

Biodiversity, bathymetric distribution, and reproductive strategies of sea stars (Echinodermata: Asteroidea) in the Argentine Sea

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Abstract: Sea stars (Echinodermata: Asteroidea) are widely distributed across all oceans, with numerous species inhabiting the Argentine Sea. This region is highly productive and sustains a rich diversity of marine invertebrates. The present work aimed to conduct a comprehensive bibliographic until 2024 review focusing on the biodiversity of Asteroidea in the different marine environments of Argentina and the reproductive strategies of sea stars inhabiting the Argentine Sea. This study focused on the geographic region from the Río de la Plata to the Burdwood Bank. We identified 105 species of sea stars, grouped into six orders, 19 families, and 60 genera. Valvatida and Forcipulatida were the most diverse orders. We noted a prevalence of sea stars in intermediate waters (50–500 m), being present across a wide range of temperatures. Regarding reproduction, our results showed that most of the brooding species were located exclusively in cold and intermediate waters, while broadcast spawner species exhibited a broad distribution from shallow to intermediate waters. This review highlights gaps in reproductive data for most species, as most studies in Argentina focus on identifying species from shallow rather than deeper waters. Enhancing sampling efforts and updating the biological information of these species will likely address these gaps in knowledge, especially in deeper areas where sampling is more challenging. Our results contribute to updating the knowledge of Asteroidea diversity in the Argentine Sea.

Key words: Echinodermata, Asteroidea, Diversity, Reproduction, Spatial distribution, South Atlantic

Resumen: “Biodiversidad, distribución batimétrica y estrategias reproductivas de estrellas de mar (Echinodermata: Asteroidea) en el Mar Argentino”. Las estrellas de mar (Echinodermata: Asteroidea) se encuentran distribuidas en todos los océanos, con numerosas especies reportadas para el Mar Argentino. Esta región, altamente productiva, sustenta una gran diversidad de invertebrados marinos. El objetivo del estudio fue realizar una exhaustiva revisión bibliográfica hasta el año 2024 sobre la biodiversidad de estrellas de mar que habitan los diferentes ambientes marinos de Argentina y analizar sus estrategias reproductivas, para aquellas que se encuentran desde el Río de la Plata hasta el Banco Burdwood. Identificamos 105 especies agrupadas en seis órdenes, 19 familias y 60 géneros. Valvatida y Forcipulatida fueron los órdenes más diversos. Observamos un predominio de estrellas de mar en aguas intermedias (50–500 m) y estando presentes a lo largo de diferentes rangos de temperatura. En cuanto a la reproducción, observamos que la mayoría de las especies incubantes predominan en aguas frías e intermedias, mientras que aquellas que liberan sus gametas al medio mostraron una distribución más amplia, desde aguas someras hasta intermedias. Esta revisión expone la falta de datos reproductivos para la mayoría de las especies, ya que generalmente los estudios en Argentina se centran en la identificación de especies, priorizando aquellas de aguas someras más que las de aguas profundas. Mejorar los esfuerzos de muestreo y actualizar la información biológica de estas especies probablemente contribuirá a mejorar este conocimiento, especialmente en zonas profundas donde el muestreo es más desafiante. Nuestros resultados contribuyen al conocimiento de la diversidad de Asteroidea en el Mar Argentino actualizando datos de estudios previos.

Palabras clave: Echinodermata, Asteroidea, Diversidad, Reproducción, Distribución espacial, Atlántico Sur

INTRODUCTION

Echinoderms (Phylum Echinodermata) are widely distributed across all oceans (Pawson, 2007). This phylum includes the class Asterozoa, one of the most representative groups, comprising approximately 1,900 species reported worldwide, ranging from intertidal to deep-water zones (Mah & Blake, 2012; Mah, 2024). In the Argentine Sea, numerous species have been reported up to 2024 (Roux, 2004; Brogger *et al.*, 2013; Fraysse *et al.*, 2018, 2020a; Rivadeneira *et al.*, 2020; Hurtado-García & Manjón-Cabeza, 2022; Fraysse *et al.*, 2024), covering an extensive area from the Río de la Plata (36°S, 56°W) to the Burdwood Bank (54°S, 59°W) and from coastal areas to the 200 m depth isobath. The Argentine Sea consists of coastal and deep continental shelf waters (Piola & Rivas, 1997) influenced by two principal currents with distinct properties: the warm Brazil Current and the cold Malvinas Current. These currents generate patterns of primary productivity that influence species distribution (Acha *et al.*, 2004; Carreto *et al.*, 2007). The Argentine continental shelf, one of the largest in the Southern Hemisphere, encompasses an area of approximately 1,000,000 km². It presents high concentrations of chlorophyll-*a* and high rates of primary productivity (Bastida & Urien, 1981; Martos & Piccolo, 1988; Acha *et al.*, 2004), supporting a rich diversity of marine invertebrates (Acha *et al.*, 2004; Rivas *et al.*, 2006; Miloslavich *et al.*, 2011).

