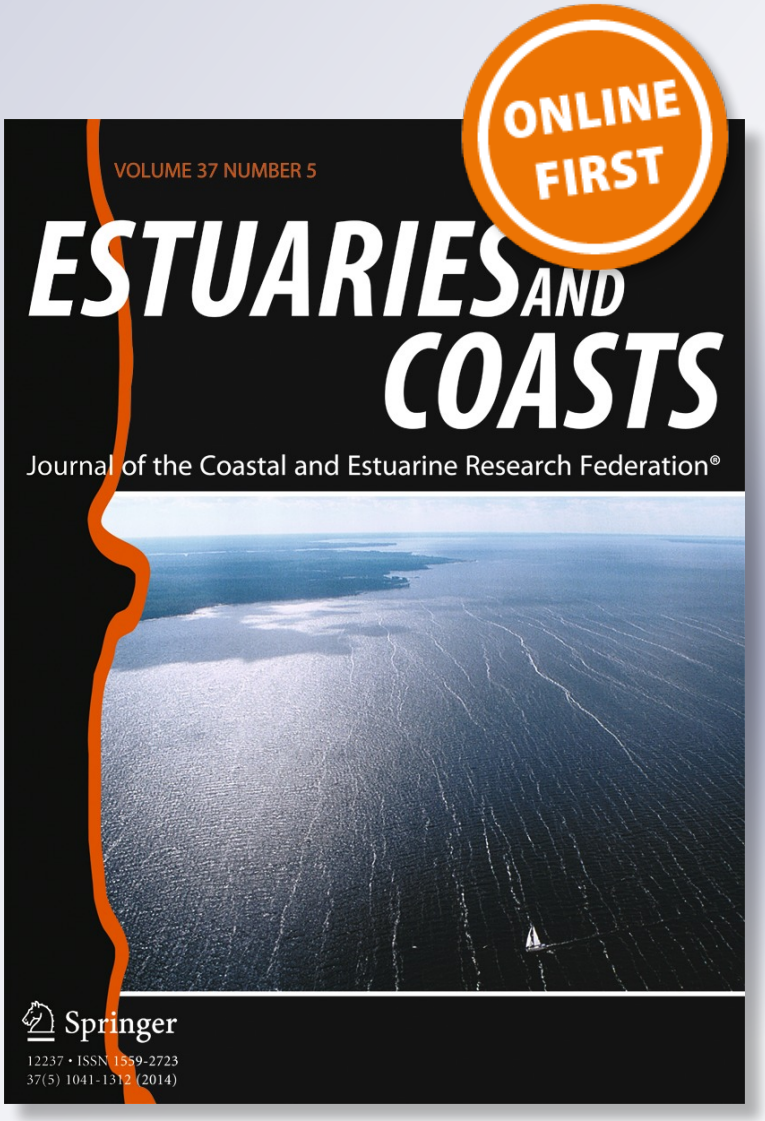
Seasonal Reproductive Biology of the Bignose Fanskate Sympterygia acuta *(Chondrichthyes, Rajidae)*

Ezequiel Mabragaña, Luis O. Lucifora, María de L. Corbo & Juan M. Díaz de Astarloa

Estuaries and Coasts
Journal of the Coastal and Estuarine Research Federation

ISSN 1559-2723

Estuaries and Coasts
DOI 10.1007/s12237-014-9888-0



Estuaries and Coasts
DOI 10.1007/s12237-014-9888-0

Seasonal Reproductive Biology of the Bignose Fanskate *Sympterygia acuta* (Chondrichthyes, Rajidae)

Ezequiel Mabragaña · Luis O. Lucifora · María de L. Corbo · Juan M. Díaz de Astarloa

Received: 16 July 2013 / Revised: 16 August 2014 / Accepted: 7 September 2014

Abstract Most skates are adapted to shelf and slope environments experiencing less seasonal variation than coastal ecosystems. Here, we analyze the reproductive ecology of *Sympterygia acuta*. We hypothesize that, like its congener *Sympterygia bonapartii*, *S. acuta* has a seasonal reproductive cycle. To test this hypothesis, we examined multiple lines of evidence: (1) time of appearance of females carrying egg cases and wild neonates; (2) seasonal variation in gonadosomatic index and follicle diameter, as indicators of reproductive activity; and (3) egg-laying season, incubation time, and fecundity in captive individuals. A total of 351 specimens were examined. Size at 50 % maturity was 475 and 478 mm total length for males and females, respectively. A marked seasonal reproductive cycle was observed. Both gonadosomatic index and follicle diameter of wild adult females increased from winter to spring and reached their lowest value during summer. Fecundity was, on average, 52 eggs per female per laying season. Egg laying of captive females peaked between August and December; eggs hatched after 119–131 days. This schedule predicts the appearance of neonates in the wild by January through April. Accordingly, wild neonates and young-of-the-year were observed between January and May. Unlike most other skates, southwest Atlantic *Sympterygia* species are adapted to life in shallow, coastal waters, matching the seasonality of the coastal environment with egg-laying activity in spring and hatching in summer. These shallow coastal waters, which are important in the life cycle of *Sympterygia* spp., are threatened by human impacts.

Keywords Skate · Rajidae · Southwest Atlantic · Fecundity · Hatching · Oviparity

Communicated by Iris C. Anderson

E. Mabragaña (✉) · M. d. L. Corbo · J. M. Díaz de Astarloa
Laboratorio de Biotaxonomía Morfológica y Molecular de Peces (BIMOPE), Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, B7602AYL Mar del Plata, Buenos Aires, Argentina
e-mail: emabraga@mdp.edu.ar

M. d. L. Corbo
Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, La Plata, Argentina

L. O. Lucifora
Instituto de Biología Subtropical-Iguazú, CONICET, Universidad Nacional de Misiones, Casilla de Correo 9, N3370AVQ Puerto Iguazú, Misiones, Argentina

Introduction

Due to their life-history characteristics, most skate species are vulnerable to overfishing (Walker and Hislop 1998). This is evident by the drastic historic declines in several populations around the world (e.g., Brander 1981; Graham et al. 2001; Devine et al. 2006; McPhie and Campana 2009). The southwest Atlantic is not an exception to this situation. Indeed, a considerable decline in the biomass of several coastal and shelf skate species has been documented in Argentine waters (Massa et al. 2004). Nonetheless, the basic life-history parameters of several skate species remain unknown. Biological parameters are known for less than 50 % of the 32 skate species reported for the southern sector of the southwest Atlantic (34° to 55° S) (e.g., Oddone et al. 2005; Arkhipkin et al. 2008; Mabragaña et al. 2012; and references therein).

Sympterygia, one of the less known genera among South American skates comprises four species endemic to South America. Two species, *Sympterygia bonapartii* and *Sympterygia acuta*, are restricted to coastal waters of the southwestern Atlantic (McEachran 1982). The scant information on the biology and ecology of species of *Sympterygia* is largely restricted to *S. bonapartii*, which is one of the most

Published online: 17 September 2014

common species of skate in the southwestern Atlantic. The reproductive ecology of *S. bonapartii* has been extensively studied during the last decade (Mabragaña et al. 2002; Oddone and Velasco 2004; Jañez and Sueiro 2007). Some of the most interesting aspects of the reproductive ecology of *S. bonapartii* are its egg-laying habitat and apparent seasonal egg laying. Off Argentina and Uruguay, *S. bonapartii* restricts its egg laying to coastal waters, and juveniles congregate in shallow (<20 m) estuarine areas (Mabragaña et al. 2002). This species appears to limit the egg-laying period to spring and summer (Mabragaña et al. 2002), although captive specimens may lay eggs year-round (Jañez and Sueiro 2007). These two characteristics of the reproductive ecology of *S. bonapartii* are unusual among skates because—with few exceptions (e.g., Hunter et al. 2005; Last and Gledhill 2007)—most skate species dwell in mid-shelf (70–200 m) or slope (>200 m) waters year-round and are not commonly associated with estuaries (Ebert and Stehmann 2013).

