



The reproductive ecology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic

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Logistical ogives gave an estimated L_{T50} value (i.e. the total length at which 50% individuals are sexually mature) of 635 mm for female and 650 mm for male *Sympterygia bonapartii*. Mature individuals of both sexes had significantly larger livers than immature ones and females had a significantly heavier liver than males. Clasper elongation was the first step in male maturation, followed by clasper calcification and the development of alar thorns. In mature females, the right ovary was larger than the left, which was apparently due to differences in stroma tissue. Gonadosomatic index and diameter of ovarian follicles of mature females peaked in late spring and was at a minimum from late summer and through the winter. Juvenile *S. bonapartii* were more abundant near estuarine areas during winter, and adults appeared in estuaries by late spring and summer. Females carrying egg-cases were found near the shore in late spring and egg-cases were found in benthic samples only in shallow waters suggesting that *S. bonapartii* deposits egg-cases in shallow waters during late spring-summer and that nursery areas are in outer estuarine zones. In the southern part (38°–42° S) of the study area *S. bonapartii* showed a strong movement to shallow waters in late spring and summer, spreading over the entire coastal area in winter. These movements are discussed in relation to water temperature and trophic interactions.

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INTRODUCTION

Skates are ubiquitous and often common components of temperate demersal ecosystems worldwide (McEachran & Miyake, 1990; Last, 1997). Skates are oviparous and studies on their reproductive biology have focused mainly on physiology and egg-case formation, with the reproductive ecology of many skate species unknown (Walmsley-Hart *et al.*, 1999). As a result, important life history information such as size and age at maturity, nursery and egg-laying grounds, fecundity, and development rates are lacking for most skate species. Skates are usually said to have a prolonged period of egg-case deposition (Hamlett & Koob, 1999). They inhabit waters from the coastline to 3000 m deep (McEachran & Miyake, 1990), however, which suggests that their reproductive ecology may be very different among species dwelling in such different habitats. While deep-water skates may deposit egg-cases all year-round, shallow-water species may have seasonal reproductive cycles (Hamlett & Koob, 1999).

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The coastal skate fauna of the subtropical and temperate south-west Atlantic is composed of the genera *Atlantoraja* (three species), *Rioraja* (one species), *Psammobatis* (three species) and *Sympterygia* (two species) (Vooren, 1997; Menni & Stehmann, 2000). The genus *Sympterygia* comprises four species of skates endemic to the temperate waters of South America (McEachran, 1982). The smallnose fanskate *Sympterygia bonapartii* Müller & Henle is one of the commonest elasmobranchs from coastal and shelf waters (from the shoreline down to 100 m depth) from southern Brazil to northern Argentina (Menni & Stehmann, 2000). Most studies on *Sympterygia* have focused on taxonomy (Menni, 1972; McEachran, 1982; Cousseau *et al.*, 2000), and the ecology of the entire genus is very poorly known. Some aspects of the trophic ecology of *S. bonapartii* are the only ecological information on the genus (Barrera Oro & Maranta, 1996; Paesch, 2000).

Skates are becoming increasingly important in south-west Atlantic fisheries (Agnew *et al.*, 1998; Paesch & Meneses, 1999). Most fishing effort off northern Argentina and Uruguay is in coastal and continental shelf waters, which results in a high fishing pressure on *S. bonapartii* (A. M. Massa, unpubl. data). Biological data (especially on reproduction) of skates are needed for the proper management of their fisheries.

In this study the reproductive ecology (size at maturity, sexual dimorphisms, egg-case laying areas and seasons) and abundance (seasonal variability and concentration areas) of *S. bonapartii* from Uruguayan and north Argentinean waters were investigated.

MATERIALS AND METHODS

Data were collected from research cruises conducted in Uruguay and north Argentina coastal waters (34°–42° S), from the shoreline down to 50 m depth. This area contains two large estuarine regions, the La Plata River estuary and the El Rincón salt marsh area, separated by marine waters (Fig. 1; Esteves *et al.*, 2000). Additional specimens were also collected during a research cruise carried out in inner-shelf waters (39°–40° S) at 45–67 m depth. All specimens were caught with a bottom trawl (200 mm mesh in the wings and 120 mm at the cod end; vertical opening 4 m, horizontal aperture 15 m). The net was trawled at 4 knots for 15–30 min.

REPRODUCTIVE CONDITION AND MATURITY

Data on reproduction of *S. bonapartii* were obtained from seven research cruises in all seasons, six from coastal waters and one from shelf waters. One research cruise surveyed the entire coastal study area (34°–42° S) in late spring (November–December 1999). Three cruises covered only the northern area (34°–38° S; late summer, March 2000; late autumn, June 2000; winter, July 2000). Two cruises sampled only the southern part of the study area (38°–41°30'S) in spring (November 2000) and late spring (December 2000). One research cruise was carried out on the inner shelf area in spring (October 2000).

Once caught, all specimens were frozen and subsequently thawed and analysed in the laboratory. Total length (L_T) and disc width (D) to the nearest mm were recorded for every specimen. The relationship between D and L_T , with L_T as the dependent variable, was estimated separately for each sex in order to estimate L_T for some *S. bonapartii* with damaged tails.

Uteri and oviducal gland width, number and diameter (to the nearest 0.5 mm) of ovarian follicles, were recorded. Females were categorized as immature when they had undeveloped thread-like uteri, ovaries containing only non-vitellogenic ovarian follicles <10 mm in diameter, and undeveloped oviducal glands. Mature females had wide uteri,