Sea stars play a key role in marine ecosystems, highlighting their ecological importance as biological indicators for environmental pollution and their use in experimental studies (Paine, 1974; Menge, 1982; Brogger & Penchaszadeh, 2008; Gil & Zaixso, 2008; Arribas *et al.*, 2016, 2017). They exhibit both sexual and asexual reproduction mechanisms (Clark & Downey, 1992; Byrne & O'Hara, 2017), displaying a variety of reproductive strategies (Menge, 1975; Tyler & Pain, 1982; McClary & Mladenov, 1989; McEdward, 1997; Pearse *et al.*, 2009; Byrne, 2013; Fraysse *et al.*, 2020). These strategies encompass a range of mechanisms and behaviors tailored to their ecological niche, contributing to their adaptability and evolutionary success. Most sea stars are gonochoric and release their gametes into the environment, where external fertilization occurs, followed by a larval feeding stage, considered an ancestral character (Lawrence, 1987; McEdward & Janies, 1993). However, some species exhibit direct development, a strategy

observed exclusively in the family Pterasteridae with a mesogen stage, which occurs between the embryo and the juvenile (McEdward & Janies, 1993; Fraysse *et al.*, 2020b). Other species brood their embryos and care for their young on the body, either internally (O'Loughlin & O'Hara, 1990; Byrne, 1996; Komatsu *et al.*, 2006) or externally (Himmelman *et al.*, 1982; Strathmann *et al.*, 1984; Gil *et al.*, 2011; Fraysse *et al.*, 2020; Rivadeneira *et al.*, 2017, 2020). Brooders may exhibit a modified larvae phase as an adaptation to this mode of reproduction (McEdward & Janies, 1993; Gillespie & McClintock, 2007). This phenomenon is particularly common in polar and deep-sea areas where environmental conditions are unfavorable for larval development (Miliekovsky, 1971; Himmelman *et al.*, 1982; Boivin *et al.*, 1986; McEdward, 1995; Fraysse *et al.*, 2018) and is considered a derived reproductive strategy (Chia & Walker, 1991; McEdward & Janies, 1993). Asexual reproduction, known as fission, is another common reproductive strategy in sea stars (Rubilar *et al.*, 2005). The reproductive activity of Asterozoa appears to be influenced by environmental conditions (*e.g.*, temperature and photoperiod) as well as endogenous factors (Olive, 1992; Thorndyke *et al.*, 1999; Pearse & Bosch, 2002; Mercier & Hamel, 2009; Cossi *et al.*, 2015; Caballes *et al.*, 2021). Although research on sea stars has increased in recent years in Argentina (Rubilar *et al.*, 2005; Gil & Zaixso, 2007; Pastor de Ward *et al.*, 2007; Gil *et al.*, 2011; Cossi *et al.*, 2015; Pérez *et al.*, 2015; Rivadeneira *et al.*, 2017, 2020; Meretta *et al.*, 2016; Pérez *et al.*, 2017; Fraysse *et al.*, 2020b), many reproductive strategies of South Atlantic species remain unstudied.

On the other hand, there is limited information about the distribution patterns of sea stars and the factors influencing them (Moreau *et al.*, 2017). Some authors have suggested that physical and biological factors play a significant role in explaining the distribution of sea stars (Gage & Tyler, 1982; Pearse *et al.*, 2009; Moreau *et al.*, 2017). For instance, Menge *et al.* (1997) found that sea temperature is one of the most limiting factors for marine species distribution. Additionally, other studies emphasize that reproductive strategies strongly influence sea star distribution patterns, as brooders and broadcasters have different dispersal capabilities (Moreau *et al.*, 2019). In light of these considerations, the aim of the present work was to conduct a comprehensive bibliographic review focusing on the biodiversity of Asterozoa in the marine environ-

ments of Argentina, and the reproductive strategies of sea stars inhabiting the Argentine Sea. This study contributes to expanding knowledge of these diverse and ecologically significant marine species along the Argentine coast.

MATERIALS AND METHODS

A bibliographic analysis of the available information on sea star species recorded in the Argentine Sea was conducted through a thorough search. The geographic scope encompassed the area from the Río de la Plata (34°S) to the Burdwood Bank (~55°S), including the Malvinas Islands, and ranged from intertidal zones to deeper waters. We analyzed published papers and reports found on various bibliographic online platforms and open databases, such as the Global Biodiversity Information Facility (GBIF.org) and the Ocean Biodiversity Information System (OBIS, 2024), as well as repositories at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'.

All collected information was categorized into two main groups for this study: **1.** marine environments of Argentina, and **2.** reproduction. The first group was further divided in two categories: **A.** species distribution according to water temperature and **B.** species distribution across depth ranges. Category **A** was subdivided into four water temperature ranges determined within the study area: **1** 'Warm-temperate waters' (WTW), **2** 'Cold-temperate waters' (CTW), **3** 'Cold waters' (CW), and **4** 'Warm-temperate to cold waters' (WT-CW). Category **B** was subdivided into three depth ranges: **1** 'Shallow waters (<50 meters)', **2** 'Intermediate waters (50–500 meters)', and **3** 'Deep waters (>500 meters)'. Each range focused on species exclusive to that range. For instance, species inhabiting only 'warm-temperate waters' were not included in the 'warm-temperate to cold waters' range. In cases of overlap within the 'depth ranges' category, additional combined ranges were established: **1, 2** shallow to intermediate waters (0–500 meters), **1, 2, 3** shallow to deep waters (0 to >500 meters), and intermediate to deep waters **2, 3** (50 to >500 meters). Seawater temperature varies across depth ranges, with cold waters typically found at intermediate and deep waters, while warm-temperate waters are generally observed in shallow and intermediate waters (Balech & Ehrlich, 2008; Acha et al., 2024). However, exceptions occurred depending on the specific area in the Argentine Sea where the species were located.

Regarding the 'reproduction' group, sea star species were classified into three distinct categories: 'Brooding' (B), 'Broadcast spawners' (S), and 'Broadcast spawners and fissiparous' (S+F). To ensure accuracy, the 'World Register of Marine Species' (WoRMS, 2024) database was consulted to verify species names, taxonomic status, and their respective orders and families.

