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REVIEW

Reproductive strategies of benthic macroinvertebrates at the Argentine shelf-break front, southwestern Atlantic Ocean

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ABSTRACT. The Argentine shelf-break front is of high ecological and economic importance and supports diverse benthic communities and key life-history processes of several commercial species. This study provides the first comprehensive synthesis of reproductive traits among benthic invertebrates inhabiting this area of the southwestern Atlantic Ocean (80-120 m depth). Information was compiled for 126 epibenthic species belonging to Porifera, Cnidaria, Annelida, Mollusca, Brachiopoda, Echinodermata, Arthropoda, Bryozoa, and Chordata (> 1 cm) from published sources, aiming to identify the dominant reproductive strategies that sustain populations persistence over time. Species-specific reproductive data were available for only 47% of the taxa, and for only five species (~ 4%) such information derived from specimens collected at the shelf-break front itself. Despite data gaps and the need for extrapolation from related taxa or regions, this synthesis reveals predominant reproductive patterns among benthic invertebrates and provides essential baseline knowledge for ecosystem-based management. Approximately 68% of the species are gonochoric, although most sponges and all ascidians are hermaphroditic, while 43% can reproduce asexually or have the ability of regeneration. Internal fertilization predominates (71%), while all bivalves and polychaetes reproduce by external fertilization. Parental care, defined as any kind of protection of embryos through incubation or encapsulation, occurs in 61% of the species, being universal among crustaceans and frequent in gastropods (89%). Indirect development characterizes 82% of the species, of which 59% produce lecithotrophic larvae and 33% planktotrophic larvae. Understanding reproductive modes and dispersal capacities is crucial to assess connectivity, resilience, and vulnerability of benthic communities in the Argentine shelf-break front.

Key words: Benthic communities, reproduction, larval dispersion, parental care, Argentina.

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Estrategias reproductivas de macroinvertebrados bentónicos en el frente del talud argentino, Océano Atlántico Sudoccidental

RESUMEN. El frente del talud continental argentino es de gran importancia ecológica y económica, y sustenta diversas comunidades bentónicas y procesos clave del ciclo de vida de varias especies comerciales. Este estudio proporciona la primera síntesis exhaustiva de los rasgos reproductivos entre los invertebrados bentónicos que habitan esta área del Océano Atlántico Sudoccidental (80-120 m de profundidad). Se recopiló información para 126 especies epibentónicas (> 1 cm) pertenecientes a los Phyla Porifera, Cnidaria, Annelida, Mollusca, Brachiopoda, Echinodermata, Arthropoda, Bryozoa y Chordata a partir de fuentes publicadas, con el objetivo de identificar las estrategias reproductivas dominantes que sustentan la persistencia de las poblaciones a lo largo del tiempo. Los datos reproductivos específicos de cada especie estaban disponibles solo para el 47% de los taxones, y para solo cinco especies (~ 4%) dicha información provino de especímenes colectados en el propio frente del talud. A pesar de la falta de datos y la necesidad de extrapolación a partir de taxones o regiones relacionadas, esta síntesis revela patrones reproductivos predominantes entre los invertebrados bentónicos y proporciona conocimientos básicos esenciales para la gestión ecosistémica. Aproximadamente el 68% de las especies son gonocóricas, aunque la mayoría de las esponjas y todas las ascidias son hermafroditas, mientras que el 43% puede reproducirse asexualmente o tiene la capacidad de regenerarse. Predomina la fecundación interna (71%), mientras que todos los bivalvos y poliquetos se reproducen por fecundación externa. El cuidado parental, definido como cualquier tipo de protección de los embriones mediante incubación o encapsulación, ocurre en el 61% de las especies, siendo universal entre los crustáceos y frecuente en los gasterópodos (89%). El desarrollo indirecto caracteriza al 82% de las especies, de las cuales el 59% produce larvas lecitotróficas y el 33% larvas planctotróficas. Comprender los modos reproductivos y las capacidades de dispersión es crucial para evaluar la conectividad, la resiliencia y la vulnerabilidad de las comunidades bentónicas en el frente del talud continental argentino.