The bignose fanskate *S. acuta* Garman is found in coastal waters (0–50 m; 23° S–45° 43′ S) from Rio de Janeiro, Brazil (Monteiro-Neto et al. 2008), to the San Jorge Gulf, Argentina (Bovcon et al. 2011). It attains a maximum total length (L_T) of 435 mm (Cousseau et al. 2007). Although common in Brazilian, Uruguayan, and Argentine coastal waters, most aspects of its biology are unknown, other than descriptions of the reproductive anatomy (Galíndez and Estecondo 2008; Díaz Andrade et al. 2009) and egg case (Oddone and Vooren 2002; Mabragaña et al. 2011) and estimation of hatching size (Oddone and Vooren 2002). Along its range, *S. acuta* is taken by shrimp and multispecies trawl fisheries that target coastal demersal fish assemblages (Van der Molen and Caille 2001; Massa et al. 2004; Segura et al. 2008; Massa and Hozbor 2011). Between 34° and 41° S, a 49 % decline in the biomass of *S. acuta* from 1993 to 2003 was observed (Massa and Hozbor 2004), although 2005 estimations showed a slight increase in biomass (Massa and Hozbor 2011). Consequently, *S. acuta* is categorized as "vulnerable" by the International Union for Conservation of Nature (Massa and Hozbor 2004).

Seasonality among oviparous chondrichthyans is less common than among viviparous ones. Two general reproductive strategies have been observed in oviparous species: reproduction throughout the year with one or two egg-laying peaks and a well-defined egg-laying season (Hamlett and Koob 1999; Wyffels 2009). Among skates (Rajiformes: Rajidae), the vast majority of species studied to date lay eggs throughout the year (Frisk 2010). In fact, year-round egg laying has been reported for no less than 15 skate species worldwide (e.g., Sulikowski et al. 2007; Ebert et al. 2008; Williams et al. 2011). On the other hand, seasonal egg laying has been reported for less than five skate species to date (e.g., Rasmussen et al. 1999; Mabragaña et al. 2002; Sulikowski et al. 2004). *Sympterygia* may be one of the few genera among skates entirely adapted to coastal ecosystems with high variability. Most skates are adapted to continental shelf, slope, and deeper waters up to 3000 m depth (McEachran and Miyake 1990; McEachran and Dunn 1998; Ebert and Compagno 2007). These environments, while not completely devoid of seasonal variability, experience less variation than coastal, shallow ecosystems. Year-round reproductive activity observed in many skate species may be related to this lack of seasonal variability (Lucifora and García 2004). Skates that secondarily adapted to coastal ecosystems would have to cope with greater environmental variability. One strategy to cope with this variability is to couple biological cycles with seasonal variation in the environment. The pattern observed in *S. bonapartii*—the only species of the genus studied so far—is consistent with this strategy.

In this paper, we analyze the reproductive ecology of *S. acuta* from Uruguayan and north Argentinean waters. We hypothesize that since *S. acuta* and *S. bonapartii* have a common ancestor (McEachran 1982) and similar niche (Menni and Stehmann 2000; Cousseau et al. 2007), they will share a seasonal reproductive cycle. To test this hypothesis, we examined multiple lines of evidence. Firstly, we examined the time of appearance of females carrying egg cases and neonates in the environment. Secondly, we examined seasonal variation in gonadosomatic index and follicle diameter, as indicators of reproductive activity. Finally, we kept specimens in captivity to estimate the egg-laying season, incubation time, and fecundity. If our hypothesis is true, we predict a match among the three lines of evidence, with egg laying in spring or early summer and hatching in summer.

Material and Methods

Sample Collection

Specimens came from different sources: (1) research cruises carried out by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) between 2000 and 2003 in Uruguayan and north Argentinean coastal waters (33° to 41° S). These cruises were conducted during March, May, July, August, October, November, and December. (2) Artisanal fishing boats from off Mar Chiquita coastal lagoon, Argentina, operating during March, October, and December 2009, March 2010, and every month from October 2010 to August 2012. (3) A research cruise conducted by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) on board the OV *Puerto Deseado* in Buenos Aires Province coastal waters, during August 2012. During sampling on artisanal boats, water temperature (°C) and salinity (psu) were recorded using a multiparametric device HORIBA G30.

Study Area

The study area covered the whole bathymetric range of *S. acuta*, from the shoreline up to 50 m depth, in Uruguayan and north Argentinean coastal waters (33° to 41° S). This rather extensive area contains two large estuarine regions, the Río de la Plata estuary and the El Rincón salt-marsh area, separated by marine waters (Fig. 1; Esteves et al. 2000). This system corresponds to the Argentine Biogeographic Province, which extends farther north up to Rio de Janeiro (23° S), Brazil (Menni et al. 2010). Water temperature is vertically homogeneous in the coastal zone and displays a pronounced seasonal cycle typical of temperate areas (Lucas et al. 2005). Bottom temperature ranges from 13 to 20 °C during late spring-summer and from 8 to 12 °C during winter (Cousseau et al. 1979; Guerrero and Piola 1997; Lucas et al. 2005).

Biological Measurements

Specimens of *S. acuta* were collected and frozen on board for subsequent examination in the laboratory. Skates were sampled typically within 1–3 days once the vessel returned to port. Specimens were allowed to thaw overnight and sampled on the subsequent morning. All measurements were taken on completely thawed individual. Each specimen was identified, sexed, and weighed. L_T and disc width (DW) to the nearest millimeter were recorded for every specimen. The relationship between DW and L_T, with L_T as the dependent variable, was used separately for each sex to estimate L_T for some skates with a damaged tail.

Maturity status of the reproductive organs was assessed visually, following Mabragaña et al. (2002) and Ebert (2005). In males, clasper length (L_C), the degree of calcification of the claspers, number of rows of thorns in the alar thorn patch (RAT), and shape of the efferent duct were recorded. 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. Males were assigned to one of three categories: immature (short, uncalcified claspers, alar thorn patch not yet developed, efferent ducts straight), maturing (longer semicalcified claspers, alar thorn patch developing, efferent ducts beginning to coil), and mature (long, fully calcified claspers, alar thorn patch fully developed, efferent ducts greatly coiled). In females, oviducal gland width (W_{OG}), follicle number, diameter (in mm) of the largest follicle, and dimensions of egg cases in the uteri (total length without horns and maximum width) were recorded. Females were categorized as immature (undeveloped thread-like uteri, ovaries with non-distinguishable follicles, and undeveloped oviducal glands) and mature (wide uteri, distinguishable follicles, and widened oviducal glands). Total (W_T) and gonad (W_G) weights to the nearest 0.1 g were recorded for each specimen.

For both sexes, the proportion of mature individuals in 10-mm L_T intervals was calculated. A logistical model was fitted to the data using a maximum likelihood approach in order to estimate the size at which 50 % of individuals were sexually mature (L_T50; Roa et al. 1999). The logistical model was

$$P_i = \alpha / \left(1 + e^{a+bL^T}\right)$$

where P_i is proportion mature at size i, α is the asymptote, a and b are intercept and slope, and L_T total length of the specimen.

Seasonal Changes in Gonadosomatic Index and Follicle Size

Temporal changes in gonadosomatic index (GSI) and maximum diameter of follicles were analyzed to test for seasonality in the reproductive cycle of *S. acuta*. GSI was calculated as GSI=W_G/W_T and was modelled as a function of season. Maximum diameter of follicles was modelled as a function of season and L_T, which was included to control for the effect of body size on the response variable. In each analysis, the best model was chosen as the one that minimized the Akaike information criterion (Anderson et al. 2000). Any independent variable included in the best model was judged to have a significant effect on the dependent variables (i.e., ovary weight or maximum diameter of follicles) (Franklin et al. 2001). These analyses were carried out only for the northern part of the study area because it was the only area with data from multiple seasons.