RESULTS

From a review of 257 scientific articles, 116 focused specifically on the class Asteroidea in the Argentine Sea, reporting a total of 105 sea star species. These species were classified into six orders, 19 families, and 60 genera (Table 1). For each species, information on distribution by water temperature range, depth ranges, and reproductive strategies was compiled (Table 1). The orders Valvatida and Forcipulatida contained the highest number of species (34 and 27 species, respectively), and were present across all water temperature ranges in the Argentine Sea (Fig. 1).

Based on marine environments of Argentina, we found 98 species belonging to the orders Forcipulatida, Valvatida, Paxillosida, and Velatida distributed from the warm-temperate waters of the Río de la Plata (34°S) to the cold waters in the southern part of the study area (~55°S) (Fig. 1). Moreover, the species from the orders Notomyotida and Spinulosida exhibited narrow distribution ranges (Fig. 1). Regarding Notomyotida, the species *Cheiraster (Luidiaster) gerlachei* was unique to the cold-water range, while *Cheiraster (Luidiaster) planeta* inhabited the warm-temperate to cold waters (Table 1). In the case of Spinulosida order, it was distributed throughout all ranges except in warm-temperate waters (Table 1).

The depth ranges analyzed showed that 21.90% of the species were exclusively recorded in intermediate waters (50–500 m), 16.19% in deep waters (>500 m), and 4.76% in shallow waters (0–50 m) (Table 2). Additionally, 26.67% of the species were located from shallow to intermediate waters (0–500 m), 15.24% from intermediate to deep waters (50 to >500 m), and 8.57% species spread from shallow to deep waters (0 to >500 m) (Table 2). Furthermore, 6.67% of the species had unknown depth ranges due to the lack of information in the literature.

Information on the sea stars' reproduction in the Argentine Sea was only available for 50 of the 105 species reviewed. The reproductive strategy results showed 29 species with brooding

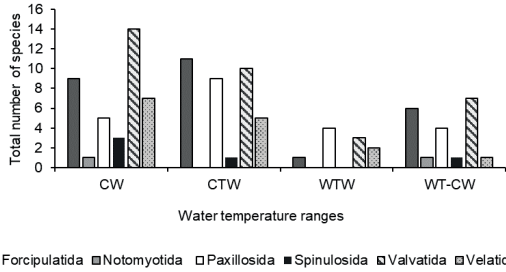


Fig. 1. Total number of Asteroidea species sorted by order in each distribution range according to water temperature in the Argentine Sea. The temperature ranges are categorized as: ‘Cold waters’ (CW), ‘Cold-temperate waters’ (CTW), ‘Warm-temperate waters’ (WTW), and ‘Warm-temperate to cold waters’ (WT-CW).

of their young primarily distributed in cold-temperate and cold waters (Fig. 2). Nineteen species were broadcast spawners and all of them were reported in the whole range of water temperatures in the Argentine Sea. Only two species, *Stichaster striatus* and *Allostichaster capensis*, displayed fissiparous reproduction, alternating with broadcast spawning (Table 1). The sea star *S. striatus* was found only in cold-temperate waters, while *A. capensis* inhabited the warm-temperate to cold waters range (Table 1 and Fig. 2).

The reproductive strategy in relation to depth ranges can be seen in the Table 2. Brooding species were distributed across all depth ranges in the study area, with nine species primarily in intermediate waters and six species from shallow to intermediate waters (0–500 m). Broadcast spawner species were more prevalent (8 species) in shallow to intermediate waters (0–500 m). Additionally, among the species that exhibit both fissiparous and broadcast spawning reproduction, *S. striatus* was found in the intermediate waters, while *A. capensis* was found in the range from shallow to intermediate waters (0–500 m).

DISCUSSION

The extensive review of literature on echinoderm species from Argentine waters (*i.e.*, over 250 manuscripts) provided information on 105 species of sea stars. Nearly half of these studies focused on the class Asteroidea, covering aspects such as biodiversity, distribution, depth range, and reproductive information. This apparent bias towards sea stars may be attributed to their abundance in shallow waters and the relative ease of sample collection. While the number of specialists has increased in recent years (*e.g.*,

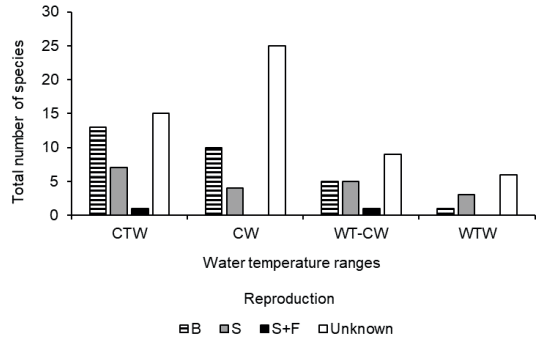


Fig. 2. Number of species by their reproductive strategy across water temperature ranges in the study area. The categories are: Brooding (B), Broadcast spawners (S), Broadcast spawners and fissiparous (S+F), and Unknown (Unknown). The distribution ranges are: ‘Cold waters’ (CW), ‘Cold-temperate waters’ (CTW), ‘Warm-temperate waters’ (WTW), and ‘Warm-temperate to cold waters’ (WT-CW).

