



# Egg capsules of the multispine skate, *Bathyraja multispinis*: the largest of the genus recorded in South American waters

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## Abstract

Egg capsules of the multispine skate, *Bathyraja multispinis* (Norman, 1937), described here for the first time, are larger (180 mm in length without horns) than those of any *Bathyraja* species from the South-west Atlantic Ocean (SWA). The capsule's surface texture is relatively smooth by the presence of woven-like fibres. However, below the fibres, it is rough to the touch by the presence of longitudinal ridges and prickles of different shapes and sizes, ending in two or more digitiform projections. An identification key to all described *Bathyraja* egg capsules occurring in the SWA from 34° to 55°S is provided.

**Keywords** Rajiformes · Arhynchobatidae · Capsules · Key · South-west Atlantic Ocean

## Introduction

Skates (order Rajiformes) are oviparous. Females lay their eggs on the seafloor encapsulated in a tough corneous structure, where the embryo develops while feeding from the yolk until hatching (Conrath and Musick 2012). The capsule is the only protection during the embryonic development period, which could range from months to a year or longer depending on the species and environmental conditions (Berestovskii 1994; Jañez and Sueiro 2007; Mabragaña et al. 2015). The specificity of egg capsule morphology (Ishiyama 1958; Ebert and Davis 2007; Concha et al. 2012) makes them a tool for taxonomical (Ishihara et al. 2012; Fischer et al. 2014), biological (Luer et al. 2007; Vazquez et al. 2020), and ecological studies (Hoff 2010; Hunt et al. 2011; Cordeiro and Oddone 2019). The latter include the identification of egg capsule

nurseries, critical areas that support sensitive life stages of oviparous chondrichthyans (Martins et al. 2018).

The genus *Bathyraja* (Arhynchobatidae) constitutes the most diverse genus within Rajiformes (Ebert and Compagno 2007; Last et al. 2016; Stehmann et al. 2021). In the sector of the South-west Atlantic Ocean (SWA) from 34° to 55°S, it is represented by thirteen species (Menni and Stehmann 2000; Figueroa 2019; Weigmann et al. in press). One of the largest species of this genus reported from the continental shelf of the SWA is the multispine skate, *Bathyraja multispinis* (Norman, 1937), which can reach a total length of 1260 mm (Cousseau et al. 2007; Last et al. 2016). It is distributed around southern South America, from southern Chile to southern Brazil on the continental shelf and between 72 and 740 m depth (Lamilla and Pequeño 1999; Last et al. 2016; Weigmann 2016; Sabadin et al. 2020). In the SWA, this species is strictly stenothermal

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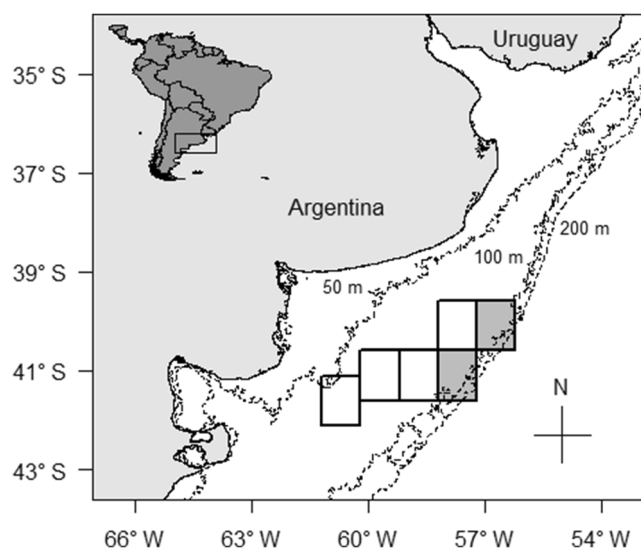
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and stenohaline, occurring mainly in mid-shelf waters and extending into waters of the outer shelf or slope (Figueroa et al. 1999; Arkhipkin et al. 2012). Currently, the International Union for Conservation of Nature (IUCN) categorizes *B. multispinis* as Near Threatened (Pollom et al. 2020).

