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Reproductive biology of the endemic skate *Psammobatis lentiginosa* in the San Matías Gulf (south-western Atlantic)

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The reproductive biology of Psammobatis lentiginosa *was studied in San Matías Gulf (Patagonia, south-west Atlantic). A total of 1033 skates was analysed, total length ranged from 17 to 52 cm for females and from 13 to 55 cm for males. Total length–total weights relationships differed between sexes, with* $TW = 0.005 \times TL^{3.02}$ *for females and* $TW = 0.005 \times TL^{2.97}$ *for males. The overall sex-ratio was 1:1. In females, the* $L_{50\%}$ *was 41.06 cm, in males the* $L_{50\%}$ *was 41.38 cm. The mean number of yolked oocytes per skate was 4.22 (±2.41). The mean number of yolked oocytes and the length of the female were linearly related. The diameter maximum of yolked oocytes was 24 mm. The species exhibited a continuous reproductive cycle throughout the year, with a peak of egg-case production during autumn that was synchronous with maximum values of the epididymis and uterus indices. This is the first record of a reproductive aggregation for* P. lentiginosa *in San Matías Gulf, North Patagonia. This finding together with its continuous presence around the year, suggest that this area is the main distribution area of* P. lentiginosa *in the south-west Atlantic.*

Keywords: reproductive cycle, egg case, Rajidae, maturity, Patagonia

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INTRODUCTION

Skates have been identified as one of the most vulnerable groups of marine fish to intensive fishing pressure, particularly due to life-history traits such as low fecundity, slow growth, delayed maturity and long incubation period (Holden, 1973; Brander, 1981). In addition to the concern over the collapse of the fisheries and possible extinction of some species, a further problem is the negative effects that drastic population declines can have on ecosystems (Holden, 1973, 1974; Brander, 1981; Walker, 1998; Castro, 1999; Dulvy *et al.*, 2000; Shepherd & Myers, 2005; Dudley & Simpfendorfer, 2006).

The genus *Psammobatis* is endemic to the south-western Atlantic Ocean and it is represented by 7 species (McEachran, 1983; Menni & Stehmann, 2000). Among these, systematic, morphological and biological aspects have been studied in the following species: *Psammobatis bergi*, *P. extenta*, *P. rudis*, *P. normani* and *P. rutrum* (McEachran, 1983; Mabragaña & Cousseau, 2004; Braccini & Chiaramonte, 2002a, b; Sánchez & Mabragaña, 2002; Braccini & Perez, 2005; Martins *et al.*, 2005; San Martín *et al.*, 2005, 2007; Cousseau *et al.*, 2007; Mabragaña, 2007; Mabragaña & Gilberto, 2007).

The skate *Psammobatis lentiginosa* is distributed between 32° and 45°S at depths ranging from 70 to 170 m. (Menni & Stehmann, 2000; Mabragaña, 2007; Cousseau *et al.*, 2007; Di Giacomo *et al.* in press). Available information deals with species description and ecological and biological aspects (McEachran, 1983; Menni & Stehmann, 2000; Cousseau *et al.*, 2007; Mabragaña, 2007; Di Giacomo *et al.*, in press). In the San Matías Gulf (41°–42°S 64°–65°W), a small-scale trawl fishery targeting the common hake, *Merluccius hubbsi*, has been developing since 1971 (Di Giacomo & Perier, 1992). *Psammobatis lentiginosa* is part of the by-catch and discarded at sea due to its small size. The objective of the present study is to determine life-history parameters of *P. lentiginosa*, with particular emphasis on its reproductive biology.

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MATERIALS AND METHODS

Sampling

Skates were caught during bottom trawl surveys performed with commercial vessels and random selected sampling from commercial catches by onboard observers. The surveys were carried out in San Matías Gulf, northern Patagonia (Figure 1), one in October–November 2004 and the other in November–December 2005, aboard the fishing vessels 'Chiarpesca 59' and 'Marina Z', respectively. These were equipped with 96-ft commercial bottom trawls. In concordance with the methodology described by Di Giacomo & Perier (1991, 1992) a variable number of hauls (35–40) of 30 minutes each were performed at a depth-range of 40–175 m. The total number of skates captured per haul and the total length (L, in cm) of each specimen were recorded during each survey.

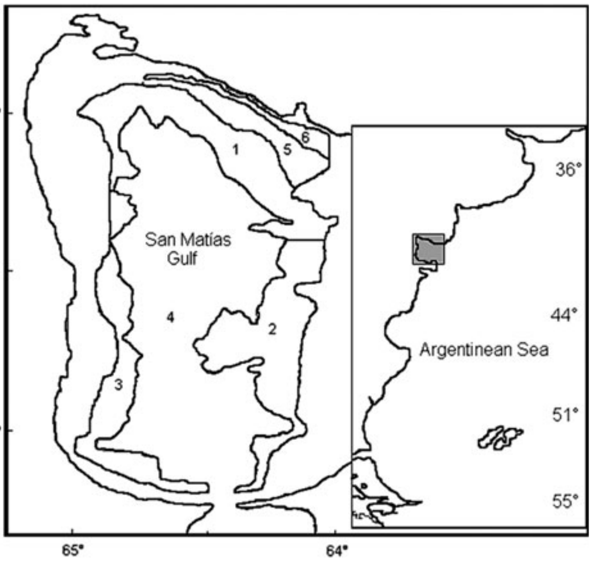

Fig. 1. San Matías gulf. Bottom trawl survey. Random stratified sampling. Strata depths 1, 2, 3 = 90–130 m; 4 > 130 m; 5 = 50–89 m; 6 = 20–49 m.