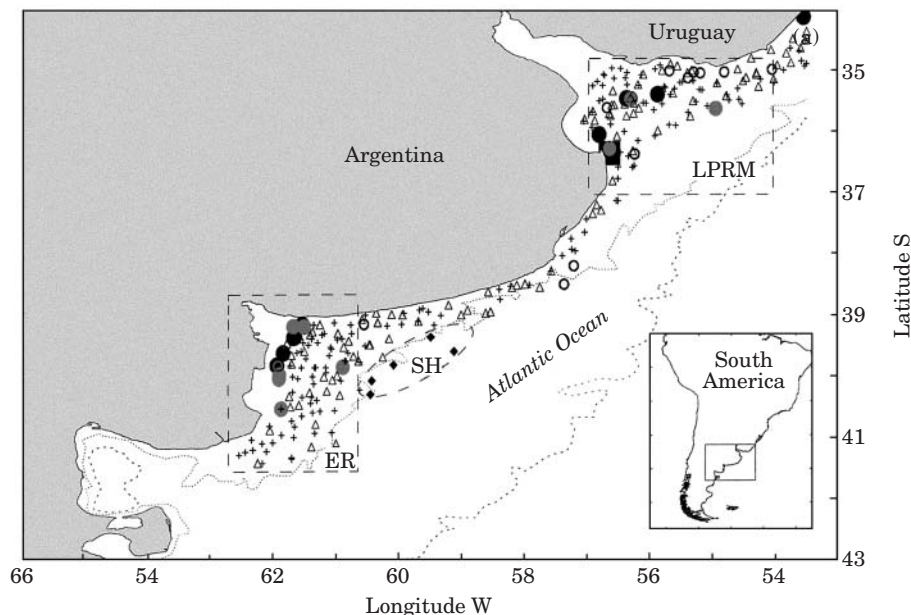


Fig. 1. Map of the study area showing estimated densities +, 0.00-0.00; Δ , 0.00-0.25; \circ , 0.25-0.50; \odot , 0.50-1.00; \bullet , 1.00-2.00; \blacksquare , 2.00-3.00 t km⁻² of *Sympterygia bonapartii*. , 50 m isobath; ----, 200 m isobaths. Enclosed zones are El Rincón area (ER), the inner shelf area (SH) and La Plata River mouth (LPRM). Sampling stations from SH (\blacklozenge) do not represent densities.

and widened oviducal glands. Also, they usually had vitellogenic ovarian follicles >10 mm in their ovaries. The masses of the right and left ovaries were recorded separately in mature females.

The degree of calcification of claspers was recorded as non-calcified (soft highly flexible claspers), calcifying (flexible claspers that could be bent) or calcified (hard, rigid claspers that could not be bent). Claspers were measured from the tip of the pelvic fins to the tip of the claspers. Thus, individuals with claspers shorter than pelvic fins had negative values of clasper length, and individuals with claspers longer than pelvic fins had positive clasper length values. The number of rows in the alar thorn patch was recorded. Males were divided into three categories: immature (short non-calcified claspers, non-developed alar thorn patch, straight efferent ducts), maturing (long calcifying claspers, developing alar thorn patch, efferent ducts beginning to coil) and mature (long fully-calcified claspers, fully grown alar thorn patch, highly coiled efferent ducts).

Male maturity was estimated from the pattern of growth of claspers relative to L_T . Female maturity was estimated from the relationship between oviducal gland and uteri widths with L_T . For both sexes, the proportion of mature individuals in 10 mm L_T intervals was calculated. A logistical ogive was fitted to the data using a maximum-likelihood approach in order to estimate the size at which 50% of individuals (L_{T50}) were sexually mature (Roa *et al.*, 1999).

Total mass (M_T), liver mass (M_L) and gonad mass (M_G) were recorded to the nearest 0.1 g for each specimen. Length and mass relationships were calculated separately for each sex; these regressions were ln-transformed and the null hypothesis of no difference between slopes was tested with the *t*-test (Zar, 1984). The hepatosomatic index (I_H) was calculated as: $I_H = 100M_L M_T^{-1}$.

In females, the null hypothesis of no difference in mean I_H between immature and mature individuals was tested with the Mann-Whitney *U* test (Zar, 1984). In males, the null hypothesis of no difference in mean I_H between immature, maturing and mature individuals was assessed with one-way ANOVA (Zar, 1984). Sexual dimorphism in M_L

was assessed by testing (*t*-test) the null hypothesis of no difference between the slopes of linear regressions between L_T and M_L estimated from ln-transformed data.

The null hypothesis of no difference between mean masses of right and left ovaries in mature females was tested with the paired-sample *t*-test (Zar, 1984). This statistical procedure was also employed for testing differences in diameter and number of ovarian follicles between right and left ovaries of mature females. The gonadosomatic index (I_G) was calculated as: $I_G = 100M_G M_T^{-1}$. The I_G of mature females was calculated separately for each season of the year.

The null hypothesis of no seasonal differences in mean I_G and mean maximum diameter of ovarian follicles was tested with one-way ANOVA. The Tukey test (Zar, 1984) was used for subsequent *post hoc* comparisons. This analysis was carried out only for the northern coastal part of the study area because it was the only area with data from all four seasons of the year.

EGG-CASE LAYING ZONES

Sympterygia bonapartii egg-cases were sampled during six research cruises between December 1998 and July 1999, designed for assessing Patagonian scallop *Zygochlamys patagonica* (King & Broderip) and mussel *Mytilus edulis platensis* d'Orbigny benthic communities. These cruises were appropriate for egg-case sampling because fishing operations were carried out with a dredge, which is a better gear than a net for obtaining representative benthic samples. Sampling positions comprised a wide depth range (i.e. 35–120 m) on part of the northern Argentinean continental shelf (38°11' to 43°19' S and 55°44' to 59°50' W), in order to cover the entire depth range of *S. bonapartii* in the area.

TEMPORAL AND SPATIAL SIZE-DISTRIBUTION

Size distributions of *S. bonapartii* were obtained from nine research cruises, eight from the coastal area and one from shelf waters. Size distributions were estimated separately for three areas: La Plata River mouth (LPRM, 34°–38° S, down to 50 m depth), El Rincón area (ER, 38°–42° S, down to 50 m depth), and inner shelf (SH, 39°–40° S, 45–67 m depth). Seasonal variations in size distributions were investigated for the LPRM area. This area was sampled twice in spring (November–December 1998, and November 1999), twice in late summer (March 1999 and 2000) and twice in winter (June–July 1998 and July 1999). Size distributions from the ER and SH areas were obtained only for late (December 1998, 1999 and 2000) and early spring (October 2000), respectively.

ABUNDANCE

Data from two research cruises were employed to estimate densities of *S. bonapartii* along the entire Uruguayan and north Argentinean coast. These research cruises were conducted during November–December 1994 ($n=178$ hauls) and 1999 ($n=106$ hauls) with the same vessel and fishing gear, and were chosen because they covered the whole study area. Densities were expressed as metric tons per km² ($t\ km^{-2}$). For each estimation of density, area was calculated as $s \times t \times ha$, where s is trawling speed (corrected for water-current speed), t is duration of trawling, and ha is horizontal aperture of the net (measured with a Doppler sensor).

Seasonal variations in densities were investigated for ER. Data from a research cruise conducted in July 1993 (winter; $n=77$ hauls) and another conducted in November–December 1998 (late spring, $n=54$ hauls) were used for this purpose. Densities of elasmobranchs may have changed in the study area in the last 4 years (A. M. Massa, unpubl. data). Therefore, densities were expressed as per cent of the maximum density observed in each research cruise to avoid a possible bias in using absolute values of densities, because of the long time (nearly 5 years) between both research cruises. Seasonal variability in the northern region could not be investigated because abundance data were not obtained in a consistent manner for different seasons and years.

