Reproductive biology of the spotback skate *Atlantoraja castelnaui* in the south-west Atlantic Ocean

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This study provides information on the reproduction of spotback skate *Atlantoraja castelnaui*. A total of 232 individuals (119 females and 113 males) were obtained from surveys carried out between 2003 and 2006, from the south-west Atlantic Ocean, between 34 and 42° S and <50 m deep; another 514 specimens (241 females and 273 males) were obtained between 2005 and 2007 from commercial fishery operations carried out in the same area and landings in the port of Mar del Plata, Argentina. Males ranged from 185 to 1250 mm total length (L_T) and females from 243 to 1368 mm L_T. Length at maturity was estimated to be 980 mm for males and 1089 mm L_T for females. Lack of variation of testis mass together with the continuous production of mature spermatocyst and spermatozoa in deferent ducts suggested that males can reproduce throughout the year. Females reproduced year-round with peaks of reproductive activity an integral part of a continuous cycle. This conclusion is corroborated by the seasonal variation of ovaries, oviducal gland and the occurrence of females with eggs in the uterus throughout the year. Results from this study indicate that *A. castelnaui* is very susceptible to fishery pressure.

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INTRODUCTION

In the south-west Atlantic Ocean, between 34 and 42° S and <50 m deep, oceano-graphic (Lucas *et al.*, 2005) and biological characteristics (Jaureguizar *et al.*, 2006; Menni *et al.*, 2010) define a coastal ecosystem (south-western Atlantic coastal ecosys-tem, SACE). Many species of chondrichthyans use this ecosystem in different ways throughout their life history (Menni & Stehmann, 2000; Barbini, 2011; Cortés *et al.*, 2011).

The SACE has been subject to fishing operations since the end of the 19th cen-tury, when the initial fishing expeditions in Argentina were recorded (Lasta *et al.*, 2001). At the beginning of the 20th century, 100 t of skates were captured annually

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without specific identification (Argentina Fishery Statistics, 1950). In the 1960s, several coastal skates were captured seasonally by the small coastal fleet and destined for the fishmeal industry (Nani, 1964). Since 1994, fishing effort in the SACE has noticeably increased as a result of a decline in traditional commercial deep-water resources (Lasta *et al*., 2001; Massa *et al*., 2004). Since 2005, >20 000 t of skates have been captured annually from the Argentinean Continental Shelf (Ministerio de la Producción, Subsecretaría de Pesca y Acuicultura, 2009) and the multispecies fishery carried out in the SACE represents the highest captured proportion (Massa *et al*., 2004). Within this fishery, the smallnose fanskate *Sympterygia bonapartii* Müller & Henle 1841, the rio skate *Rioraja agassizi* (Müller & Henle 1841) and the spotback skate *Atlantoraja castelnaui* (Miranda Ribeiro 1907) are the main skates captured (Massa *et al*., 2004).

Atlantoraja castelnaui is distributed from Rio de Janeiro (23° S, Brazil) to Chubut (42° S, Argentina) (Menni & Stehmann, 2000; Cousseau *et al*., 2007). In the SACE, this species lives down to a depth of 70 m (Menni & Stehmann, 2000; Cousseau *et al*., 2007), attains a maximum total length (L_T) of 1400 mm (Cousseau *et al*., 2007) and feeds mainly on teleosts, crustaceans, cephalopods and chondrichthyans (Barbini, 2011; Barbini & Lucifora, 2012). In southern Brazilian waters, *A. castelnaui* can be found down to a depth of 200 m (Vooren & Klippel, 2005; Casarini, 2006). The maximum recorded L_T is 1160 mm and the size at maturity varies between 915 and 1000 mm L_T in males and between 1055 and 1100 mm L_T in females (Ponz Louro, 1995; Casarini, 2006; Oddone *et al*., 2008).

In Argentina, the number of biological studies on chondrichthyans has increased in the last 10 years and recently, the national action plan, PAN tiburón (Ministerio de la Producción, Subsecretaría de Pesca y Acuicultura, 2009), for chondrichthyan conservation and management was developed according to FAO guidelines (FAO, 2000). Biological knowledge of several species, however, remains fragmentary. This is the case for *A. castelnaui*, where reproductive variables remain unknown. Therefore, the purpose of this study was to analyse the reproductive ecology of *A. castelnaui* in the SACE, focusing on determining the size at maturity, as well as critical reproductive periods.

MATERIALS AND METHODS

In total, 232 *A. castelnaui* (119 females and 113 males) were obtained between 2003 and 2006 from surveys carried out using R.V. *Dr. Eduardo L. Holmberg* and R.V. *Cap. Oca Balda* of the Instituto Nacional de Investigación y Desarrollo Pesquero (National Institute for Fisheries Research and Development, Argentina). The gear used was a standard Engel-type bottom trawl of 120 mm inner mesh-size, with a vertical height of 5 m and a horizontal opening of 20 m. The standard tow duration was 15 min at a speed of 4 knots (7·41 km h^{-1}). An additional 514 individuals (241 females and 273 males) were obtained between 2005 and 2007 from commercial hauls with an operational zone in the SACE from the Mar del Plata Port. All samples were used to examine sexual development and reproduction. Each individual fish was measured, weighed and sexed. Total length (L_T, mm), disc width (W_D, mm), total body mass (M_{TB}, g) and liver mass (M_L, g) were recorded. Morphometric relationships L_T and M_{TB} and M_{TB} and M_L were calculated for each sex, the data were ln transformed for regressions and the null hypothesis of no differences between slopes was tested using ANCOVA (Zar, 1984).