Skates caught by commercial vessels were bimonthly sampled by onboard observers (Instituto de Biología Marina y Pesquera Almirante Storni, Onboard Observers Program) between March 2005 and May 2007. In each commercial trip, when observers were onboard, all skates caught were kept for sampling. Samples of two sources were properly labelled and kept cold onboard before being sent to the laboratory for the morphometric and reproductive analyses described below.

Morphometric analysis and sex-ratio

Sex, total length (TL, cm), disc width (DW, cm) and total weight (TW, g) were recorded for each fish. Total length and disc width were measured to nearest cm from the top of the rostrum to the tip of the tail and the maximum distance between the edges of pectoral fins, respectively. The relationships between TL and DW ($TL = a + bDW$) and between TL and TW ($TL = a.\ TW^b$) were calculated for each sex; data were log-transformed and a Student's *t*-test was used for comparisons of slopes and intercepts. Differences in the proportions of sexes for each season were evaluated by the Chi square ($\chi 2$)-test (Zar, 1984).

Reproductive analysis

Sexual maturity degree was determined following the classification of Holden & Raitt (1975) and Stehmann (2002). In males, sexual maturity was determined by the rigidity and length of the myxopterygia or claspers (Holden & Raitt, 1975; Stehmann, 2002), which were measured to nearest mm from the caudal end of the cloaca to their tip (CL). Specimens were dissected to expose the reproductive system. Liver and reproductive organs were drained and the mass determined. Testes and epididymis were weighed (g).

Males were classified as virginal or immature (claspers not reaching margin of pectoral fin), maturing (semi-calcified claspers exceeding the pectoral fins but flexible) and mature (fully calcified and rigid claspers longer than pectoral fins).

In females, ovaries, oviducal glands and oviducts were weighed (g). All the oocytes of diameter larger than 1 mm where counted and the yolked oocytes were measured (mm). Females were classified as virginal or immature (oviducts, oviducal gland and ovaries undeveloped), maturing (oviducts and oviducal gland developing and ovarian follicles without yolk) or mature (oviducal glands fully developed, oviducts with or without egg cases and ovarian follicles with yolk). Differences in the proportions of mature to immature specimens for the entire dataset and for each season were evaluated by the χ^2-test (Zar, 1984).

In mature females, differences in the number of yolked oocytes between right and left ovaries were assessed by the Wilcoxon paired-sample test. Ovarian fecundity was determined as the number of follicles with yolk in the ovaries. Regression analyses were performed to evaluate the possible relationships between the number and diameter of mature oocytes and female length. The number of females carrying egg cases and total length (without horns), width, thickness (all mm) and weight (g) of completely formed egg cases were determined on a seasonal basis.

The length of the smallest mature specimen was recorded for each sex. Size at 50% of maturity (LT50%) was estimated using the FISHPARM. 3.05 program (Prager *et al.*, 1987).

The reproductive activity was indirectly assessed using several indices. The gonadosomatic index (GI = ovaries or testes weight * 100/total weight) and hepatosomatic index (HI = liver weight * 100/TW) were calculated for both sexes. The oviducal gland index (OGI = oviducal gland weight * 100/TW) and uterus index (UI = uterus weight * 100/TW) indices were calculated for females and the epididymis index (EI = epididymis weight * 100/TW) for males. The condition factor ($CF = TW/TL^b$, where b is the exponent of the relationship between TL and TW obtained for each sex) was calculated for males and females.

Comparisons of TL–TW relationship and TW versus liver weight (LW) were analysed for seasonal and individual variations and related to the reproductive cycle.

The mean values of the indices were analysed for each season in order to characterize the reproductive cycle of the skate. Differences were tested by the Kruskal–Wallis nonparametric ANOVA, followed by multiple comparisons (Q) when they were necessary (Zar, 1984).

RESULTS

Morphometric analysis

Female length ranged from 17 to 52 cm, while male length ranged from 13 to 55 cm (Figure 2). A total of 1033 skates, 514 females and 519 males, were sampled in the two surveys. The DW–TL relationship was $DW = 0.56 * TL - 0.34$ ($N = 269$, $r^2 = 0.93$) for females, and $TW = 0.56 * TL - 0.44$ ($N = 268$, $r^2 = 0.94$) for males. There were no significant differences between the sexes in either the slopes or intercepts of these relationships (*t*-test, $df = 552$, $P > 0.05$ for slopes and *t*-test, $df = 553$, $P > 0.05$ for intercepts). The TL–TW relationship differed significantly between sexes, with females being heavier than males (*t*-test, $df = 1028$, $P > 0.05$ for slopes and *t*-test, $df = 1029$, $P < 0.05$ for intercepts) (Figure 3).