RESULTS

REPRODUCTIVE CONDITION AND MATURITY

A total of 527 (245 females and 282 males) specimens were analysed. Females ranged from 227 to 808 mm L_T . The relationship between D and L_T in females was linear ($r^2=0.96$) with a slope of 1.447 and an intercept of 7.542. The smallest mature female was 415 mm L_T and the largest immature one was 675 mm L_T . Most mature females, however were >524 mm L_T and most immature specimens were <650 mm L_T [Fig. 2(a)]. The estimate of female L_{T50} from the logistical curve was 636 mm [Fig. 2(b)].

The size range of examined males was between 200 and 746 mm L_T . The D and L_T relationship for males was linear ($r^2=0.93$) with slope 1.490 and intercept 0.790. The smallest mature male was 470 mm L_T , and the largest immature male was 692 mm L_T . Most mature individuals were between 525 and 660 mm L_T , but maturing males ranging from 516 to 717 mm L_T were observed [Fig. 3(a)]. The logistical curve fitted produced an estimated L_{T50} of 651 mm [Fig. 3(b)]. The number of rows in the alar thorn patch varied from 0 to 6. Immature males had 0 to 1, maturing males had 1 to 3 and mature males had 1–6 rows of alar thorns (Fig. 4).

Some aspects of the male maturation process can be obtained from the analysis of alar thorns and clasper growth. Five immature individuals with uncalcified claspers had long claspers (70–92 mm) well in the range of mature males (48–93 mm) with calcified claspers [Fig. 3(a)]. In spite of being large and having long (though uncalcified) claspers, however, these immature males had 0–1 rows of alar thorns. Furthermore, all maturing males with calcifying claspers also had clasper lengths (70.5–85 mm) in the range of mature males, but their counts of alar thorn rows were intermediate (1–3) between immature and mature males.

Length and mass relationships (females: $M_T=2E-6 \cdot L_T^{3.24}$; males: $M_T=5E-6 \cdot L_T^{3.03}$; Fig. 5) were significantly different between sexes, with adult females heavier at a given length than males ($t=3.698$; d.f.=488; $P=2.41 \times 10^{-4}$).

Liver size varied significantly through ontogeny in both sexes. Mature females had significantly higher mean I_H than immature females (mean \pm s.d. mature $I_H=4.75 \pm 1.26$; immature $I_H=2.82 \pm 0.98$; $U=777$; n immature=178; n mature=50; $P<0.000001$). Significant differences in mean I_H among immature ($I_H=2.48 \pm 0.91$; $n=207$), maturing ($I_H=2.34 \pm 0.90$; $n=14$) and mature males ($I_H=3.30 \pm 1.75$; $n=32$) were also found ($F_{2,250}=8.948$; $P=1.76 \times 10^{-4}$), with mature males having heavier livers than each of the other groups (Tukey test corrected for unequal sample size; immature v. mature: $P=0.0047$; maturing v. mature: $P=0.041$). Liver size was sexually dimorphic as indicated by significant differences found in the L_T and M_L relationships (females: $M_L=3E-10 \cdot L_T^{4.03}$; males: $M_L=1E-8 \cdot L_T^{3.41}$; $t=5.75$; d.f.=483; $P=1.59 \times 10^{-8}$).

Mature females had slightly asymmetric gonads as shown by significant differences in mass between right (mean \pm s.d. 45.07 \pm 31.61 g) and left (38.03 \pm 23.88 g) ovaries ($t=2.237$; $n=35$; $P=0.032$). There were no significant differences, however, between right and left ovarian follicle number (mean right and left: 10.42 and 10.22, respectively; $t=0.487$; d.f.=31; $P=0.629$) and diameter

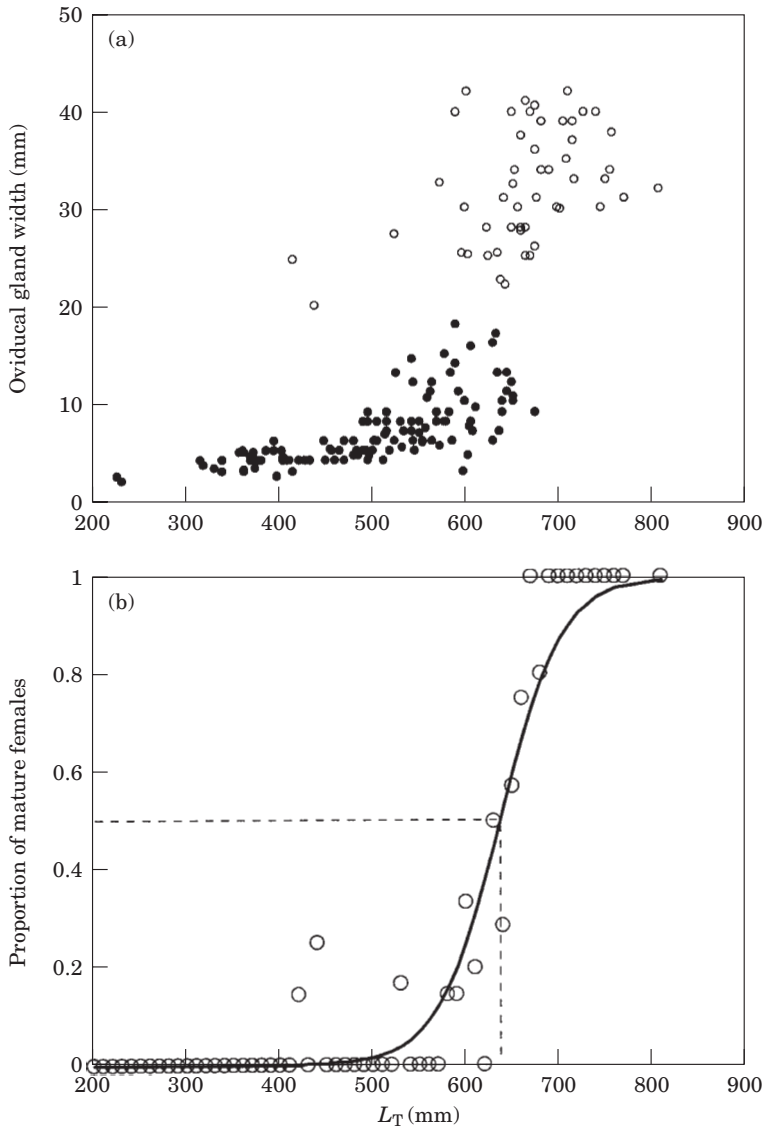


FIG. 2. (a) Relationship between oviducal gland width and total length in *Sympterygia bonapartii*. ●, Immature females; ○, mature females. (b) Proportion of mature females per size class. ○, Observed values. The line is a logistical ogive fitted by maximum-likelihood techniques. ---, Size at 50% maturity (636 mm L_T).

