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ORIGINAL ARTICLES

Exploring nursery sites for oviparous chondrichthyans in the Southwest Atlantic (36°S–41°S)

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ABSTRACT
The aim of this paper was to explore egg-laying areas of oviparous chondrichthyans occurring in the northern part of the Southwest Atlantic Ocean (36°S–41°S) at between 50 and 200 metres depth and the Mar del Plata Canyon (from 200 to 3447 m). A total of 515 capsules were collected corresponding to 10 species. Four species accounted for 87.6% of the total catch: *Psammobatis normani*, *Bathyraja macloviana*, *Amblyraja doellojuradoi* and *Bathyraja brachyurops.* The remaining corresponded to *Schroederichthys bivius*, *Psammobatis rudis*, *Zearaja chilensis*, *Bathyraja albomaculata*, *Psammobatis lentiginosa* and *Bathyraja* sp. Most hauls were monospecific and relatively few hauls contained four or five species (southern part of the area, in sites located at 75 and 94–105 m depth). No egg capsules were recorded between 1712 m and 3447 m. Highest densities (>3000 capsules/km^2) were mainly found between 39° 46.2′ and 40°29.9′S from 85 to 105 m and they were also recorded near the Mar del Plata Canyon at 37°59.7′S and at 852 m. The highest value recorded was 12,326 capsules/km^2 (located at 40°18.9′S and 85.4 m). The highest densities for each of the most abundant species are discussed. The finding of high densities of egg cases near the Argentine shelf-break front indicates that many skate species use this area as a nursery site. The egg-laying areas explored here are the first reported sites of this kind in the Southwest Atlantic Ocean. Recognizing and protecting egg-laying habitats may be important steps to a long-term conservation of oviparous chondrichthyan populations.

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Introduction

Chondrichthyans, which include around 1200 species (Naylor et al. 2012; Weigmann 2016) have life-history traits characterized by slow growth, late age at sexual maturity, few young production per litter, long incubation and gestation periods, and relatively high longevity. These features make them especially vulnerable to overfishing as either targeted or by-catch species (Compagno 1990; Pratt & Cassey 1990; Musick 2004).

Oviparism is a reproductive mode observed in all species of skates (order Rajiformes, families Arhynchobatidae, Rajidae, Anacanthobatidae and Crurirajidae, following Weigmann 2016), holocephalans and some sharks and is characterized by the production of fertilized eggs which are encapsulated in a protein structure (ovarian capsule) produced by the mother and deposited onto the seafloor (Hamlett et al. 2005). Egg laying seems to be spatially restricted to sites known as nursery areas where embryo development and subsequent hatching occurs (Hoff 2008; Love et al. 2008). The incubation period is unknown for most species of skates but previous reports indicate that it lasts from a few months to several years depending on the species and environmental factors (Berestovskii 1994; Oddone & Vooren 2002; Jañez & Sueiro 2007; Hoff 2008; Mabragaña et al. 2015). Skate nursery grounds are characterized by high egg densities. For example, a small nursery site (< 2 km^2) harboured an egg density exceeding 500,000 eggs/km^2 (Hoff 2007). Different nursery areas have been discovered during exploratory trawling. The Bering Sea is known to be a nursery for several species of *Bathyraja* (Hoff 2010) and the North Pacific is important for *Raja binoculata* Girard, 1855 (Hitz 1964). In the Atlantic Ocean, a site for *Fenestraja plutonia* (Garman, 1881) off North Carolina, USA was found (Quattrini et al. 2009) and

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numerous nursery sites in Portuguese waters have been reported for seven *Raja* species (Serra-Pereira et al. 2014). Nursery sites have also been discovered during photographic or video surveys of the seafloor and include one in the Sea of Japan (Hunt et al. 2011), one in a submarine canyon in the Southern California Bight (Love et al. 2008) and others in the Mediterranean Sea (Treude et al. 2011). Finally, in the Antarctic Peninsula a possible nursery area for one species of *Bathyraja* has recently been reported through photographic images (Amsler et al. 2015). However, sites have not yet been reported in the Southwest Atlantic Ocean and information about nursery grounds is scarce. In this sense, it is known that marine fronts play an important role in ecological processes of the ocean; they are areas of high biological productivity, generating great food availability (Acha et al. 2004, 2015). It would be expected that these areas are preferentially utilized for egg-laying of oviparous chondrichthyans which inhabit shelf waters.

Twenty-eight species of oviparous chondrichthyans have been found to occur in the Argentine Sea (Menni & Stehmann 2000; Cousseau et al. 2007; Menni & Lucifora 2007; Díaz de Astarloa et al. 2008). Specifically, on the northern part of the Argentine Continental Shelf (nACS) from 36°S to 41°S, between 50 and 200 m depth, the presence of 12 species of skates, the elephant fish *Callorhinchus callorynchus* (Linnaeus, 1758) and the narrowmouthed catshark *Schroederichthys bivius* (Müller & Henle, 1838) has been recorded so far (Cousseau et al. 2007; Mabragaña 2007; Díaz de Astarloa et al. 2008; Sánchez et al. 2009; Cousseau & Perrotta 2013). Chondrichthyan egg cases have morphological features that make them species-specific (Ishiyama 1958; Ebert & Davis 2007; Mabragaña et al. 2011; Ishihara et al. 2012). Their morphology provides information about phylogenetic interrelationships between both recent and fossil oviparous chondrichthyans (Fischer et al. 2014). Capsules can also be useful for studying distribution and reproductive biology traits (breeding season, fertility, incubation period) that are useful parameters for conservation that can provide better management for effective fishing. Egg cases of most of the Argentine Sea oviparous chondrichthyans have been described morphologically, allowing identification at the species level (Oddone & Vooren 2008; Mabragaña et al. 2011; Scenna 2011). Even though detailed descriptions of cases have been made, little is known about the location and importance of egg-laying areas for each species. Knowledge of the location of nursery areas of elasmobranch fishes has been considered as a research requirement for the management of elasmobranch fisheries (Castro 1993).