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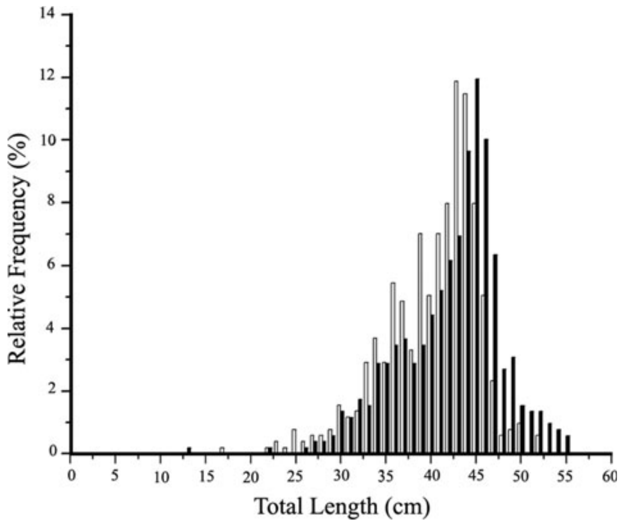

Fig. 2. Size–frequency distribution of *Psammobatis lentiginosa*. Female (black bars), N = 514; male (white bars), N = 519.

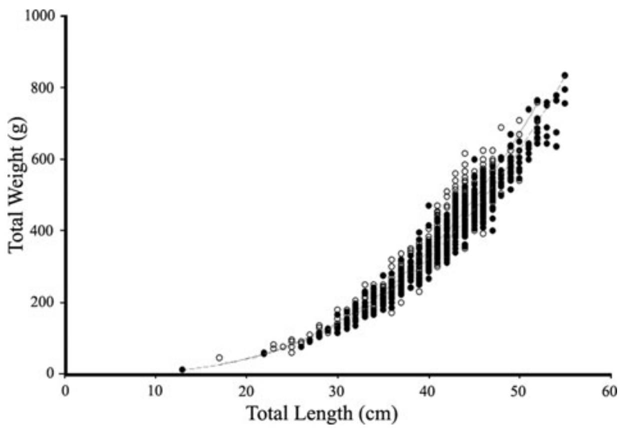

Fig. 3. Total length–total weight relationship of *Psammobatis lentiginosa*. Female, N = 508, (-), R2 = 0.94; male, N = 518, (- -) R2 = 0.96.

The LW–TL relationship was LW = 7 * 10–05 TL3, 20 ($r^2 = 0.67$) for females, and LW = 1* 10–4 TL2, 66 ($r^2 = 0.61$) for males. These relationships differed significantly between sexes (*t*-test, df = 394, $P < 0.05$ for slopes) with livers of females being heavier than those of males at given TL. There was a noticeable individual variation in hepatic mass for each length-class (class interval = 1 cm) as males and females reach sexual maturity (Figure 4).

Sex-ratio

No significant differences from the expected 1:1 ratio were found for the overall female:male ratio ($\chi^2 = 0.001$; df = 1; $P > 0.05$; N = 1032), the immature female:male ratio ($\chi2 = 3.6$; df = 3; $P > 0.05$; N = 452) and the mature female: male ratio ($\chi^2 = 7.65$; df = 3; $P > 0.05$; N = 580). Seasonal significant difference in female : male ratio was found in spring ($\chi^2 = 12.39$; df = 3; $P > 0.05$; $N = 407$).

Maturity and reproductive analysis

The smallest mature male was 38 cm L and all males > 46 cm L were mature showing well-calcified claspers (Figure 5) and fully developed testis and epididymis (Figure 6). Transition

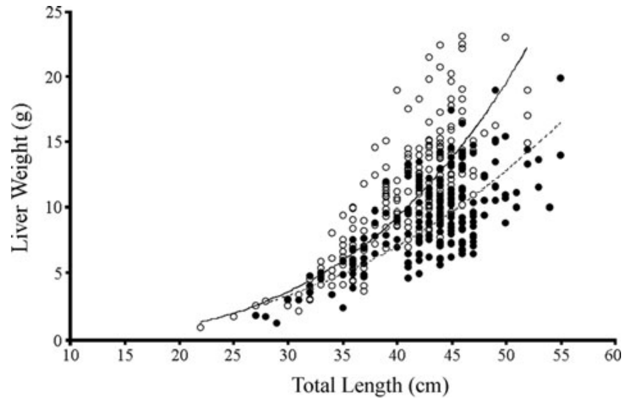

Fig. 4. Total length–liver weight relationship of *Psammobatis lentiginosa*. Female (o), N = 223, (-), R2 = 0.71; male (•), N = 183, (- -) R2 = 0.61.

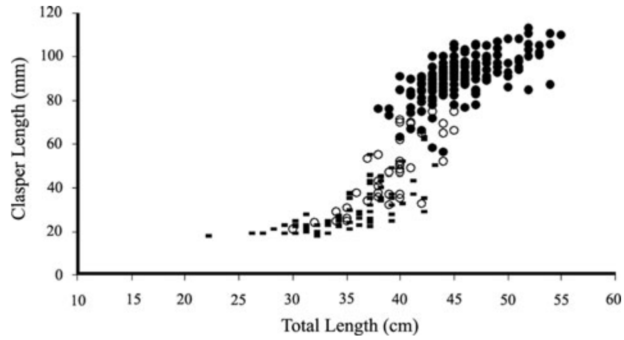

Fig. 5. Total length–clasper length relationship by maturity stages of males of *Psammobatis lentiginosa*. Immature ( ) N = 83; maturing (o) N = 44; mature (•) N = 202.