Incubation Period and Hatching

Two adult females (580 and 582 mm L_T) of *S. acuta* were collected in nearshore waters off Mar del Plata, Argentina, in January 2001, using commercial gill nets, and were transported to an aquarium located at Museo del Mar, Mar del Plata. The aquarium contained 20,000 l of natural seawater in a closed system. Seawater passed through several filters (mechanic, biological, and ultraviolet); then, it was cooled and constantly aerated. Water temperature was maintained between 15 to 17 °C and salinity between 33 and 34 psu. The tank had physicochemical conditions intended to mimic the natural conditions found in the northern Argentinean coasts. The two females used in the experiment shared this aquarium with other fishes but had no contact with any male skate during their captivity. Each day, egg cases were removed from the aquarium and placed in other tanks, maintained in aerated seawater at 17–19 °C, with mechanic and biological filters. Eggs were monitored daily to record the incubation period and hatching time and to remove egg cases with embryos that were not viable.

Results

A total of 351 specimens of *S. acuta* (166 females and 185 males) were collected from waters off Uruguay and northern Argentina (Fig. 1). Skates were caught during all months sampled from 5 to 40 m depth. Bottom water temperature off Mar Chiquita coastal lagoon (4 to 12 m depth) ranged from 8.2 °C (winter) to 22.7 °C (summer).

Males ranged from 98 to 560 mm L_T (Fig. 2). The smallest mature male was 422 mm L_T (L_C=57 mm; RAT=3), and the largest immature was 485 mm L_T (L_C=31 mm; RAT=0) (Fig. 3). Clasper length increased rapidly between 420 and 470 mm L_T (Fig. 3) being all individuals with claspers longer than 40 mm (measured from the tip of the pelvic fin) mature. All males >473 mm L_T, except for two, were mature. Maturity occurred at 75 % of maximum L_T and size at maturity (L_T50) was estimated at 475 mm L_T. Parameters of the logistical model were a=33.8753891 and b=−0.07132748.

Females ranged from 89 to 585 mm L_T. The smallest mature female was 444 mm L_T (OG=18 mm) and the largest immature was 530 L_T (OG=8 mm) (Fig. 4). Oviducal gland width increased between 445 and 540 mm L_T (Fig. 4), being most individuals with OG wider than 15 mm mature. The exception was a female 465 mm L_T with developed OG (16.5 mm) that was maturing. Except for two individuals, all females >510 mm L_T were mature. Maturity occurred at 76 % of maximum L_T, and L_T50 was estimated at 478 mm L_T. Parameters of the logistical model were a=32.3107049 and b=−0.06756375.

Egg Laying and Occurrence of Neonates in the Environment

Females carrying egg cases were found only in November and December off Mar Chiquita lagoon at 5 m depth and off southern Buenos Aires Province at depths shallower than 35 m, at temperatures ranging from 15.6 to 18 °C. Neonates and young-of-the-year (88 to 100 mm L_T) were observed in January, March, and May off Mar Chiquita coastal lagoon at 5 m depth, at temperatures of 20.6, 21.3, and 13.5 °C, respectively.

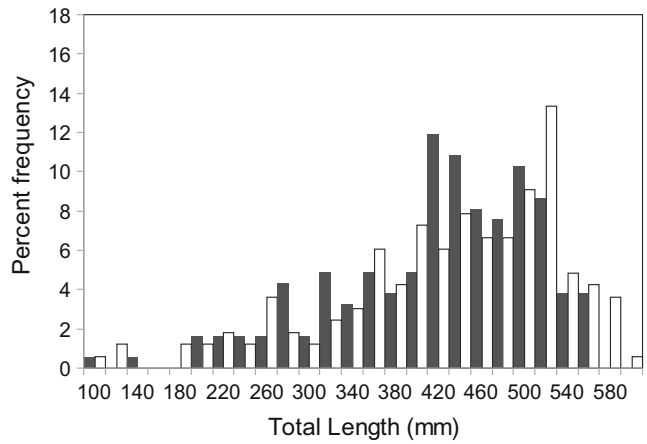


Fig. 2 Length frequency distribution of bignose fanskates, *Sympterygia acuta*, from off Uruguay and northern Argentina. Females (n=166) are represented by *white bars* and males (n=185) by *gray bars*

Seasonal Changes in Gonadosomatic Index and Follicle Size

Temporal changes in GSI and maximum diameter of follicles were found. GSI increased from winter to spring and reached its lowest value during summer (Fig. 5a). The best model explaining variation in ovary size included season (Table 1). Parameters of the best model were (season parameters are given relative to "winter" as a baseline): intercept=0.0164, season: summer=−0.0092, spring=0.0082.

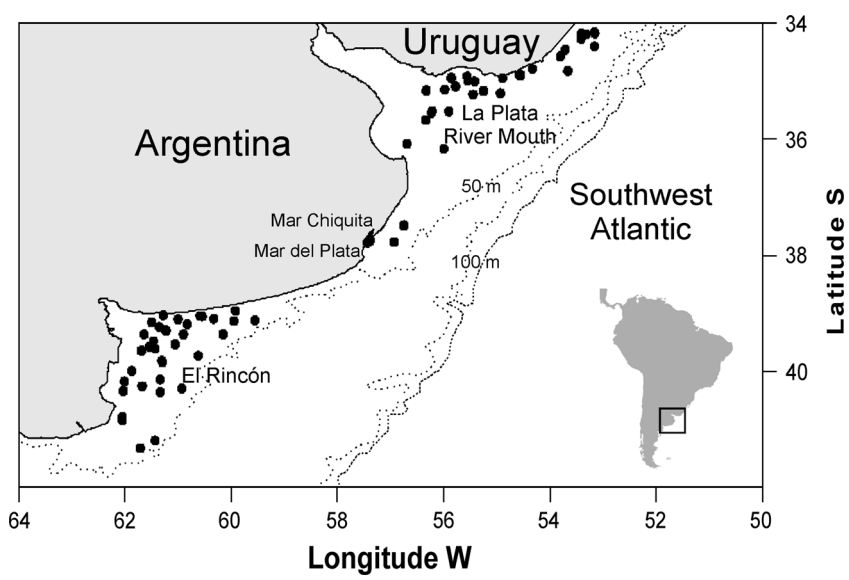


Fig. 1 Map of the study area showing locations where samples of bignose fanskates, *Sympterygia acuta*, were obtained off Uruguay and northern Argentina

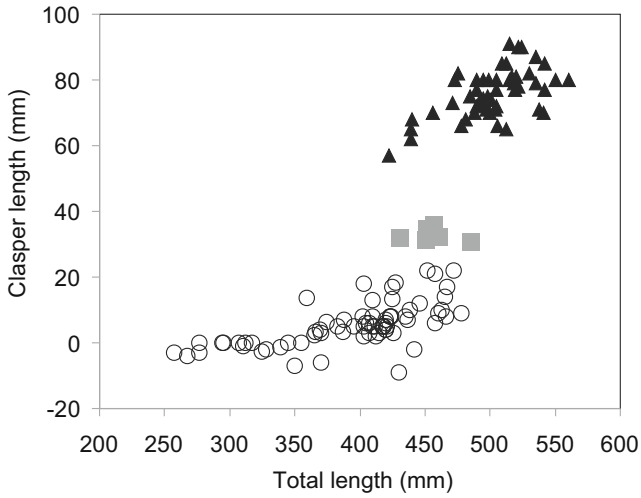


Fig. 3 Relationship between clasper length and total length for male bignose fanskates, *Sympterygia acuta*, from off Uruguay and northern Argentina. *Empty circles* represent immature males, *gray squares* maturing males, and *black triangles* mature males. See "Materials and Methods" for explanation of some clasper length values lower than 0

Coincidently, maximum diameter of follicles also peaked from winter to spring and was lowest in summer (Fig. 5b). The best model included season and total length (Table 1). Parameters of the best model were (season parameters are given relative to winter as a baseline): intercept=17.083, season: summer=−3.683, spring=3.028.

