Revista de Biología Marina y Oceanografía
ISSN: 0717-3326
revbiolmar@gmail.com
Universidad de Valparaíso
Chile

Oddone, María C.; Amorim, Alberto F.; Mancini, Patricia L.
Reproductive biology of the spotback skate, Atlantoraja castelnaui (Ribeiro, 1907) (Chondrichthyes, Rajidae), in southeastern Brazilian waters
Revista de Biología Marina y Oceanografía, vol. 43, núm. 2, agosto, 2008, pp. 327-334
Universidad de Valparaíso
Viña del Mar, Chile

Revista de Biología Marina y Oceanografía 43(2): 327-334, agosto de 2008

Reproductive biology of the spotback skate, *Atlantoraja castelnaui* (Ribeiro, 1907) (Chondrichthyes, Rajidae), in southeastern Brazilian waters

Biología reproductiva de la raya a lunares, *Atlantoraja castelnaui* (Ribeiro, 1907) (Chondrichthyes, Rajidae), en aguas del sudeste brasileño

María C. Oddone[1], Alberto F. Amorim[2] and Patricia L. Mancini[3]

[1]*Secretaria Especial de Aqüicultura e Pesca da Presidência da República, Esplanada dos Ministérios,*
Bloco D, 2º andar, Sala 238, CEP: 70.043-900, Brasília, DF
[2]*Instituto de Pesca, Av. Bartolomeu de Gusmão, 192, Ponta da Praia, CEP: 11030-906, Santos, SP, Brazil*
[3]*Projeto Albatroz. Av. Rei Alberto I, N. 450, sala 5, Ponta da Praia, CEP: 11030-906, Santos, SP, Brazil*
cristina_oddone@yahoo.com

Resumen.- Especimenes de *Atlantoraja castelnaui* fueron obtenidos a través de siete barcos de pesca comercial operando en aguas del sudeste brasilero, desde marzo de 2005 hasta abril de 2006. Un total de 53 machos fueron capturados y analizados, con longitudes totales comprendidas entre 17,9 y 111,0 cm. De acuerdo con el análisis de la longitud del clásper y de la glándula del clásper, peso de los testículos, diámetro de los lóbulos testiculares y espinas alares, el tamaño de primera madurez sexual fue estimado en 91,0 cm. Cincuenta y cuatro hembras de entre 17,4 y 116,0 cm de longitud total fueron capturadas. De acuerdo con las observaciones del ancho del útero y de la glándula oviductal, del peso de los ovarios y del diámetro del mayor folículo vitelogénico, el tamaño de primera madurez sexual fue estimado en 105,0 cm. La vitelogénesis comenzaría cuando los folículos alcanzan un tamaño de 1,0 cm y la ovulación cuando alcanzan 3,0 cm de diámetro. El número máximo de folículos vitelogénicos observado en esta especie fue de 20. A pesar de ser *A. castelnaui* una especie ovípara y por tanto, con una fecundidad relativamente alta en comparación con otros elasmobranquios, su gran tamaño la convierte en una especie sumamente susceptible a la presión de pesca, siendo incluso ya considerada como especie en peligro de extinción. Por tales motivos, el conocimiento de sus parámetros reproductivos podrá resultar en un manejo adecuado de los stocks.

Palabras clave: Hembras con huevo, elasmobranquios, tamaño de madurez sexual, folículo vitelogénico, clásper

Abstract.- Specimens of *Atlantoraja castelnaui* were obtained from seven commercial fishing vessels operating in southeastern Brazilian waters, from March 2005 to April 2006. A total of 53 males, ranging from 17.9 to 111.0 cm in total length (TL), were examined. Based on analyses of the clasper gland and clasper length, testes weight, testicular lobes diameter and alar thorns, size at maturity was estimated to be 91.0 cm TL. Fifty-four females were examined ranging from 17.4 to 116.0 cm TL. According to observations of uterus width, oviducal gland width, ovary weight and diameter of the largest vitellogenic follicle, size at maturity was estimated as 105.0 cm TL. Vitellogenesis would start when follicles attain a diameter of 1.0 cm, and ovulation when attaining 3.0 cm of diameter. The maximum number of vitellogenic follicles of this species was 20. In spite of the fact that *A. castelnaui* is an oviparous species, and therefore, with a relatively high fecundity when compared with other elasmobranchs, its big size makes it an extremely vulnerable species to fishery pressure, being even already considered as an endangered one. Because of that, the knowledge of its reproductive parameters will lead to an adequate management of the stocks.

Key words: Egg-bearing females, elasmobranchs, size at maturity, vitellogenic follicle, clasper

Introduction

The distribution of *Atlantoraja castelnaui* (Ribeiro, 1907) ranges from Rio de Janeiro, Brazil, to northern Argentina. This species is common between 30°S and 41°S, where it is the largest rajid (Figueiredo 1977, Menni 1973, Menni *et al.* 1981). In Southern Brazilian waters, the species occurs at depths between 20 and 220 m and it is commonly captured between 24 and 120 m deep, being sympatric to the congeneric species *A. platana* and *A. cyclophora* (Vooren 1998, Oddone & Amorim 2007). *Atlantoraja castelnaui* is the largest species within the genus, with males and females attaining lengths of up to 110 and 116 cm TL, respectively (Oddone & Amorim 2007).

