-8649.2001.TB00134.X
- Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (Chondrichthyes), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**, 476–494. doi:10.1006/JMSC.2000.0724
- Walker, T. I. (2005). Reproduction in fisheries science. In 'Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras'. (Eds. W. C. Hamlett.) pp. 81–127. (Science Publishers: Enfield, NH.)
- Walker, P. A., and Hislop, J. R. G. (1998). Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES Journal of Marine Science* **55**, 392–402. doi:10.1006/JMSC.1997.0325