Maturity was assessed macroscopically for females and males. The oviducal gland width (W_{OG}, mm), uterus width (W_U, mm), number and diameter of the largest ovarian follicles

(D_{LOF}, mm) and ovary mass (M_O, g) were recorded for females. Ovary mass was expressed as a gonado-somatic index ($I_G = 100M_O M_{TB}^{-1}$). Symmetry and functional parity of the ovaries were analysed. For this purpose, the null hypothesis of no differences between the mean mass of ovaries and the number and diameter of the largest ovarian follicles of each ovary was tested with a paired-sample *t*-test (Zar, 1984). The inner clasper length (L_C, mm) of males, as measured from the end of the cloaca to the tip of the claspers, the number of alar thorn rows and testis mass (M_T, g) were recorded for each fish.

Maturity was assessed by visual inspection of the reproductive organs following Stehmann (2002). Females were considered to be juvenile when the ovarian follicles were undifferentiated, oviducal glands indistinct from the anterior oviduct and the uterus was uniformly thin. Sub-adult females included those whose ovarian follicles were translucent with some of them accumulating yolk, the oviducal glands were still undifferentiated and the uterus was narrow and constricted. Adult females had ovaries with yellow ovarian follicles ≥3 mm, oviducal glands that were distinctly differentiated and the uterus was pendulous. Males were assessed as juveniles when testes were thin, the efferent ducts were straight and the claspers were shorter than the pelvic fins and uncalcified. Sub-adult males had lobular testes, efferent ducts beginning to coil, elongate and flexible, but without calcified claspers. Mature males had enlarged testes, highly coiled efferent ducts and large and calcified claspers. A logistic ogive was fitted to the data using a maximum likelihood approach in order to estimate size at 50% maturity (L_{T50}) (Aubone & Wöhler, 2000). Differences in L_{T50} between the sexes were evaluated through a log-likelihood test (Aubone & Wöhler, 2000).

To assess temporal changes in female reproductive conditions, the hepato-somatic index ($I_H = 100M_L M_{TB}^{-1}$) and gonado-somatic index I_G ($I_G = 100M_O M_{TB}^{-1}$), oviducal glands width and diameter of the largest ovarian follicle were calculated. Male I_H and I_G ($I_G = 100M_T M_{TB}^{-1}$) were calculated to assess monthly changes in their reproductive condition. Monthly differences were tested using ANOVA ($P < 0.05$) followed by *post hoc* comparisons with Tukey's test (Zar, 1984).

The timing of the male reproductive cycle was determined macroscopically through monthly variation of the I_G and the presence of sperm in the deferent ducts. Histological assays of testes and genital ducts to verify the macroscopic assessments were conducted. For this purpose, cross-sectional samples were removed and fixed in 10% formalin. In the laboratory, samples were placed in tissue cassettes, dehydrated and embedded in paraffin wax. A 1–3 μm thick segment was sectioned and stained with standard haematoxylin and eosin. Prepared slides were examined and classified into spermatogenic stages based on the method of Maruska *et al.* (1996). The number of spermatocysts at each stage was measured across representative full-lobe sections of the testis. The mean proportions of the testis occupied by each stage throughout the different months of the year were compared to determine seasonal variation in testis development. Following previous histological studies of elasmobranch testes (Maruska *et al.*, 1996; Sulikowski *et al.*, 2004), three stages were focused on: immature (spermatocytes I and II), maturing (spermatids) and mature (after spermiation).

RESULTS

SIZE DISTRIBUTION

Males ranged from 185 to 1250 mm L_T and females from 243 to 1368 mm L_T. There were very few specimens <300 mm L_T. The majority of specimens >1200 mm L_T were females (Fig. 1).

MORPHOMETRIC RELATIONSHIPS

Morphometric relationships L_T and W_D, L_T and M_{TB} and M_{TB} and M_L were sexually dimorphic (ANCOVA, L_T and W_D: $F_{1,750} = 22.32$, $P < 0.001$; L_T and M_{TB}:
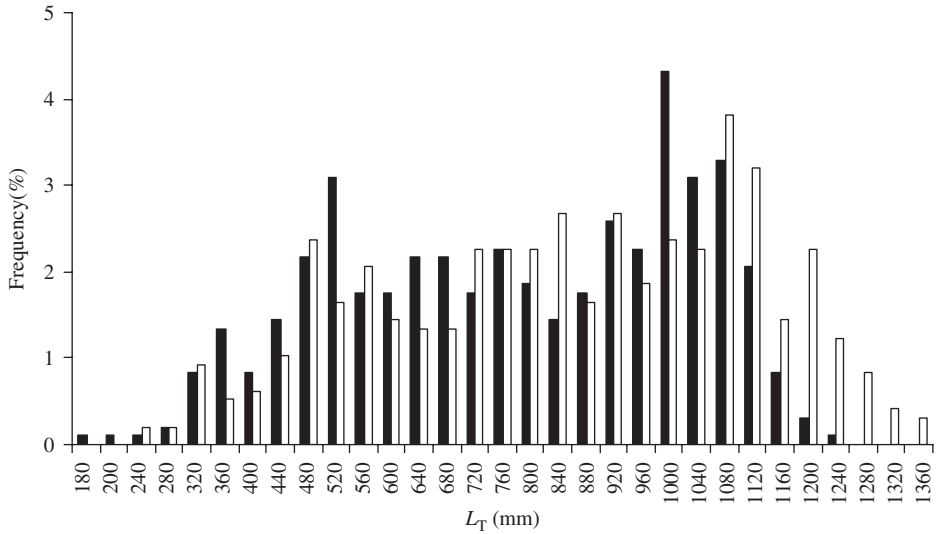
FIG. 1. Total length (L_T) frequency distribution of male (■, 386 individuals) and female (□, 360 individuals) *Atlantoraja castelnaui*.