Specimens of *Atlantoraja* spp. are commonly landed and marketed in the cities of Santos and Guarujá, especially the larger individuals. From 1999 to present, its meat started to be exported to Asia, especially to South

Korea (Casarini 2006). Intensive fisheries have led to overexploitation of several species of demersal elasmobranchs in the southwestern Atlantic (Vooren & Klippel 2005), rendering *Atlantoraja castelnaui* an endangered species (Hozbor *et al*. 2004). Due to overexploitation of this species, current information on its basic biology is needed for stock management purposes.

With regard to the reproductive biology of *A. castelnaui*, Ponz Louro (1995) provided a description of the reproductive tract of both sexes and analysed various aspects of its reproduction off Southeast Brazil. Oddone *et al*. (2005) estimated a size at maturity at 110-114 cm and 91-95 cm TL for females and males respectively, off the coast of Uruguay. The aim of the present work was to analyse the sexual development of *A. castelnaui*, by examining reproductive tracts of males and females and to estimate size at maturity in southeastern Brazilian waters.

Material and methods

Sampling

Specimens of *A. castelnaui* were obtained monthly from seven commercial vessels from March 2005 through March 2006. The study area was situated in southeast Brazil, between latitudes 23°37´S and 27°40´S, covering the States of Rio de Janeiro, São Paulo, Paraná and Santa Catarina, at depths between 10 and 146 m (Fig. 1). Latitude and longitude of hauls were recorded by fishermen, however, the exact number of hauls with occurrence of the species was uncertain; therefore, in Fig. 1 the total number of hauls registered is represented.

Reproductive data recorded

Specimens were measured to the nearest millimetre below as total length (TL, measured from the tip of the snout to the distal end of the caudal fin). Electronic scales used had 1 and 5 g precision and to weigh material with less than 1 g, a precision scale (0.001 g) was used.

For males, the following reproductive variables were recorded: clasper length (measured from the insertion in the pelvic region to the distal end) clasper gland length (measured from the anterior to the posterior end) (both in cm), number of alar thorn rows, number of thorns, number of developing thorns (as described by Oddone & Vooren (2005)), diameter of the largest testicular lobe at the widest point (cm) and testes weight (g). Claspers were classified as ‘rigid’ or flexible’ for maturity assessment. For females, maximum oviducal gland width, maximum uterus width (cm), diameter (cm) and colour of the largest ovarian follicle, number of vitellogenic follicles of the ‘maturing group’ (Fitz & Daiber 1963) and presence of egg capsules in the uteri or cloaca were recorded.

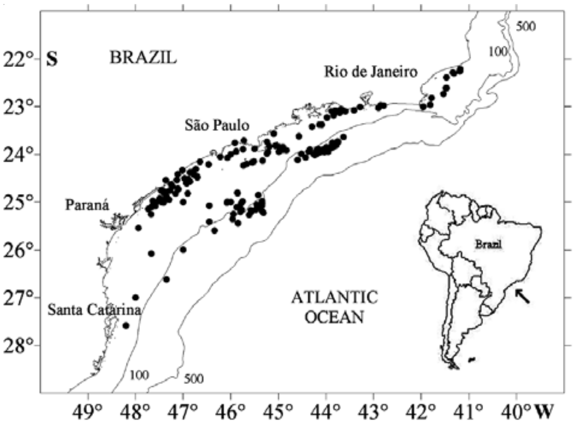

Figure 1

Map of the study area off the coast of Southeast Brazil, Southwestern Atlantic Ocean. Symbols represent the total number of fishing hauls reported by fishermen in the area where samples of *Atlantoraja castelnaui* were collected

Mapa del área de estudio en la plataforma del sudeste del Brasil, océano Atlántico Sudoccidental. Los símbolos representan el numero total de lances de pesca registrados por los pescadores en el área de donde las muestras de *Atlantoraja castelnaui* fueron recolectadas

Specimens were categorised according to Oddone *et al*. (2007), in immature, adolescent and mature.

Estimation of median size-at-maturity

A logistic curve was fitted to the relationship between the proportion of mature males or females as a function of TL: $P_{TL}=1/(1-e^{(a+b*TL)})$, where P_{TL} is the fraction of mature individuals in length class TL, and *a* and *b* are model parameters. In this model, median size at maturity, TL_{50}, is given by *-a/b*, which represents the body size at which 50% of the population was mature (Restrepo & Watson 1991).

Statistical analyses

To determine whether parametric or non-parametric tests would be utilized, normality of residuals and homogeneity of variance were tested by Lilliefors’ and Levene’s tests, respectively. Parametric comparisons were performed using a Student’s t-test (Sokal & Rohlf 1995). Values of all measures considered were expressed as the mean and standard deviation (SD).