The aim of the present paper is to explore nursery sites for oviparous chondrichthyan species in the nACS between 50 and 200 m depth and in the Mar del Plata Canyon.

Materials and methods

Sample collection

Sampling was carried out in the northern part of the Argentine Continental Shelf (nACS) (36°S–41°S) between 50 and 200 m depth, approximately. Additionally, data from the continental slope up to the Mar del Plata Canyon (from 200 to 3447 m depth), which is located at the continental margin off northern Argentina at around 38°S, were considered (Figure 1). Samples mainly came from eight research cruises carried out by the O/V Puerto Deseado (OVPD) between 2009 and 2014. Samples were collected using two bottom trawls, a shrimp net (50 mm mesh in the wings, and 20 mm in the cod end; vertical height 1 m, horizontal opening 4 m) and a bottom trawl net (135 mm mesh in the wings, and 60 mm in the cod end; vertical height 3.7 m, horizontal opening 10 m). Two dredges (horizontal openings 0.6 and 0.8 m) were also used. Tow duration was between 20 and 30 minutes and the trawling speed was from 1.5 to 3 knots. Additional samples were obtained from commercial vessels. A total of 122 fishing hauls considering all sources were carried out and for each date, latitude, longitude and depth were recorded (Figure 1).

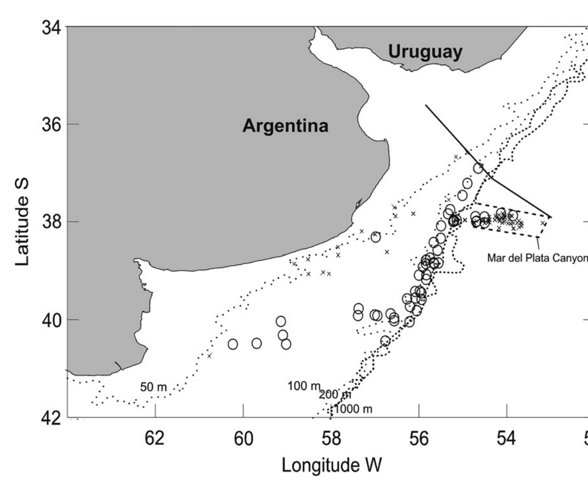

Figure 1. Map of the study area showing the location of fishing stations along the northern part of the Southwest Atlantic continental shelf and continental slope. Empty circles indicate positive hauls; crosses indicate those sites where no catches were reported. The line in the upper right quadrant indicates the international limit between Argentina and Uruguay. The Mar del Plata Canyon location is surrounded by a dotted line.

Egg-case identification

Samples were collected and frozen on board for subsequent examination in the laboratory. Capsules were identified following Paesch & Oddone (2008) and Mabragaña et al. (2011) and length (excluding horns) and maximum width were recorded. Capsules were fixed in 4% formalin and stored in 70% alcohol.

Distribution, richness and abundance patterns

After taxonomic identification, the number of capsules per haul for each species was recorded. To describe distribution and richness patterns, data from both research and commercial vessels were considered. To estimate the abundance of each species only data from research cruises carried out by the OVPD were considered. Only hauls sampled with nets were used to avoid bias in the analysis. The relative abundance of egg capsules was estimated by the swept area method (Alverson & Pereyra 1969), expressed as individuals per km^2 (Ind × km^{-2}). For each estimation of density, area was calculated as $s \times t \times ha$, where s is trawling speed, t is duration of trawling and ha is horizontal aperture of the net. Relative abundance was initially performed for all species taken together and then for each of the most abundant species. Distribution, richness and abundance maps were produced using Surfer 10.

Results

Collection and identification of egg cases

One hundred and twenty-two hauls were sampled. Of these, 59 were carried out in shelf waters (71.2% positives) and 63 in continental slope waters (17.5% positives). Overall, 515 egg cases of 10 species of Chondrichthyes were collected (Figures 1 and 2). For these egg cases, the number and measurements of each species are summarized in Table I. All capsules were identified to species level except two, which were assigned to the genus *Bathyraja*. No egg capsules were collected beyond a depth of 1712 m. From those capsules, 87.6% corresponded to four species: *Psammobatis normani* McEachran, 1983, *Bathyraja macloviana* (Norman, 1937), *Amblyraja doellojuradoi* (Pozzi, 1935) and *Bathyraja brachyurops* (Fowler, 1910). The remaining capsules belonged to *Schroederichthys bivius* (6.2%), *Psammobatis rudis* Günther, 1870 (1.55%), *Zearaja chilensis* (Guichenot, 1848) (1.55%), *Bathyraja albomaculata* (Norman, 1937) (1.35%), *Psammobatis lentiginosa* McEachran, 1983 (1.35%) and *Bathyraja* sp. (0.4%).