(mean right and left: 23.54 and 23.29 mm, respectively; $t=0.382$; d.f.=35; $P=0.705$).

The I_G of mature females showed significant seasonal changes ($F_{2,14}=7.65$; $P=0.0057$), and peaked during late spring, with a minimum in late summer to winter [Fig. 6(a)]; late spring v. late summer $P=0.0096$; late spring v. winter $P=0.016$; late summer v. winter $P=0.910$). The maximum diameter of ovarian follicles also showed seasonal changes paralleling those of I_G [Fig. 6(b)] ($F_{3,37}=19.63$; $P<0.000001$; late summer v. late autumn $P=0.911$; late summer v.

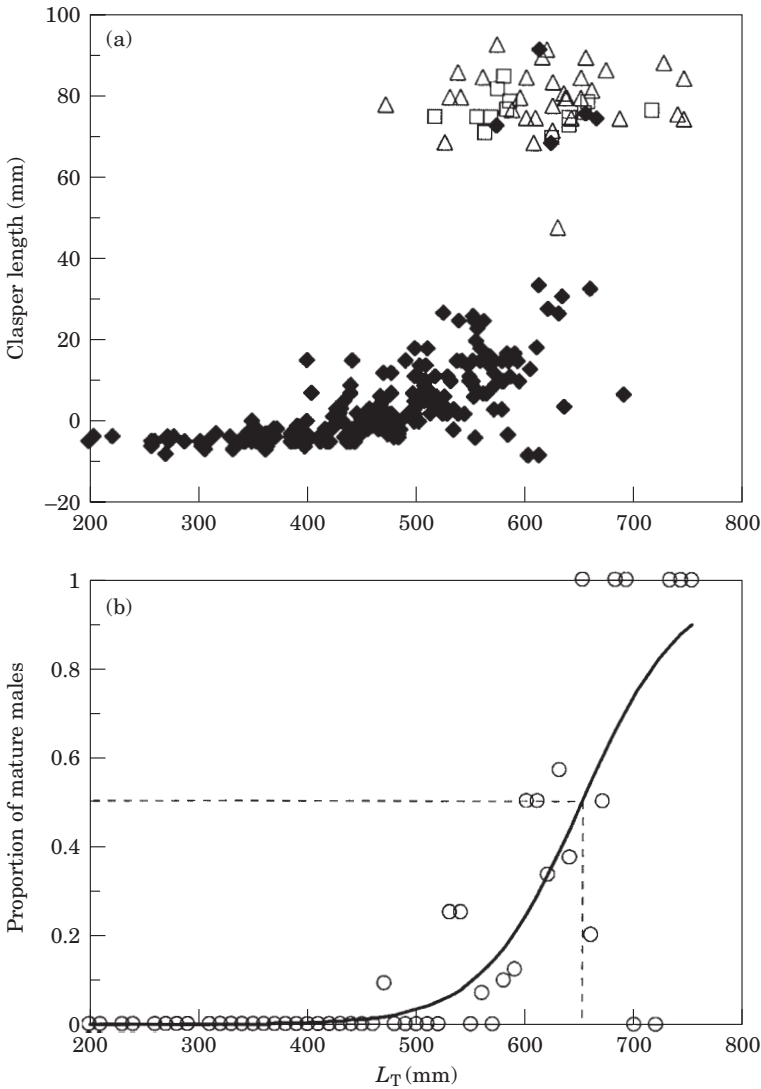


FIG. 3. (a) Relationship between clasper length and total length in *Sympterygia bonapartii*. ◆, Immature males with uncalcified claspers; □, maturing males with semicalcified claspers; △, mature males with fully calcified claspers. (b) Proportion of mature males per size class. ○, Observed values. The line is a logistical ogive fitted by maximum-likelihood techniques. ---, Size at 50% maturity (651 mm L_T).

winter $P=0.0551$; late summer *v.* late spring $P=0.001$; late autumn *v.* winter $P=0.088$; late autumn *v.* late spring $P=0.001$; winter *v.* late spring $P=0.0002$).

EGG-CASE LAYING AREAS

Five females containing egg-cases were found. Four were obtained during late spring off LPRM and the other caught in spring off ER. All these females were caught in waters <50 m depth. Egg-cases were barrel-shaped with the anterior part (that part adjacent to the oviducal gland) wider than the posterior part (that part towards the cloaca) [Fig. 7(a)]. The egg-cases were smooth and amber in

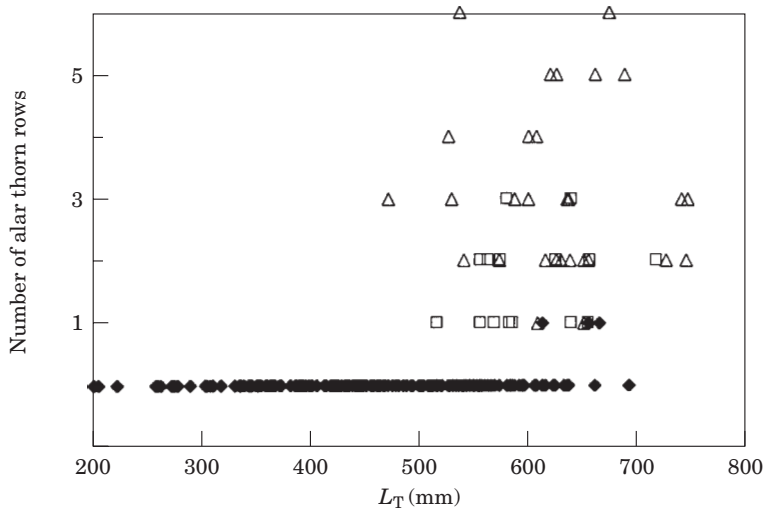


FIG. 4. Relationship between number of thorn rows in the alar thorn patch and total length in male *Sympterygia bonapartii*. \blacklozenge , Immature males; \square , maturing males; \triangle , mature males.