Results

Male sexual development

Immature stage

A total of 53 males, ranging from 17.9 to 111.0 cm (65.3±23.6) were captured and analyzed. Individuals from 17.9 to 77.8 cm TL were immature, with uncalcified claspers ranging from 0.3 to 7.8 cm long (3.1±2.3cm, n=36, Fig. 2A). Clasper glands grew with TL describing a sigmoid curve (*r*=0.948, n=53, a=5.924, b=0.058). In males smaller than 48 cm TL, clasper glands ranged from undeveloped (0) to 3.6 cm (1.25±1.34, n=29), becoming evident at 48 cm TL onward and growing slowly relative to TL (Fig. 2B). Testes weight ranged from 0.1 to 15.0 g (4.0±3.70, n=32) and lobes diameter from 0.2 to 0.5 cm (0.3±0.08, Fig. 2C).

Adolescent stage

Individuals between 80.5 and 99.0 cm TL were adolescent, with claspers ranging from 6.2 to 22.0 cm long (15.1±6.5, n=9, Fig. 2A). In specimens larger than 80.5 cm TL, the clasper gland grew faster relatively to TL, representing the adolescent phase. The clasper glands varied from 2.8 to 9.0 cm at this phase (5.7±2.37, n=10, Fig. 2B). Testes ranged from 11.0 to 45.0 g (18.2±5.50, n=10) in weight and lobes from 0.4 to 0.9 (0.6±0.20, n=10, Fig. 2C). Developing thorns occurred in two males, in number of 2 and 4 respectively. Fully formed alar thorns began to occur at 84 cm TL (Fig. 2D). The number of alar thorns per fin varied from 17 to 42 on the right and 17 to 46 on the left pectoral fin, with no significant difference between means (26.8±9.09, n=7; 28.7±11.5, n=7, respectively, t=-0.49, g.l.=12, *P*=0.6328).The

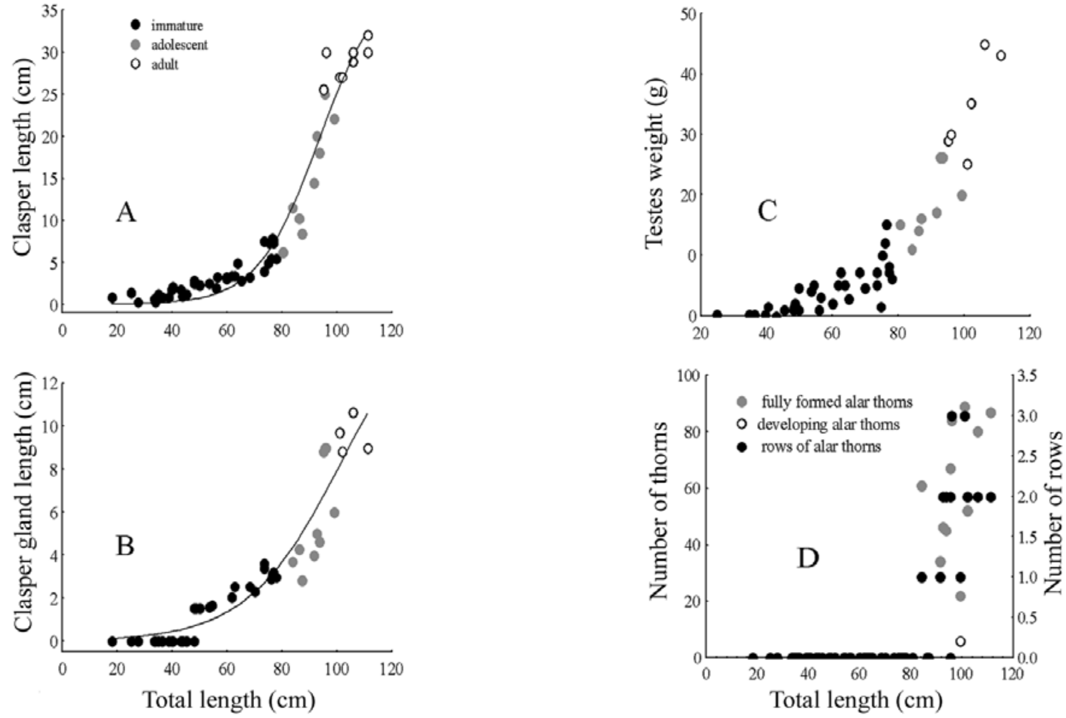

Figure 2

Relationship between total length (cm) and (A) clasper length (cm) (n immature=36; n adolescent=9; n mature=5); (B) clasper gland length (cm) (n immature=29; n adolescent=10; n mature=4) (and the logistic curve adjusted for both relationships); (C) testes weight (g)(n immature=32; n adolescent=10; n mature=6) (g) and (D) number of fully formed alar thorns, developing alar thorns and alar thorns rows (n=11) for males of *Atlantoraja castelnaui*

Relación entre longitud total (cm) y (A) longitud del clásper (cm) (n inmaduros=36; n adolescentes=9; n maduros=5); (B) longitud de la glándula del clásper (cm) (n inmaduros=29; n adolescentes=10; n maduros=4) (y la curva logística ajustada para ambas relaciones); (C) peso de los testículos (g) (n inmaduros=32; n adolescentes=10; n maduros=6) (g) y (D) numero de espinasalares completamente formadas, de espinas alares en desarrollo y de hileras de espinas alares (n=11) para machos de *Atlantoraja castelnaui* number of alar thorn rows varied from 1 to 3 on both fins (1.7±0.76, on both). The inflexion point of the logistic curve adjusted to the clasper length/TL ratio was at 93.4 cm (R=0.97, n=53, *a*=8.39, *b*=0.09).