In spite of its wide distribution and conservation status, little is known about the reproductive biology of *B. multispinis* (Scenna 2011; Arkhipkin et al. 2012). In an attempt to fill this gap, and as a first step to recognize possible nursery sites in the SWA, here we describe for the first time the egg capsule of *B. multispinis*, and compare it with those of congeners from the SWA whose egg capsules are known: *Bathyrāja brachyurops* (Fowler, 1910), *Bathyrāja magellanica* (Philippi, 1902), *Bathyrāja macloviana* (Norman, 1937), *Bathyrāja albomaculata* (Norman, 1937), *Bathyrāja scaphiops* (Norman, 1937), and *Bathyrāja griseocauda* (Norman, 1937) (Paesch and Oddone 2008; Mabragaña et al. 2011, 2017). Egg capsules of *B. multispinis* were also compared with those of *Bathyrāja eatonii* (Günther, 1876) and *Bathyrāja maccaini* Springer, 1971, two Southern Ocean species (Last et al. 2016) also recorded north of 55°S in the SWA, between Malvinas and South Georgia Islands (Weigmann et al. in press). In these cases, information available is limited to their size or images (Meissner 1987; Ishihara et al. 2012; Last et al. 2016; Chagnoux 2022).

## Material and methods

An egg-bearing female of *B. multispinis* (1158 mm total length) was caught in October 2019 by a commercial vessel fishing in the SWA between 38° and 41° 56' S, 55° and 58° W,



**Fig. 1** Fishing area (white square) on the Argentine continental shelf where the commercial bottom-trawl vessel operated; (gray square) probable areas where the adult female *Bathyrāja multispinis* was collected. Map created in R Core Team (2021); [www.R-project.org](http://www.R-project.org)

at a depth range of 70 to 350 m (Fig. 1). The specimen was examined during routine sampling of fishery landings at a fish processing plant in the Mar del Plata harbor, where two egg capsules were retrieved from its uteri. In the laboratory, egg capsules were described and measured following Ebert and Davis (2007), Mabragaña et al. (2011), and Stehmann et al. (2021). Morphometric measurements were: egg case total length including horizontal length of bent horns ( $TL_{EC}$ ), egg case length without horns ( $L_{EC}$ ), maximum egg case width ( $W_{max}$ ), minimum egg case width ( $W_{min}$ ), anterior border width (distances between the bases of the anterior horns) ( $W_{AB}$ ), posterior border width (distances between the bases of the posterior horns) ( $W_{PB}$ ), central body length (excl. aprons) ( $L_{CB}$ ), central body width (excl. lateral keels) ( $W_{CB}$ ), capsule height ( $H_C$ ), anterior horn length ( $L_{AH}$ ), straight distance from the anterior horn base to the tips ( $L_{AH2}$ ), posterior horn length ( $L_{PH}$ ), straight distance from the posterior horn base to the tips ( $L_{PH2}$ ), lateral keel width ( $W_{LK}$ ), keel thickness ( $T_{LK}$ ), anterior apron ( $A_A$ ), posterior apron ( $A_P$ ), and straight distance from anterior apron to apex of anterior horn ( $L_{AH3}$ ). All measurements were taken with a digital caliper (0.1 mm precision). For characterizing and photographing the capsule surface, a Leica MC 170 Full High Definition 1080 P camera under a stereoscopic microscope (Leica M165C) with reflected light was used. Finally, the egg capsules were fixed in 4% formalin, preserved in 75% ethanol, cataloged, and deposited in the Ichthyological Collection of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Mar del Plata, Argentina), as INIDEP 864.