$F_{1,791} = 23 \cdot 68$, $P < 0 \cdot 001$; M_{TB} and M_L: $F_{1,725} = 247 \cdot 9$, $P < 0 \cdot 001$). Females weighed more than males and the livers were heavier in females than males at any given L_T (Fig. 2).

MACROSCOPIC ANALYSIS OF REPRODUCTIVE ORGANS: MALES

The smallest mature male measured 900 mm L_T and the largest juvenile 1110 mm L_T (Fig. 3). Clasper length increased linearly with L_T at the three reproductive stages, but the rate was higher in individuals between 850 and 1050 mm L_T (stage 2; Fig. 3). The difference between the smallest mature claspers and the highest imma- ture claspers was 55 mm (320–375 mm), suggesting that the development implies growth in size and finally calcification. Testis mass also increased linearly with L_T, but a wide range of values was observed for each L_T (Fig. 3). In the largest indi- viduals of stage 1, germinal signs of alar thorns were observed, whereas the largest individuals of stage 2 showed two rows of developed thorns; mature males had a maximum of three rows of thorns. The L_{T50} was estimated to be 980 mm, repre- senting 78·4% of the maximum L_T recorded for males [Fig. 3(d)]. Non-differences were recorded in the maturity estimation considering stages of reproductive organs (claspers, epididymis and testes) separately.

REPRODUCTIVE CYCLE: MALES

Mean values of I_G were higher in July, September and November, whereas mini- mum values were observed in August and October [Fig. 4(a)]; however, differences were not significant ($F_{10,77} = 1 \cdot 32$, $P \geq 0 \cdot 05$). Some variations were observed in I_H throughout the year, with higher values in August, but differences were not
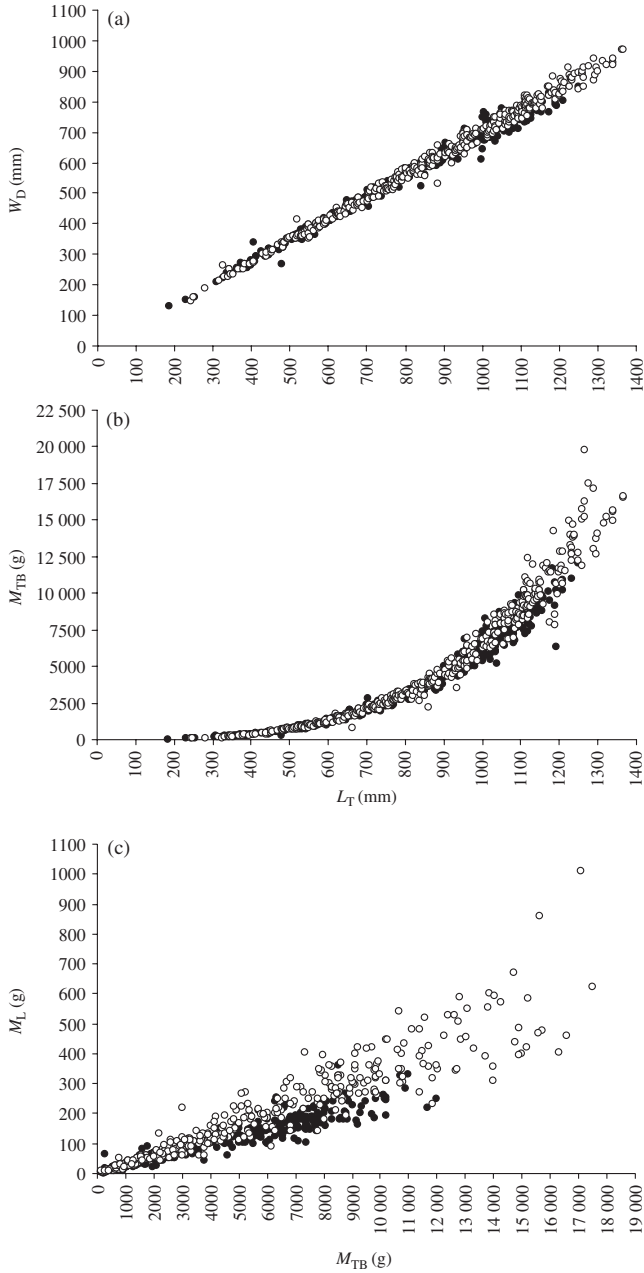
FIG. 2. Relationships between total length (L_T) and (a) disc width (W_D) and (b) total body mass (M_{TB}) and (c) liver mass (M_L) and M_{TB} of male (●) and female (○) *Atlantoraja castelnaui*.