Mature stage and size at maturity

Mature males ranged from 95.5 to 111.0 cm of TL, with claspers varying from 27.0 to 30.0 cm (28.6±1.5, n=5, Fig. 2A). From 101.0 cm TL onward, the growth of the clasper glands was slower again. Clasper gland length ranged from 8.8 to 10.6 cm (9.5±0.81, n=4, Fig. 2B). Testes weight varied from 25.0 to 35.0 g (34.5±8.04, n=6). Lobes ranged from 0.7 to 1.0 cm (0.9±0.14, n=7) in diameter, following the same pattern of the testes weight with TL (Fig. 2C). The number of alar thorns per fin varied from 17 to 44 on the right and 17 to 47 on the left pectoral fin, with no significant difference between means (31.7±10.55, n=11; 30.2±10.4, n=11, respectively, t=0.35, g.l.=20, *P*=0.9680). The number of alar thorn rows varied from 1 to 3 on both fins (2.0±0.63, on both). Developing thorns were not observed in mature males.

Maturity stages were well delimited, with no overlapping of the variables. The application of the logistic curve to the proportion of mature males per TL classes of 5 cm (Fig. 3) resulted in an estimated TL_{50} of 91.1 cm (R=0.99, *a*=26.89, *b*=0.29, n=11), which corresponds to 83% of the maximum TL observed for males of this species.

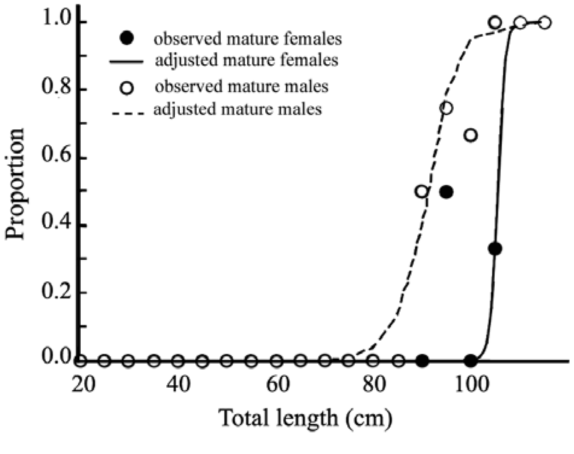

Figure 3

Size at 50% maturity ogives for males (n=53) and females (n=54) of *Atlantoraja castelnaui*. Total length classes considered were 5 cm

Ojivas de tamaño de 50% de madurez para machos (n=53) y hembras (n=54) de *Atlantoraja castelnaui*. Las clases de tamaño consideradas fueron de 5 cm

Female sexual development

Immature stage

A total of 54 females, ranging from 17.4 to 116.0 cm TL (68.0±24.8) were analysed. Immature females ranged from 28.0 to 95.0 cm of TL, with ovary weight varying from 0.1 to 31.0 g (3.4±7.1, n=38) and uterus width from 0.1 to 5.0 cm (0.7±0.90, n=30, Fig. 4A). Oviducal gland width varied from undifferentiated to 3.5 cm (1.1±0.96, n=22, Figure 4B). Follicles were white and varied from 0.1 to 0.8 cm (0.36±0.25, n=9) in diameter (Fig. 4D).

Adolescent stage

Two adolescent females measuring 96.5 and 101.5 cm of TL were recorded. In these specimens, ovary weights were 34.0 and 43.0 g, respectively, whilst uteri widths were 2.6 and 3.0 cm, respectively (Fig. 4A, B). Widths of the oviducal glands were 3.9 and 4.8 cm, respectively. Vitellogenesis began when follicles attained 1.0 cm of diameter. Follicles were light yellow with diameters of 1.0 and 1.3 cm, respectively (Fig. 4A, B).

Mature stage and size-at-maturity

Mature, non egg-bearing females had ovaries ranging from 39.0 to 230.0 g (117.1±55.15 g, n=9) in weight and uteri from 2.8 to 6.0 cm wide (4.0±1.70, n=3), whereas in egg-bearing specimens, ovary weight ranged from 80.0 to 147.0 g (n=2) and uteri width from 7.0 to 7.5 cm (n=2, Fig. 4A, B). Oviducal gland varied from 4.0 to 7.5 cm wide (4.7±1.44, n=4) in non egg-bearing individuals and from 5.9 to 6.7 cm (6.2±0.43, n=3) in egg-bearing females. Follicles diameter varied from 2.1 to 4.0 cm in mature females with empty uteri (3.0±0.78, n=4) and from 2.7 to 3.3 in egg-bearing individuals (n=2, Fig. 4C, D). Therefore, the ovulation size for this species was assumed to be approximately 3.0 cm. A mature female with empty uteri showed 17 vitellogenic follicles in the ovaries, whereas an egg-bearing female carried 20, varying the number of these follicles from 5 to 20 (n=4).

According to the analysis of the abovementioned variables, females were classified as immature or mature and TL_{50} resulted in 105.5 cm (R=0.94, *a*=141.12, *b*=1.34, n=22), which corresponds to 91.0% of the maximum TL observed (Fig. 3).