## Results

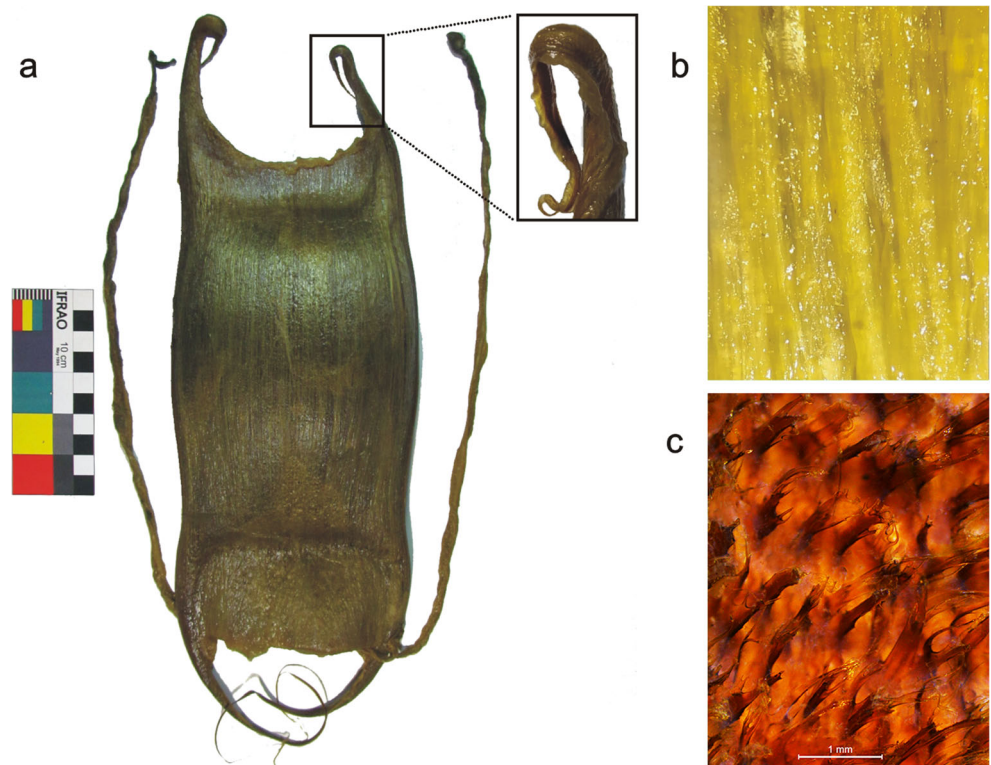
All morphometric measurements are provided in Table 1. Both egg capsules (Fig. 2a) were 180 mm  $L_{EC}$ , with  $W_{max}$  51–52% of  $L_{EC}$ . The egg capsule surface was covered with soft woven-like fibres giving a smooth texture (Fig. 2b). Under these fibres, the surface texture was relatively rough to touch, with longitudinal ridges and prickles of different shapes and sizes that ended in two or more digitiform projections (Fig. 2c). All these ornamentations were embedded in a gelatinous matrix. Attachment fibres originated in the region of the posterior horns, close to the end of the posterior apron. Their length 1.6–1.9 times  $L_{EC}$  and 3.2–3.8 times  $W_{max}$ . Respiratory fissures were relatively large (78 mm) and were located latero-ventrally on each horn. Each anterior horn had an internal transparent flange at its end (Fig. 2a). The  $T_{LK}$  was > 2 mm and the  $W_{LK}$  was narrow (5% of  $W_{max}$ ). The posterior apron was wider (2.55 times) than the anterior apron. Posterior horns curved inward and were slightly longer (1.4 times) than the anterior ones. Colour before preservation was uniformly light greenish (Fig. 2a).

**Table 1** Morphometric measurements (in mm) of two egg capsules from a female *Bathyraja multispinis* from the northern Argentine continental shelf, deposited in the Ichthyological Collection of Instituto Nacional de Investigación y Desarrollo Pesquero, INIDEP

| Morphometric measurements | INIDEP 864.1 (left egg capsule) | INIDEP 864.2 (right egg capsule) |
|---------------------------|---------------------------------|----------------------------------|
| TL <sub>EC</sub>          | 291                             | 270                              |
| L <sub>EC</sub>           | 180                             | 180                              |
| W <sub>max</sub>          | 91.8                            | 92.4                             |
| W <sub>min</sub>          | 85.1                            | 84.3                             |
| W <sub>AB</sub>           | 62                              | 57                               |
| W <sub>PB</sub>           | 68                              | 67                               |
| L <sub>CB</sub>           | 126                             | 130                              |
| W <sub>CB</sub>           | 79,8                            | 88                               |
| H <sub>C</sub>            | 38                              | 45                               |
| L <sub>AH</sub>           | 136                             | 128                              |
| L <sub>AH2</sub>          | 65                              | 64                               |
| L <sub>AH3</sub>          | 49.6                            | 52.3                             |
| L <sub>PH</sub>           | 205                             | 165                              |
| L <sub>PH2</sub>          | 92                              | 84                               |
| W <sub>LK</sub>           | 5.3                             | 4.4                              |
| T <sub>LK</sub>           | 3.4                             | 4.7                              |
| A <sub>A</sub>            | 14.02                           | 15.5                             |
| A <sub>P</sub>            | 39.9                            | 34.4                             |