significant ($F_{10,91} = 1.54$, $P > 0.05$) [Fig. 4(b)]. Males had two functional and synchronic testes of the compound type (Pratt, 1988). With regard to sperm production, mature and immature cysts appeared to persist throughout the year as well as spermatozoa in male genital ducts (Fig. 5).
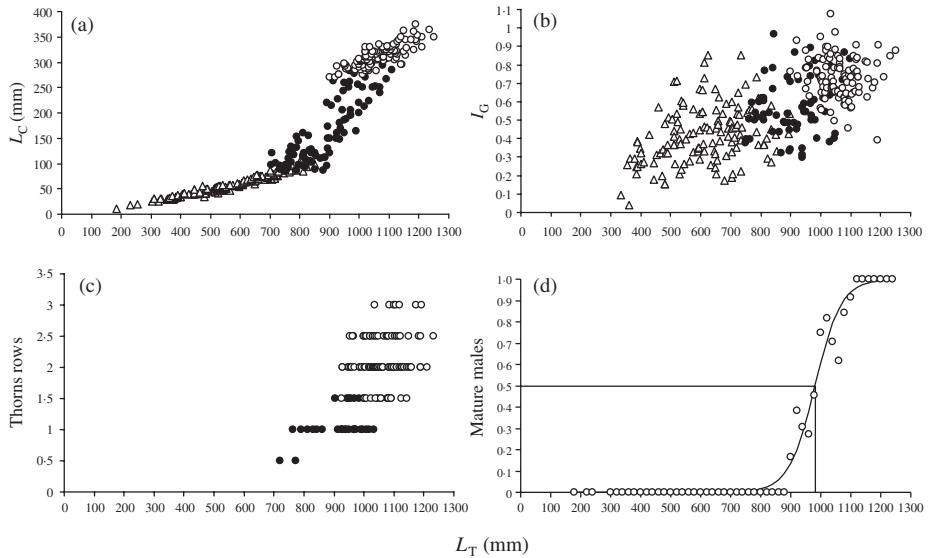
FIG. 3. Relationships between total length (L_T) with (a) inner clasper length (L_C), (b) gonado-somatic index (I_G), (c) number of alar thorn rows and (d) proportion of mature individuals in male *Atlantoraja castelnaui* according to maturity stage (stage 1: △, stage 2: ● and stage 3: ○).

MACROSCOPIC ANALYSIS OF REPRODUCTIVE ORGANS: FEMALES

The range between the smallest mature and largest juvenile was 980–1232 mm L_T (Fig. 6). Immature females at stage 1 showed oviducal glands and uterus <10 mm in width that were not related to L_T. In mature females without egg cases, these organs increased from 10 mm to 70 and 40 mm, respectively [Fig. 6(a), (b)]. Only one female had oviducal glands >75 mm.
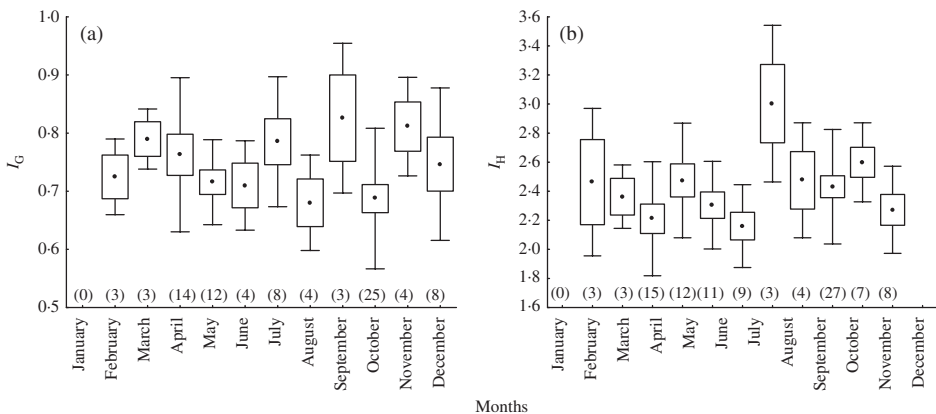