Observations in Aquarium

Females (n=2) were maintained in the aquarium from the time of capture in January 2001 to February 2002. A total of 80 egg cases were laid by these females. Egg cases of *S. acuta* had extremely long posterior horns and a thick lateral keel (Fig. 6). Oviposition took place from 6 August to 21 December 2001, but only the capsules that had been laid between August and

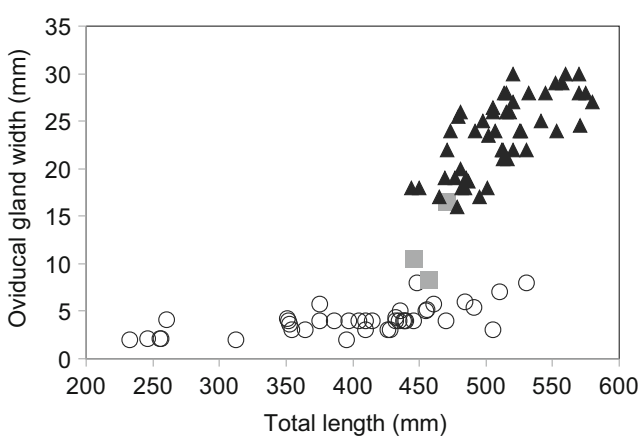


Fig. 4 Relationship between oviducal gland width and total length of bignose fanskates, *Sympterygia acuta*, from off Uruguay and northern Argentina. *Empty circles* represent immature females, *gray squares* maturing females, and *black triangles* mature females

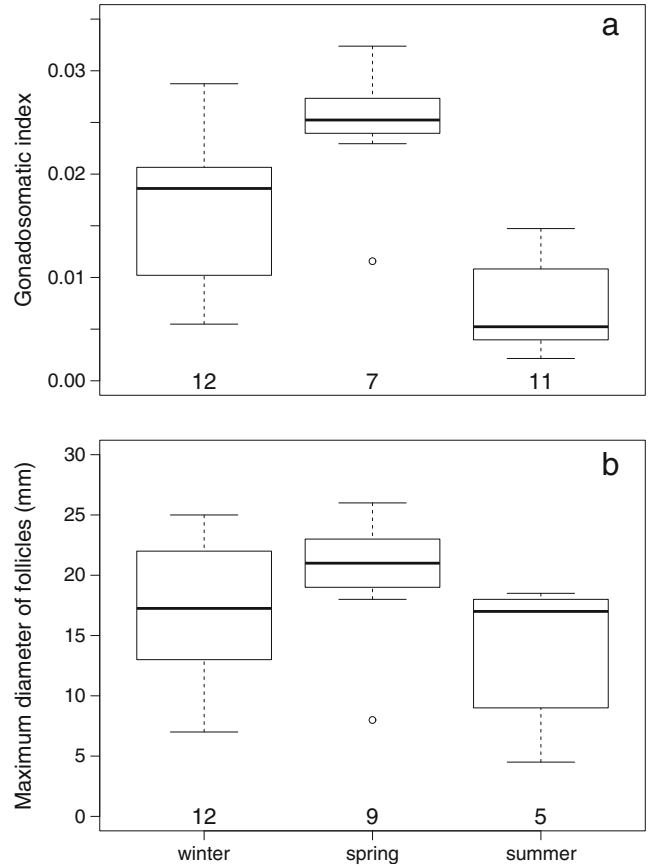


Fig. 5 Seasonal variation in gonadosomatic index (**a**) and maximum diameter of follicles (**b**) in bignose fanskates, *Sympterygia acuta*, from off Uruguay and northern Argentina. The *central*, *bold lines* of the boxplots indicate the median; *boxes* span the interquartile range, *whiskers* encompass values less than 1.5 box lengths away from the box, and *circles* are outliers more than 1.5 box lengths away from the box

October hatched successfully. Indeed, almost all capsules laid during August (n=12) hatched successfully, whereas only two individuals hatched from those laid during September (n=24) and October (n=14) and none from eggs laid during November and December. Overall, hatching percentage was low

Table 1 Models explaining variation in gonadosomatic index (GSI) and maximum diameter of follicles (MOD) of bignose fanskates, *Sympterygia acuta*, from off Uruguay and northern Argentina

Model	AIC	w
GSI~season	−302.8	0.999
GSI~k	−281.52	2.4×10^{-5}
MOD~season	93.27	0.419
MOD~k	93.96	0.298
MOD~season+L_T	95.21	0.159
MOD~L_T	95.71	0.124

Akaike information criterion (AIC) and Akaike weight (w) are given for each model. For each dependent variable, models with the lowest AIC and the highest w are the best

L_T total length, k constant

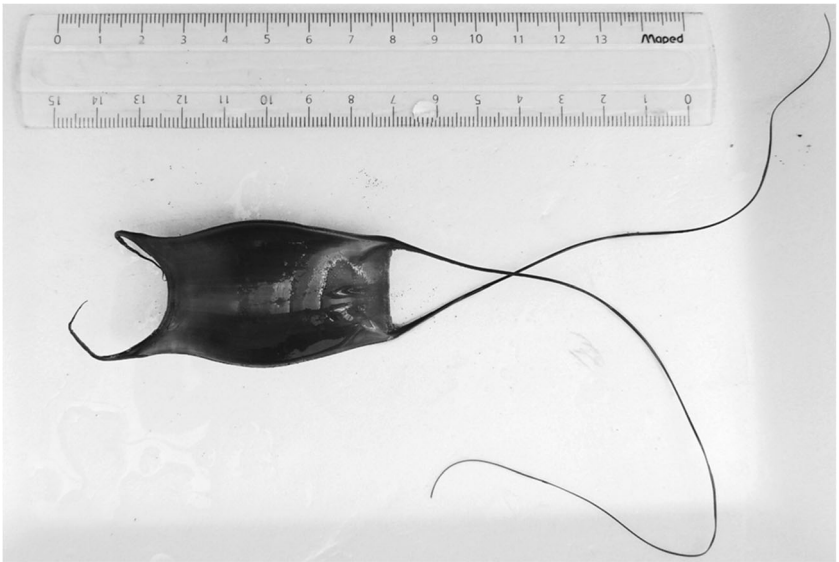


Fig. 6 Egg case of the bignose fanskate, *Sympterygia acuta. Left* anterior

(15 %), and dead embryos at different stages of development were recorded. Oviposition was not a continuous event; typically 1–2 weeks were observed between pulses of oviposition. Within these pulses, oviposition took place every 4 days on average, but more frequently between August and October.

The first hatching event occurred on 3 December 2001. The last viable egg cases were laid on 16 October and hatched on 21 February 2002. Empty egg cases (n=4) and capsules with double vitellogenic oocytes (n=5) were also recorded, but none of the latter hatched successfully. The incubation period at 17–19 °C and 34 psu was between 119 and 131 days. Neonates (84–92 mm L_T at birth) did not present the long snout typical of adult specimens (Fig. 7).