TL<sub>EC</sub>, egg capsule total length incl. horizontal length of bent horns; L<sub>EC</sub>, egg capsule length without horns; W<sub>max</sub>, maximum egg capsule width; W<sub>min</sub>, minimum egg capsule width; W<sub>AB</sub>, posterior border width (distances between the bases of the posterior horns), W<sub>PB</sub>, posterior border width (distances between the bases of the posterior horns); L<sub>CB</sub>, central body length (excl. aprons); W<sub>CB</sub>, central body width (excl. lateral keels); H<sub>C</sub>, capsule height; L<sub>AH</sub>, anterior horn length; L<sub>AH2</sub>, straight distance from the anterior horn base to the tips; L<sub>AH3</sub>, straight distance from the anterior apron to the apex of the anterior horn; L<sub>PH</sub>, posterior horn length; L<sub>PH2</sub>, straight distance from the posterior horn base to the tips; W<sub>LK</sub>, lateral keel width; T<sub>LK</sub>, keel thickness; A<sub>A</sub>, anterior apron; A<sub>P</sub>, posterior apron

**Fig. 2** **a** Dorsal view of *Bathyraja multispinis* egg capsule (each block 1 cm); with **b** magnified view (20×) of the capsule surface showing the woven-like fibres; and **c** magnified view (20×) of the capsule surface showing the ornamentation below the fibres. Portion of the capsule observed in **b** and **c** have the same orientation than capsule of **a**



## Discussion

Recognizing and protecting nursery habitats may be one important step to long-term conservation of oviparous chondrichthyan populations (Hoff 2016). Different egg nursery sites of *Bathyraja* spp. have been identified in several regions of the world (Hoff 2010; Hunt et al. 2011; Treude et al. 2011; Amsler et al. 2015), including the SWA (Vazquez et al. 2016). A requirement for the identification of these areas is the accurate taxonomic identification of the egg capsules (Mabragaña et al. 2017).

Currently, there is available information for more than 70% of the 52 valid species of *Bathyraja* regarding their egg capsules (Ebert 2005; Ebert and Davis 2007; Paesch and Oddone 2008; Ishihara et al. 2012; Last et al. 2016; Mabragaña et al. 2011, 2017; Stehmann and Merrett 2001; Stehmann et al. 2021). The specific description of the egg capsule morphology of *B. multispinis* reported here may allow future studies to identify egg nurseries for this species in the SWA and South East Pacific. Morphologically, the egg capsules of this species have one distinctive feature, their large size: the capsules of *B. multispinis* are indeed the largest known from any SWA *Bathyraja* (Meissner 1987; Ishihara et al. 2012; Last et al. 2016; Mabragaña et al. 2011, 2017). Even more, it is one of the largest egg capsules of the world within the genus *Bathyraja*, only surpassed by those of *B. pallida* (Forster, 1967) ( $L_{EC} = c. 300$  mm) and *B. richardsoni* (Garrick, 1961) ( $L_{EC} = c. 208$  mm) (Stehmann and Merrett 2001). It is

worth mentioning that the size of the capsule of *B. pallida* was estimated from an incomplete egg capsule and those of *B. richardsoni* were reconstructed from a photograph (Stehmann and Merrett 2001).