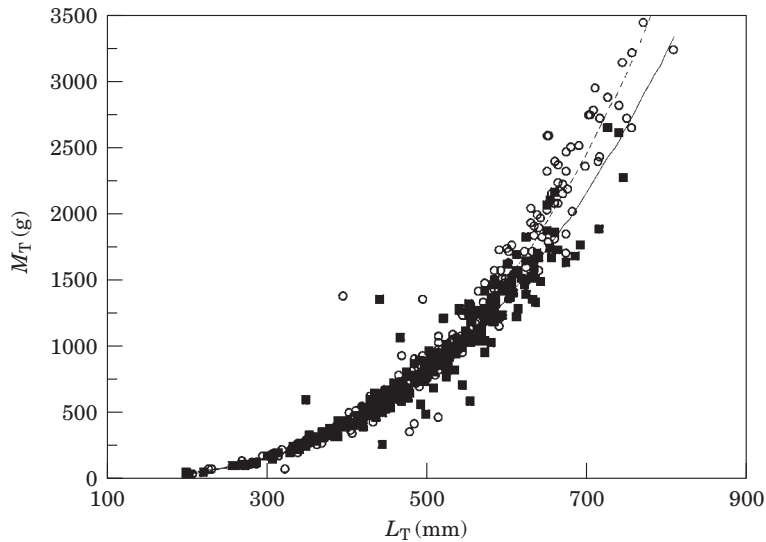


FIG. 5. Total length and total mass relationship in *Sympterygia bonapartii*. \circ , Females; \blacksquare , males; differences between sexes are statistically significant.

colour when recently laid, becoming darker during development. The anterior and posterior margins were flattened, with the anterior margin concave and the posterior margin relatively straight. The posterior horns were longer than the anterior ones. Lateral edges truncated forming a vertical plane [Fig. 7(b)]. Mean (\pm s.d.) egg-case length (without horns) was 76.75 ± 3.92 mm, and mean width was 48.37 ± 0.74 mm ($n=8$).

Egg-cases which could be positively assigned to *S. bonapartii* were found only in the shallower benthic samples (32–44 m depth; $n=2$), but were absent from all

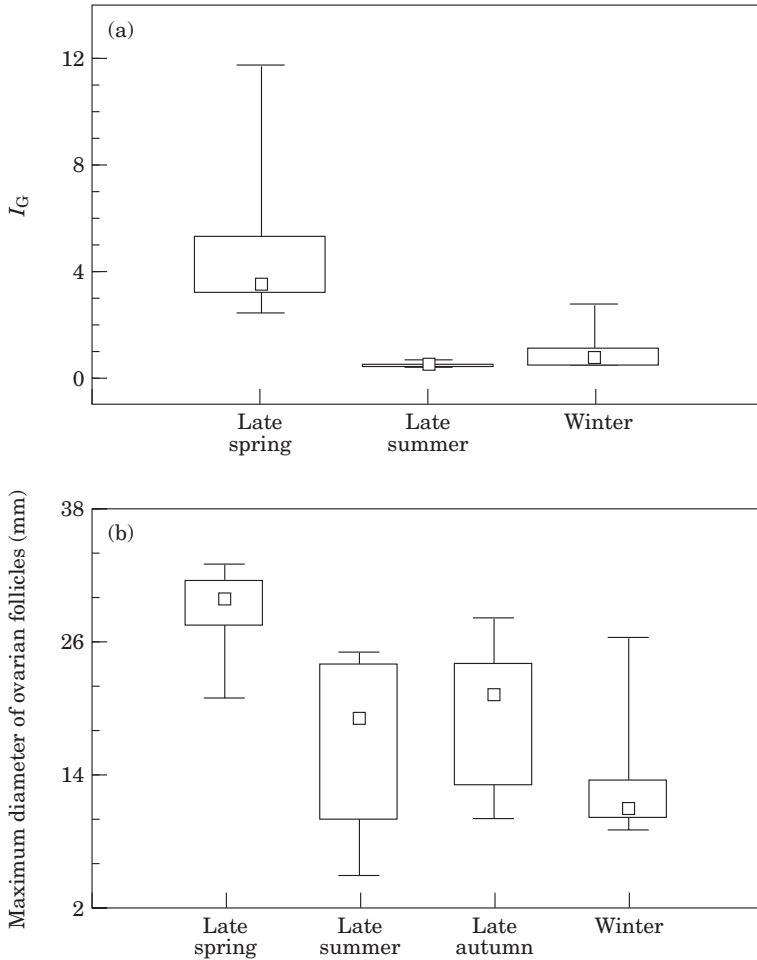


FIG. 6. Seasonal distributions of gonadosomatic index (a) and maximum diameter of ovarian follicles (b) in mature female *Sympterygia bonapartii*. Squares are median values, box enclose values between the 25 and 75 percentiles and whiskers are minimum and maximum values. In both cases late spring distributions are significantly different to the other seasons.

other samples, which ranged in depth from 85 to 120 m ($n=62$). It is noteworthy that egg-cases of *S. bonapartii* were absent from deep samples despite the high sampling effort in that area.

TEMPORAL AND SPATIAL SIZE-DISTRIBUTION

Most smallnose fanskates present in the LPRM in winter were juveniles <490 mm L_T ($n=190$ males and 278 females) [Fig. 8(a)]. This situation was different to that occurring in spring ($n=63$ males and 67 females) [Fig. 8(b)] and summer ($n=183$ males and 197 females) [Fig. 8(c)] when adults >600 mm L_T of both sexes appeared in the area. Juveniles <590 mm L_T dominated spring size distribution in the ER area ($n=134$ males and 147 females) [Fig. 9(a)] while individuals >500 mm L_T (mostly adults) predominated in the SH area ($n=25$ males and 33 females) in early spring [Fig. 9(b)].