Palabras clave: Comunidades bentónicas, reproducción, dispersión larval, cuidado parental, Argentina.

INTRODUCTION

Understanding how organisms maintain populations over time within a given marine area requires consideration of both environmental variables (e.g. temperature, salinity, substrate type) and intrinsic biological factors, such as food availability, recruitment, larval supply from nearby populations, and their variability (Caley et al. 1996; Todd 1998; Ostrovsky 2021). Species employ a variety of strategies to persist, often involving seasonal changes and responses to natural or anthropogenic disturbances. Reproductive strategies and modes have been the focus of extensive research worldwide, enabling the identification of patterns across taxonomic groups and environments, and shedding light on traits that make certain species more sensitive or better adapted to specific conditions (e.g. Thorson 1950; Vance 1973; Jackson 1983; Ostrovsky 2021). In this context, organisms may colonize and persist in a given environment by employing both sexual and asexual reproductive strategies. Special attention must be paid to the most vulnerable stages in the life cycle, which often occur during reproduction and larval development, when species' requirements are most critical (Thorson 1950; Wangensteen et al. 2017). A study by Thorson (1950), for example, identified broad biogeographic patterns in reproductive traits, noting a prevalence of planktotrophic development in tropical waters and a higher frequency of brooding species in polar and deep-sea environments, potentially linked to food availability. Numerous ecological models have since been developed to evaluate the relative importance of pre- and post-settlement processes and to distinguish between open and closed population structures (e.g. Caley et al. 1996; Todd 1998; Fraschetti et al. 2003). These approaches provide essential insights into the persistence and dynamics of marine ecosystems across biogeographic regions.

The diversity of life cycles among organisms that reproduce sexually can, in broad terms, be classified into two main reproductive strategies. The first, which is the most common across taxa and species, involves the production of many offspring without any form of parental care. The second strategy entails the allocation of a portion of the available resources toward parental care (Giangrande et al. 1994; Ostrovsky 2021). Within these two predominant strategies, a wide range of reproductive variants can be found. These include: species capable of releasing hundreds or thousands of gametes into the environment, where external fertilization occurs and is typically followed by the development of a planktotrophic larva (which feeds on plankton during development); species that retain female gametes within the parental body, where internal fertilization occurs upon the entry of male gametes, followed by the release of either planktotrophic or lecithotrophic larvae (the latter relying solely on yolk-derived nutrients); oviposition of embryos or larvae by females, often accompanied by the formation of gelatinous masses, dense capsules, or cocoons that provide a degree of protection during development and, in other cases, internal incubation of embryos within the adult body, with juveniles being released directly into the environment (Thorson 1950; Mileikovsky 1971; Giangrande et al. 1994; Ostrovsky 2021).

The number of eggs, larvae or offspring produced by benthic invertebrates varies widely among species and across geographic regions. Consequently, their dispersal potential also differs substantially. Species that produce large numbers of planktotrophic larvae are generally associated with greater dispersal capacity, allowing them to colonize new environments due to the extended duration of their planktonic larval stage, which can last from several weeks to months. In contrast, species that produce fewer but larger offspring, such as lecithotrophic larvae or encapsulated embryos, tend to have higher survival rates but more limited dispersal capabilities (Mileikovsky 1971; Strathmann 1978, 1985).

In sessile or low-mobility organisms such as cnidarians, sponges, bryozoans and some mollusks, the ability of larvae or juveniles to locate suitable habitats for settlement and development is a key determinant of reproductive success and survival (e.g. Roberts et al. 1991; Altieri 2003; Maldonado 2006; Bremec et al. 2008). Settlement often occurs in areas where food is more abundant or where the risk of predation is lower. In some cases, proximity to conspecifics or other organisms may enhance survival, while in others it may hinder it due to increased competition for space or resources (Jackson 1983).