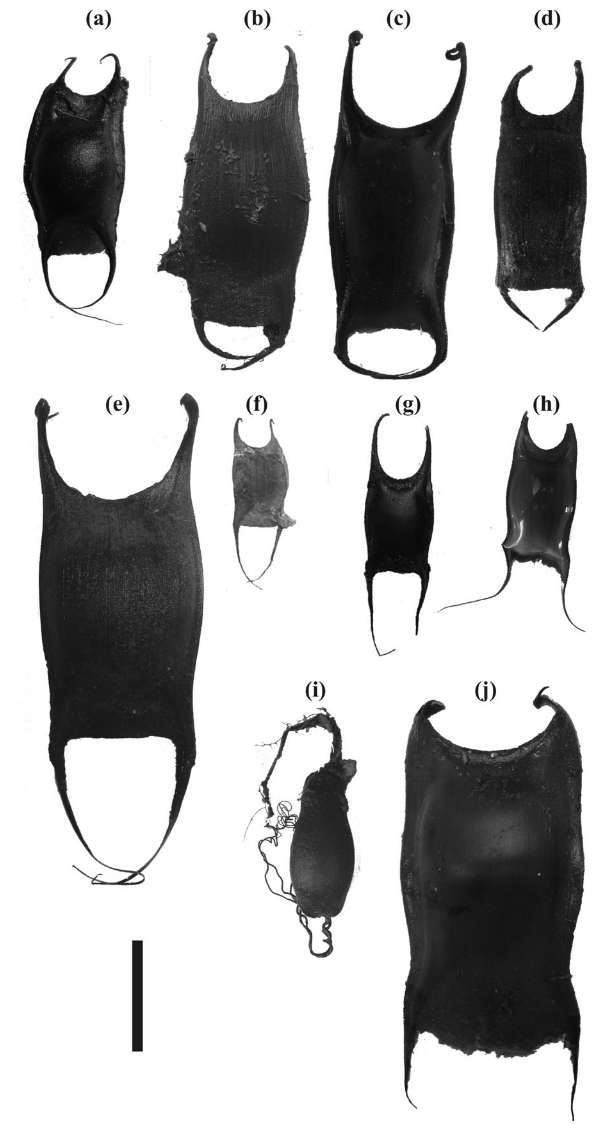

Figure 2. Collected egg cases of (a) *Amblyraja doellojuradoi* (Pozzi, 1935); (b) *Bathyraja albomaculata* (Norman, 1937); (c) *Bathyraja brachyurops* (Fowler, 1910); (d) *Bathyraja macloviana* (Norman, 1937); (e) *Bathyraja* sp.; (f) *Psammobatis lentiginosa* McEachran, 1983; (g) *Psammobatis normani* McEachran, 1983; (h) *Psammobatis rudis* Günther, 1870; (i) *Schroederichthys bivius* (Müller & Henle, 1838); and (j) *Zearaja chilensis* (Guichenot, 1848). Scale bar = 5 cm.

Distribution patterns

The egg case distribution for each species from shallower to deeper trawls is described here. Sites with empty capsules and those with eggs are shown in Figure 3. Egg cases of *Zearaja chilensis* were collected in three hauls located at 38°18.6′S and 40°29.9′S from 63 to 75 m depth; capsules with eggs occurred only in the deepest haul (75 m; Figure 3a). Those of *Psammobatis lentiginosa* were recorded in two hauls coinciding with those further south of *Z. chilensis* and capsules with eggs were present at 63 m (Figure 3b).

Table I. Number of egg cases and measurement ranges of 10 species of oviparous chondrichthyans caught in the northern part of the Southwest Atlantic continental shelf and continental slope.

Species	Total egg cases (*n*)	Open egg cases (*n*)	Closed egg cases (*n*)	ECL[a] range (mm)	MAW[b] range (mm)
Amblyraja doellojuradoi (Pozzi, 1935)	70	51	19	60.9–81.6	36.6–55.8
Bathyraja albomaculata (Norman, 1937)	7	4	3	92.4–99.4	53.8–59.4
Bathyraja brachyurops (Fowler, 1910)	49	28	21	74.7–107.4	44.4–65.4
Bathyraja macloviana (Norman, 1937)	94	72	22	68–95.1	39–51
Bathyraja sp.	2	1	1	98–99	62–67
Psammobatis lentiginosa McEachran, 1983	7	2	5	34–36	23.2–25
Psammobatis normani McEachran, 1983	238	227	11	39–54.9	27.9–37.7
Psammobatis rudis Günther, 1870	8	4	4	44.6–57	28.9–34.3
Schroederichthys bivius (Müller & Henle, 1838)	32	24	8	57.3–78.3	19–29.1
Zearaja chilensis (Guichenot, 1848)	8	4	4	105–144.1	60.3–77.8
	515	**417**	**98**		
		80.81%	**19.19%**		

[a]ECL: egg case length (without horns); [b]MAW: egg case width (maximum).