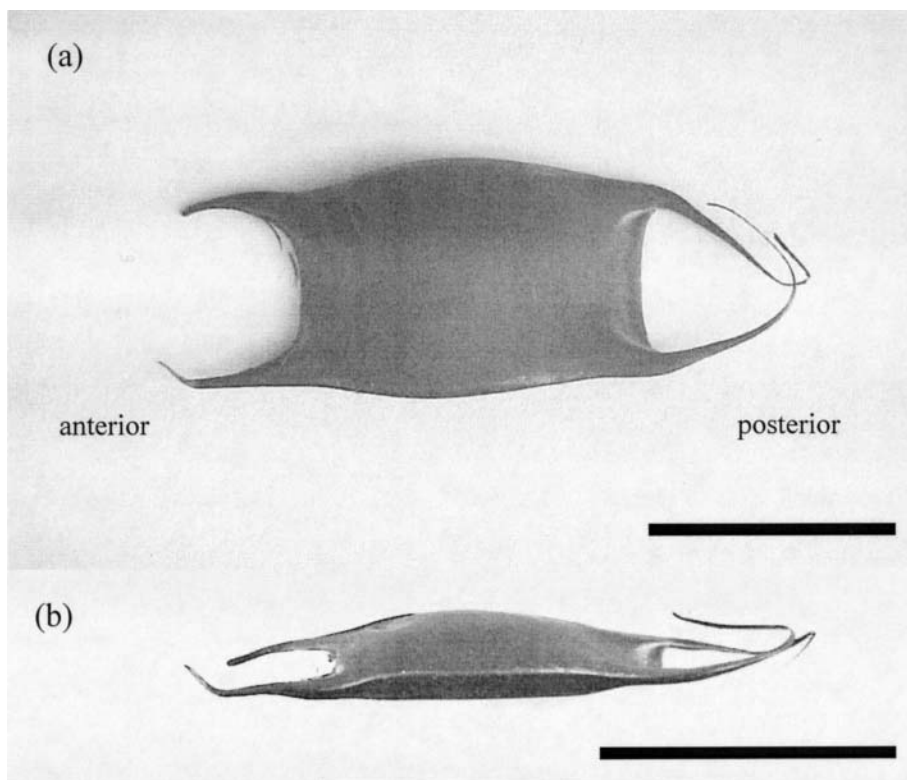


FIG. 7. Egg-case of *Sympterygia bonapartii*, scale bars: 5 cm. (a) Dorsal and (b) lateral view, the latter showing the truncated lateral edges forming a vertical plane.

ABUNDANCE

Two major areas of abundance of *S. bonapartii* were found (Fig. 1), both clearly associated with estuarine zones. One area was located in the LPRM with densities of up to 2.80 t km^{-2} , and the other was in the southern part of the study area in front of Blanca and Anegada Bays (El Rincón area, densities up to 1.92 t km^{-2}). A possible third area of high abundance of *S. bonapartii* was located in the northern extreme of the study area (i.e. 34° S ; the Brazilian-Uruguayan border), also near the mouth of a large estuarine system, Patos Lagoon, where maximum density was 1.40 t km^{-2} (Fig. 1).

The distribution of per cent densities of *S. bonapartii* in the southern part of the study area was different in winter and in late spring-early summer. In winter, smallnose fanskates were almost evenly distributed over the coastal area with a maximum per cent density of 4.70 [Fig. 10(a)]. In late spring-early summer they were concentrated in the shallower parts of the coastal area off Blanca Bay and maximum per cent density was 8.32 [Fig. 10(b)].

DISCUSSION

The L_{T50} values for both female and male *S. bonapartii* (636 and 650 mm, respectively) are the largest for any species of *Sympterygia* for which data are

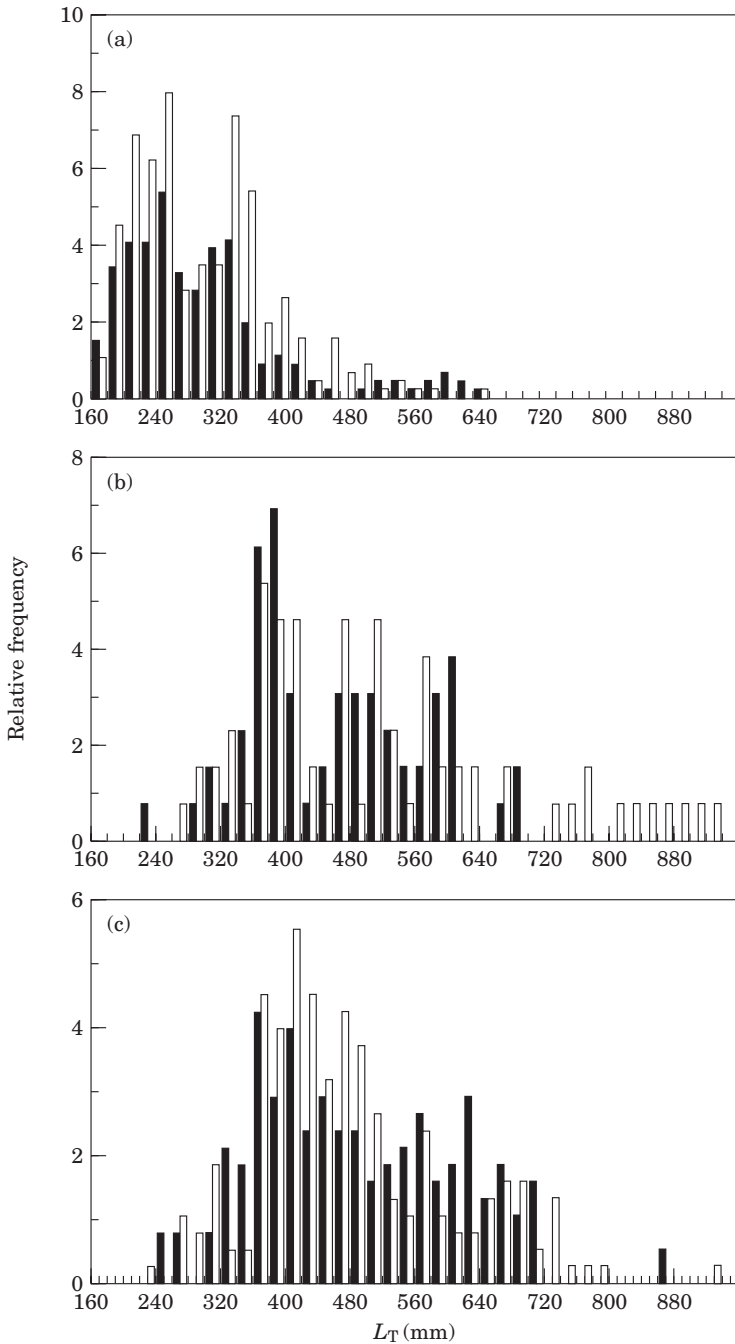


FIG. 8. Size-frequency distributions of *Sympterygia bonapartii* off La Plata River mouth. □, Females; ■, males. (a) Winter, (b) late spring and (c) summer.

available. The bignose fanskate *Sympterygia acuta* Garman, is a much smaller species with a maximum L_T of *c.* 470 and 500 mm for males and females respectively (Cousseau *et al.*, 2000). Photographs of fully mature male shorttail