The Argentine shelf-break front is a dynamic region where continental shelf waters converge with those of the Malvinas Current, forming a permanent thermohaline front (Acha et al. 2004; Piola et al. 2024). This area exhibits high seasonal primary productivity (Dogliotti et al. 2014; Guinder et al. 2024), which is also associated with elevated zooplankton concentrations observed during summer and early autumn (Sabatini and Álvarez Colombo 2001; Cepeda et al. 2024). These conditions are optimal for the feeding and/or reproduction of nektonic species such as fishes and squids (Alemany et al. 2024). Furthermore, the shelf-break front may act as a retention area for the larvae of both fish (i.e. Ehrlich et al. 2025) and benthic species (i.e. Mauna et al. 2008; Torres Alberto et al. 2025), thus favoring the establishment of adult populations. Several of Argentina's most economically important species, such as the Argentine hake (*Merluccius hubbsi*), the shortfin squid (*Illex argentinus*), the Argentine anchovy (*Engraulis anchoita*) and the Patagonian scallop (*Zygochlamys patagonica*), occur in this region and carry out key life-history processes here (Schejter et al. 2017a; Giberto et al. 2024).

Benthic communities of the shelf-break front region, particularly between 80 and 120 m depth, are dominated by the Patagonian scallop, along with other benthic invertebrates such as echinoderms, sponges, gastropods, and crustaceans (Bremec et al. 2003; Schejter et al. 2017a; Campodónico et al. 2019; Giberto et al. 2024). These benthic assemblages have been extensively studied in recent decades through the analysis of bycatch from bottom trawl fisheries, mainly targeting the Patagonian scallop and the Argentine hake (Gaitán et al. 2014; Schejter et al. 2017a, 2024; Gaitán and Souto 2020).

The overarching goal of the study is to identify dominant reproductive strategies employed by benthic invertebrates in the Argentine shelf-break region, southwestern Atlantic Ocean, that enable the persistence of their populations and communities over time. In this sense, particular objectives are: 1) to compile available information on the reproductive modes of the most common invertebrate species inhabiting the Argentine shelf-break front between 37° and 45° S and at 80 to 120 m depths, approximately; 2) to identify main reproductive strategies employed by benthic invertebrates in this region enabling the persistence and maintenance of their populations and communities over time, and 3) to determine which species potentially exhibit the highest and lowest dispersal capacities. This information is particularly relevant in the context of global change and may contribute to management strategies for ecosystems exposed to current and potential anthropogenic pressures (i.e. fisheries, hydrocarbon exploitation).

MATERIALS AND METHODS

Study area

The study area is located along the slope front of the southwestern Atlantic Ocean, between approximately 37° and 45° S and at depths ranging from 80 to 120 m depth. The region encompassing the shelf-break front is primarily characterized by soft-bottom habitats, mostly sandy substrates, as is the case for much of the Argentine continental shelf (Parker et al. 1997). At approximately 100 m depth, bottom water temperatures typically range between 6 and 8 °C. Salinity values vary from 33.7 to 34.0 in the outer portion of the front, while more shelf-influenced inner areas can present salinities as low as 33.4. During autumn and winter, thermoclines and pycnoclines are disrupted by vertical mixing driven by convective processes, resulting in bottom water temperatures that are approximately 1-2°C higher (Guerrero and Piola 1997).

This region is primarily influenced by the northward-flowing Malvinas Current (Figure 1). Within this area, particle transport occurs in the direction of the prevailing current, and vertical fluxes have been described that may facilitate benthic-pelagic coupling (Franco et al. 2017; Piola et al. 2024). In this area, main fishing grounds of the Patagonian scallop *Z. patagonica* are located.