Gil *et al.*, 2011; Brogger *et al.* 2013; Pérez *et al.*, 2014; Arribas *et al.*, 2016, 2023; Fraysse *et al.*, 2024; Pérez *et al.* 2024), there are still significant knowledge gaps regarding Asteroidea. The foundation of echinoderm research in various Latin American countries can be traced back to early European and United States expeditions (Alvarado & Solís-Marín, 2013). Over time, each country has developed its own research focus. A pioneer in the taxonomic identifications of echinoderms in Argentina was Dr. Irene Bernasconi, who mainly specialized in the taxonomy of Asteroidea describing many species and revising seven families of sea star (*e.g.*, Bernasconi, 1935, 1937, 1941, 1962, 1963, 1964, 1973, 1980). In Latin America, a notable example is Mexico, where researchers have focused much of their studies on the echinoderms presenting a diverse range of habitats, encompassing both the Pacific and Atlantic Oceans (Alvarado & Solís-Marín, 2013). Their collection includes around 650 species of echinoderms recorded up to that time, of which approximately 185 belong to the Asteroidea (Alvarado & Solís-Marín, 2013).

This review compiles the current state of knowledge of the class Asteroidea in the Argentine Sea, updating data from previous studies (Sladen, 1889; Fisher, 1940; Tommasi, 1970; Bernasconi, 1966, 1973; Penchaszadeh, 1973; Hernández, 1981; Tablado, 1982; Hernández & Tablado, 1985; Tablado & Maytia, 1988; Brogger *et al.*, 2013; Pérez *et al.*, 2014; Souto *et al.*, 2014; Bigatti & Signorelli, 2018; Fraysse *et al.*, 2018, 2024). The most recent species records pro-

Table 1: Sea stars reported for the Argentine Sea with their taxonomic levels and information from reviewed literature. The table includes the **Distribution of species according to water temperature**: ‘Warm-temperate waters’ (WTW), ‘Cold-temperate waters’ (CTW), ‘Cold waters’ (CW), and ‘Warm-temperate to cold waters’ (WT-CW). **Depth ranges** are categorized as follows: 1) ‘Shallow waters (<50 meters)’, 2) ‘Intermediate waters (50–500 meters)’, and 3) ‘Deep waters (>500 meters)’. **In cases of species overlap**, the ranges are specified as: 1, 2) ‘From shallow to intermediate waters (0–500 meters)’, 1, 2, 3) ‘From shallow to deep waters (0–>500 meters)’, and 2, 3) ‘From intermediate to deep waters (50–>500 meters)’. **Reproduction** is classified according to the reproductive strategies as: ‘Brooding’ (B); ‘Broadcast spawners’ (S), and ‘Broadcast spawners and fissiparous’ (S+F).

Order	Family	Genus	Species	Distribution of species according to water temperature	Depth ranges	Reproduction
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias spirabilis</i> (Bell, 1881) ^{1,2}	CTW	1	B
Forcipulatida	Asteriidae	<i>Cryptasterias</i>	<i>Cryptasterias brachiata</i> Koehler, 1923 ^{3,4}	CTW	1	B
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias studei</i> Perrier, 1891 ^{3,5}	CTW	1,2	B
Forcipulatida	Asteriidae	<i>Diplasterias</i>	<i>Diplasterias meridionalis</i> (Perrier, 1875) ^{6,7}	CTW	2	B
Forcipulatida	Asteriidae	<i>Lethasterias</i>	<i>Lethasterias australis</i> Fisher, 1940 ^{8,9}	CTW	2	B
Forcipulatida	Asteriidae	<i>Lysasterias</i>	<i>Lysasterias perrieri</i> (Studer, 1885) ^{10,11}	CTW	2	B
Forcipulatida	Stichasteridae	<i>Cosmasterias</i>	<i>Cosmasterias lurida</i> (Philippi, 1858) ^{4,5,8,12}	CTW	1,2,3	S
Forcipulatida	Stichasteridae	<i>Stichaster</i>	<i>Stichaster striatus</i> Müller & Troschel, 1840 ^{13,14}	CTW	2	S+F
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias minuta</i> Perrier, 1875 ^{15,16,17,18}	CTW	1,2	B
Forcipulatida	Asteriidae	<i>Bernasconiaster</i>	<i>Bernasconiaster pipi</i> Rivadeneira, Martínez, Penchaszadeh & Brogger, 2020 ¹⁹	CTW	3	B
Forcipulatida	Asteriidae	<i>Diplasterias</i>	<i>Diplasterias brucei</i> (Koehler, 1907) ^{4,20,21}	CTW	1,2,3	B
Forcipulatida	Asteriidae	<i>Lysasterias</i>	<i>Lysasterias</i> sp. ^{4,13}	CW		B
Forcipulatida	Asteriidae	<i>Diplasterias</i>	<i>Diplasterias octoradiata</i> (Studer, 1885) ^{9,22}	CW	1	B
Forcipulatida	Asteriidae	<i>Cryptasterias</i>	<i>Cryptasterias turqueti</i> (Koehler, 1906) ^{3,4,23,24}	CW	1,2	B
Forcipulatida	Asteriidae	<i>Psalidaster</i>	<i>Psalidaster mordax mordax</i> Fisher, 1940 ^{5,11,23,25}	CW	1,2,3	B
Forcipulatida	Asteriidae	<i>Adelasterias</i>	<i>Adelasterias papillosa</i> (Koehler, 1906) ⁶⁵	CW	2	
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias asterinoides</i> Perrier, 1875 ⁶⁵	CW	2	
Forcipulatida	Stichasteridae	<i>Neosmilaster</i>	<i>Neosmilaster steineri</i> (Studer, 1885) ^{2,3,11,15}	CW	2	B
Forcipulatida	Stichasteridae	<i>Smilasterias</i>	<i>Smilasterias scalprifera</i> (Sladen, 1889) ^{9,11,26}	CW	2	B
Forcipulatida	Asteriidae	<i>Anteliasier</i>	<i>Anteliasier australis</i> (Fisher, 1940) ^{9,22}	CW	2,3	
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias antarctica</i> (Lütken, 1856) ^{4,5,11,27}	WT-CW	1,2	B
Forcipulatida	Asteriidae	<i>Anasterias</i>	<i>Anasterias pedicellaris</i> (Koehler, 1923) ^{4,5,17,24}	WT-CW	1,2	B
Forcipulatida	Stichasteridae	<i>Allostichaster</i>	<i>Allostichaster capensis</i> (Perrier, 1875) ^{8,17,28}	WT-CW	1,2	S+F
Forcipulatida	Helasteridae	<i>Labidaster</i>	<i>Labidaster radiosus</i> Loven in Lütken, 1871 ^{4,5}	WT-CW	1,2	
Forcipulatida	Asteriidae	<i>Diplasterias</i>	<i>Diplasterias brandtii</i> (Bell, 1881) ^{3,4,5,17}	WT-CW	1,2,3	B
Forcipulatida	Asteriidae	<i>Psalidaster</i>	<i>Psalidaster mordax</i> Fisher, 1940 ^{5,9,23}	WT-CW	1,2,3	B
Forcipulatida	Asteriidae	<i>Perissasterias</i>	<i>Perissasterias polycantha</i> H.L. Clark, 1923 ^{8,9,29}	WTW	1,2,3	
Paxillosida	Astropectinidae	<i>Dytaster</i>	<i>Dytaster grandis grandis</i> (Verrill, 1884) ^{8,31}	CTW	3	
Paxillosida	Astropectinidae	<i>Dytaster</i>	<i>Dytaster grandis nobilis</i> Sladen, 1889 ^{8,30}	CTW	3	
Paxillosida	Astropectinidae	<i>Dytaster</i>	<i>Dytaster</i> sp. ³¹	CTW	3	
Paxillosida	Astropectinidae	<i>Leptychaster</i>	<i>Leptychaster kerguelensis</i> E. A. Smith, 1876 ^{3,9,30}	CTW	2,3	B