FIG. 4. Monthly changes in (a) the gonado-somatic index (I_G) and (b) hepato-somatic index (I_H) in mature male *Atlantoraja castelnaui*. For each month, the median (•), S.E. (□), S.D. (⊥) and the number of samples analysed (in parentheses) are given.
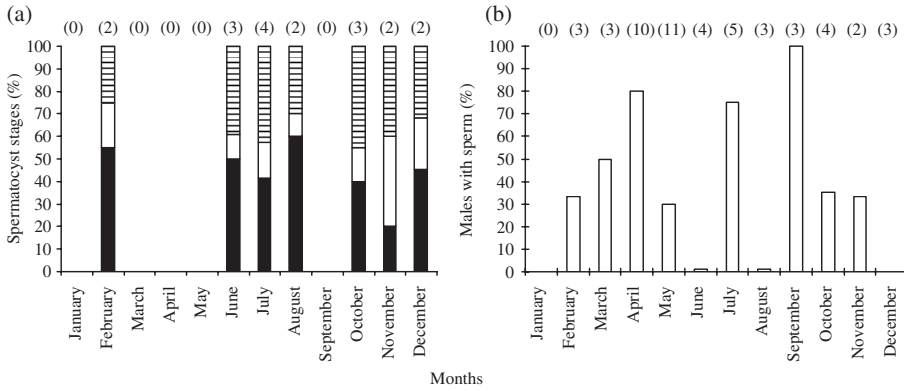
FIG. 5. Monthly frequency (%) changes in (a) spermatogenesis [immature (■), maturing (□) and mature (⊟)] and (b) frequency (%) of individuals with spermatozoa in the deferent ducts of male *Atlantoraja castelnaui*. The number of samples analysed is given in parentheses above data bars.

Both ovaries were functional and no significant differences were observed between mass (I_G) ($t = 0.18$, d.f. $= 180$, $P > 0.05$) and the maximum diameter of ovarian follicles ($t = 0.89$, d.f. $= 138$, $P > 0.05$). The L_{T50} of females was estimated to be 1089 mm (80% of maximum L_T) [Fig. 6(d)] and no differences were observed when considering the stage of each reproductive organ (uterus, oviducal glands and ovaries) separately. All females >1200 mm L_T were mature. The size at maturity of females was significantly higher than the estimated one for males ($t = 33.29$, d.f. $= 1$, $P < 0.001$).
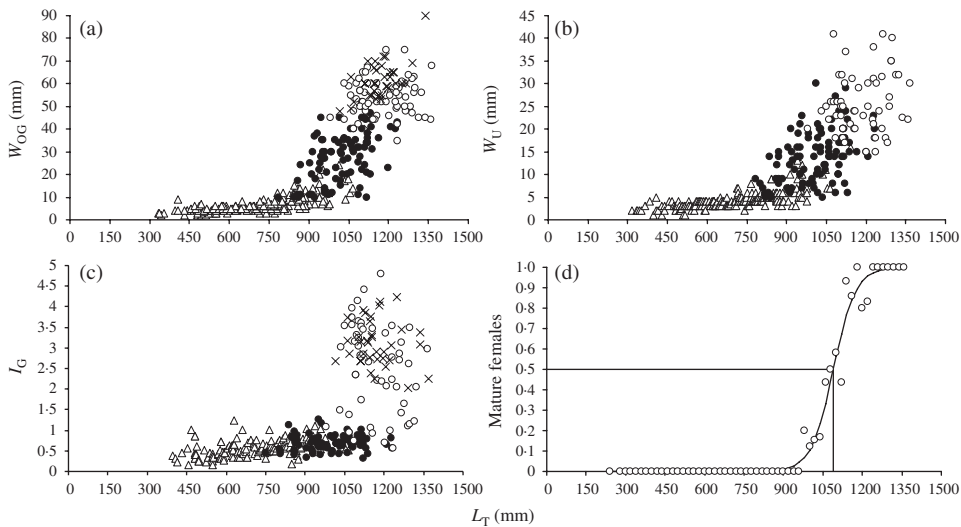

FIG. 6. Relationship between total length (L_T) with (a) oviducal glands width (W_{OG}), (b) uterus width (W_U), (c) gonado-somatic index (I_G) and (d) proportion of mature individuals in female *Atlantoraja castelnaui* according to maturity stage (stage 1: △, stage 2: ●, stage 3: ○ and stage 4: ✕).
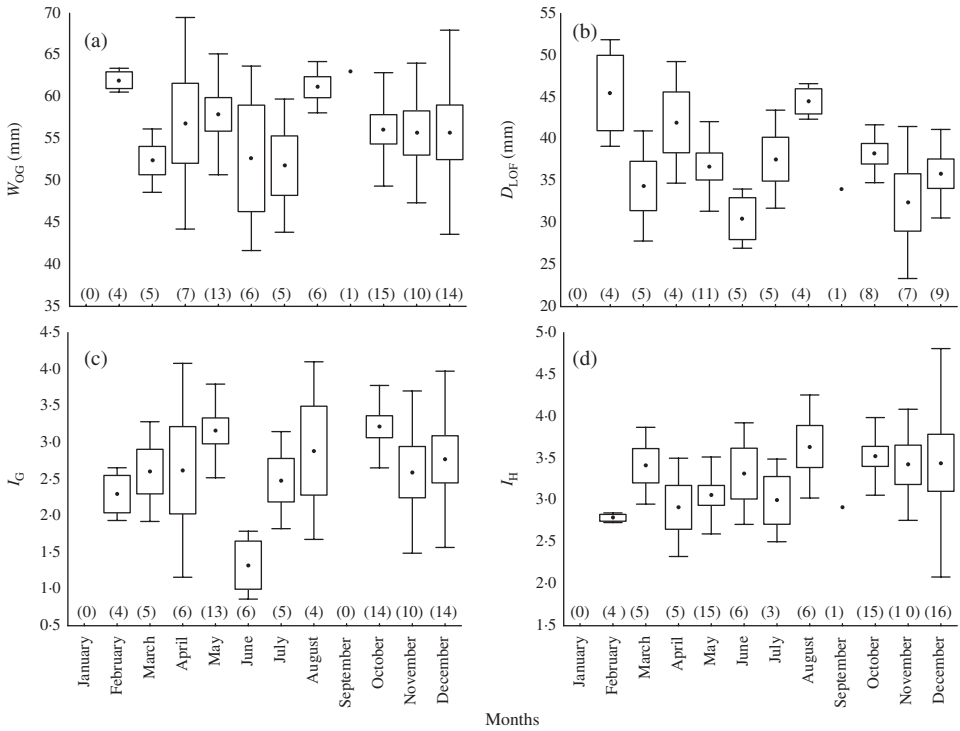
FIG. 7. Monthly changes in (a) oviducal gland width (W_{OG}), (b) diameter of the largest ovarian follicle (D_{LOF}), (c) gonado-somatic index (I_G) and (d) hepato-somatic index (I_H) in female *Atlantoraja castelnaui*. For each month, the median (•), S.E. (□), S.D. (⊥) and the number of samples analysed (in parentheses) are given.