Bibliographic sources

A comprehensive literature search was performed to gather published information relevant to each species or faunal group. Searches were conducted in multiple scientific databases and platforms, including ASFA (Aquatic Sciences and Fisheries Abstracts), Academia.edu, PubMed, Scopus, Web of Science, JSTOR, and Google Scholar, to maximize coverage. To complement database searches, we also queried ChatGPT (OpenAI) with same targeted prompts to identify other potential literature sources. All suggestions were manually verified (see Ruksakulpiwat et al. 2024). Search strategies combined keywords and prompts of ChatGPT including each species names in combination with the following terms: 'larvae', 'reproduction', 'fecundity', 'larval development', 'incubation', 'embryo', and 'parental care'. We considered peer-reviewed articles, books, technical reports, and gray literature relevant to each taxonomic group, with no restrictions on publication date or language. In cases where species-specific reproductive data were unavailable, reproductive modes were inferred based on information from related species at the genus, family, or higher taxonomic levels.

RESULTS

Information on the reproductive strategies of 126 epibenthic invertebrate species (typically bigger than 1 cm) recorded in this region was compiled (Appendix, Table A1).

A total of 55 species (approximately 44%) exhibit some form of asexual reproduction or regeneration (Table 1). Regarding sexual reproduction, sixty-eight percent (68%) of the species are gonochoric (with separate sexes), although the Ascidiacea group is entirely composed of hermaphroditic organisms; most sponge species are also hermaphroditic (Table 2). Internal fertilization occurs in

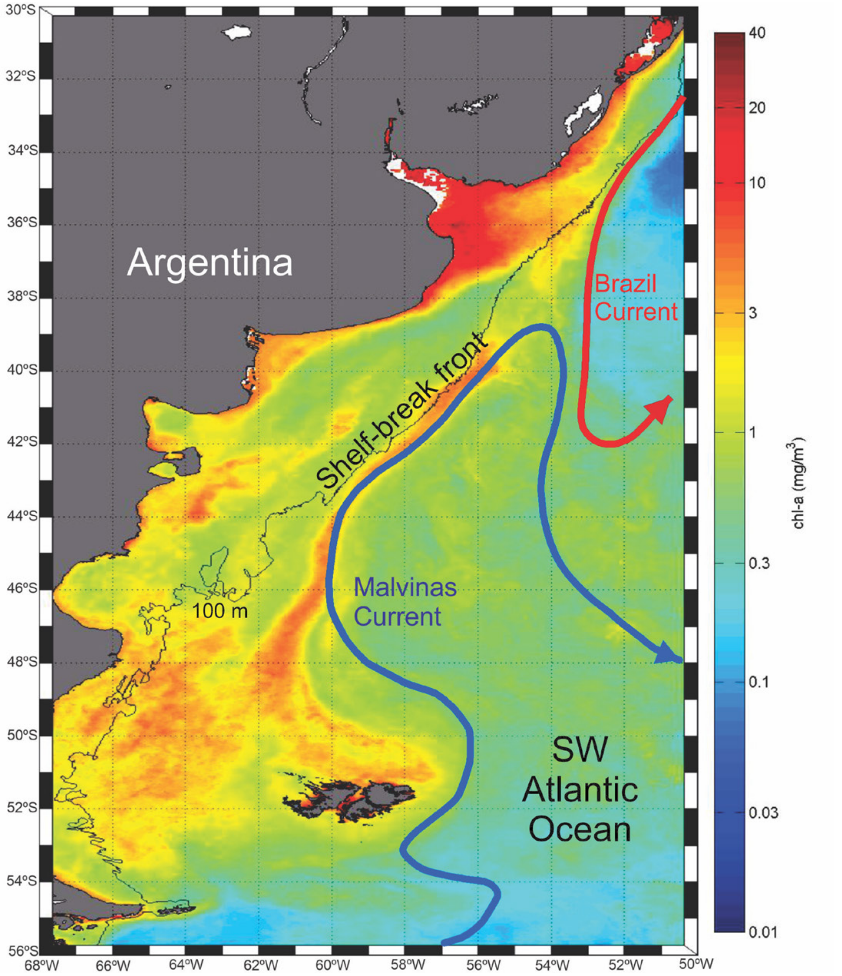

Figure 1. Study area: location of the shelf-break front in Argentina. The image shows monthly averages of chlorophyll-*a* concentration derived from MODIS-Aqua satellite images for the period January-March 2024 (data obtained from https://oceandata.sci.gsfc.nasa.gov; 2022). The circulation of the main surface ocean currents (Brazil Current in red and Malvinas Current in blue) was digitized and vectorized in QGIS 3.40 using geospatial analysis tools, based on Franco et al. (2018). Courtesy of the Remote Sensing Program, INIDEP.