Capsules of *Schroederichthys bivius* occurred in three hauls at approximately the same latitude as those of *P. lentiginosa*, from 75 to 105 m depth, with the presence of full egg cases at 87 m (Figure 3a). Capsules of *Psammobatis normani* were collected in 19 hauls between 36°54′S and 40°29.9′S from 73.7 to 112 m depth, finding full egg cases in hauls at 75 and 95 to 97 m (Figure 3c). Egg cases of *Bathyraja brachyurops* came from 18 hauls between 84 and 251 m ranging between 37°12.7′S and 40°26′S. Capsules with eggs of this species were present at the central zone, between 37°59.7′S and 39°35′S from 95 to 251 m (Figure 3d). Capsules of *Bathyraja macloviana* were collected in 30 hauls situated between 37°12.7′S and 40° 29.9′S, most of which were recorded at depths between 84 and 201 m, and capsules with eggs were generally scattered following this distribution pattern, between 84 and 117 m (Figure 3e). Egg cases of *Psammobatis rudis* were observed in seven hauls between 37°45′S and 39°54.7′S, most of them between 91.3 and 150 m, with capsules containing eggs at 108 m. One egg case with egg of *P. rudis* was also recorded at 998 m (Figure 3b). Capsules of *Amblyraja doellojuradoi* were collected in 24 hauls between 84 and 1006 m depth from 37°53.5′S to 40°26′S (Figure 3f). For this species, capsules with eggs were observed north of 38°50′S between 95 and 1006 m. Egg cases of *Bathyraja albomaculata* occurred in four hauls between 251 and 1006 m from 37°57.7′S to 38°0.98′S, and those capsules with eggs at lower depths (Figure 3a). Finally, the two capsules (one with egg) of *Bathyraja* sp were collected in the same haul at 37°52.15′S and 1712 m (Figure 3a).

Richness and abundance patterns

Figure 4 shows the egg case richness in the surveyed area. Positive hauls ranged from one up to five species. Most hauls (37.7%) were monospecific, but some contained two (26.4%) or three (28.3%) species. Relatively few hauls (<4% each) contained four or five species. The highest richness was found in the southern part of the area, in sites located at 75 and 94–105 m depth. In shallower hauls, capsules of *Zearaja chilensis*, *Schroederichthys bivius*, *Psammobatis lentiginosa* and *Psammobatis normani* were recorded. The deepest hauls contained capsules of *Amblyraja doellojuradoi*, *Bathyraja brachyurops*, *Bathyraja macloviana*, *P. normani* and *S. bivius*.

Figure 5 shows the relative abundance of capsules (considering all species) in the surveyed area. Densities ranged from 135 to 12,326 capsules/km^2. Highest densities (> 3000 capsules/km^2) were mainly found between 39°46.2′S and 40°29.9′S from 85 to 105 m and they were also recorded near the Mar del Plata Canyon at 37°59.7′S and 852 m. The highest value recorded was 12,326 capsules/km^2 and was located at 40°18.9′S and 85.4 m. The next two highest values were 7284 capsules/km^2 (39°46.2′S and 95.7 m) and 7138 capsules/km^2 (40°29.9′S and 87 m).

Psammobatis normani was the most abundant species in hauls, with capsule densities between 72 and 12,326 capsules/km^2. The major concentrations were observed between 39°46.2′S and 40°29.9′S over a depth range of 85.4–105 m (Figure 6a). Hauls containing *A. doellojuradoi* were obtained with densities between 169 and 3726 capsules/km^2. The highest density was observed on the continental slope at 37° 59.7′S and 852 m. Of the 11 hauls where this species was present, six were located on the continental slope (Figure 6b). Densities of *B. brachyurops* ranged from 62 to 540 capsules/km^2. High densities of capsules were recorded in three areas: at 37°59.7′S and 251 m, three hauls between 39°33′S and 40°2.4′S from 94 to 145 m and at 37°12.7′S and 97 m, the latter having the highest number. Hauls with densities over 1000 capsules/km^2 were not recorded (Figure 6c). *Bathyraja macloviana* occurred in densities of between 169 and