REPRODUCTIVE CYCLE: FEMALES

Ovarian follicle diameters ranged between 2 and 55 mm and the frequency distribution was composed of seven groups: <6, 6–14, 14–18, 18–28, 28–36, 36–46 and >46 mm. The number of follicles <6 mm was an estimate because it was very difficult to count them. Presumably, the incipient yolked ovarian follicles were represented by those <6 mm, whereas pre-ovulatory ones were represented by those >36 mm. Mature females were too scarce to analyse seasonal variation of these follicle groups.

No significant differences were detected in the D_{LOF} follicle ($F_{10,46} = 1.02$, $P > 0.05$), M_O (I_G; $F_{9,65} = 1.28$, $P > 0.05$) and W_{OG} ($F_{10,70} = 0.66$, $P > 0.05$) (Fig. 7). Females with presumed pre-ovulatory follicles were observed during all months (Fig. 7) and those with eggs in the uterus were observed during most of the year (Fig. 8).

EGG CASES

Egg case sizes of *A. castelnaui* exceeded 90 mm in length (excluding horns) and 70 mm in width and increased with female L_T, although the correlation was only significant with respect to the capsule width (length: $r^2 = 0.003$, $F_{1,12} = 0.04$,
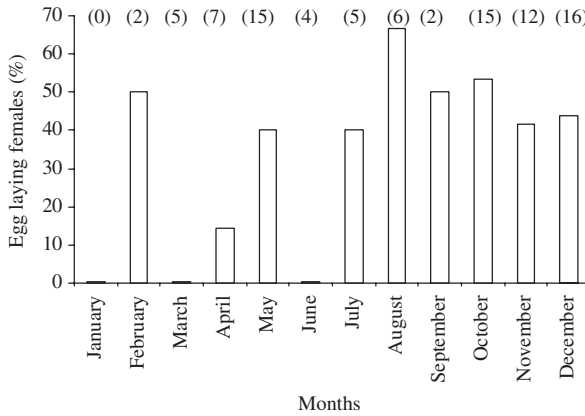
Fɪɢ. 8. Monthly changes in the frequency (%) of egg-laying female *Atlantoraja castelnaui*.

$P > 0.05$; width: $r^2 = 0.506$, $F_{1,12} = 12.3$, $P < 0.01$). In one station (40° 32′ S; 61° 03′ W) of a research cruise carried out during November 2008 (this cruise was not included in the analysis), a free egg case was obtained (Fig. 9). The size of this egg was 105 mm in length and 77 mm in width containing a male embryo of 157 mm L_T, 109 mm W_D and 28 g M_{TB} (including external vitelline vesicle; Fig. 9). The dorsal pattern of colouration was similar to that seen in neonates, characterized by a spot,
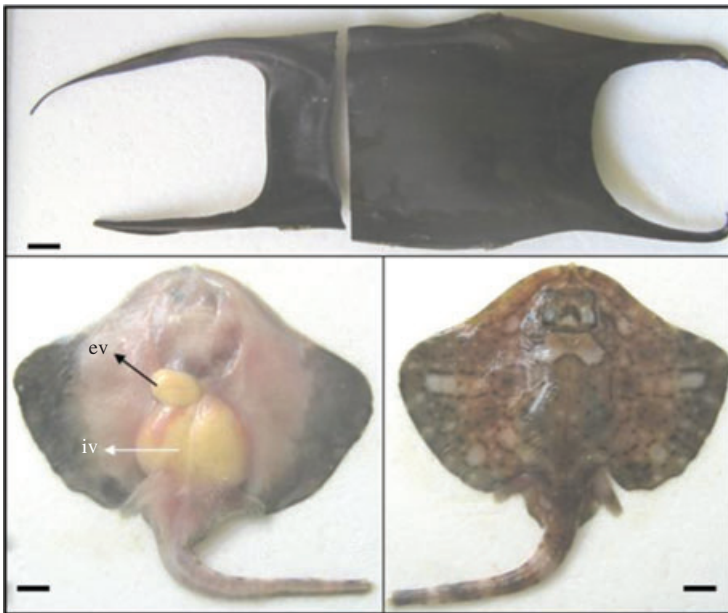

Fɪɢ. 9. Free egg case of *Atlantoraja castelnaui* obtained in a research cruise (November 2008) containing a developed embryo of 157 mm total length L_T with an external (ev) and internal (iv) vitelline vesicle and a dorsal spot, with the appearance of a butterfly, between the eyes and spiracles typical of neonates. Bar = 1 cm.

with the appearance of a butterfly, between the eyes and spiracles. Considering this embryo and the smallest free swimming neonate (186 mm L_T), the size at hatching was estimated to be *c*. 170 mm L_T.