Order	Family	Genus	Species	Distribution of species according to water temperature	Depth ranges	Reproduction
Paxillosida	Astropectinidae	<i>Plutonaster</i>	<i>Plutonaster</i> sp. ³¹		3	S
Paxillosida	Astropectinidae	<i>Psilaster</i>	<i>Psilaster</i> sp. ³¹		3	S
Paxillosida	Astropectinidae	<i>Leplychaster</i>	<i>Leplychaster</i> sp.1 ⁴			
Paxillosida	Benthopectinidae	<i>Gaussaster</i>	<i>Gaussaster</i> sp.			
Paxillosida	Pseudarchasteridae	<i>Pseudarchaster</i>	<i>Pseudarchaster</i> sp.			
Paxillosida	Ctenodiscidae	<i>Ctenodiscus</i>	<i>Ctenodiscus procurator</i> Sladen, 1889 ⁶⁵		2	
Paxillosida	Astropectinidae	<i>Plutonaster</i>	<i>Plutonaster bifrons</i> (Wyville Thomson, 1873) ^{9,32}		3	S
Paxillosida	Radiasteridae	<i>Radiaster</i>	<i>Radiaster elegans</i> (Perrier, 1881) ⁹		3	
Paxillosida	Astropectinidae	<i>Leplychaster</i>	<i>Leplychaster</i> sp.2 ⁴			
Paxillosida	Luidiidae	<i>Luidia</i>	<i>Luidia patriciae</i> Bernasconi, 1941 ³³			
Paxillosida	Pseudarchasteridae	<i>Pseudarchaster</i>	<i>Pseudarchaster discus</i> Sladen, 1889 ^{8,9}		2	
Paxillosida	Ctenodiscidae	<i>Ctenodiscus</i>	<i>Ctenodiscus australis</i> Loven in Lütken, 1871 ^{4,5,8,34,35}		2,3	B
Paxillosida	Astropectinidae	<i>Psilaster</i>	<i>Psilaster herwigii</i> (Bernasconi, 1972) ^{5,31,36}		2,3	S
Paxillosida	Astropectinidae	<i>Bathyiaster</i>	<i>Bathyiaster loripes</i> Sladen, 1889 ^{4,5,21,36}		1,2	S
Paxillosida	Astropectinidae	<i>Astropecten</i>	<i>Astropecten brasiliensis</i> Müller & Troschel, 1842 ^{17,37,38,39}		1,2	S
Paxillosida	Astropectinidae	<i>Astropecten</i>	<i>Astropecten cingulatus</i> Sladen, 1883 ^{5,37,40}		1,2	S
Paxillosida	Luidiidae	<i>Luidia</i>	<i>Luidia alternata alternata</i> (Say, 1825) ^{8,41,42}		1,2	
Paxillosida	Luidiidae	<i>Luidia</i>	<i>Luidia ludwigi scotti</i> Bell, 1917 ^{8,41,42}		1,2	
Notomyotida	Benthopectinidae	<i>Cheiraster</i>	<i>Cheiraster (Luidiaster) gerlachei</i> Ludwig, 1903 ^{4,43}		2	S
Notomyotida	Benthopectinidae	<i>Cheiraster</i>	<i>Cheiraster (Luidiaster) planeta</i> (Sladen, 1889) ^{5,9,44}		2	S
Spinulosida	Echinasteridae	<i>Echinaster</i>	<i>Echinaster (Ophilia) brasiliensis</i> Müller & Troschel, 1842 ^{8,45}		1	S
Spinulosida	Echinasteridae	<i>Henricia</i>	<i>Henricia studeri</i> (Perrier, 1891) ^{4,8,46,47}		2	S
Spinulosida	Echinasteridae	<i>Henricia</i>	<i>Henricia diffidens</i> (Koehler, 1923) ⁶⁵		2,3	
Spinulosida	Echinasteridae	<i>Henricia</i>	<i>Henricia pagenstecheri</i> (Studer, 1885) ⁹		2,3	
Spinulosida	Echinasteridae	<i>Henricia</i>	<i>Henricia obesa</i> (Sladen, 1889) ^{5,16,47}		1,2	S
Valvatida	Asterinidae	<i>Asterina</i>	<i>Asterina fimbriata</i> Perrier, 1875 ⁴⁸		1,2	B
Valvatida	Odontasteridae	<i>Diploodontias</i>	<i>Diploodontias singularis</i> (Müller & Troschel, 1843) ^{17,47,49}		1,2	S
Valvatida	Solasteridae	<i>Lophaster</i>	<i>Lophaster stellans</i> Sladen, 1889 ^{5,8,44}		2	B
Valvatida	Ganeridae	<i>Cyathra</i>	<i>Cyathra cingulata</i> Koehler, 1923 ⁵		1,2	
Valvatida	Ganeridae	<i>Ganeria</i>	<i>Ganeria hahni</i> Perrier, 1891 ^{5,16}		1,2	
Valvatida	Odontasteridae	<i>Odontaster</i>	<i>Odontaster meridionalis</i> (E. A. Smith, 1876) ^{4,20,21}		3	S
Valvatida	Poranidae	<i>Glabraster</i>	<i>Glabraster antarctica</i> (E. A. Smith, 1876) ^{4,5,50}		1,2	S
Valvatida	Odontasteridae	<i>Acodontaster</i>	<i>Acodontaster elongatus</i> (Sladen, 1889) ^{21,51}		2,3	S
Valvatida	Ganeridae	<i>Vemaster</i>	<i>Vemaster sudatlanticus</i> Bernasconi, 1965 ⁵²		3	
Valvatida	Goniasteridae	<i>Peltaster</i>	<i>Peltaster placenta</i> (Müller & Troschel, 1842) ⁵		1,2,3	
Valvatida	Odontasteridae	<i>Acodontaster</i>	<i>Acodontaster capitatus</i> (Koehler, 1912) ⁶⁵		1,2	
Valvatida	Ganeridae	<i>Ganeria</i>	<i>Ganeria falklandica</i> Gray, 1847 ^{5,8,17,53}		1,2	
Valvatida	Asterinidae	<i>Perknaster</i>	<i>Perknaster fuscus</i> Sladen, 1889 ⁶⁵		1,2	