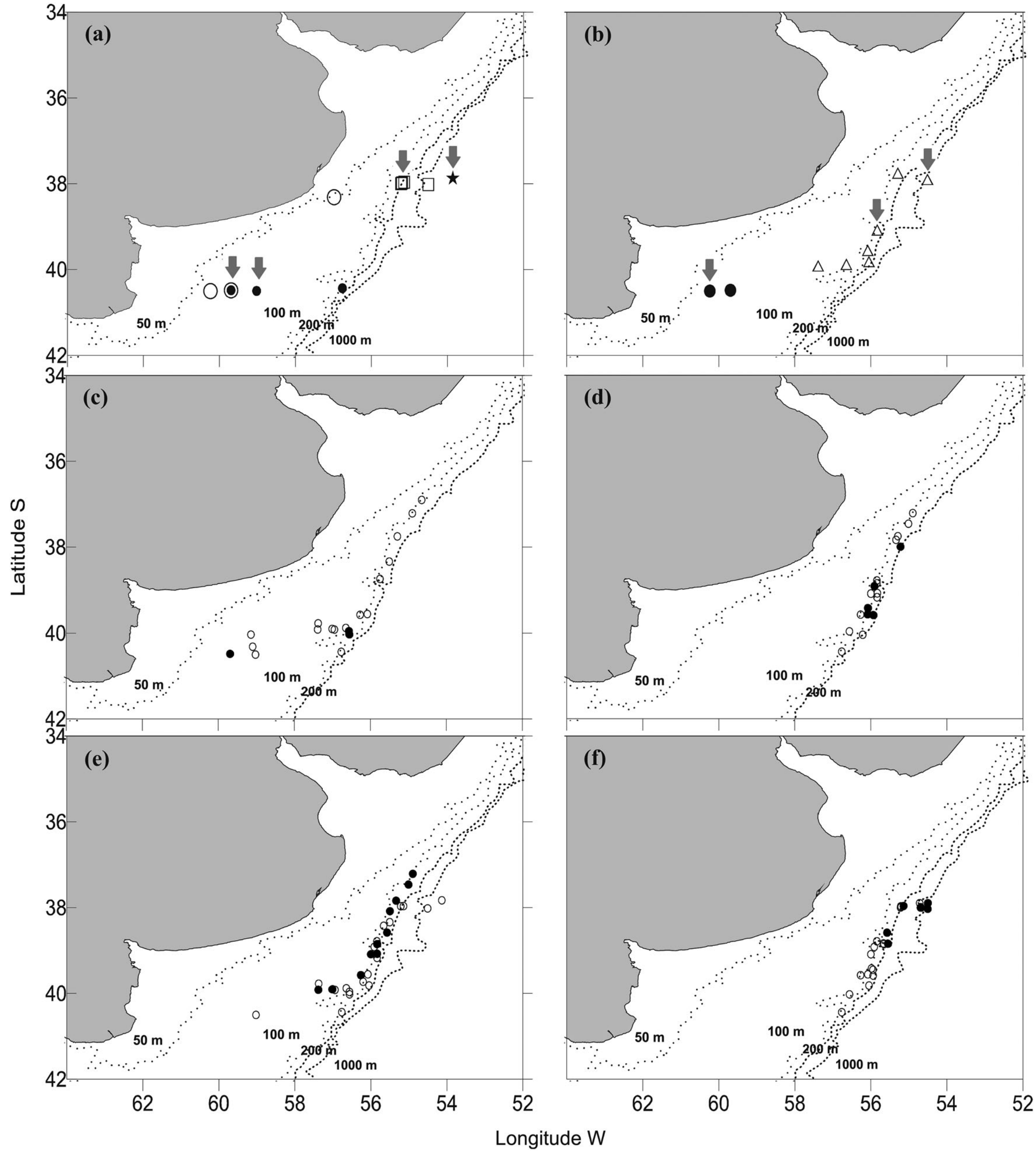

Figure 3. Egg case distribution of (a) *Bathyraja* sp. (★), *Bathyraja albomaculata* (□), *Schroederichthys bivius* (●) and *Zearaja chilensis* (○); (b) *Psammobatis lentiginosa* (●) and *Psammobatis rudis* (△); (c) *Psammobatis normani*; (d) *Bathyraja brachyurops*; (e) *Bathyraja macloviana*; and (f) *Amblyraja doellojuradoi*. Arrows in (a) and (b), and black circles in (c), (d), (e) and (f), indicate sites where capsules with eggs were recorded.

1619 capsules/km^2. The highest densities were recorded between 39°34.3′S and 40°26′S, from 91.3 to 105 m (Figure 6d). There were no hauls with densities of more than 3000 capsules/km^2.

In the case of the less abundant species such as *S. bivius*, egg cases were collected in three hauls with densities of between 108 and 1265 capsules/km^2. The highest density was located at 40°29.9′S and 87 m. Capsule densities of *P. lentiginosa* ranged between 36 and 450 capsules/km^2 and those of *Z. chilensis* from 144 to 150 capsules/km^2. The highest value for both species was located at 40°29.9′S and 63 m.

Discussion

Chondrichthyans, particularly skates, are a cosmopolitan group distributed in all oceans of the world. Besides the 14 species of oviparous chondrichthyans reported to be occurring in the nACS (50 to 200 m depth), three species of skates have been recorded

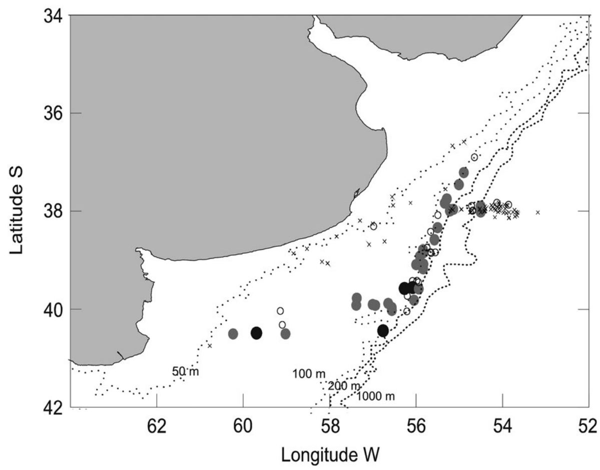

Figure 4. Egg case richness in the surveyed area. Species number in each haul was grouped in × 0, ○ 1, ● 2 and 3 and ● 4 and 5.

from deep waters off the Buenos Aires province (beyond 800 m): the thickbody skate *Amblyraja frerichsi* (Krefft, 1968), the butterfly skate *Bathyraja papilionifera* Stehmann, 1985 and the whitemouth skate *Bathyraja schroederi* (Krefft, 1968) (Cousseau et al. 2007). Although numerous taxonomic and biological studies on chondrichthyans of the Argentine Sea have been published (Díaz de Astarloa et al. 2008; Scenna & Díaz de Astarloa 2014, and references therein), no detailed studies describing the distribution and abundance of egg cases deposited by these species have been performed so far.