DISCUSSION

Secondary sexual dimorphism (L_T and W_D relationships) appears to be common in skates (Mabragaña *et al.*, 2002; Oddone & Vooren, 2004; Ruocco *et al.*, 2006; Colonello *et al.*, 2007*a*; Ebert *et al.*, 2008*a*), but not universal (Ebert *et al.*, 2008*a*). Species exhibiting significantly different relationships between L_T and W_D also show sexual dimorphism in the disc shape (Ebert *et al.*, 2008*a*). Behavioural implications of this dimorphism, if any, remain unknown. In agreement with this trend, *A. castelnaui* is sexually dimorphic, with females larger and heavier than males. Dimorphic characteristics of the L_T and M_{TB} relationship observed in *A. castelnaui* are consistent with the observations in skates of small (Braccini & Chiaramonte, 2002; Mabragaña & Cousseau, 2004) and medium sizes (Mabragaña *et al.*, 2002; Oddone *et al.*, 2005; Ruocco *et al.*, 2006; Colonello *et al.*, 2007*a*; Ebert *et al.*, 2008*a*). This dimorphism could be related to the higher reproductive energy requirements of females. Differences in trophic niche have also been proposed to explain this difference (Oddone *et al.*, 2007). Both sexes of *A. castelnaui*, however, feed on similar prey (Barbini, 2011; Barbini & Lucifora, 2012).

The magnitude of sexual dimorphism in maximum L_T is quite variable in skates. Usually, small and medium-sized skates exhibit small differences and in those skates that attain large sizes, the differences can be substantial (Ebert *et al.*, 2008*a*). Although the magnitude of dimorphism in *A. castelnaui* is large (115 mm), it represents 8·4% of the maximum L_T. This is similar to other medium and large sizes, where the difference is <10% of the maximum L_T. Differences in maximum L_T were accomplished by differences in L_{T50} for males and females. In oviparous elasmobranchs, however, sexual dimorphism in size at maturity is not as clear, with the sexes maturing at similar sizes (Ebert, 2005; Ruocco *et al.*, 2006; Ebert *et al.*, 2008*a*, *b*), females maturing at a larger size than males (Ebert, 2005; Oddone & Vooren, 2005; Oddone *et al.*, 2005; Colonello *et al.*, 2007*a*; Ebert *et al.*, 2008*a*, *b*) or *vice versa* (Braccini & Chiaramonte, 2002; Mabragaña *et al.*, 2002; Mabragaña & Cousseau, 2004). There are no advantages for oviparous females in attaining a larger size to produce larger young (Ebert *et al.*, 2008*a*).

Maturity estimations for *A. castelnaui* in south Brazil during the last 20 years have fallen from 110·0 cm L_T (1985–1987) (Ponz Louro, 1995) to 103·2 cm L_T (1995–1997) (Casarini, 2006) to 105·5 cm L_T (2005–2006) (Oddone *et al.*, 2008) for females and from 100·0 cm L_T (1985–1987) (Ponz Louro, 1995) to 94·0 cm L_T (1995–1997) (Casarini, 2006) to 91·0 cm L_T (2005–2006) (Oddone *et al.*, 2008) for males. In Uruguayan waters, the L_{T50} at 50% maturity was estimated to be 112 cm for females and the L_T at first maturity was estimated to be 93 cm for males (Oddone *et al.*, 2005). Oddone *et al.* (2008) attributed the maturity changes observed in Brazilian waters to heavy fishing pressure over the last decade. Taking into account the life history of chondrichthyans, however, it is unlikely that a compensatory response will be detected in a time scale of 10 years. Sampling bias may be another reason for these differences. Maximum L_T and size at 50% maturity estimated in

SACE are higher than that in south Brazilian and Uruguayan waters. Geographical trends in vital rates are relatively unstudied in batoids; however, several regional variations in life-history patterns have been observed in skates with a latitudinal increase in maximum L_T and size at maturity (Frisk, 2010).

The absence of seasonality in reproductive condition is common in male skates (Braccini & Chiaramonte, 2002; Colonello *et al.,* 2007a; Oddone *et al.*, 2008), but few studies have correlated this pattern to the capacity to produce sperm throughout the year (Maruska *et al.*, 1996; Sulikowski *et al.*, 2004; Ebert *et al.*, 2008b). The lack of variation in I_G together with the continuous production of mature spermatocysts and spermatozoa in deferent ducts suggests that male *A. castelnaui* can reproduce throughout the year. Continuous spermatozoa production represents selective advantages in species with nomadic behaviour and low encounter rate (Pratt & Tanaka, 1994), when production and release of sperm is determined by the balance between the opportunity to mate and sperm competition. It is likely that there is an adjustment at the individual level in the production of sperm, according to certain signals associated with the risk of sperm competition (Parker *et al.*, 1997).