Regarding their congeners from the SWA, the egg capsules of *B. multispinis* are similar to those of *B. griseocauda*. However, in the latter, the capsule surface texture is relatively smooth, without prickles, spines, or other ornamentations (Mabragaña et al. 2017), whereas in *B. multispinis*, even though it seems smooth due to the woven-like fibres, below these fibres, the surface is rough to the touch with longitudinal ridges and prickles. In addition, egg capsules of *B. multispinis* are larger than those of *B. griseocauda* (180 vs 140 mm  $L_{EC}$ ). Their large size also allows a clear differentiation from the other rough-surface egg capsules (e.g., *B. albomaculata*, *B. macloviana*, *B. scaphiops*, and *B. magellanica*; Paesch and Oddone 2008; Mabragaña et al. 2011, 2017). Meissner (1987) illustrated an egg capsule of *B. eatonii*. Similarly to that of *B. multispinis*, it possesses very large attachment fibres in the region of the posterior horns, close to the end of the posterior apron. But, a picture provided by Chagnoux (2022) also shows the absence of woven-like fibres in *B. eatonii* egg capsules, a diagnostic feature of *B. multispinis* egg capsules. Finally, in addition to the above, the egg capsules of *B. multispinis* are larger than those of *B. maccaini* and *B. eatonii* (180 vs 156 and 120 mm  $L_{EC}$ , respectively) (Meissner 1987; Ishihara et al. 2012; Last et al. 2016).

## Key to *Bathyraja* egg capsules from the SWA (34° to 55° S)

1. Very large egg capsules, length > 110 mm, surface covered (or not) with woven-like fibres in fresh capsules; below the fibres, surface texture rough to the touch or surface relatively smooth; attachment fibres on posterior horns ..... 2
  - Medium to large egg capsules, length < 100 mm, surface relatively smooth but with denticles under magnification or surface rough to the touch ..... 5
2. Surface covered with woven-like fibres in fresh capsules; below the fibres, surface texture rough to the touch with longitudinal striations and prickles of different sizes visible under magnification;  $L_{EC} > 170$  mm ..... *B. multispinis*
  - Fresh capsules surface without woven-like fibres,  $L_{EC} < 160$  mm; surface texture relatively smooth or rough ..... 3
3.  $L_{EC} > 150$  mm ..... *B. maccaini*
  - $L_{EC} < 150$  mm, surface texture relatively smooth or rough ..... 4
4. Surface texture relatively smooth, finely striated, without denticles, prickles or any ornamentation under magnification;  $L_{EC} > 130$  mm ..... *B. griseocauda*
  - Surface texture relatively rough, with longitudinal striations,  $L_{EC} < 130$  mm ..... *B. eatonii*
5. Surface texture relatively smooth, finely striated, with rasp-like denticles under magnification but without prickles; attachment fibres on posterior horns only ..... *B. brachyurops*
  - Surface texture rough to the touch, with longitudinal striations having prickles; attachment fibres absent or on both anterior and posterior horns ..... 6

6. Lateral keel remarkably lighter in colour than rest of the capsule, > 6 mm;  $W_{LK}$  relatively broad, 12–16% of the  $W_{max}$ ; surface of capsule with long, thin prickles of similar size visible under magnification ..... *B. magellanica*
- Lateral keel similar in colour to rest of the capsule, ≤ 6 mm;  $W_{LK}$  relatively narrow (< 11% of  $W_{max}$ ); surface of capsule with other pattern of ornamentation under magnification..... 7
7. Egg capsule length < 85 mm, maximum width < 50 mm, surface texture coarse and rough to touch, covered by papillose longitudinal ridges; prickles with different sizes and shapes visible under magnification ..... *B. macloviana*
- Egg capsule length > 85 mm, maximum width > 50 mm, surface of capsule with other pattern of ornamentation ..... 8
8. Surface of capsule with long and thin prickles of different sizes under magnification, giving a velvety texture to touch; attachment fibres are absent;  $W_{LK}$  less than 16 times in  $W_{max}$  ..... *B. albomaculata*
- Surface with prickles of similar size visible under magnification; attachment fibres on both anterior and posterior horns,  $W_{LK}$  more than 30 times in  $W_{max}$  ..... *B. scaphiops*

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## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethical approval** No animal testing was performed during this study. Ethical review and approval was not required for the specimen study because it was based on egg capsules retrieved from uteri of a skate collected by a commercial bottom-trawl vessel.

**Sampling and field studies** All necessary permits for sampling have been obtained by the authors from the competent authorities.

**Data availability** The manuscript has no associated data. All data is included in the manuscript.

**Author contribution** JMR, EM, and SAB: conceptualization. JMR and DES: obtained the samples. JMR and EM: generated and analysed the data and prepared the first draft of the manuscript. JMR and DES: prepared the egg capsule figures. All six authors corrected the draft and approved the final version of the manuscript.