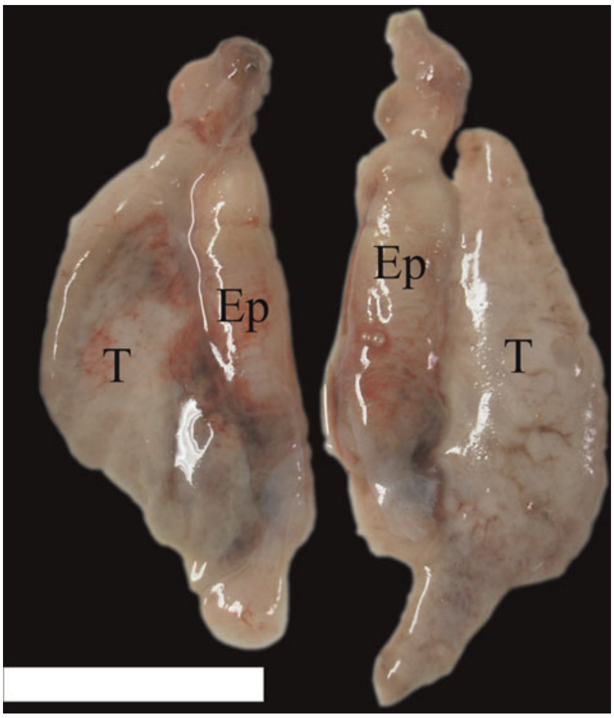

Fig. 6. Dissected reproductive of mature male of *Psammobatis lentiginosa*. T, testis; Ep, epididymis. White bar = 3 cm.

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from immaturity to maturity was observed in males between 38 and 46 cm L. For males, L50% was estimated to be 41.38 cm, representing 75.3% of the largest male sampled (Figure 7A). All females < 37 cm L were immature or maturing, while those > 45 cm L were mature having fully developed oviducts, oviducal glands and ovaries with mature yolked oocytes. In females the transition from immaturity to maturity was observed between 37 and 45 cm L. The L50% for females was estimated to be 41.06 cm L, which represented 79% of the largest female sampled (Figure 7B). The smallest female carrying egg cases, was 39 cm L.

There were no significant differences in the number of mature yolked oocytes between the left and right ovaries (Mann–Whitney, N = 43, $P > 0.05$). The mean number of yolked oocytes per skate (ovarian fecundity) was 4.22 (N = 43, SD = 2.41). A linear relationship was found between the mean number of yolked oocytes and the L of the female (F, N = 50, $P > 0.05$). The diameter of yolked oocytes ranged between 6 and 24 mm.

Dimensions of the egg cases are shown in Table 1 (Figure 8). There were no significant differences in the length and width of the egg cases (Mann–Whitney, N = 9, $P > 0.05$), between the left and right oviducts. Mature females carrying egg cases represented 13.4% (Figure 9)

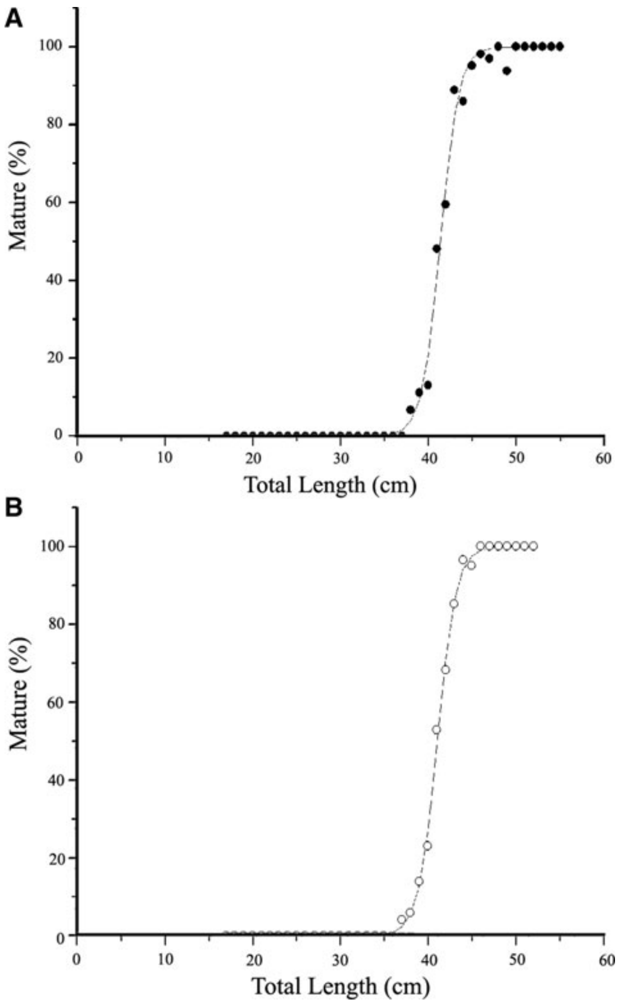

Fig. 7. (A) Size at first maturity (L50%T) of males of *Psammobatis lentiginosa*; (B) size at first maturity (L50%T) of females of *P. lentiginosa*.

Table 1. Length, width and thickness (mm) of egg case of *Psammobatis lentiginosa*.

	Egg case left (mm)			Egg case right (mm)		
Female (cm)	Length	Width	Thickness	Length	Width	Thickness
40	40.3	21.1	11	41.0	21.4	9.2
43	45.5	28.7	9.3	46.6	28.6	6.2
41	47.7	28.3	9.3	43.3	27.9	9.0
42	42.0	30.0	8.0	45.0	29.0	7.0
43	43.6	28.8	–	–	28.5	–
43	44.1	28.3	–	43.7	28.8	–
46	39.0	30.0	–	39.0	30.0	10.0
45	39.0	29.0	–	39.0	28.0	9.0
43	44.0	31.0	–	38.0	21.0	–

–, not available.