As was observed in other skates, follicle development was asynchronous since follicles at different developmental stages, from presumptive incipient yolked to pre-ovulatory, are present in mature and egg-laying females. Size dependency on the total number of follicles is difficult to analyse because of the continuous ovarian cycle and the results are diverse and inconclusive. The number of follicles may provide an estimate of ovarian fecundity. The relationship between this number and actual reproductive output is, however, not clear.

Female oviparous chondrichthyans show, within the same reproductive strategy, a wide range of morphological and physiological adaptations related to three reproductive cycles: (1) reproduction throughout the year, (2) partially defined reproductive cycle with one or two peaks of activity and (3) defined annual or biennial reproductive cycle (Wourms & Demski, 1993). According to this classification and the results obtained, *A. castelnaui* reproduce throughout the year with peaks of activity an integral part of the continuous cycle. This conclusion is corroborated by the seasonal variation of ovaries, oviducal gland and the occurrence of females with eggs in the uterus throughout the year. The year-round reproductive cycle with seasonal peaks of activity is consistent with other skates of the SACE such as *S. bonapartii* (Mabragaña *et al.*, 2002), zipper sand skate *Psammobatis extenta* (Garman 1913) (Braccini & Chiaramonte, 2002) and *R. agassizi* (Colonello *et al.*, 2007a; Estalles *et al.*, 2008). Contrarily, in deeper waters where physical conditions remain stable, the lack of seasonal peaks was observed in white-dotted skate *Bathyraja albomaculata* (Norman 1937) (Ruocco *et al.*, 2006) and eyespot skate *Atlantoraja cyclophora* (Regan 1903) (Oddone & Vooren, 2005). These differences could be explained by the less variable conditions in deeper water.

The extended juvenile stage and the small number of mature individuals collected during the research cruises indicate that juvenile individuals dominate the population structure of *A. castelnaui* in the SACE. The same happens in south Brazilian waters (Ponz Louro, 1995; Casarini, 2006; Oddone *et al.*, 2008).

Following a general characteristic of chondrichthyans, *A. castelnaui* matures at *c.* 80% of maximum L_T. Reproductive analysis indicates that, in proportion, this fish has a long juvenile stage, followed by a short adolescent stage prior to maturity once mature growth is limited. This finding conforms to observations on other oviparous

elasmobranchs (Ebert, 2005; Ebert *et al.*, 2008*a*). Late maturity also has implications for life cycles with reproductive activity. From individuals of *A. castelnaui* collected in Brazil between Rio de Janeiro (23° S) and Lagoa dos Patos (31° S), the period between maturity and maximum age in females was determined to be 7 years (Casarini, 2006). This estimation translates into a small number of spawning seasons. The ratio of age at maturity to longevity is generally higher in skates than in other groups of elasmobranchs (Frisk, 2010).

Within the same fishery, diverse responses are expected for chondrichthyans depending on life-history variables. Larger species with late maturity and longevity are usually more vulnerable (Dulvy *et al.*, 2000; Stevens *et al.*, 2000; García *et al.*, 2008). Along with this hypothesis, it could be argued that *A. castelnaui* is one of the most vulnerable elasmobranchs of the SACE. By contrast, the extinction risk is significantly affected by the reproductive mode and is the lowest in oviparous species (García *et al.*, 2008). Substantial differences in annual fecundity are expected between *A. castelnaui* and triennial elasmobranchs with extremely low fecundities, such as the tope shark *Galeorhinus galeus* (L. 1758) (Lucifora *et al.*, 2004), the angular angel shark *Squatina guggenheim* Marini 1936 (Colonello *et al.*, 2007*b*) and the lesser guitarfish *Zapteryx brevirostris* (Müller & Henle 1841) (Colonello *et al.*, 2011). Although oviparous elasmobranchs also show higher annual fecundity than annual viviparous relatives, a high ratio of age at maturity to longevity (Frisk, 2010) and the rates of egg predation (*c*. 24%) (Lucifora & García, 2004) suggest that effective differences in fecundities throughout the reproductive life are not substantial. To attain an integral perspective of the vulnerability of *A. castelnaui*, different intrinsic (*e.g.* growth and migrations) and extrinsic (*e.g.* fishery) population aspects must be analysed in an ecosystem context. Trophic studies on food interactions on the SACE (Milessi, 2008) and particularly on *A. castelnaui* (Barbini, 2011; Barbini & Lucifora, 2012) demonstrate consumption of teleosts, elasmobranchs, cephalopods and decapods. Probably, *A. castelnaui* occupying the higher tropic level of the SACE, being consumed only by the sand tiger shark *Carcharias taurus* Rafinesque 1810 (Lucifora *et al.*, 2009*a*), *G. galeus* (Lucifora *et al.*, 2006) and copper shark *Carcharhinus brachyurus* (Günther 1870) (Lucifora *et al.*, 2009*b*). These characteristics underlie the high susceptibility of *A. castelnaui* to fishery pressure and the cascading effects on the communities as result of their decline.

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