Order	Family	Genus	Species	Distribution of species according to water temperature	Depth ranges	Reproduction
Valvatida	Goniasteridae	<i>Mediaster</i>	<i>Mediaster pedicellaris</i> (Perrier, 1881) ⁶⁵	CW	1,2	
Valvatida	Odontasteridae	<i>Odontaster</i>	<i>Odontaster</i> sp. ⁴	CW	1,2,3	
Valvatida	Odontasteridae	<i>Aodontaster</i>	<i>Aodontaster hodgsoni</i> (Bell, 1908) ⁶⁵	CW	2	
Valvatida	Goniasteridae	<i>Ceramaster</i>	<i>Ceramaster patagonicus</i> (Sladen, 1889) ^{5,54}	CW	2	
Valvatida	Goniasteridae	<i>Pillsburiaster</i>	<i>Pillsburiaster calvus</i> (Mah, 2011) ⁵⁵	CW	2,3	
Valvatida	Asterinidae	<i>Anseropoda</i>	<i>Anseropoda antarctica</i> (Fisher, 1940) ^{5b}	CW	2,3	
Valvatida	Goniasteridae	<i>Hippasteria</i>	<i>Hippasteria falklandica</i> Fisher, 1940 ^{5a}	CW	2,3	B
Valvatida	Asterinidae	<i>Tremaster</i>	<i>Tremaster mirabilis</i> Verrill, 1880 ^{8,56}	CW	2,3	
Valvatida	Goniasteridae	<i>Chitonaster</i>	<i>Chitonaster johannae</i> Koehler, 1907 ⁶⁵	CW	3	
Valvatida	Solasteridae	<i>Paralophaster</i>	<i>Paralophaster lorioti</i> (Koehler, 1907) ⁹	CW	3	
Valvatida	Goniasteridae	<i>Notioceramus</i>	<i>Notioceramus anomalus</i> Fisher, 1940 ⁴	CW		
Valvatida	Goniasteridae	<i>Tostia</i>	<i>Tostia</i> sp. ^{13,57}	WT-CW	1	
Valvatida	Ganeridae	<i>Cyathra</i>	<i>Cyathra verrucosa</i> (Philippi, 1857) ^{5a,16,17}	WT-CW	1,2	
Valvatida	Odontasteridae	<i>Odontaster</i>	<i>Odontaster penicillatus</i> (Philippi, 1870) ^{5a,24}	WT-CW	1,2	S
Valvatida	Odontasteridae	<i>Aodontaster</i>	<i>Aodontaster elongatus granuliferus</i> (Koehler, 1912) ^{5a}	WT-CW	1,2,3	
Valvatida	Goniasteridae	<i>Cladaster</i>	<i>Cladaster analogus</i> Fisher, 1940 ^{5a,58}	WT-CW	2,3	
Valvatida	Ganeridae	<i>Perknaster</i>	<i>Perknaster densus</i> (Sladen, 1889) ⁴⁴	WT-CW	2,3	
Valvatida	Solasteridae	<i>Solaster</i>	<i>Solaster regularis</i> Sladen, 1889 ^{4,5a}	WT-CW	2,3	
Valvatida	Asterinidae	<i>Asterina</i>	<i>Asterina stellifera</i> (Möbius, 1859) ^{5,5,59}	WTW	1,2	S
Valvatida	Goniasteridae	<i>Hippasteria</i>	<i>Hippasteria phrygiana</i> (Parelius, 1768) ⁹	WTW	1,2	
Valvatida	Poraniidae	<i>Poraniopsis</i>	<i>Poraniopsis echinaster</i> Perrier, 1891 ^{5a}	WTW	1,2	
Velatida	Korethrasteridae	<i>Remaster</i>	<i>Remaster gourdoni</i> Koehler, 1912 ^{8,9}	CTW	1,2	
Velatida	Pterasteridae	<i>Diplopteraster</i>	<i>Diplopteraster verrucosus</i> (Sladen 1882) ^{4,5a,22}	CTW	2	B
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster gibber</i> (Sladen, 1882) ^{9,11}	CTW	2	
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster flabellifer</i> (Sladen, 1882) ⁹	CTW	2,3	
Velatida	Pterasteridae	<i>Calyptroster</i>	<i>Calyptroster vitreus</i> Bernasconi, 1972 ^{5a,60}	CTW	3	
Velatida	Pterasteridae	<i>Calyptroster</i>	<i>Calyptroster tenuissimus</i> Bernasconi, 1966 ⁶⁰	CW	2	B
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster rugatus</i> Sladen, 1882 ¹¹	CW	2	
Velatida	Korethrasteridae	<i>Peribolaster</i>	<i>Peribolaster folliculatus</i> Sladen, 1889 ^{4,5a,47}	CW	2	S
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster affinis</i> Smith, 1876 ^{3,11}	CW	3	B
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster affinis lebruni</i> Perrier, 1891 ^{8,53}	CW	2	
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster</i> sp. ⁴	CW	3	
Velatida	Pterasteridae	<i>Pteraster</i>	<i>Pteraster stellifer</i> Sladen, 1882 ^{5b,61}	CW	2,3	B
Velatida	Pterasteridae	<i>Hymenaster</i>	<i>Hymenaster pergamentaceus</i> (Sladen, 1882) ^{8,9}	WT-CW	3	
Velatida	Pterasteridae	<i>Diplopteraster</i>	<i>Diplopteraster clarki</i> Bernasconi, 1937 ^{5a,62}	WTW	2	B
Velatida	Myxasteridae	<i>Pythonaster</i>	<i>Pythonaster murrayi</i> Sladen, 1889 ^{63,64}	WTW	3	