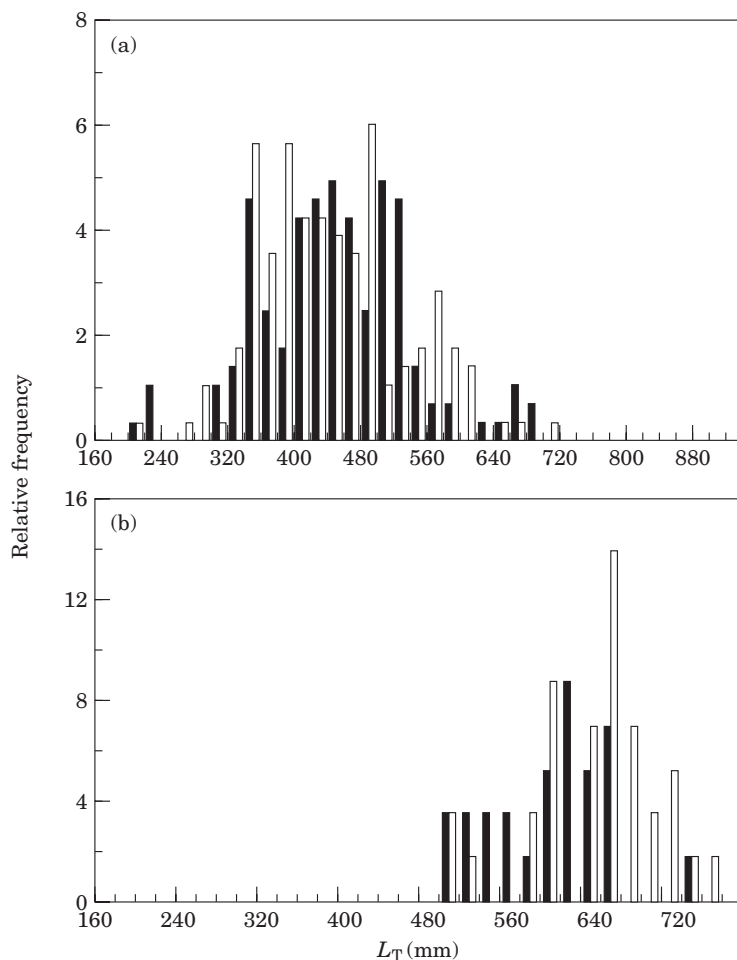


FIG. 9. Size-frequency distributions of *Sympterygia bonapartii* in the El Rincón area, Argentina. □, Females; ■, males. (a) Coast, late spring and (b) inner shelf, spring.

fanskates *Sympterygia brevicaudata* (Cope) published by McEachran (1982) show that they are sexually mature at 353 mm L_T .

Both sexes of *S. bonapartii* appear to mature at about the same size. It is common among elasmobranchs that females mature at larger sizes than males. Sexual dimorphism in size at maturity, however, is quite variable among different skate species. Jardas (1973) and Nottage & Perkins (1983) have shown that female thornback skates *Raja clavata* L. reach sexual maturity at a larger size than males. The same trend has been found in the mottled skate *Raja pulchra* Liu (Yeon *et al.*, 1997). In contrast, in yellowspot skate *Leucoraja wallacei* (Hulley) (Walmsley-Hart *et al.*, 1999), cuckoo skate *Leucoraja naevus* (Müller & Henle), and Maltese skate *Leucoraja melitensis* (Clark) (Capapé, 1975), there are no intersexual differences in size at maturity, as reported in the present study for *S. bonapartii*. Even within the same species, there are populations with sexes maturing at different size and populations with sexes having the same size at

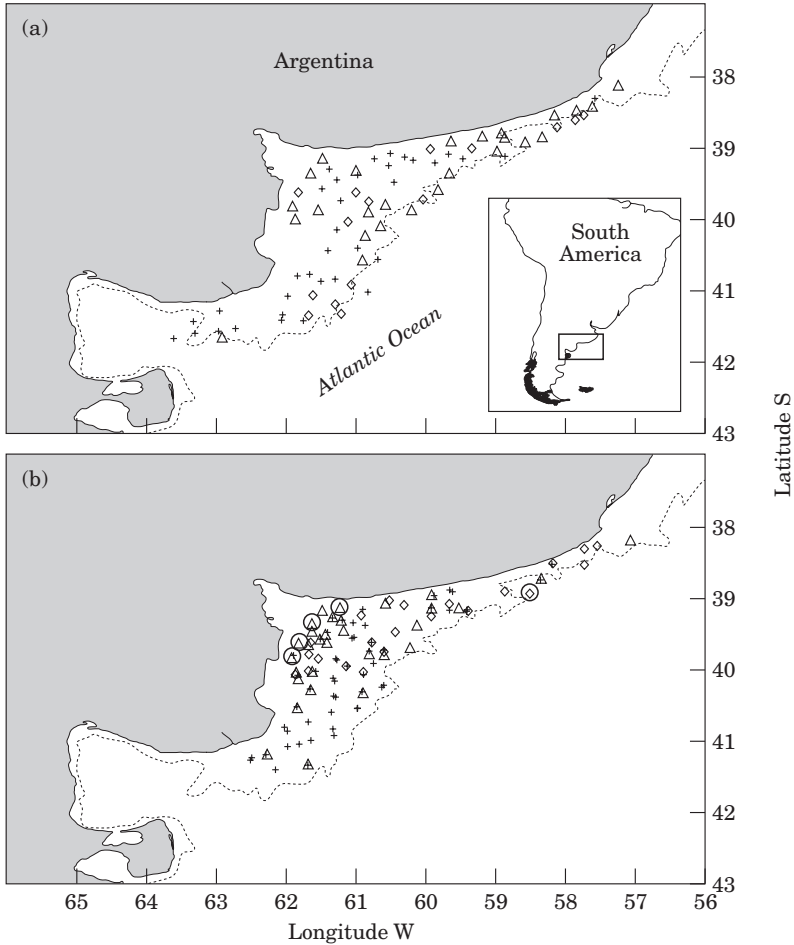


FIG. 10. Relative abundances of *Sympterygia bonapartii* in the El Rincón area expressed as per cent of maximum density. (a) Winter and (b) late spring. +, 0-00; ◇, 0-00-0-50; △, 0-50-5-00 and ○, 5-00-10-00%.

maturity, as shown for the thorny skate *Amblyraja radiata* (Donovan) (Templeman, 1987). These data suggest that local ecological characteristics may affect size at maturity, as well as other reproductive traits, which may result in interspecific and interpopulational differences in the sexual dimorphism of skates.

The present data show that the first step in the male maturation process of *S. bonapartii* is clasper elongation, followed by clasper hardening and appearance of the alar thorn patch. This suggests that tissue mineralization is the last step in the process as is the rule for most ontogenetic changes vertebrates.