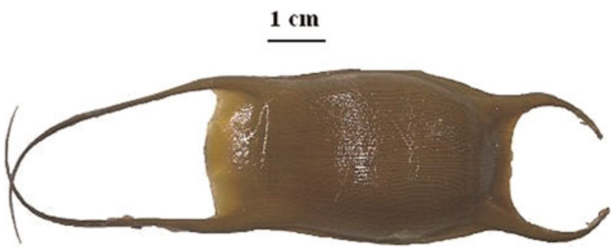

Fig. 8. Egg case dimension of *Psammobatis lentiginosa*.

of all mature females; they were found all year round, with the highest percentage being recorded in autumn (Figure 10).

The male IH did not vary significantly among seasons (Kruskal–Wallis, df = 3, $P > 0.05$) and the highest value was observed in summer (Figure 11A). The GI showed significant differences among seasons (Kruskal–Wallis,

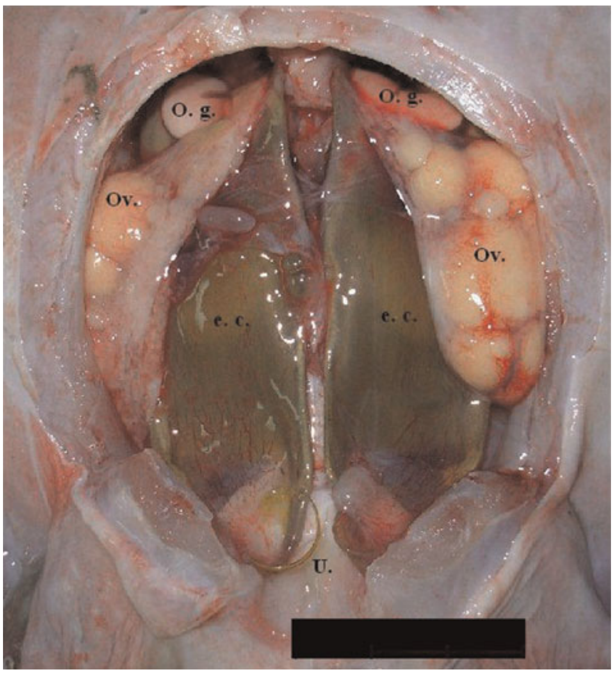

Fig. 9. Dissected reproductive female tract of *Psammobatis lentiginosa* with egg case in uterus. Ov. : ovaries; O.g., oviducal glands; U, uterus; e.g., egg case. Black bar = 3 cm.

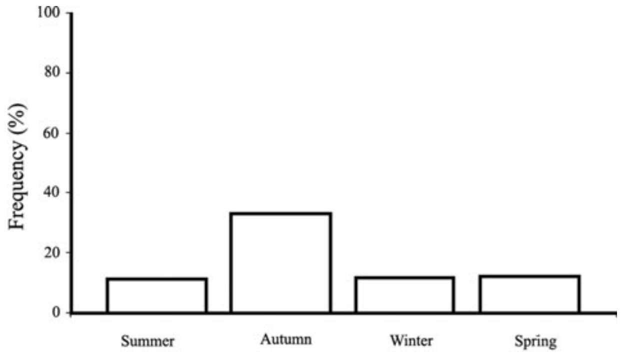

Fig. 10. Seasonal variation of percentage of females with egg-cases in uterus of *Psammobatis lentiginosa*.

df = 3, $P < 0.05$) and pairwise comparisons revealed that IG values were significantly lower and higher in summer and spring, respectively (Q, df = 4, $P < 0.05$; Figure 11B). The IE did not vary significantly among seasons (Kruskal–Wallis, df = 3, $P > 0.05$), with the maximum value being obtained in spring and summer (Figure 11C). The CF showed lowest and highest values in autumn and winter, respectively (Figure 11D).

The female HI showed significant differences among seasons (Kruskal–Wallis, df = 3, $P < 0.05$) but contrasts were non-significant (Q, df = 4, $P > 0.05$) (Figure 12A). The highest HI value was obtained in summer. The GI differed significantly among seasons (Kruskal–Wallis, df = 3, $P < 0.05$; Figure 12B), although contrasts showed no significant differences. The highest GI value was recorded in spring.

The mean oviducal gland index (OI) did not vary significantly among seasons (Kruskal–Wallis, df = 3, $P > 0.05$) and the higher values were reached in summer and spring (Figure 12C). The mean uterus index (UI) varied significantly among seasons (Kruskal–Wallis, df = 3, $P < 0.05$) and pairwise comparisons indicated significant differences between summer autumn, autumn–spring and spring–winter (Q, df = 4, $P < 0.05$). The highest and lowest values of this index were recorded in autumn and spring, respectively (Figure 12D). The condition factor showed its highest value during spring. The lowest value was observed during autumn (Figure 12E).