Many of the species considered here are distributed in both the southwest Atlantic Ocean (SAO) and the southeast Pacific Ocean (SPO). However, in this paper the distribution of egg cases will be discussed only in relation to the SAO distribution of all of the species. The shallower egg cases collected in this study corresponded to *Zearaja chilensis* and *Psammobatis lentiginosa*. *Zearaja chilensis* is distributed from Rio Grande do Sul in Brazil (29°46′S) to 32°S in Chile (14 to 600 m) (Menni & Stehmann 2000; Cousseau et al. 2007; Vargas Caro et al. 2015; Weigmann 2016). The highest abundance in the SAO is recorded between 50 and 150 m (Cousseau et al. 2007). Although this species is abundant in the nACS (Colonello & Cortés 2014), females bearing egg cases have only been reported from the sea of northern Patagonia (Chubut) at 50 m depth (Mabragaña et al. 2011). Even if the density was low, the presence of capsules with eggs in the nACS suggests a possible nursery site near the surveyed area. This information is relevant, taking into account that *Z. chilensis* is the most exploited skate species in the ACS (Massa et al. 2004). *Psammobatis lentiginosa* is only distributed in the SAO between 35°15′S and 45°19′S, with a gap in its range between 39°20′S and 44°22′S and from 28 to 170 m depth (Mabragaña et al. 2012; Weigmann 2016). Interestingly, the highest densities of capsules (with eggs) of *P. lentiginosa* were found south of the known distribution for nACS (40°29.9′S) expanding the latitudinal range of this species southwards.

Psammobatis normani is distributed from 35°24′S in the SAO to 30°S in the SPO (from 30 to 358 m depth) (Cousseau et al. 2007; Mabragaña 2007; Bustamante 2014; Weigmann 2016). In the nACS the highest abundances are between 40°S and 42°S and between 81 and 90 m depth (Mabragaña 2007). Mabragaña et al. (2011) reported the presence of females bearing eggs along the shelf from 71 to 182 m. Here, capsules of this species were observed between 36°54′S and 40°29.9′S and from 73.7 to 112 m depth, with the highest densities between 39°46.2′S and 40°29.9′S and from 85.4 to 95.7 m depth. The depth range of greatest abundance of *P. normani* overlaps with that of high concentrations of egg cases, of which some contain eggs, suggesting that this is an important nursery site for this species in the nACS close to the 80 and 90 m isobaths. This area would include both the Argentine shelf-break front and the 85 m isobath, which at latitudes near 40°S is far from the front.

Schroederichthys bivius is found from 25°50′S in southern Brazil to Valparaiso (33°S), from 12 to 359 m depth (Soto 2001; Sánchez et al. 2009; Bornatowski et al. 2014; Weigmann 2016). The highest concentrations in the SAO are recorded from 90 to 110 m depth (Sánchez et al. 2009). Capsules were observed near 40°S between 87 and 105 m. The location of the highest density (with eggs) is consistent with the

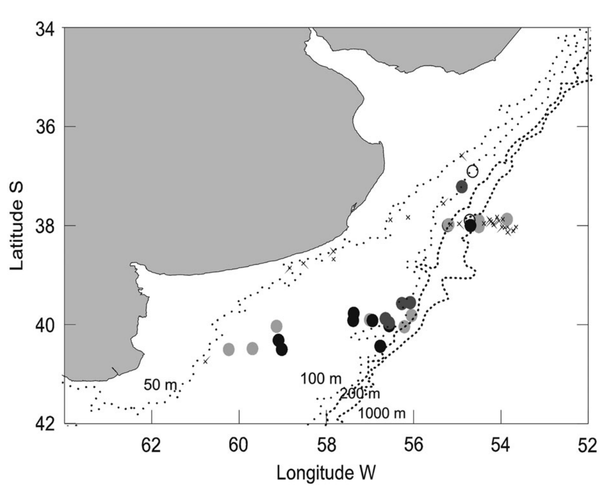

Figure 5. Egg case density considering all species. Density is expressed as number of egg cases/km^2: × 0, ○ 1 to 300, ● 301 to 1000, ● 1001 to 3000 and ● 3001 to 15,000.