References Table 1:	²² Fisher (1940)	⁴⁵ Lopes & Ventura (2016)
¹ Perrier (1891)	²³ Pearse <i>et al.</i> (2009)	⁴⁶ O'Hara (1998)
² Mah (2024)	²⁴ Bernasconi (1970)	⁴⁷ Frayse <i>et al.</i> (2020a)
³ Hyman (1955)	²⁵ Mah <i>et al.</i> (2015)	⁴⁸ Alarcón <i>et al.</i> in prep.
⁴ Frayse <i>et al.</i> (2018)	²⁶ O'Loughlin & O'Hara (1990)	⁴⁹ Bernasconi (1962)
⁵ Bernasconi (1973a)	²⁷ Pérez <i>et al.</i> (2017)	⁵⁰ Bosch (1989)
⁶ Bosch & Slattery (1999)	²⁸ Rubilar <i>et al.</i> (2005)	⁵¹ Pérez <i>et al.</i> (2024)
⁷ Perrier (1878)	²⁹ Tablado & Maytia (1988)	⁵² Bernasconi (1965)
⁸ Clark & Downey (1992)	³⁰ Alvarado & Solís-Marín (2013)	⁵³ Bernasconi (1964)
⁹ Hurtado-García & Monjon-Cabeza (2022)	³¹ Rivadeneira (2020)	⁵⁴ Carrera-Rodríguez & Tommasi (1977)
¹⁰ Koehler (1906)	³² Tyler & Pain (1982)	⁵⁵ Mah (2011)
¹¹ Moreau <i>et al.</i> (2018)	³³ Bernasconi (1941)	⁵⁶ O'Loughlin & Waters (2004)
¹² Pastor de Ward (2007)	³⁴ Rivadeneira <i>et al.</i> (2017)	⁵⁷ Pérez <i>et al.</i> (2014)
¹³ Mah & Blake (2012)	³⁵ Lieberkind (1926)	⁵⁸ Mah (2006)
¹⁴ Lawrence & Larrain (1994)	³⁶ Moreau <i>et al.</i> (2019)	⁵⁹ Carvalho & Ventura (2002)
¹⁵ Salvat (1985)	³⁷ Bernasconi (1957)	⁶⁰ Bernasconi (1972)
¹⁶ Hernández & Tablado (1985)	³⁸ Roux (2004)	⁶¹ Janies (1995)
¹⁷ Arribas <i>et al.</i> (2016)	³⁹ Ventura <i>et al.</i> (1997)	⁶² Bernasconi (1937)
¹⁸ Gil <i>et al.</i> (2011)	⁴⁰ Ventura <i>et al.</i> (1998)	⁶³ Souto (2014)
¹⁹ Rivadeneira <i>et al.</i> (2020)	⁴¹ Tommasi (1970)	⁶⁴ Sladen (1889)
²⁰ Pearse <i>et al.</i> (1991)	⁴² Bernasconi (1943)	⁶⁵ Frayse <i>et al.</i> (2024)
²¹ Pearse & Bosch (1994)	⁴³ MacBride (1910)	
	⁴⁴ Moreau <i>et al.</i> (2015)	