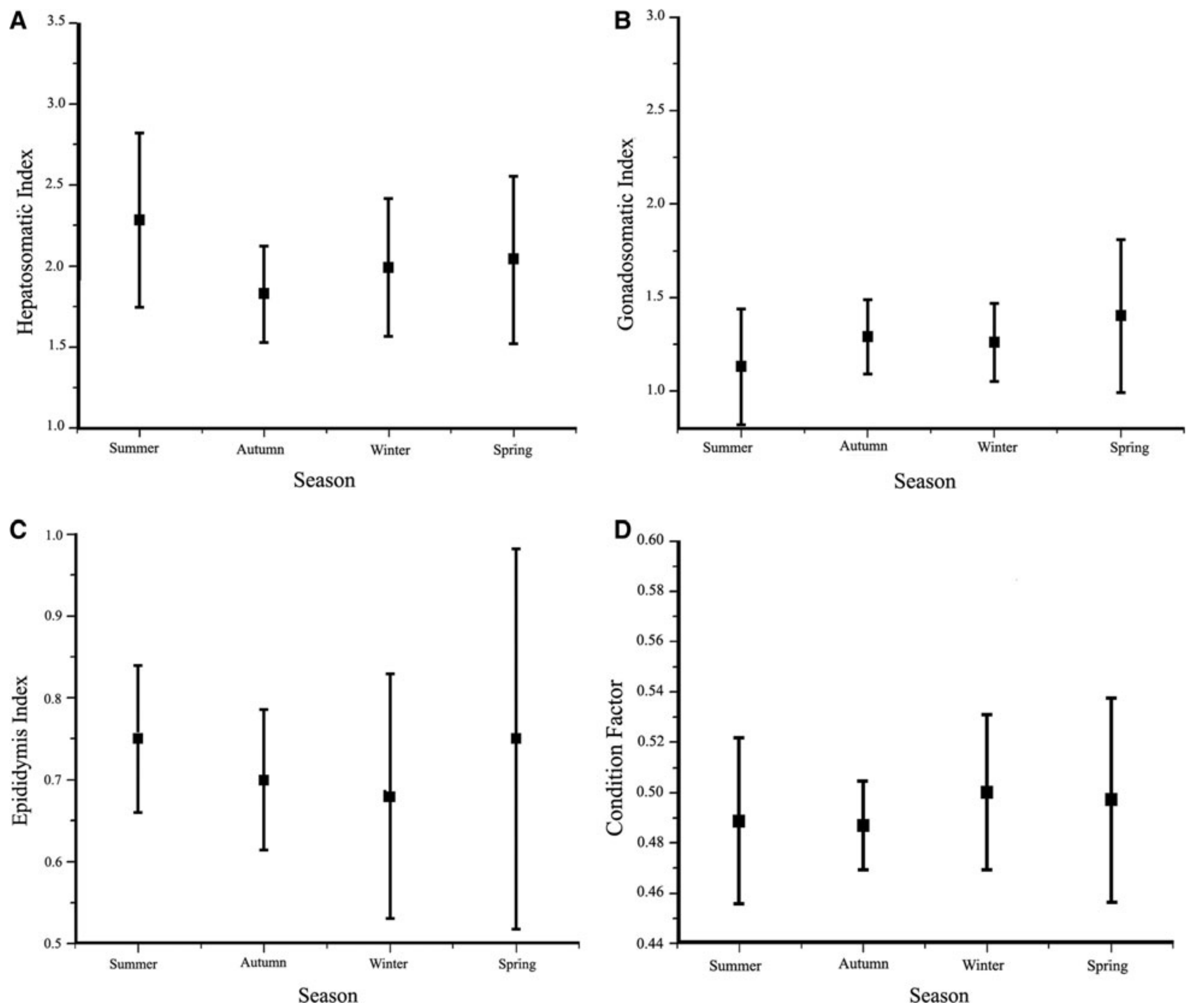

Fig. 11. Seasonal variation of mature male reproductive indices of *Psammobatis lentiginosa*. (A) Hepatosomatic index; (B) gonadosomatic index; (C) epididymis index; (D) condition factor. Black squares represent mean values and bars ±1 standard deviation.