## References

- Amsler MO, Smith KE, McClintock JC, Stingh H, Thatje S, Vos SC, Brothers CJ, Brown A, Ellis D, Anderson J, Aronson RB (2015) In situ observations of a possible skate nursery off the western Antarctic Peninsula. *J Fish Biol* 86:1867–1872. <https://doi.org/10.1111/jfb.12679>
- Arkipkin A, Brickle P, Laptikhovsky V, Pompert J, Winter A (2012) Skate assemblage on the eastern Patagonian Shelf and Slope: structure, diversity and abundance. *J Fish Biol* 80:1704–1726. <https://doi.org/10.1111/j.1095-8649.2012.03260.x>
- Berestovskii EG (1994) Reproductive biology of skates of the family Rajidae in the seas of the far north. *J Ichthyol* 34(6):26–37
- Chagnoux S (2022) The fishes collection (IC) of the Muséum national d'Histoire naturelle (MNHN - Paris). Version 57.265. MNHN - Museum national d'Histoire naturelle. Occurrence dataset 10.15468/tm7whu accessed via [GBIF.org](https://www.gbif.org/occurrence/583511612) on 28 June 2022. <https://www.gbif.org/occurrence/583511612>
- Concha F, Oddone MC, Bustamante C, Morales N (2012) Egg capsules of the yellownose skate *Zearaja chilensis* (Guichenot 1848) and the roughskin skate *Dipturus trachyderma* (Kreff & Stehmann 1974) (Rajiformes: Rajidae) from the south-eastern Pacific Ocean. *Ichthyol Res* 59:323–327. <https://doi.org/10.1007/s10228-012-0293-z>
- Conrath CL, Musick JA (2012) Reproductive biology of elasmobranchs. In: Carrier C, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives*. CRC Press, Boca Raton, pp 291–311
- Cordeiro L, Oddone MC (2019) Diversidad y abundancia de casquillos de huevos de raya eclosionada (Chondrichthyes: Elasmobranchii: Rajoidei) en Cassino Beach, Rio Grande do Sul, Brasil. *Bol Soc zoológica Urug* 28(2):38–58. <https://doi.org/10.26462/28.2.1>
- Cousseau MB, Figueroa DE, Díaz de Astarloa JM, Mabragna E, Lucifora LO (2007) Rayas, Chuchos y Otros Batoideos del Atlántico Sudoccidental (34° – 55° S). Publicaciones especiales INIDEP, Mar del Plata
- Ebert DA (2005) Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. *J Fish Biol* 66:618–649. <https://doi.org/10.1111/j.1095-8649.2005.00628.x>
- Ebert DA, Compagno LJD (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environ Biol Fishes* 80: 111–124. <https://doi.org/10.1007/s10641-007-9247-0>
- Ebert DA, Davis CD (2007) Description of skate egg cases (Chondrichthyes: Rajiformes: Rajoidei) from the eastern North Pacific. *Zootaxa* 1393:1–18. <https://doi.org/10.11646/zootaxa.1393.1.1>
- Figueroa DE (2019) Clave de Peces Marinos del Atlántico Sudoccidental, entre los 33° S y 56° S. INIDEP, Mar del Plata
- Figueroa DE, Martos P, Reta R, Cousseau MB, Díaz de Astarloa JM (1999) Distribución de las rayas de Argentina y Uruguay y su relación con las masas de agua. VIII Congreso Latinoamericano de Ciencias Del Mar. Perú. Expanded abstract, 148–149
- Fischer J, Licht M, Kriwet J, Schneider JW, Buchwitz M, Bartsch P (2014) Egg capsule morphology provides new information about the interrelationships of chondrichthyan fishes. *J Syst Paleontol* 12(3):389–399. <https://doi.org/10.1080/14772019.2019.762061>