Discussion

Growth of the clasper gland was concomitant with clasper and testes growth in *A. castelnaui*. This was also recorded for *Rioraja agassizi* (Oddone *et al*. 2007). The male reproductive structures that appear later in development include the alar thorns, as these structures are used as

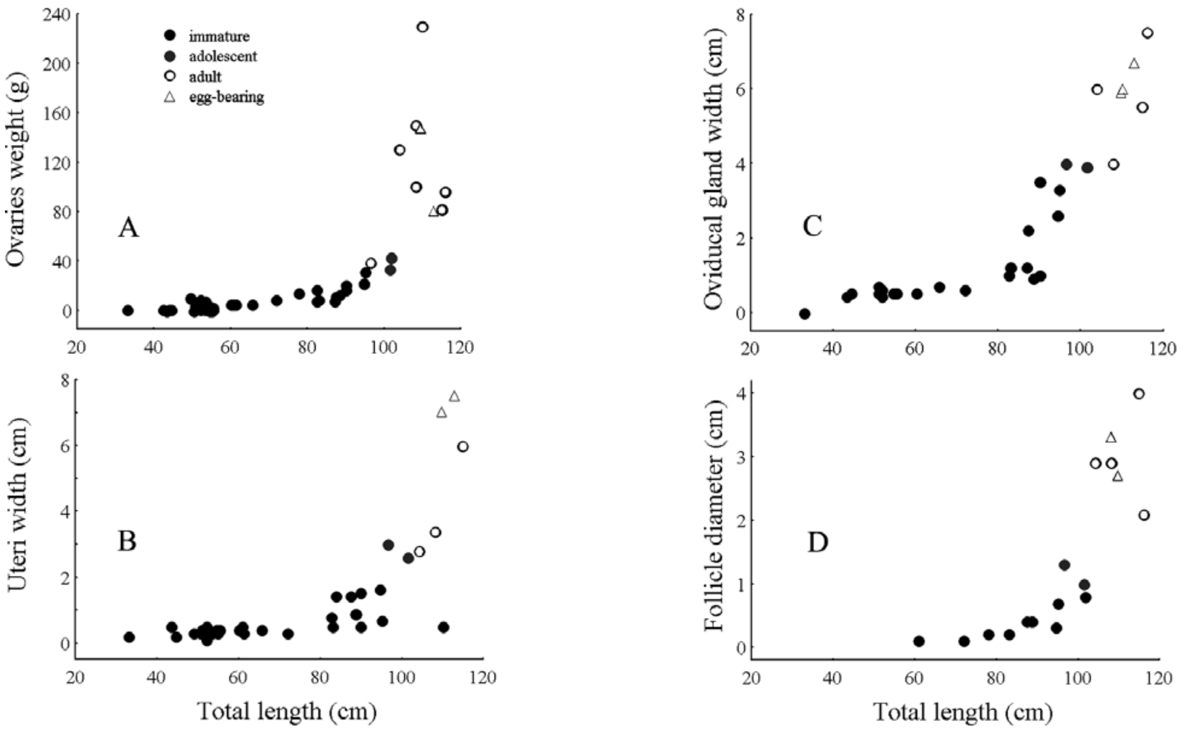

Figure 4

Relationship between total length (cm) and (A) ovaries weight (g) (n immature=38; n adolescent=2; n mature=9); (B) uteri width (cm) (n immature=30 n adolescent=2; n mature=7); (C) oviducal gland width (cm) (n immature=22; n adolescent=2; n mature=7) and (D) largest follicle diameter (cm) (n immature=9; n adolescent=2; n mature=6) for females of *Atlantoraja castelnaui*

Relación entre longitud total (cm) y (A) peso de los ovarios (g) (n inmaduras=38; n adolescentes=2; n maduras=9); (B) ancho de los úteros (cm) (n inmaduras=30 n adolescentes=2; n maduras=7); (C) ancho de las glándulas oviductales (cm) (n inmaduras=22; n adolescentes=2; n maduras=7) y (D) diámetro del mayor folículo (cm) (n inmaduras=9; n adolescentes=2; n maduras=6) para hembras de *Atlantoraja castelnaui*

hold-fast devices during copulation (McEachran & Konstantinou 1996). Similar results were reported for *Sympterygia bonapartii* with regard to the clasper and the alar thorns (Mabragaña *et al*. 2002). Developing thorns have been reported to occur commonly in adolescent and adult stages of other rajids, such as *A. cyclophora* and *R. agassizi (*Oddone & Vooren 2005, Oddone *et al.* 2007); however, none was noted in adults of this species; occurring only in adolescents, which could be related to the low sample size. For *A. cyclophora*, Oddone & Vooren (2005) recorded up to 6 rows of alar thorns, whereas for *A. platana* and *R. agassizi*, Oddone *et al*. (2007) and Oddone & Amorim (2008) recorded up to 5 rows. *Atlantoraja castelnaui*, the largest member of the genus, was found to bear the least number of rows, *i.e.*, 3 rows per pectoral fin.