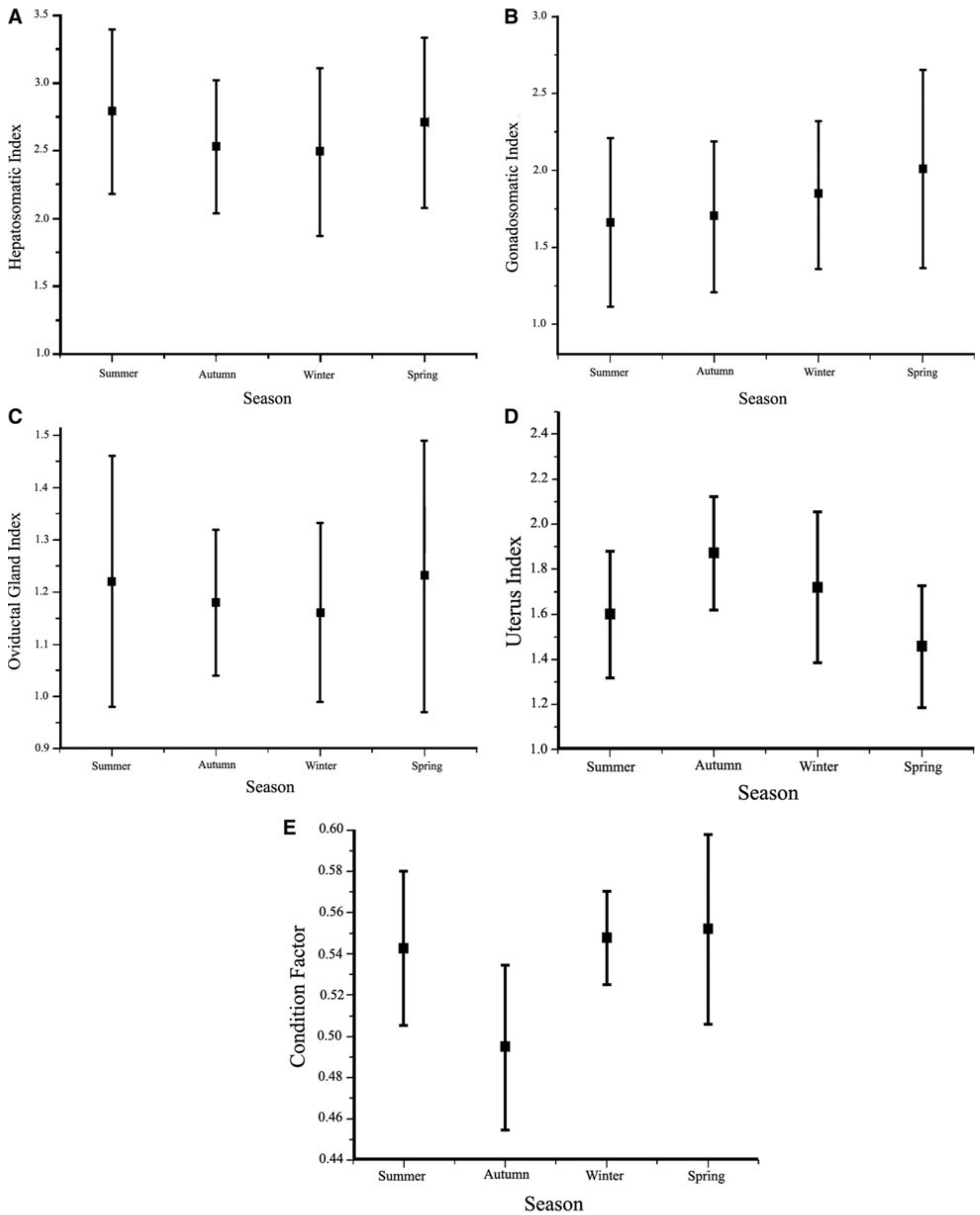

Fig. 12. Seasonal variation of mature female reproductive indices of *Psammobatis lentiginosa*. (A) Hepatosomatic index; (B) gonadosomatic index; (C) oviducal gland index; (D) uterus index; (E) condition factor. Black squares represent mean values and bars ±1 standard deviation.

DISCUSSION

The present study reports for the first time basic information on the reproductive cycle of the skate *Psammobatis lentiginosa*, endemic to the south-western Atlantic, and on the reproductive aggregation of this species in San Matías Gulf. Individuals reproductively active—female with egg case in formation—were reported for the north of the Argentinean continental shelf by Mabragaña (2007).

Sexual size dimorphism favouring larger females is common in chondrichthyans (Mellinger, 1989). In *P. lentiginosa*, females are heavier than males of the same size. The

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relationship between total length and total mass was allometric for both sexes. This feature has been reported for almost all species of the genus *Psammobatis* studied so far except for *P. rudis* (Mabragaña & Couuseau, 2004). Many species of Arhynchobatidae show allometry (*P. extenta*, Braccini & Chiaramonte, 2002a; *P. normani*, Mabragaña & Cousseau, 2004; genus *Atlantoraja*, Odone & Amorin, 2007).

In the studied *P. lentiginosa* population, overall sex-ratio was 1:1, similarly to that observed for *P. rudis* (Mabragaña & Cousseau, 2004; Mabragaña, 2007), and seasonal sexual segregation was detected, in concordance with *P. bergi*, *P. normani* and *P. extenta* (Bracini & Chiaramonte, 2002b; Mabragaña & Cousseau, 2004; San Martín *et al.*, 2007).

In comparison with the reproductive and morphometric patterns of other species of *Psammobatis* from the south-western Atlantic, *P. lentiginosa* attains sexual maturity at a value of TL50% lower than the maximum one reported in literature. This feature suggests that *P. lentiginosa* is the least vulnerable species of the genus because more than 60% of the size–length distribution was adults.

Some species of Rajiformes, *P. lentiginosa* included, show significant differences in the hepatic weight between sexes (Mabragaña *et al.*, 2002; Odone & Vooren, 2004), while others do not (Braccini & Chiaramonte, 2002b; Ruocco *et al.*, 2006). The analysis of the hepatic weight–total length relationship of *P. lentiginosa* during its ontogeny shows a variation in the interval of body length corresponding approximately to the stage of sexual maturity, possibly related to changes in morphology and physiology. This may also explain the large dispersion of hepatic weight values in individuals of the studied species at the onset of sexual maturity. This result has also been observed for *A. cyclophora*.

Storage of lipids in the liver and their mobilization during vitellogenesis have been described in chondrichthyans by Rossouw (1987) and mentioned in some rajiform species by Odone & Velasco (2006). In *P. lentiginosa*, the maximum hepatic index values were obtained in summer. This result is possibly explained by the fact that the maximum egg case production is found in the following season (autumn), when lipid storage is expected to be the highest.

The variation of the condition factor may help to elucidate the mobilization of energetic reserves (Nikolsky, 1963) and in Rajidae, this index has been used as a complementary indicator of energy status (Du Buit, 1975). In *P. lentiginosa*, the lowest CF of females was obtained in autumn, when, as mentioned above, there is a peak in egg case production. This activity would be achieved at the expense of increased energetic cost, which may ultimately result in a decline in the general condition.