71% of the species (Table 3). All bivalves included in this study as well as polychaete species (Annelida) reproduce by external fertilization, although in some tube-dwelling polychaetes, fertilization may occur externally within the tube water, followed by parental care and embryo incubation on radioles or opercula, depending on the taxon (see more detailed information below, within Annelida).

With regard to parental care, in this study it is considered that a species exhibits parental care when the parent protects at least part of the embryonic development of its offspring either through incubation within the body or by providing some type of egg capsule that protects early embryonic stages, regardless of whether larvae or juveniles hatch from it. Based on this criterion, 61% of the species included in this study exhibit some form of parental care (Table 4). Among them, crustaceans (Malacostraca) stand out, with 100% of the species studied showing parental care, followed by

Table 1. List of taxa (N = 126) according to their reproductive capabilities, arranged in alphabetical order. RS: sexual reproduction; RS-RA: sexual and asexual reproduction.

Phylum	Class	RS	RS-RA	Total
Annelida	Polychaeta	2	5	7
Arthropoda	Malacostraca	11		11
	Thecostraca	2		2
	Pycnogonida	1		1
Brachiopoda	Rhynchonellata	3		3
Bryozoa	Gymnolaemata		6	6
	Stenolaemata		1	1
Chordata	Ascidiacea	2	3	5
Cnidaria	Hexacorallia	3	4	7
	Hydrozoa		11	11
	Octocorallia	1	1	2
Echinodermata	Asteroidea	10		10
	Crinoidea		1	1
	Echinoidea	5		5
	Holothuroidea	2		2
	Ophiuroidea	5		5
Mollusca	Bivalvia	5		5
	Gastropoda	19		19
Porifera	Calcarea		1	1
	Demospongiae		22	22
Total		71	55	126

gastropods with 89%. On the other hand, 21% of the species do not exhibit any type of parental care, while for another 18%, no adequate information was found in the literature to assess this parameter (Table 4). Finally, 82% of the species exhibit an indirect life cycle with a larval stage. Of these, 59% produce lecithotrophic larvae, 33% planktotrophic larvae, and for the remaining species, the larval type remains unknown (Table 5).

It is important to note that species-specific reproductive information is available for only 47% of the studied species (Table 6). Moreover, the available data are highly heterogeneous and range from complete reproductive cycles to isolated observations of particular parameters. In this study, it is considered that there is species-specific information if there is at least one piece of data on embryo incubation, larvae, or some other reproductive parameter. Only five species (~ 4%), namely the scallop *Z. patagonica*, the bivalve *Hiatella umbonata*, the gastropod *Coronium acanthodes*, the hermit crab *Sympagurus dimorphus*, and the sea cucumber *Psolus patagonicus*, have reproductive studies or data derived from specimens collected specifically in the shelf-break front region. For the remaining species, the species-specific information was compiled from studies conducted in other environments (e.g. deep slope, Argentine Patagonian coast and gulfs, Chile, or Antarctica).

Table 2. Information on the reproductive system of the studied taxa (N = 126), arranged in alphabetical order. GO: gonochoric; HE: hermaphroditic; HE-GO: both reproductive modes; SD: no data.