- Forster GR (1967) A new deep-sea ray from the Bay of Biscay. *J Mar Biol Assoc U K* 47(2):281–286. <https://doi.org/10.1017/S0025315400056393>
- Fowler HW (1910) Notes on batoid fishes. *Proc Acad Nat Sci Philadelphia* 62:468–475
- Garrick JAF (1961) Studies on New Zealand Elasmobranchii. Part XIII—a new species of *Raja* from 1,300 fathoms. *Trans R Soc N Z* 88(4):743–748
- Günther A (1876) Remarks on fishes, with descriptions of new species in the British Museum, chiefly from southern seas. *Ann Mag Nat Hist (Series 4)* 17(101):389–402
- Hoff GR (2010) Identification of skate nursery habitat in the eastern Bering Sea. *Mar Ecol Prog Ser* 403:243–254. <https://doi.org/10.3354/meps08424>
- Hoff GR (2016) Identification of multiple nursery habitats of skates in the eastern Bering Sea. *J Fish Biol* 88:1746–1757. <https://doi.org/10.1111/jfb.12939>
- Hunt JC, Lindsay DJ, Shahalemi RR (2011) A nursery site of the golden skate (Rajiformes: Rajidae: *Bathyrāja smirmovi*) on the Shiribeshi Seamount, Sea of Japan. *Mar Biodivers Rec* 4:e70. <https://doi.org/10.1017/S1755267211000728>
- Ishihara H, Treloar M, Bor PHF, Senou H, Jeong CH (2012) The comparative morphology of skate egg capsules (Chondrichthyes: Elasmobranchii: Rajiformes). *Bull Kanagawa Prefect Mus (Nat Sci)* 41:9–25
- Ishiyama R (1958) Studies on the rajid fishes (Rajidae) found in the waters around Japan. *J Shimonoseki Univ Fish* 7:191–394
- Jañez JA, Sueiro MC (2007) Size at hatching and incubation period of *Sympterygia bonapartii* (Müller & Henle, 1841) (Chondrichthyes, Rajidae) bred in captivity at the Temaiken Aquarium. *J Fish Biol* 70:648–650. <https://doi.org/10.1111/j.1095-8649.2007.01332.x>
- Lamilla J, Pequeño G (1999) Descripción esquelética comparativa y primer registro en el Océano Pacífico de *Bathyrāja multispinis* (Norman, 1937) (Rajiformes; Rajoidei), con referencia a otras especies de *Bathyrāja*. *Rev Biol Mar Oceanogr* 34(2):281–290
- Last PR, Stehmann MFW, Séret B, Weigmann S (2016) Softnose skates, family Arhynchobatidae. In: Séret B, Stehmann MFW, Naylor GJP (eds) Last PR, White WT, Carvalho MRde. *Rays of the world*. CSIRO Publishing, Melbourne, pp 364–472
- Luer CA, Walsh CJ, Bodine AB, Wyffels JT (2007) Normal embryonic development in the clearnose skate, *Raja eglanteria*, with experimental observations on artificial insemination. *Environ Biol Fishes* 80(2–3):239–255. <https://doi.org/10.1007/s10641-007-9219-4>
- Mabragaña E, Figueroa DE, Scenna LB, Díaz de Astarloa JM, Colonello JH, Delpiani G (2011) Chondrichthyan egg cases from the south-west Atlantic Ocean. *J Fish Biol* 79:1261–1290. <https://doi.org/10.1111/j.1095-8649.2011.03111.x>
- Mabragaña E, Lucifora LO, Corbo ML, Díaz de Astarloa JM (2015) Seasonal reproductive biology of the bignose fanskate *Sympterygia acuta* (Chondrichthyes, Rajidae). *Estuaries Coast* 38:1466–1476. <https://doi.org/10.1007/s12237014-9888-0>
- Mabragaña E, Vazquez DM, Gabbanelli V, Sabadin D, Barbini SA, Lucifora LO (2017) Egg cases of the graytail skate *Bathyrāja griseocauda* and the cuphead skate *Bathyrāja scaphiops* from the South-west Atlantic Ocean. *J Fish Biol* 91:968–974. <https://doi.org/10.1111/jfb.13380>
- Martins APB, Heupel MR, Chin A, Simpfendorfer CA (2018) Batoid nurseries: definition, use and importance. *Mar Ecol Prog Ser* 595:253–267. [10.3354/meps12545](https://doi.org/10.3354/meps12545)