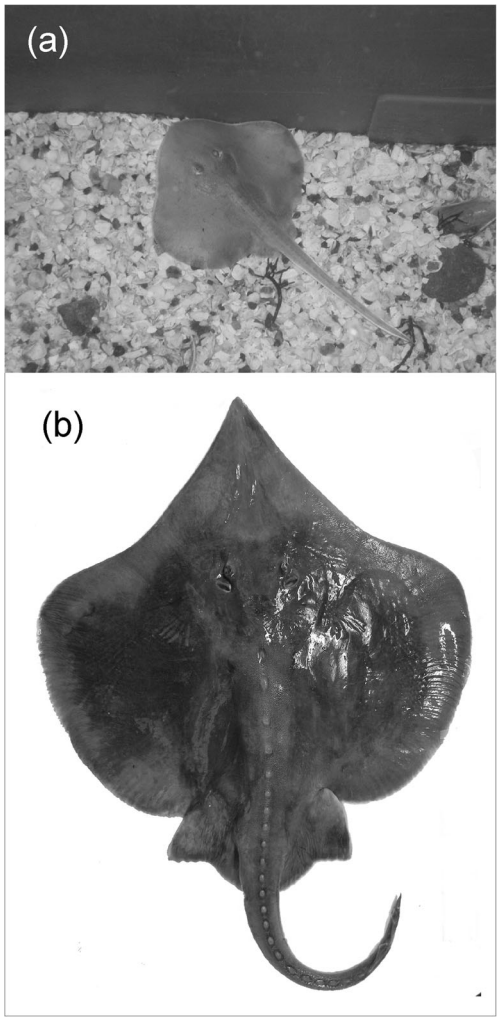


Fig. 7 **a** Neonate specimen of bignose fanskate, *Sympterygia acuta*, 84 mm total length, born in captivity at Museo del Mar aquarium (Mar del Plata, Argentina); **b** adult female of 541 mm total length. Note the difference in snout shape and length between **a** and **b**

Discussion

Our results indicate a seasonal reproductive cycle in *S. acuta*, similar to other species within the genus. Both gonadosomatic index of wild females and egg laying of captive females peak between August and December (Fig. 8). Aquarium observations indicate that hatching occurs after approximately 4 months at 17–19 °C. This schedule predicts the appearance of neonates by January through April. Our observations confirm this prediction, since neonates and young-of-the-year were observed between January and May (Fig. 8). These results support the hypothesis that the genus *Sympterygia* is adapted to life in shallow, coastal waters. The reproductive cycle of *Sympterygia* species studied so far matches the seasonality of the coastal environment with maximum egg-laying activity in spring and hatching in summer.

The general trend in most oviparous chondrichthyans is to lay eggs throughout the year with or without seasonal peaks in

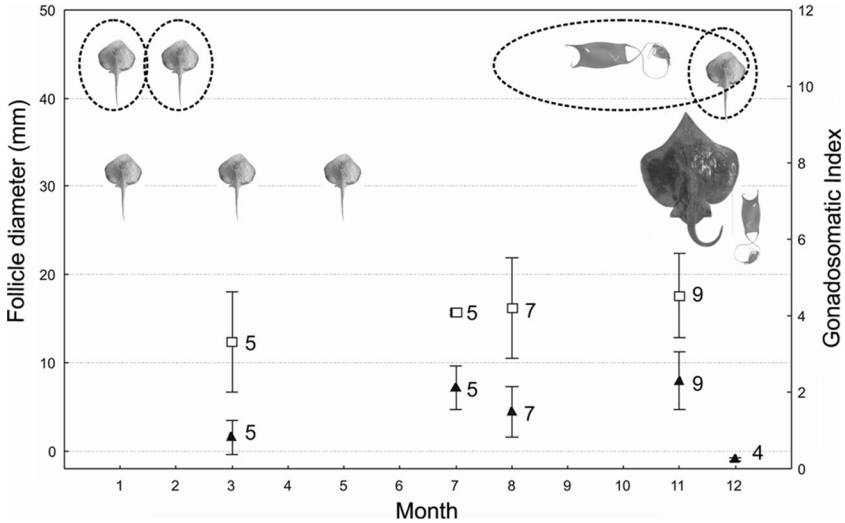


Fig. 8 Integrated diagram showing the reproductive cycle of the bignose fanskate, *Sympterygia acuta*, from off Uruguay and northern Argentina over the span of a year. *Squares* represent mean follicle diameter (mm), *triangles* represent gonadosomatic index, and *error bars* are one standard deviation. The *number beside each square or triangle* represents sample size. The *large skate* with an associated egg case represents the time of occurrence of females carrying egg cases in the wild; *small skates* represent the time at which neonates were found in the wild. *Small skates* and *egg cases enclosed in dotted circles* indicate captive oviposition and hatching times, respectively

the proportion of females carrying egg cases (Hamlett et al. 2005; Sulikowski et al. 2007; Williams et al. 2011; and references therein). Cases of oviparous species that exhibit clear seasonal reproductive cycles are scarce, e.g., the clearnose skate *Raja eglanteria* and the epaulette shark *Hemiscyllium ocellatum* (Heupel et al. 1999; Rasmussen et al. 1999). Seasonal egg laying is also uncommon in skates of the southwest Atlantic and appears to be correlated with the type of environment. A well-defined egg-laying season has been observed in only three species off Argentina: *Rioraja agassizii* (Colonello et al. 2007; Estalles et al. 2009) and two species of *Sympterygia* (Mabragaña et al. 2002; this study). These three species have in common a shallow, coastal habitat (<50 m depth) subject to seasonal variability (Menni and Stehmann 2000; Cousseau et al. 2007). Southwest Atlantic skates inhabiting deeper, mid-shelf waters have a loosely defined seasonal (Perier et al. 2011; Mabragaña et al. 2012) or continuous egg laying (Mabragaña and Cousseau 2004; Ruocco et al. 2006). Oceanographic conditions are very different in these habitats. In mid-shelf waters (70–200 m depth), temperature ranges from 6 to 15 °C during summer and from 5 to 11 °C during winter, whereas salinity shows no seasonal variation (Cousseau et al. 1979). On the contrary, coastal waters experience more variation seasonally. Temperature ranges from 13 to 20 °C during summer and 8 to 12 °C during winter (Cousseau et al. 1979). Salinity fluctuates (20 to >32 psu) in some areas as a consequence of seasonal changes in wind patterns and river discharge (Acha et al. 2008). This general pattern can be observed intraspecifically. Rio skates, *R. agassizii*, tend to lay eggs in a well-defined season, during spring and summer off Argentina (Colonello et al. 2007; Estalles et al. 2009), whereas egg laying occurs year-round off southern Brazil (Oddone et al. 2007). This year-round reproduction off southern Brazil may indicate egg laying in deep water, since neonates and young-of-the-year are absent from Brazilian shallow, coastal areas (Vooren et al. 2005). It is noteworthy that the egg-laying period of some coastal species is not-so well defined (e.g., *Psammobatis bergi*, *P. extenta*, *Atlantoraja castelnaui*; Braccini and Chiaramonte 2002; Martins et al. 2005; San Martín et al. 2005; Colonello et al. 2012), which warrants further research into the causes of reproductive seasonality (or lack of it) in skates of the southwest Atlantic.

Even though skates are among the easiest elasmobranchs to keep in captivity, most reproductive studies on skates fail to describe the egg-case incubation period, oviposition rate, and size at hatching (Frisk 2010). In fact, the egg-laying habits of only nine species of skates have been described from captive studies (Wyffels 2009). The only southwest Atlantic skate in which breeding was recorded from females kept in captivity is *S. bonapartii* (Jañez and Sueiro 2007, 2009). These authors estimated an incubation period of 135±10 days for *S. bonapartii*. Oddone and Vooren (2002), based on egg cases collected on Cassino Beach (Brazil) and maintained in the laboratory under constant conditions (~20 °C), reported the hatching of seven eggs of *S. acuta* after 4–5 weeks of incubation from stage at collection. This faster embryo development may have resulted from the fact that, at the start of the laboratory rearing period, the embryos were already 10–15 mm L_T (e.g., they already presented external branchial filaments). According to Menni and Stehmann (2000), the incubation period in captivity for *S. acuta* from southern Brazilian waters was 90 days, although no data on incubation temperature was provided. Our results showed that at 17–

19 °C and 34 psu, the incubation period of *S. acuta* in Argentine waters ranged from 119 to 131 days, similar to its congener *S. bonapartii*. A shorter incubation period at lower latitudes could be indicative of temperature influence, since skate species living in warm waters tend to have a shorter incubation period than species from cold waters (Luer and Gilbert 1985; Palm et al. 2011). For example, clearnose skates *R. eglanteria* from the Gulf of Mexico have the shortest known incubation period—72.9±8.9 days at 20–27 °C (Luer and Gilbert 1985) and 85±6 days at 20 °C (Luer et al. 2007). On the other hand, thorny skates *Amblyraja radiata* from the Barents Sea have an incubation period of 2–2.5 years at −0.3 to 9.5 °C (Berestovskii 1994), and Alaska skates *Bathyraja parmifera* from the Bering Sea possess the longest known incubation time—3.5 years at 4.4 °C (Hoff 2008).