The general pattern observed in several rajid species for the relationship between clasper and TL is a three-phased sigmoid curve (Capapé 1974, Capapé & Quignard 1974, Templeman 1987, Oddone & Velasco 2004, Oddone & Vooren 2005, Oddone *et al*. 2007). However, in *A. castelnaui*, claspers appear to grow continuously in the adult phase, contrasting with the general pattern. This could be a species-specific pattern, as was also recorded by Ponz Louro (1995) for *A. castelnaui.* A similar pattern in the clasper gland/TL ratio was recorded for *A. cyclophora* and for *R. agassizi* (Oddone & Vooren 2005, Oddone *et al*. 2007).

Female sexual development in *A. castelnaui* was concomitant with respect to the ovaries, uteri, oviducal gland and follicles development, a fact also observed in

R. agassizi and *A. cyclophora* (Oddone & Vooren 2005, Oddone *et al*. 2007).

Another interesting fact occurs in *A. castelnaui*, *i.e.*, the three maturity stages in both sexes were well delimited with regard to TL. Conversely, species like *R. agassizi*, a high overlap among mature and immature/adolescent occurs in both sexes, especially regarding to testes and number of alar thorns for the males, and ovaries weight and number of follicles for the females (Oddone *et al*. 2007).

Vitellogenesis in *A. castelnaui* begins when follicles attain a diameter of 1.0 cm. In *R. agassizi* this process begins when follicles attain a diameter of 0.5-0.6 cm (Ponz Louro 1995, Oddone *et al*. 2007) and in *A. cyclophora* when follicles attain a diameter of 0.9 cm (Oddone & Vooren 2005). These differences in follicular diameters suggest that follicular size at the onset of vitellogenesis could be species-specific. Follicles would be ready for ovulation at a diameter of 3 cm for *A. castelnaui*. Follicles ovulation size would be species-specific as well, since follicles are ready to ovulate with diameter of 2.6 cm for *A. cyclophora* and 2.0 cm for *R. agassizi* (Oddone & Vooren 2005, Oddone *et al.* 2007).

The maximum number of follicles recorded in this work for *A. castelnaui* was 20, in an egg-bearing female. Ponz Louro (1995) reported up to 15 follicles in this species. In *R. agassizi*, a number of up to 30 follicles was recorded (Oddone *et al*. 2007) and in *Psammobatis extenta*, Martins *et al.* (2005) recorded up to 10. Licandeo & Cerna (2007) recorded up to 85 vitellogenic follicles for *Zearaja chilensis* and Licandeo *et al.* (2007), up to 68 in *Dipturus trachyderma*.

Female *A. castelnaui* attained 50% maturity at 91% of their maximum observed size while males were mature at 83% of their maximum observed size. Cortés (2000) noted that elasmobranchs generally mature at 75% of their maximum size, while Frisk *et al*. (2001) observed that dogfishes, skates and rays mature at 73% of their maximum size. In *Rioraja agassizi*, males and females mature at 68% of the maximum size (Oddone *et al*. 2007), whereas in *Atlantoraja cyclophora*, males attain maturity when they reach 76 % and females 82% of their maximum size (Oddone & Vooren 2005). In *Atlantoraja platana*, males mature when they reach 86% and females 94% of their maximum sizes (Marçal 2003).

Ponz Louro (1995) estimated size at maturity at 100 cm for males and *ca*. 110 cm TL for females, in specimens caught between 1985 and 1987. In the present study, performed 20 years after that of Ponz Louro (1995) the observed size at maturity for the same area diminished in 9 cm for males, and approximately 5 cm for females. Natural fish stocks are complex mixtures of genotypes, responding differently to fishing pressure, which somewhat erodes natural genetic diversity in order to select the genotypes that are better able to withstand the impacts, and the change in size at maturity is one of the more worrisome genetic changes (Walters & Martell 2004).

The difference in size at maturity between this work and Ponz Louro (1995), thus, may reflect the effects of decades of fishing pressure upon *A. castelnaui* in southeastern Brazilian waters. Frisk *et al*. (2005), by performing elasticity and perturbation analyses, noted that compensatory responses to exploitation in elasmobranchs were more likely to be expressed as changes in juvenile and adult mortality and stage durations, *i.e.*, size and age at maturity, than changes in other parameters as fertility. Further, according to Fogarty *et al.* (1989) (*apud* Walker & Ellis 1998), the negative effects of exploitation, may be counteracted by compensatory mechanisms such as density dependent changes in fecundity, age or size at maturation.

Differences in size at maturity for a given species may be also related to other reasons as the area in which the species live. Templeman (1987) for instance, observed that maturity in *Amblyraja radiata* occurred at relatively small sizes off northern Iceland and West Greenland, off Baffin Island and Labrador, on the Northeast Newfoundland Shelf and in the Gulf of St. Lawrence, and at considerably larger sizes on the Grand Bank and St. Pierre Bank. Mabragaña & Cousseau (2004) also noted latitudinal variations in the size at maturity for *Psammobatis rudis* and *P. normani*, arguing that this could be a consequence of oceanographic conditions, apart from the effect of fishing pressure.