Liver size was significantly larger for mature than for immature individuals in both sexes. Also, females had significantly larger livers than males. Both results can be related to reproduction. The liver of mature females produces vitellogenin, the precursor of yolk, during oocyte maturation (García-Garrido *et al.*, 1990; Henningsen, 1999). In addition, some liver lipids are used in yolk

anabolism (Rossouw, 1987; García-Garrido *et al.*, 1990). These facts may help to explain the occurrence of larger livers in mature females than in males and immature females as an adaptation to maximize yolk formation. Mature males with larger livers than immature ones have been observed in the viviparous lesser guitarfish *Rhinobatos annulatus* Smith (Rossouw, 1987), and in the oviparous small-spotted cat shark *Scyliorhinus canicula* (L.) (García-Garrido *et al.*, 1990). This difference was thought to be related to metabolic requirements other than gamete formation during the reproductive season, such as migration to mating grounds and resistance to starvation (Rossouw, 1987). The role of the liver during spermatogenesis in elasmobranchs, however, is not yet fully understood and needs further research (García-Garrido *et al.*, 1990).

Many elasmobranchs have asymmetric ovaries, with such large size differences that one ovary may become atrophied or absent (Hamlett & Koob, 1999). In *S. bonapartii*, the difference in mass between right and left ovaries is not due to differences in number or size of ovarian follicles. It is likely that the amount of stroma tissue is different between both ovaries. This hypothesis and its functional implications, if any, need to be tested.

Gonadosomatic indices are good indicators of periodicity of spawning (Jons & Miranda, 1997). Ovaries of many oviparous elasmobranchs with extended egg-case laying seasons do not show significant changes in size throughout the year (Du Buit, 1976; Cross, 1988; Taniuchi, 1988). Ellis & Shackley (1997) found a significant increase in I_G just prior to the maximum in egg-case laying rate in *S. canicula*. The present data show that most female *S. bonapartii* carrying egg-cases were caught in late spring, and this correlates with a peak in mature female I_G in late spring. This evidence indicates that smallnose fanskates lay their egg-cases during late spring and summer. Unfortunately, the duration of embryo development is not known for *S. bonapartii*. Embryonic development can be extremely variable among species and environments (Berestovskii, 1994). The present observations on seasonality in the egg-laying of *S. bonapartii* agree with data indicating a short egg-laying season in temperate shallow-water oviparous elasmobranchs (Hamlett & Koob, 1999). A marked seasonality and instability in shallow-water temperate ecosystems as compared to deep-water ones may limit the egg-case deposition period to the more favourable season (usually spring and summer) and the appearance of well-protected nursery areas for deposition of egg-cases and growth of neonates. More comparative data between shallow- and deep-water oviparous elasmobranchs are needed for testing this hypothesis.

Seasonal changes in size distributions off LPRM agree with the above conclusions on the egg-laying season. Juveniles were dominant (by size distribution) during winter. In contrast, in late spring and summer mature male and females appeared [Fig. 8(b)(c)]. This shows that adults move towards coastal waters in summer possibly in relation to reproductive requirements.

The data show that *S. bonapartii* lays its egg-cases in the shallower parts of its range. Because of the opportunistic nature of the sampling design, there are no data on egg-case occurrence in the depth range 44–85 m. Because of this, the possibility of egg-case laying in mid-shelf waters cannot be excluded. Observations, however, agree with the fact that most egg-cases found washed ashore (both empty and embryo-carrying ones) on the Province of

Buenos Aires coastline belong to the genus *Sympterygia* (L. O. Lucifora, pers. obs.).

Juveniles occur only in coastal waters <50 m depth, while only subadult and adult specimens were found on the continental shelf. These facts indicated that nursery areas of *S. bonapartii* are located in nearshore waters, much like the egg-case laying areas. Furthermore, the combination of data on abundance and size distribution indicates that nursery areas of *S. bonapartii* are located near estuarine zones. Estuarine zones are known nursery areas for a number of sharks (Castro, 1993) and some rays (Martin & Cailliet, 1988; Snelson *et al.*, 1988), but not for skates. Given that skates are strictly marine fishes, the association of *S. bonapartii* to estuarine systems is rather surprising. *Sympterygia bonapartii*, however, always occurs in the outer part of estuaries (A. Jaureguizar, pers. comm.) with salinity values >30‰ (Menni & Stehmann, 2000). This association may be linked to the high densities of crabs and other benthic invertebrates in south-west Atlantic estuaries (Esteves *et al.*, 2000), which constitute the main prey of *S. bonapartii* (Barrera Oro & Maranta, 1996; Paesch, 2000).

In the ER area, densities showed seasonal variations. In late spring-summer smallnose fanskates were more abundant in shallow waters, whereas in winter they spread over the coastal area down to 50 m [Fig. 10(a)(b)]. Juvenile individuals dominated in ER in late spring. Thus, reproductive activities could not explain seasonal differences in densities. An important factor may be temperature. Smallnose fanskates may avoid low winter temperatures of shallow waters by moving to deeper waters until shallow water temperatures rise again. Another important factor may be predator avoidance. During late spring and summer, large copper *Carcharhinus brachyurus* (Günther) and sand tiger sharks *Carcharias taurus* Rafinesque arrive to the area between Blanca and Anegada Bays (L. O. Lucifora, unpubl. data). These sharks are known predators of skates (L. O. Lucifora, unpubl. data). South American sea lions *Otaria flavescens* (Shaw) occur all year in the ER area and may potentially predate on skates, although elasmobranchs are not generally taken (Koen Alonso *et al.*, 2000). Thus sharks appear to be the main predators of skates in the area. Skates may evade predation by retreating to the shallowest parts of the region, which are unavailable for sharks. This predator avoidance strategy has already been suggested for the La Plata River dolphin *Pontoporia blainvillei* (Gervais & D'Orbigny) in the same area (Bordino *et al.*, 1999). Prey availability could also be important in determining skate seasonal distribution. Unfortunately, seasonal variations in crab abundance have not been investigated in the study area. These hypotheses are not exclusive to each other and further research is needed to test them.

Many aspects of the life-history of *S. bonapartii* important for management (e.g. age at maturity, fecundity and mortality) are still unknown. This is true for most south-west Atlantic skates. This study shows that some areas are especially relevant for the life cycle of *S. bonapartii*. These areas are also important reproductive grounds for many other fish species (Macchi & Acha, 1998) and feeding and resting areas for wildlife (Esteves *et al.*, 2000). Thus, an appropriate management tool for these zones could be the implementation of marine protected areas.

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