The existence of functional symmetry of the female reproductive system is a common feature among species of Rajiformes (Braccini & Chiaramonte, 2002b; Mabragaña & Cousseau, 2004; Martins *et al.*, 2005; San Martín *et al.*, 2005; Odone & Vooren, 2005; Ruocco *et al.*, 2006). In *P. lentiginosa* both the right and left ovaries showed to be functional and no significant differences in the number of oocytes were found between them. Likewise, no functional asymmetry was detected between the two uteri of females carrying eggs (one egg capsule per uterus). The maximum diameter of the mature oocyte in the ovary was 24 mm. The lack of data on this subject in other species of the genus prevents any further comparison.

The suitability of the indices of reproductive activity for defining reproductive cycles or to distinguish immature from mature individuals has been confirmed for several fish species (Wilk *et al.*, 1990; Di Giacomo & Perier, 1994; Perier & Di Giacomo, 2002; Sulikowski *et al.*, 2005). In the present study, they proved to be useful tools to investigate temporal variations in the reproductive pattern of *P. lentiginosa*.

The following two reproductive cycles have been identified in species of Rajiformes: an annual reproductive cycle with one or two seasonal peaks in *Atlantoraja cyclophora* (Oddone & Vooren, 2005), *Psammobatis bergi* (San Martín *et al.*, 2005), *Raja clavata* (Holden, 1975) and an annual reproductive cycle with no marked seasonality in *P. extenta* (Martins *et al.*, 2005) and *Bathyraja albomaculata* (Ruocco *et al.*, 2006). Taking into account the percentage of females with egg cases in development or ready to be laid, *P. lentiginosa* has an annual reproductive cycle with a peak in autumn and a decline in winter.

The peak of egg capsule production was synchronous with the maximum development of the glandular caudal portion of the uterus, as indicated by the highest value of UI obtained at that time. Seasonal variations in UI values may reflect an active role of the caudal portion during the formation, storage and release of the egg capsules, although in Rajiformes, it is not known if this uterine glandular portion secretes substances for capsule production (Hamlett & Koob, 1999).

In the uterus of *P. lentiginosa*, a fecundated ovule was found in egg capsules over 50% of development, in agreement with that found in many oviparous fish species, particularly Rajiformes and holocephalans (Di Giacomo & Perier, 1994; Hamlett *et al.*, 2005). In Rajiformes, spermatophores have been detected in the cephalic portion of the nidamental gland (Holden, 1975; Hamlett & Koob, 1999), but their presence could not be confirmed in *P. lentiginosa* because of the impossibility of performing serial histological sections of the reproductive system.

Another particularity in the reproductive cycle is related to the mating period. Our results suggest that although mating showed a seasonal pattern for most of the population, it may take place throughout the year in some individuals. On the other hand, the highest percentage of mature males and females in summer is related to an intense mating period previous to the maximum production of eggs in autumn. This observation is supported by the highest values of IE and IH shown by males in summer, before the peak in the number of egg capsules appearing in females in the next season. A similar pattern has been observed for *Raja clavata* by Holden (1975). In addition, the high variability of the indirect indicators of reproductive activity in each length-class suggests the coexistence of individuals at different maturity stages, with some females producing capsules and others undergoing mating.

The frequency of mating could not be established for *P. lentiginosa* due to the lack of data on the physiological duration of spermatophores in the reproductive system of female skates after mating. In the different Rajiformes, the egg-laying areas vary according to the bathymetric distribution of each species. For example, egg capsules of the species *Bathyraja albomaculata*, which is distributed up to slope waters, have been found in deep waters simultaneously with females carrying developing or fully developed egg-cases (Ruocco *et al.*, 2006), while species of genera *Atlantoraja* and *Raja* lay their egg capsules in coastal areas (Holden, 1975; Mabragaña *et al.*, 2002; Odonne *et al.*, 2007). No egg capsules of *P. lentiginosa* were

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found in the present work, probably because the sampling area did not overlap the oviposition area of the species (between 50 and 171 m), or because the fishing gear used to catch skates (trawl nets) was not appropriate to collect egg capsules from the bottom.

These constraints in sampling egg capsules have been pointed out by Odone & Vooren (2004), who also mentioned that egg capsules could be severely damaged or buried in the sediment while the nets are being dragged. The permanent presence of the species and the reproductive aggregation revealed by the seasonal samplings, together with the almost complete absence of the species on the continental shelf—only is reported in the north of San Jorge Gulf, 54°S and in the fishing area common to Argentina and Uruguay (McEacrhan, 1983; Cousseau *et al.*, 2007; Mabragaña, 2007)—indicate that San Matías Gulf is the main distribution area of *P. lentiginosa* in the south-western Atlantic.

The negative impact of fishing over the exploitation of Rajiformes species has been documented by Holden (1973, 1974), Brander (1981) and Dulvy *et al.* (2000). *Psammobatis lentiginosa* is not targeted by the fishery in San Matías Gulf and all catch of this species is discarded. The lack of capture records makes it difficult to estimate fishing mortality of the population, and although experiments have been made to ascertain the likely survival rate of another species of skates discarded during commercial fishing (Chiaramonte, 2006), information on *P. lentiginosa* is needed for the appropriate management of the local fishery.

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