In addition, for *Rioraja agassizi*, Colonello *et al*. (2007) estimated size at maturity for the area situated between southern Brazil and northern Argentina, considerably greater that the ones estimated by Oddone *et al.* (2007) for southeastern Brazil. For the species in question, Oddone *et al*. (2005) observed that off Uruguay, (Argentinean-Uruguayan Common Fishing Zone, 34°30´-39°30´) males and females matured at total length of 93 and 112 cm, respectively. These values of TL_{50} are close to those obtained for males in the present study, whilst for females; a 7 cm difference is observed. However, samples from the earlier study were caught from 7-11 years before the current work, and these maturity estimates may have changed.

As in other rajid species, females of *A. castelnaui* attained size at maturity at larger lengths than males. This delayed onset of maturity in females, known as 'bimaturism', could be related to the need of females to carry the pups, and as such, to invest on growth in favour to reproduction (Cortés 2000). However, exceptions exist within the Rajidae family. For instance, Ebert (2005) and Ruocco *et al*. (2006) noted that in *Bathyraja* species, males and females attained maturity at the same size.

Dulvy & Reynolds (2002) found that skate species which have disappeared from substantial parts of their ranges (considered as «locally extinct»), have larger body sizes compared to all other skates, as a large body size is related to higher mortality rates and to life-history parameters such as late age at maturity. Moreover, García *et al*. (2007) also noted that (after the reproductive mode), a large body size increased the extinction risk in elasmobranchs. This is a matter of concern for *A. castelnaui*, because it is the largest skate species caught in the area. However, according with these authors, oviparous species would be subjected to the lowest extinction risk than elasmobranches with other reproductive modes. Further, Frisk *et al.* (2005) observed that fecundity in the family Rajidae is higher than in other elasmobranchs. Therefore, the extinction risk due to the large body size in this species, could be somewhat compensated with the high fecundity. However, *A. castelnaui* has already become an endangered species (Hozbor 2004) and this should be considered for management and conservation purposes.

Acknowledgments

To Walter Norbis and Paul G. Kinas for statistical advice; skippers of the CV 'Cigano do Mar II & III', 'Antares I & Polares III', 'Franzese III', 'São Paulo IV', 'São Paulo II', 'Dourado & Araguaia', 'São Paulo VI & XI', 'Jangadeiro XV' for providing the samples, Gonzalo Velasco for collaborating in sampling, Luis O. Lucifora and Verónica B. García for revising the English grammar and four anonymous referees, for making important comments on the submitted version. This study was financed by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil).

Literature cited

Capapé C. 1974. Contribution à la biologie des Rajidae des côtes tunisiennes. 2. *Raja radula*. Archives de l'Institut Pasteur Tunis 51: 211-228.

Capapé C & JP Quignard. 1974. Contribution à la biologie des Rajidae des côtes tunisiennes. 1. *Raja miraletus*, Linné, 1758: répartition géographique et bathymétrique, sexualité, reproduction, fécondité. Archives de I'Institut Pasteur Tunis 51: 39-60.

Casarini LM. 2006. Dinâmica populacional de raias demersais do gênero *Atlantoraja* e *Rioraja* (Elasmobranchii, Rajidae) da costa sudeste e sul do Brasil. Tesis de doctorado. Universidade de São Paulo, São Paulo, 206 pp.

Colonello JH, ML García & CA Lasta. 2007. Reproductive biology of *Rioraja agassizi* from the coastal southwestern Atlantic ecosystem between northern Uruguay (34°S) and northern Argentina (42°S). Environmental Biology of Fishes 80(2-3): 277-284.

Cortés E. 2000. Life-history patterns and correlations in sharks. Reviews in Fisheries Science 8: 299-344.

Dulvy NK & JD Reynolds. 2002. Predicting extinction vulnerability in skates. Conservation Biology 16: 440-450.

Ebert DA. 2005. Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea Continental Slope. Journal of Fish Biology 66: 618-649.

Figueiredo JL. 1977. Manual de Peixes Marinhos do Sudeste do Brasil. Introdução, cações, raias e quimeras. 104 pp Museu de Zoologia da Universidade de São Paulo, São Paulo.

Fitz, ES Jr. & FC Daiber. 1963. An introduction to the biology of *Raja eglanteria* Bosc 1802 and *Raja erinacea* Mitchill 1825 as they occur in Delaware Bay. Bulletin Bingham Oceanographic Collection 18: 69-97.

Frisk MG, TJ Miller & MJ Fogarty. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: A comparative life history study. Canadian Journal of Fisheries and Aquatic Science 58: 969-981.

Frisk MG, TJ Miller & NK Dulvy. 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. Journal of the Northwest Atlantic Fishery Science 35: 27–45.

Hozbor N, AM Massa & CM Vooren. 2004. *Atlantoraja castelnaui*. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <http://www.iucnredlist.org> [Downloaded on February 12, 2007].

Licandeo R & FT Cerna. 2007. Geographic variation in life-history traits of the endemic kite skate *Dipturus chilensis* (Batoidea: Rajidae), along its distribution in the fjords and channels of southern Chile. Journal of Fish Biology 71(2): 421-440.

Licandeo R, F Cerna & R Céspedes. 2007. Age, growth, and reproduction of the roughskin skate, *Dipturus trachyderma*, from the southeastern Pacific. ICES Journal of Marine Science 64(1): 141-148.

Mabragaña E & MB Cousseau. 2004. Reproductive biology of two sympatric skates in the south-west Atlantic: *Psammobatis rudis* and *Psammobatis normani*. Journal of Fish Biology 65: 559-573.