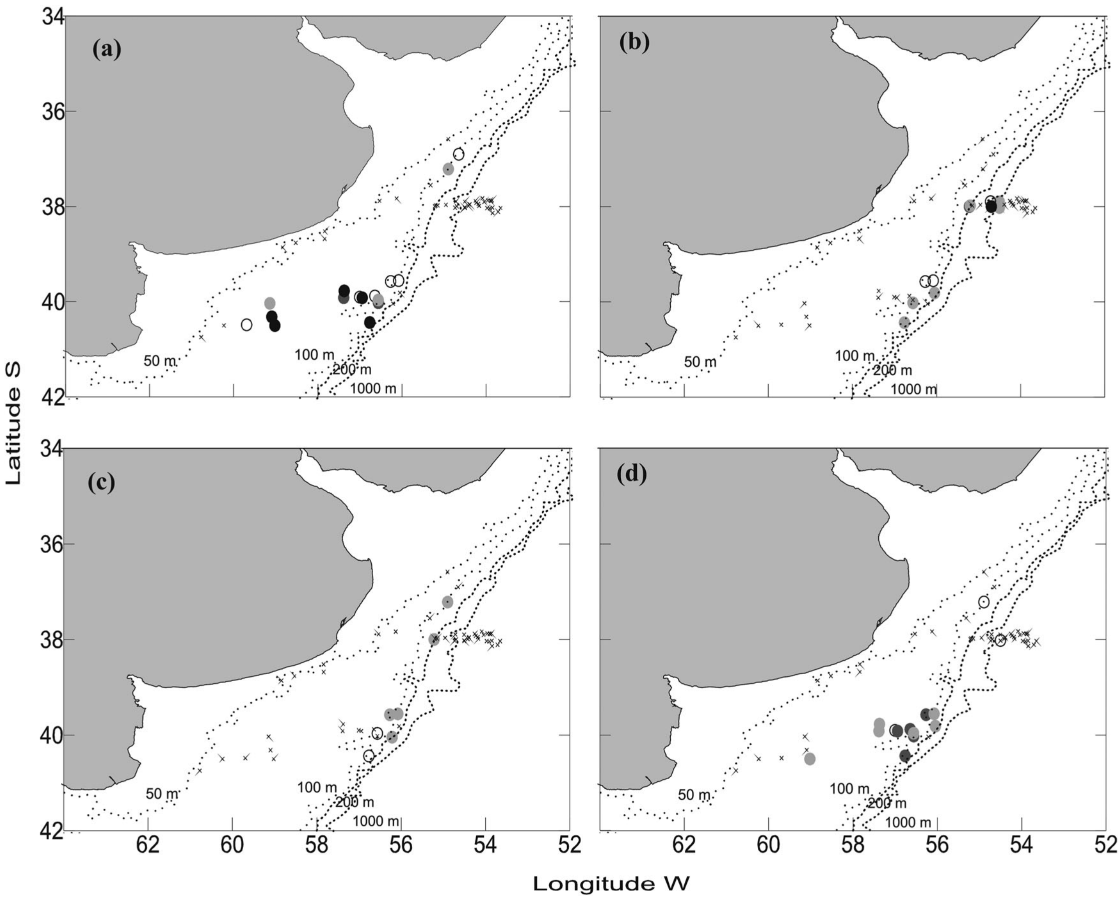

Figure 6. Egg case density of (a) *Psammobatis normani*; (b) *Amblyraja doellojuradoi*; (c) *Bathyraja brachyurops*; and (d) *Bathyraja macloviana*. Density is expressed as number of egg cases/km^2: × 0, ○ 1 to 300, ● 301 to 1000, ● 1001 to 3000 and ● 3001 to 15,000.

depths of greater abundance of the species and also with one of the oviposition sites of *P. normani*.

Psammobatis rudis is found from 35°18′S in the SAO to Valparaiso (33°S) in the SPO, at depths ranging from 30 to 475 m (Cousseau et al. 2007; Mabragaña 2007; Bustamante 2014; Weigmann 2016). In the nACS the highest abundances are recorded between 37°S and 38°S at depths from 81 to 90 m (Mabragaña 2007; Mabragaña & Giberto 2007). Mabragaña et al. (2011) only reported females of *P. rudis* bearing capsules in Patagonian waters (45°–55°S and from 75 to 116 m depth). The results of the present study also suggest possible nursery sites in the nACS.

Amblyraja doellojuradoi occurs from 36°S in the SAO to southern Chile (off Punta Arenas), between 51 and 1000 m depth (Menni & Stehmann 2000; Bizikov et al. 2004; Arkhipkin et al. 2012; Bustamante 2014; Weigmann 2016). The highest frequency in the SAO is between 36°S and 42°S (Cousseau et al. 2007). Capsules with eggs of *A. doellojuradoi* were found within this distribution range at depths from 95 to 1006 m. The present results indicate that the area near the head of the Mar del Plata Canyon would be an important nursery site for *A. doellojuradoi*. The highest density of capsules is found on the continental slope, since this species has deep-water habits. Additionally, *A. doellojuradoi* lays eggs in shelf waters (from 84 m) and this coincides with Mabragaña et al. (2011), who indicated the presence of females bearing eggs at 40° 59′S and 143 m depth.

Bathyraja brachyurops and *B. macloviana* occur from 36°S in the SAO to 51°S in the SPO, from 28 to 604 m depth for the former and 48 to 514 m for the latter (Bellisio et al. 1979; Menni & Stehmann 2000; Cousseau et al. 2007; Bustamante 2014; Weigmann 2016). Capsules of both species have been collected in the SAO within this distribution range. In the case of *B. macloviana*, although the known distribution in the SAO is from 63 m (Menni & Stehmann 2000), capsules with eggs were found from 84 m. Therefore, the shallower areas would not be oviposition sites for this species, at least in the nACS. The capsule distribution of *B. brachyurops* was limited to shelf waters, with no records beyond 251 m. A large number of hauls were carried out in the submarine canyon off Mar del Plata but no capsules of this species were collected, suggesting that it would not use this area as a nursery site, preferring the shallower shelf waters. *Bathyraja macloviana* was found at a greater density than *B. brachyurops*, but these values are well below those reported for other *Bathyraja* species (Hoff 2010). Both species showed a similar egg case distribution pattern and their highest densities were mostly observed south of 39°S. Mabragaña et al. (2011) found females of *B. brachyurops* and *B. macloviana* bearing egg cases only in Patagonian waters within a range of 104–137 m and 106–144 m depth, respectively. Nursery areas for these two species are closely related to the Argentine shelf-break front, where dense beds of the Patagonian scallop *Zygochlamys patagonica* (King & Broderip, 1832) are found (Lasta & Bremec 1998).

Bathyraja albomaculata occurs from 37°S in the SAO to 38°S in the SPO, from 55 to 945 m depth (Cousseau et al. 2000; Menni & Stehmann 2000; Cousseau et al. 2007; Bustamante 2014; Weigmann 2016). High numbers of *B. albomaculata* egg cases have been found in the waters off central Patagonia (43°S–60°W) in benthic samples (Lucifora & García 2004; Scenna 2011), suggesting that this area is an important nursery site for *B. albomaculata* in the SAO. In the nACS, this species is present at a depth range of 65–310 m, with the highest densities between 250 and 310 m (Ruocco et al. 2006). Females bearing capsules were reported along the shelf, between 80 and 180 m (Ruocco et al. 2006; Mabragaña et al. 2011). In this survey, capsules were recorded above 250 m, but the low number of egg cases collected does not allow a clear interpretation of these observations.