Both sexes of *S. acuta* mature at about the same size, similar to most other oviparous chondrichthyans which do not show the typical bimaturism observed among viviparous elasmobranchs. The result is a mosaic of maturity differences among both sexes, composed of species with (e.g., Ebert 2005; Colonello et al. 2007; Oddone et al. 2008) and without (e.g., Mabragaña et al. 2002; Chen and Liu 2006; Ruocco et al. 2006) bimaturism. This pattern is hypothesized to result from a lack of selective pressure on females to reach a larger body size, which would increase fecundity. As skates are oviparous, their body size is no longer a limit to the number of offspring they can produce (Lucifora and García 2004; Sims 2005).

Female *S. acuta* laid (on average) two egg cases every 4 days. Therefore, 14 eggs were laid monthly. If the laying period in nature extends from August to December/January, each female could lay approximately 70–84 eggs in a laying season. But considering captivity dates, both females laid 80 egg cases in 138 days, equivalent to 104 egg cases in 180 days (52 per female on average). Caution should be taken in interpreting these fecundity data. Stress in captivity may alter normal oviposition of skates. The females in our study were large (580 and 582 mm L_T), bigger than the maximum size observed previously for this species. Smaller mature females could lay fewer eggs than larger ones, since follicle number tend to increase with female size (Ebert 2005).

The estimated fecundity is higher than that of viviparous elasmobranchs of similar size, but when viability is accounted for, the fertility of *S. acuta* is substantially lower. The fecundity of viviparous elasmobranchs is limited by the size of the body cavity; oviparous skates are free of this limitation and could have a higher fecundity (Lucifora and García 2004). However, oviparity adds a new life stage, the egg, with its own rate of mortality which needs to be taken into consideration in the estimation of fertility. If a mean mortality of 24 % from predation by gastropods is considered (Lucifora and García 2004), 12 embryos could die from predation out of an average annual fecundity of 52 eggs; then, annual fertility is reduced to 40 eggs per female. As was previously stated, taking into consideration that sample size was low (n=2), that individuals were held in captivity, and that females were large, caution in the interpretation of these fecundity/fertility figures must be taken.

Female cartilaginous fishes are able to store sperm for long periods in their oviducal glands, which ensures a supply of sperm for progressive fertilization of oocytes over a period of several weeks or months (Carrier et al. 2004; Hamlett et al. 2005). Information available on sperm storage in oviparous chondrichthyans is scarce. Oviparous catsharks may store sperm for a year or more, as observed in *Scyliorhinus canicula* and *S. retifer* (Ellis and Shackley 1997; Carrier et al. 2004; Griffiths et al. 2011), with a maximum of 843 days of sperm storage being recorded in the latter species (Castro et al. 1988). Luer et al. (2007) reported viable sperm for at least 6 months in the clearnose skate *R. eglanteria*. Female *S. acuta* seems to have a great capacity of sperm storage in its oviducal glands since it was capable of laying viable eggs, even after 10 months isolated from males. This is the first inference of sperm storage in *S. acuta*. Previous histological work did not find stored sperm in oviducal glands of *S. acuta* (Galíndez and Estecondo 2008); direct observations of sperm storage in this species are needed.

S. acuta appears to complete its life cycle in impacted, shallow, coastal waters. All life stages of *S. acuta*, from eggs to adults, are found in shallow waters of the southwest Atlantic, from south Brazil to central Patagonian waters, off Argentina. These habitats are also among the most impacted of the southwest Atlantic, with high levels of fishing resulting in declining populations of elasmobranchs (Massa et al. 2004; Barbini et al. 2011; Massa and Hozbor 2011). Given the dependence of *S. acuta* on the coastal environment, measures to alleviate anthropic effects on this habitat (Vooren and Klippel 2005) and reverse the declining population trend of *S. acuta* (Massa and N. Hozbor 2004; Massa and Hozbor 2011) are urgently needed. These measures could include identifying important areas in the life cycle of *S. acuta*, regulating fishing effort in these areas, and promoting live release of this non-commercial, vulnerable species.

Acknowledgments We thank the crews of the research vessels *Dr. E. L. Holmberg* and *Puerto Deseado* for the assistance in the collection of samples. We thank Ariel Martinez for his logistical support when collecting samples off Mar Chiquita coastal lagoon. We appreciate the collaboration of Carlos Jurado, Nicolás Lajud, Paula Orlando, Matías Delpiani, Mariano González Castro, Daniel Bruno, and Gabriela Blasina (Universidad Nacional de Mar del Plata) in the collection of samples. We also thank Pablo Sisterna for Museo del Mar facilities and Facundo Bernatene and Valeria Saicha for the assistance in captivity experiments. Finally, we thank two anonymous reviewers and Robert Latour, Associate Editor of Estuaries and Coasts, whose suggestions greatly improved this paper. This research was partially supported by funding from Consejo Nacional de Investigaciones Científicas y Técnicas, PIP CONICET 0942, and Universidad Nacional de Mar del Plata (Argentina),

References

Acha, E.M., H. Mianzan, R. Guerrero, J. Carreto, D. Giberto, N. Montoya, and M. Carignan. 2008. An overview of physical and ecological processes in the Rio de la Plata estuary. *Continental Shelf Research* 28: 1579–1588.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64: 912–923.

Arkhipkin, A.I., N. Baumgartner, P. Brickle, V.V. Lapthikovsky, J.H.W. Pompert, and Z.N. Shcherbich. 2008. Biology of the skates *Bathyraja brachyurops* and *B. griseocauda* in waters around the Falkland islands, southwest Atlantic. *ICES Journal of Marine Science* 65: 560–570.

Barbini, S.A., L.O. Lucifora, and N.M. Hozbor. 2011. Feeding habits and habitat selectivity of the shortnose guitarfish, *Zapteryx brevirostris* (Chondrichthyes: Rhinobatidae), off north Argentina and Uruguay. *Marine Biology Research* 7: 365–377.

Berestovskii, E.G. 1994. Reproductive biology of skates of the family Rajidae in the seas of the Far North. *Journal of Ichthyology* 34: 26–37.

Bovcon, N.D., P.D. Cochia, M.E. Góngora, and A.E. Gosztonyi. 2011. New records of warm-temperate water fishes in central Patagonian coastal waters (southwestern South Atlantic Ocean). *Journal of Applied Ichthyology* 27: 832–839.

Braccini, J.M., and G.E. Chiaramonte. 2002. Reproductive biology of *Psammobatis extenta*. *Journal of Fish Biology* 61: 272–288.

Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. *Nature* 290: 48–49.

Carrier, J.C., H.L. Pratt Jr., and J.I. Castro. 2004. Reproductive biology of elasmobranchs. In *Biology of sharks and their relatives*, ed. J.C. Carrier, J.A. Musick, and M.R. Heithaus, 269–286. Boca Raton: CRC Press.

Castro, J.I., P.M. Bubucis, and N.A. Overstrom. 1988. The reproductive biology of the chain dogfish *Scyliorhinus retifer*. *Copeia* 1988: 740–746.

Chen, W.-K., and K.-M. Liu. 2006. Reproductive biology of whitespotted bamboo shark *Chiloscyllium plagiosum* in northern waters off Taiwan. *Fisheries Science* 72: 1215–1224.

Colonello, J.H., M.L. García, and C.A. 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: 277–284.

Colonello, J.H., M.L. García, C.A. Lasta, and R.C. Menni. 2012. Reproductive biology of the spotback skate *Atlantoraja castelnaui* in the south-west Atlantic Ocean. *Journal of Fish Biology* 80: 2405–2419.