Mabragaña E, LO Lucifora & AM Massa. 2002. The reproductive biology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic. Journal of Fish Biology 60: 951-967.

Marçal AS. 2003. Biologia reprodutiva de *Atlantoraja platana* (Günther, 1880) (Elasmobranchii, Rajidae) no Sul do Brasil. Rio Grande. Tesis de maestría. Fundação Universidade Federal do Rio Grande, Rio Grande, 65 pp.

Martins IA, CL Martins & MHA Leme. 2005. Biological parameters and population structure of *Psammobatis extenta* in Ubatuba region, north coast of the State of São Paulo, Brazil. Journal of the Marine Biological Association of the United Kingdom 85: 1113-1118.

McEachran J & H Konstantinou. 1996. Survey of the variation in alar and malar thorns in skates: Phylogenetic implications (Chondrichthyes: Rajoidei). Journal of Morphology 228: 165-178.

Menni RC. 1973. Rajidae del litoral bonaerense. I. Especies de los géneros *Raja*, *Bathyraja* y *Sympterygia* (Chondrichtyes). Physis A 32 (85): 413-439.

Menni RC, HL López & ML García. 1981. Lista comentada de las especies de peces colectadas durante la campaña V del B/I «Shinkai Maru» en el Mar Argentino. Contribuciones del Instituto Nacional de Investigaciones Pesqueras 383: 267-280.

Oddone MC & G Velasco. 2004. Size at maturity of the smallnose fanskate *Sympterygia bonapartii* (Müller and Henle, 1841) (Pisces, Elasmobranchii, Rajidae) in the SW Atlantic. ICES Journal of Marine Science 61(2): 294-297.

Oddone MC, L Paesch & W Norbis. 2005. Length at first sexual maturity of two species of rajoid skates, genera *Atlantoraja* and *Dipturus* (Pisces, Elasmobranchii, Rajidae), from the Southwestern Atlantic Ocean. Journal of Applied Ichthyology 21(1): 70-72.

Oddone MC & CM Vooren. 2005. Reproductive biology of *Atlantoraja cyclophora* (Regan 1903) (Elasmobranchii, Rajidae) off southern Brazil. ICES Journal of Marine Science 62(6): 1095-1103.

Oddone MC, AF Amorim, PL Mancini, W Norbis & G Velasco. 2007. The reproductive biology and cycle of *Rioraja agassizi* (Müller and Henle, 1841) (Chondrichthyes, Rajidae), in southeast Brazil, SW Atlantic Ocean. Scientia Marina 71(3): 593-604

Oddone MC & AF Amorim. 2007. Length-weight relationships, condition and population structure of the genus *Atlantoraja* (Elasmobranchii, Rajidae, Arhynchobatidae) in South-eastern Brazilian waters, SW Atlantic Ocean. Journal of the Northwest Atlantic Fishery Science 38: 43-52.

Oddone MC & AF Amorim. 2008. Size at maturity of *Atlantoraja platana* (Günther, 1880) (Chondrichthyes: Rajidae: Arhynchobatinae) in the SW Atlantic Ocean. Journal of Fish Biology 72: 1515–1519.

Ponz Louro M. 1995. Estratégias e tácticas reprodutivas de elasmobrânquios no ecossistema de Ubatuba, SP, Brasil. São Paulo. Master Thesis Universidade de São Paulo, São Paulo, 95 pp.

Restrepo VR & RA Watson. 1991. An approach to modelling crustacean egg-bearing fractions as function of size and season. Canadian Journal of Fisheries and Aquatic Science 48: 1431-1436.

Ruocco NL, LO Lucifora, JM Díaz de Astarloa & O Wöhler. 2006. Reproductive biology and abundance of the white-dotted skate, *Bathyraja albomaculata*, in the Southwest Atlantic. ICES Journal of Marine Science 63: 105-116.

Sokal RR & FJ Rohlf. 1995. Biometry, 887 pp. Freeman WH, San Francisco.

Templeman W. 1987. Differences in sexual maturity and related characteristics between populations of thorny skate (*Raja radiata*) in the northwest Atlantic. Journal of the Northwest Atlantic Fishery Science 7: 155–167.

Vooren CM. 1998. Elasmobrânquios demersais. In: Seeliger U, C Odebrecht & JP Castello (eds), Os ecossistemas costeiro e marinho do extremo sul do Brasil, Rio Grande pp. 157-162. Ecoscientia, Rio Grande.

Vooren CM & S Klippel. 2005. Ações para a conservação de tubarões e raias no sul do Brasil, 262 pp. Igaré, Porto Alegre.

Walker PA & J Ellis. 1998. Ecology of rays of the north-eastern Atlantic. In: Biology of Skates. Proceedings of the Biology of Skates Symposium (New Orleans, 1996), pp. 7-29, Princeton Press, New Orleans.

Walters CJ & SJD Martell (eds). 2004. Strategies requirements for sustainable fisheries. In: Fisheries Ecology and Management, pp. 43-64. Princeton University Press, Princeton, New Jersey, 399 pp.

Recibido el 11 de enero de 2008 y aceptado el 15 de mayo de 2008