Table 2: Number of reported brooding species (B), broadcast spawners (S), broadcast spawners and fissiparous (S+F), and species with unknown reproduction (Unknown) in various depth ranges: **1**) Shallow waters (<50 m), **2**) Intermediate waters (50–500 m), **3**) Deep waters (>500 m), and waters with unknown depths (Unknown). In cases of species overlap, the ranges are specified as: **1,2**) from shallow to intermediate waters (0–500 m), **2,3**) from intermediate to deep waters (50 to >500 m) and **1,2,3**) from shallow to deep waters (0 to >500 m).

Depth ranges	Total number of species	Reproduction			
		B	S	S+F	Unknown
1. (<50 m)	5	3			2
2. (50–500 m)	23	9	4	1	9
3. (>500 m)	17	2	4		11
1,2. (0–500 m)	28	6	8	1	13
1,2,3. (0 to >500 m)	9	4	1		4
2,3. (50 to >500 m)	16	4	2		10
Unknown	7	1			6

posed by Hurtado-García and Manjón-Cabeza (2022) for the study area include *Plutonaster bifrons*, *Radiaster elegans*, *Pillsburiaster calvus*, *Paralophaster lorioli*, and *Pteraster flabellifer*.

Several studies have demonstrated that the reproductive strategies of sea stars play a crucial role in their distribution patterns (Moreau *et al.*, 2017). Brooding species tend to have limited dispersal capacity, while broadcast spawners exhibit higher dispersal capacity (Moreau *et al.*, 2017). Our results showed that most brooding species are frequently found in cold-temperate and cold waters, primarily in shallow to intermediate

waters (0–500 m) and in intermediate waters (50–500 meters). This may be because brooding typically occurs in deep waters (Thompson, 1878; Chia, 1968; Boivin *et al.*, 1986; McEdward, 1995; Bosch & Slattery, 1999) and under lower temperatures (Mercier & Hamel, 2008; Fraysse *et al.*, 2024). Moreover, some authors propose that deep and cold waters constitute stable environments that favor brooding species (Poulin *et al.*, 2002; Mercier & Hamel, 2009). In contrast, broadcast spawner species exhibit a broad distribution across all temperature ranges, with a higher prevalence in cold-temperate waters, and

are primarily found from shallow to intermediate waters (0–500 meters).

However, explaining distribution patterns based solely on reproductive strategy is insufficient, as environmental factors such as temperature, depth range, and the possibility of passively rafting on kelp, among others, also play significant roles in species distribution (Edgar, 1987; Poulin *et al.*, 2002; Pearse *et al.*, 2009; Pérez-Ruzafa *et al.*, 2013). In particular, sea temperature is an important factor affecting the distribution and survival of these organisms, creating distinct distribution patterns (Stanwell-Smith & Peck, 1998; Poulin *et al.*, 2002; Moreau *et al.*, 2017).

Regarding the analyzed reproductive data, information was available for approximately 48% of the species. Recently, some brooding species from deep areas along the Argentine continental shelf have been studied, such as *Ctenodiscus australis* (Rivadeneira *et al.*, 2017) and *Diplopteraster verucosus* (Frayse *et al.*, 2020b). In contrast, other brooding species have been studied from shallow waters, for example, *Anasterias minuta* (Arribas *et al.*, 2023), *A. antarctica* (Frayse *et al.*, 2021) and *Asterina fimbriata* (Alarcón *et al.* in prep.). Despite the increase in the number of species reported here, there remains a significant lack of information in the literature on this subject.

The limited reproductive data in our study may be attributed to the fact that most research in Argentina focuses on identifying and classifying species, which is a critical first step in understanding their biology and ecology. Additionally, research tends to prioritize species found in shallow waters, likely because they are more accessible and require fewer resources to study directly. In contrast, studying species in deep waters requires more resources and effort, primarily due to the high costs of using oceanographic vessels for sampling. We believe it is important to implement complementary reproductive studies to support bibliographic reviews and provide a more comprehensive understanding of these gaps in reproductive data. Enhancing sampling efforts and updating the biological information of these species will be crucial to addressing this gap, particularly in deeper areas where sampling is more challenging.

CONCLUSIONS

This review summarizes the current knowledge of Asteroidea in the Argentine Sea and updates previous available data. Our study identi-

fies 105 sea star species, most of which belong to the orders Valvatida and Forcipulatida, highlighting the rich diversity of this class in the region. Species distribution varies with depth and temperature, with the highest number of species recorded in intermediate waters. The data indicate that, with few exceptions, brooding species tend to have restricted distributions, primarily in colder and deeper waters, while broadcast spawners exhibit broader dispersal capabilities across various temperature ranges and depths. Despite recent advancements, there remains a significant lack of reproductive information for many species, underscoring the need for further research, especially in less accessible deep-water habitats. Future studies should incorporate reproductive investigations and enhance sampling efforts to address these knowledge gaps, ultimately contributing to a more comprehensive understanding of marine biodiversity along the Argentine coast.

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