Finally, egg cases of *Bathyraja* sp. collected at 37° 52.15′S and 1712 m represent the deepest record of an egg case in the Southwest Atlantic Ocean. They were assigned to the genus *Bathyraja* based on features of the posterior horns (Mabragaña et al. 2011), but are different from other *Bathyraja* capsules from the ACS described so far. There are three other species of *Bathyraja* that inhabit the deepest part of the shelf, that are also present on the slope: the graytail skate *Bathyraja griseocauda* (Norman, 1937), the multispine skate *Bathyraja multispinis* (Norman, 1937), and the cuphead skate *Bathyraja scaphiops* (Norman, 1937). In addition, two species of *Bathyraja* distributed exclusively on the slope have been recorded: *B. papilionifera* and *B. schroederi* (Menni & Stehmann 2000; Cousseau et al. 2007; Stehmann & Pompert 2014). However, since no descriptions of capsules of all of these species have yet been made, they could belong to any of these skate species. The specific identification of a tissue sample of the embryo by means of molecular analysis (DNA barcoding) is in process.

In this work, sites with high concentrations of egg cases generally presented both full and empty eggs (e.g. capsules with eggs and the ones without eggs), suggesting that these sites are, in fact, nursery grounds. Areas with viable or full eggs were surrounded by areas with empty eggs, which is more or less in agreement with Hoff (2010). The author observed that, in general, skate nursery sites possess areas of high numbers of viable eggs (> 30%) surrounded by broadly scattered areas of predominantly (> 70%) empty egg cases.

Most of the skate species considered in this paper (*A. doellojuradoi*, *B. brachyurops*, *B. macloviana*, *P. rudis* and *P. normani*) had egg case distributions near the Argentine shelf-break front. Marine fronts are areas of high biological productivity, both primary and secondary (Acha et al. 2015); therefore, they represent areas of high food availability. The Argentine shelf-break front is a permanent feature that characterizes the border of the shelf where subantartic shelf waters meet the cooler and more saline waters of the Malvinas current, producing a thermohaline front (Martos & Piccolo 1988; Lutz & Carreto 1991). It is located along the boundary of the shelf and its inner boundary lies between the 90 and 100 m isobaths. Dense beds of *Z. patagonica* coincide with this front between 90 and 150 m, from about 38°30′S to 43°S (Lasta & Bremec 1998). High concentrations of organisms of several taxonomic groups (phytoplankton, zooplankton, high densities of eggs and larvae of teleost fishes) associated with this front have demonstrated the high productivity of the Argentine shelf-break zone (Acha et al. 2004), offering valuable feeding and/or reproductive habitats for benthic fishes such as skates. Data collected for the present paper indicate that many skate species use the Argentine shelf-break front for laying eggs. As stated by Hoff (2008), areas of high biological productivity, such as marine fronts, may be a requirement for nursery sites because of the energy requirements of adults for reproduction. He also proposed that the habitat requirements of newly hatched juvenile skates may not be the same as those for nursery-site selection, because very few neonates have been found in the same location where capsules occurred (Hoff 2008). Lucifora et al. (2012) analysed the distribution patterns of chondrichthyan species in the Southwest Atlantic and concluded that diversity is more likely to occur on marine fronts than elsewhere as a result of an abundant supply of prey organisms (e.g. benthic invertebrates). The results of this study are therefore consistent with those of

Lucifora et al. (2012), with high densities of egg cases at marine fronts where chondrichthyan diversity is high. Love et al. (2008) suggest other reasons for the differential distribution of egg cases in the California Bight. They observed that significantly more capsules were laid over the highest relief areas than over the other habitats and concluded that they would be most exposed to currents and therefore less available to at least some predators than eggs laid at lower levels.

The identification and conservation of nursery sites for oviparous elasmobranchs have been stressed over the last decade (Ellis et al. 2004; Hoff 2008, 2010; Hunt et al. 2011; Serra-Pereira et al. 2014; Amsler et al. 2015). Egg-laying areas explored here are the first report of this kind in the Southwest Atlantic Ocean. This study represents an initial approach, since relatively important nursery sites were found for at least four of the 14 oviparous chondrichthyan species occurring in the nACS. The egg case densities obtained at these sites are much lower (one order of magnitude) than those reported by Love et al. (2008) and Hoff (2010). This could be attributed to two reasons: (1) marine fronts in the Southwest Atlantic Ocean cover a large area along the shelf and therefore there are many productive habitats to be occupied. Most skate species have a wide distribution in the ACS, so nursery areas would be more widespread and less confined to small areas as those previously reported; or (2) trawls were not conducted in the centre of the nursery areas. Future studies surveying those areas surrounding sites of high density would be necessary to test this hypothesis.

Recognizing and protecting egg-laying habitats may be one important step to a long-term conservation of oviparous chondrichthyan populations. In this way, two important aspects must be noted, given the vulnerability of this group: most of these species are commercially exploited in the Southwest Atlantic, and nursery sites associated with scallop beds could be strongly disturbed by fishing activities. Therefore, a continuous monitoring of these areas, assessing how they change and how they are affected by fishing activities over time, is a priority.

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