Cousseau, M.B., J. Hansen, and D. Gru. 1979. Campañas realizadas por el buque japonés Shinkai Maru en el Mar Argentino desde abril de 1978 hasta abril de,1979 Organización y reseña de datos básicos obtenidos. *Contribuciones INIDEP* 373: 1–625.

Cousseau, M.B., D.E. Figueroa, J.M. Díaz de Astarloa, E. Mabragaña, and L.O. Lucifora. 2007. *Rayas, chuchos y otros batoideos del Atlántico Sudoccidental (34°S-55°S)*. Mar del Plata: INIDEP.

Devine, J.A., K.D. Baker, and R.L. Haedrich. 2006. Deep-sea fishes qualify as endangered. *Nature* 439: 29.

Díaz Andrade, M.C., E. Galíndez, and S. Estecondo. 2009. The ovary of the bignose fanskate *Sympterygia acuta* Garman, 1877 (Chondrichthyes, Rajidae) in the Bahía Blanca estuary, Argentina: morphology and reproductive features. *Brazilian Journal of Biology* 69: 405–413.

Ebert, D.A. 2005. Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology* 66: 618–649.

Ebert, D.A., and L.J.V. Compagno. 2007. Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* 80: 111–124.

Ebert, D.A., and M.F.W. Stehmann. 2013. Sharks, batoids and chimaeras of the North Atlantic. *FAO Species Catalogue for Fisheries Purposes* 7: 1–523.

Ebert, D.A., L.J.V. Compagno, and P.D. Cowley. 2008. Aspects of the reproductive biology of skates (Chondrichthyes: Rajiformes: Rajoidei) from southern Africa. *ICES Journal of Marine Science* 65: 81–102.

Ellis, J.R., and S.E. Shackley. 1997. The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, U.K. *Journal of Fish Biology* 51: 361–372.

Estalles, M., J.E. Perez Comesaña, L.L. Tamini, and G.E. Chiaramonte. 2009. Reproductive biology of the skate, *Rioraja agassizii* (Müller and Henle, 1841), off Puerto Quequén, Argentina. *Journal of Applied Ichthyology* 25(Suppl. 1): 60–65.

Esteves, J.L., N.F. Ciocco, J.C. Colombo, H. Freije, G. Harris, O. Iribarne, I. Isla, P. Nabel, M.S. Pascual, P.E. Penchaszadeh, A.L. Rivas, and N. Santinelli. 2000. The Argentine Sea: The southeast South American shelf marine ecosystem. In *Seas at the millennium: An environmental evaluation. Volume I. Regional chapters: Europe, the Americas and west Africa*, ed. C.R. Sheppard, 749–771. Amsterdam: Pergamon.

Franklin, A.B.., T.M. Shenk, D.R. Anderson, and K.P. Burnham. 2001. Statistical model selection: An alternative to null hypothesis testing. In *Modelling in natural resource management: Development, interpretation, and application*, ed. T.M. Shenk and A.B.. Franklin, 75–90. Washington: Island Press.

Frisk, M.G. 2010. Life history strategies of batoids. In *Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation*, ed. J.C. Carrier, J.A. Musick, and M.R. Heithaus, 283–316. Boca Raton: CRC Press.

Galíndez, E.J., and S. Estecondo. 2008. Histological remarks of the oviduct and the oviducal gland of *Sympterygia acuta* Garman, 1877. *Brazilian Journal of Biology* 68: 359–365.

Graham, K.J., N.L. Andrew, and K.E. Hodgson. 2001. Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research* 52: 549–561.

Griffiths, A.M., D.M. Jacoby, D. Casane, M. McHugh, D.P. Croft, M.J. Genner, and D.W. Sims. 2011. First analysis of multiple paternity in an oviparous shark, the small-spotted catshark (*Scyliorhinus canicula* L.). *Journal of Heredity* 103: 166–173.

Guerrero, R., and A.R. Piola. 1997. Masas de agua en la plataforma continental. In *El Mar Argentino y sus recursos pesqueros*, ed. E.E. Boschi, 107–118. Mar del Plata: INIDEP.

Hamlett, W.C., and T.J. Koob. 1999. Female reproductive system. In *Sharks, skates, and rays: The biology of elasmobranch fishes*, ed. W.C. Hamlett, 398–443. Baltimore: Johns Hopkins University Press.

Hamlett, W.C., D.P. Knight, F.T.V. Pereira, J. Steele, and D.M. Sever. 2005. Oviducal glands in chondrichthyans. In *Reproductive biology and phylogeny of Chondrichthyes: Sharks, batoids and chimaeras*, ed. W.C. Hamlett, 301–335. Enfield: Science Publishers.

Heupel, M.R., J.M. Whittier, and M.B. Bennett. 1999. Plasma steroid hormone profiles and reproductive biology of the epaulette shark, *Hemiscyllium ocellatum*. *Journal of Experimental Zoology* 284: 586–594.

Hoff, G.R. 2008. A nursery site of the Alaska skate (*Bathyraja parmifera*) in the eastern Bering Sea. *Fishery Bulletin* 106: 233–244.

Hunter, E., A.A. Buckley, C. Stewart, and J.D. Metcalfe. 2005. Migratory behaviour of the thornback ray, *Raja clavata*, in the southern North Sea. *Journal of the Marine Biological Association of the United Kingdom* 85: 1095–1105.

Jañez, J.A., and M.C. Sueiro. 2007. Size at hatching and incubation period of *Sympterygia bonapartii* (Müller & Henle, 1841) (Chondrichthyes, Rajidae) bred in captivity at the Temaiken Aquarium. *Journal of Fish Biology* 70: 648–650.

Jañez, J.A., and M.C. Sueiro. 2009. Oviposition rate of the fanskate *Sympterygia bonapartii* (Elasmobranchii, Rajidae) (Müller & Henle, 1841) held in captivity. *Pan-American Journal of Aquatic Sciences* 4: 580–582.

Last, P.R., and D.C. Gledhill. 2007. The Maugean skate, *Zearaja maugeana* sp. nov. (Rajiformes: Rajidae)—a micro-endemic, Gondwanan relict of Tasmanian estuaries. *Zootaxa* 1494: 45–65.

Lucas, A.J., R. Guerrero, H. Mianzán, E.M. Acha, and C.A. Lasta. 2005. Coastal oceanographic regimes of the northern Argentine continental shelf (34°–43°S). *Estuarine, Coastal and Shelf Science* 65: 405–420.

Lucifora, L.O., and V.B. García. 2004. Gastropod predation on egg cases of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: Quantification and life history implications. *Marine Biology* 145: 917–922.

Luer, C.A., and P.W. Gilbert. 1985. Mating behavior, egg deposition, incubation period and hatching in clearnose skate *Raja eglanteria. Environmental Biology of Fishes* 13: 161–171.

Luer, C.A., C.J. Walsh, A.B.. Bodine, and J.T. Wyffels. 2007. Normal embryonic development in the clearnose skate, *Raja eglanteria*, with experimental observations on artificial insemination. *Environmental Biology of Fishes* 80: 239–255.

Mabragaña, E., and M.B. 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., L.O. Lucifora, and A.M. Massa. 2002. The reproductive ecology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic. *Journal of Fish Biology* 60: 951–967.

Mabragaña, E., D.E. Figueroa, L.B. Scenna, J.M. Díaz de Astarloa, J.H. Colonello, and G. Delpiani. 2011. Chondrichthyan egg cases from the southwest Atlantic. *Journal of Fish Biology* 79: 1261–1290.

Mabragaña, E., P. Ibáñez, and M.B. Cousseau. 2012. Reproductive biology and abundance of the freckled sandskate *Psammobatis lentiginosa* McEachran, 1983 in the southwest Atlantic. *Marine Biology Research* 8: 292–299.

Martins, I.A., C.L. Martins, and M.H.A. 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.