- Meissner EE (1987) A new species of ray (Rajidae, Batoidei) from the Indian Ocean sector of the Antarctic. *Zool Zhurnal* 66(12):1840–1849
- Menni RC, Stehmann M (2000) Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. *Rev Mus Argent Cienc Nat* 2(1):69–109
- Norman JR (1937) Coast fishes. Part II. The Patagonian region. In: *Discovery Reports Vol.16*. University Press, Cambridge, pp. 1–150
- Paesch L, Oddone MC (2008) Size at maturity and egg capsules of the softnose skates *Bathyrāja brachyrops* (Fowler 1910) and *Bathyrāja macloviana* (Norman 1937) (Elasmobranchii: Rajidae) in the SW Atlantic (37° 00′ – 39° 30′ S). *J Appl Ichthyol* 25(S1):66–71. <https://doi.org/10.1111/j.1439-0426.2008.01114.x>
- Philippi RA (1902) Descripción de cinco especies nuevas chilenas del orden de los Plagiostomos. *An Univ Chile* 109:303–315
- Pollon R, Dulvy NK, Acuña E, Bustamante C, Charvet P, Chiamonte GE, Cuevas JM, Herman K, Paesch L, Pompert J, Velez-Zuazo X (2020) *Bathyrāja multispinis*. The IUCN Red List of Threatened Species 2020: e.T63144A3121878. <https://doi.org/10.2305/IUCN.UK.2020-3.RTLS.T63144A3121878>. Accessed 29 November 2021
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Sabadin DE, Lucifora LO, Barbini SA, Figueroa DE, Kittlein M (2020) Towards regionalization of the chondrichthyan fauna of the Southwest Atlantic: a spatial framework for conservation planning. *ICES J Mar Sci* 77(5):1893–1905. <https://doi.org/10.1093/icesjms/fsaa064>
- Scenna LB (2011) Biología y ecología reproductiva de las especies del género *Bathyrāja* (Elasmobranchii: Rajidae) en la plataforma continental argentina. PhD Thesis, Universidad Nacional de Mar del Plata
- Springer S (1971) Three species of skates (Rajidae) from the continental waters of Antarctica. In: Llano GA, Wallen IE (eds) *Biology of the Antarctic seas IV*, vol 17. American Geophysical Union, Washington D.C., pp 1–10
- Stehmann MFW, Merrett NT (2001) First records of advanced embryos and egg capsules of *Bathyrāja* skates from the deep north-eastern Atlantic. *J Fish Biol* 59:338–349. <https://doi.org/10.1006/jfbi.2001.1645>
- Stehmann MFW, Weigmann S, Naylor GJP (2021) First complete description of the dark-mouth skate *Raja arctowskii* Dollo, 1904 from Antarctic waters, assigned to the genus *Bathyrāja* (Elasmobranchii, Rajiformes, Arhynchobatidae). *Mar Biodivers* 51:18. <https://doi.org/10.1007/s12526-020-01124-1>
- Treude T, Kiel S, Linke P, Peckmann J, Goedert JL (2011) Elasmobranch egg capsules associated with modern and ancient cold seeps: a nursery for marine deep-water predators. *Mar Ecol Prog Ser* 437:175–181. <https://doi.org/10.3354/meps09305>
- Vazquez DM, Mabragaña E, Gabbanelli V, Díaz de Astarloa JM (2016) Exploring nursery sites for oviparous chondrichthyans in the Southwest Atlantic (36° S - 41°S). *Mar Biol Res* 12:715–725. <https://doi.org/10.1080/17451000.2016.1203948>
- Vazquez DM, Díaz de Astarloa JM, Gabbanelli V, Mabragaña E (2020) Comparative embryonic development patterns in three deep-water skates from the Southwest Atlantic. *Deep-Sea Res I* 161:103–301. <https://doi.org/10.1016/j.dsr.2020.103301>
- Weigmann S (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *J Fish Biol* 88:837–1037. <https://doi.org/10.1111/jfb.12874>
- Weigmann S, Stehmann MFW & Bürkel DL (in press) Order Rajiformes - Skates. In: Gon O, Gon J (eds) *Fishes of the Southern Ocean*, 2nd edition. NISC (Pty) Ltd, Grahamstown

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