Massa, A.M., and N.M. Hozbor. 2011. Evolución de las estimaciones de abundancia de los peces carilaginosos demersales de mayor valor comercial del Atlántico Sudoccidental, capturados entre 34° y 41° S, a profundidades menores de 50 m. In *Contribuciones sobre biología, pesca y comercialización de tiburones en la Argentina. Aportes para la elaboración del Plan de Acción Nacional*, ed. O.C. Wöhler, P. Cedrola, and M.B. Cousseau, 193–205. Buenos Aires: Consejo Federal Pesquero.

Massa A.M., and N.M. Hozbor. 2004. *Sympterygia acuta*. In: IUCN 2010. IUCN red list of threatened species. Version 2010.1. <www.iucnredlist.org>. Accessed 13 April 2010.

Massa, A.M., L.O. Lucifora, and N.M. Hozbor. 2004. Condrictios de las regiones costeras bonaerense y uruguaya. In *El Mar Argentino y sus recursos pesqueros. Tomo 4. Los peces marinos de interés pesquero. Caracterización biológica y evaluación del estado de explotación*, ed. R.P. Sánchez and S.I. Bezzi, 85–99. Mar del Plata: INIDEP.

McEachran, J.D. 1982. Revision of the South American skate genus *Sympterygia* (Elasmobranchii: Rajiformes). *Copeia* 1982: 867–890.

McEachran, J.D., and K.A. Dunn. 1998. Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chondrichthyes: Rajidae). *Copeia* 1998: 271–290.

McEachran J.D., and T. Miyake. 1990. Phylogenetic interrelationships of skates: A working hypothesis (Chondrichthyes: Rajoidei). In: *Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries*, ed. H.L. Pratt Jr., S.H. Gruber, and T. Taniuchi. *NOAA Technical Report NMFS* 90: 285–304.

McPhie, R.P., and S.E. Campana. 2009. Reproductive characteristics and population decline of four species of skate (Rajidae) off the eastern coast of Canada. *Journal of Fish Biology* 75: 223–246.

Menni, R.C., and M.F.W. Stehmann. 2000. Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. *Revista del Museo Argentino de Ciencias Naturales, nueva serie* 2: 69–109.

Menni, R.C., A.J. Jaureguizar, M.F.W. Stehmann, and L.O. Lucifora. 2010. Marine biodiversity at the community level: Zoogeography of sharks, skates, rays, and chimaeras in the southwestern Atlantic. *Biodiversity and Conservation* 19: 775–796.

Monteiro-Neto, C., R.A. Tubino, L.E.S. Moraes, J.P.M. Neto, G.V. Esteves, and W.L. Fortes. 2008. Associações de peixes na região costeira de Itaipu, Niterói, RJ. *Iheringia, Série Zoologia* 98: 50–59.

Oddone, M.C., and G. Velasco. 2004. Size at maturity of the smallnose fanskate *Sympterygia bonapartii* (Müller & Henle, 1841) (Pisces, Elasmobranchii, Rajidae) in the SW Atlantic. *ICES Journal of Marine Science* 61: 293–296.

Oddone, M.C., and C.M. Vooren. 2002. Egg-cases and size at hatching of *Sympterygia acuta* in the south-western Atlantic. *Journal of Fish Biology* 61: 858–861.

Oddone, M.C., L. Paesch, and W. Norbis. 2005. Size at first sexual maturity of two species of rajoid skates, genera *Atlantoraja* and *Dipturus* (Pisces, Elasmobranchii, Rajidae), from the south-western Atlantic Ocean. *Journal of Applied Ichthyology* 21: 70–72.

Oddone, M.C., A.F. Amorim, P.L. Mancini, W. Norbis, and G. Velasco. 2007. The reproductive biology and cycle of *Rioraja agassizi* (Müller & Henle, 1841) (Chondrichthyes: Rajidae) in southeastern Brazil, SW Atlantic Ocean. *Scientia Marina* 71: 593–604.

Oddone, M.C., W. Norbis, P.L. Mancini, and A.F. Amorim. 2008. Sexual development and reproductive cycle of the eyespot skate, *Atlantoraja cyclophora* (Regan, 1903) (Chondrichthyes: Rajidae: Arhynchobatinae), in southeastern Brazil. *Acta Adriatica* 49: 73–87.

Palm, B.D., D.M. Koester, W.B. Driggers III, and J.A. Sulikowski. 2011. Seasonal variation in fecundity, egg case viability, gestation, and neonate size for little skates, *Leucoraja erinacea*, in the Gulf of Maine. *Environmental Biology of Fishes* 92: 585–589.

Perier, R., M. Estalles, M. Coller, and E.E. Di Giacomo. 2011. Reproductive biology of the endemic skate *Psammobatis lentiginosa* in the San Matías Gulf (south-western Atlantic). *Journal of the Marine Biological Association of the United Kingdom* 91: 1165–1173.

Rasmussen, L.E.L., D.L. Hess, and C.A. Luer. 1999. Alterations in serum steroid concentrations in the clearnose skate, *Raja eglanteria*: Correlations with season and reproductive status. *Journal of Experimental Zoology* 284: 575–585.

Roa, R., B. Ernst, and F. Tapia. 1999. Estimation of size at maturity: An evaluation of analytical and resampling procedures. *Fishery Bulletin* 97: 570–580.

Ruocco, N.L., L.O. Lucifora, J.M. Díaz de Astarloa, and 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.

San Martín, M.J., J.E. Perez, and G.E. Chiaramonte. 2005. Reproductive biology of the South West Atlantic marbled sand skate *Psammobatis bergi* Marini, 1932 (Elasmobranchii, Rajidae). *Journal of Applied Ichthyology* 21: 504–510.

Segura, A.M., E.A. Delgado, and A. Carranza. 2008. La pesquería de langostino en Punta del Diablo (Uruguay): un primer acercamiento. *Pan-American Journal of Aquatic Sciences* 3: 232–236.

Sims, D.W. 2005. Differences in habitat selection and reproductive strategies of male and female sharks. In *Sexual segregation in vertebrates: Ecology of the two sexes*, ed. K.E. Ruckstuhl and P. Neuhaus, 127–147. Cambridge: Cambridge University Press.

Sulikowski, J.A., P.C.W. Tsang, and W.H. Howell. 2004. An annual cycle of steroid hormone concentrations and gonad development in the winter skate, *Leucoraja ocellata*, from the western Gulf of Maine. *Marine Biology* 144: 845–853.

Sulikowski, J.A., E. Scott, J. Kneebone, J. Jurek, W.H. Howell, and P.C.W. Tsang. 2007. The reproductive cycle of the smooth skate, *Malacoraja senta*, in the Gulf of Maine. *Marine and Freshwater Research* 58: 98–103.

Van der Molen, S., and G. Caille. 2001. Bahía Engaño: a north Patagonian nursery area for the smoothhound shark *Mustelus schmitti* (Carcharhiniformes: Triakidae). *Journal of the Marine Biological Association of the United Kingdom* 81: 851–855.

Vooren, C.M., and S. Klippel. 2005. Diretrizes para a conservação de espécies ameaçadas de elasmobrânquios. In *Ações para a conservação de tubarões e raias no sul do Brasil*, ed. C.M. Vooren and S. Klippel, 213–228. Porto Alegre: Igaré.

Vooren, C.M., S. Klippel, and A.B.. Galina. 2005. Os elasmobrânquios das águas costeiras da plataforma sul. In *Ações para a conservação de tubarões e raias no sul do Brasil*, ed. C.M. Vooren and S. Klippel, 113–120. Porto Alegre: Igaré.

Walker, P.A., and J.R.G. Hislop. 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES Journal of Marine Science* 55: 392–402.

Williams, L.J., A.M. Cicia, G.B. Pellegrin, K.M. Smith, and J.A. Sulikowski. 2011. The reproductive cycle of the roundel skate *Raja texana*. *Journal of Fish Biology* 79: 298–305.

Wyffels, J.T. 2009. Embryonic development of Chondrichthyan fishes—a review. In *Development in non-teleost fishes*, ed. Y.W. Kunz, C.A. Luer, and B.G. Kapoor, 1–103. Enfield: Science Publishers.