Phylum	Class	GO	HE	HE-GO	SD	Total
Annelida	Polychaeta	4	3			7
Arthropoda	Malacostraca	11				11
	Pycnogonida	1				1
	Thecostraca	1	1			2
Brachiopoda	Rhynchonellata	3				3
Bryozoa	Gymnolaemata		6			6
	Stenolaemata			1		1
Chordata	Ascidiacea		5			5
Cnidaria	Hexacorallia	7				7
	Hydrozoa	11				11
	Octocorallia	1			1	2
Echinodermata	Asteroidea	10				10
	Crinoidea	1				1
	Echinoidea	5				5
	Holothuroidea	2				2
	Ophiuroidea	5				5
Mollusca	Bivalvia	4	1			5
	Gastropoda	15	4			19
Porifera	Calcarea				1	1
	Demospongiae	5	16		1	22
Total		86	36	1	3	126

Detailed reproductive traits by taxonomic group

Porifera

Over 50 sponge species have been recorded in the study area, and their occurrence is strongly dependent on the availability of suitable substrate, often provided by other benthic organisms or their remains (Schejter et al. 2025). For the purposes of this investigation, we considered 23 sponge species that are probably the most representative and frequently recorded. Reproductive timing in sponges is highly variable, ranging from restricted periods to continuous reproduction throughout the year, depending on intrinsic genetic factors and environmental conditions such as primary production blooms (Maldonado 2006). Although specific reproductive data for sponge species in the shelf-break front region are limited, it is expected that they share characteristics with closely related taxa from other regions.

Only one species from the class Calcarea has been recorded in the area, *Sycon* sp. (Schejter and Bremec 2007), a group known to produce amphiblastula larvae (Maldonado 2006). The remaining recorded species belong to the class Demospongiae, with nearly half of them belonging to the order Poecilosclerida, which is the largest order of sponges concerning the numbers of families and genera. These are generally ovoviviparous (with embryos that develop inside their body tissues in a variable

Table 3. Fertilization type in the studied taxa (N = 126). FE: external fertilization; FI: internal fertilization; SD: no data.

Phylum	Class	FE	FI	SD	Total
Annelida	Polychaeta	7			7
Arthropoda	Malacostraca		11		11
	Pycnogonida	1			1
	Thecostraca		2		2
Brachiopoda	Rhynchonellata		3		3
Bryozoa	Gymnolaemata	1	5		6
	Stenolaemata		1		1
Chordata	Ascidiacea	2	3		5
Cnidaria	Hexacorallia	2	5		7
	Hydrozoa	1	10		11
	Octocorallia	1		1	2
Echinodermata	Asteroidea	5	5		10
	Crinoidea		1		1
	Echinoidea	4	1		5
	Holothuroidea	1	1		2
	Ophiuroidea	3	2		5
Mollusca	Bivalvia	5			5
	Gastropoda	2	17		19
Porifera	Calcarea		1		1
	Demospongiae		22		22
Total		35	90	1	126

period that can extend from a few weeks to months to complete their development) and hermaphroditic (individuals with functional organs of both sexes, either simultaneous or successive), releasing lecithotrophic parenchymella larvae after variable internal embryonic developments (Maldonado et al. 2002). This has been reported in families such as Myxillidae, Microcionidae, Mycalidae, Hymedesmiidae, Isodictyidae, and Latrunculiidae (Erekovsky 2000; Maldonado 2006; Baldacconi et al. 2007; Maldonado and Riesgo 2009; Koutsouveli et al. 2018). Embryos at early developmental stages have been found in September in *Mycale (Aegogropila) magellanica*, commonly present in the region –reported by Schejter et al. (2012)– as well as in *Isodictya* spp. such as *I. kerguelensis* and *I. setifera*, suggesting a seasonal spawning pattern (see Burton 1932). *Tedania (Tedaniopsis) charcoti* has been observed to develop embryos internally from unsegmented eggs until larval release (Burton 1932). Embryonic development at different stages was reported in *Clathria (Clathria) discreta* and *Spongia magellanica* (Burton 1932), and the presence of embryos in the mesohyl was also recorded for *Iophon proximum* (Burton 1940). Gonochorism has been observed in genera such as *Callyspongia*, *Calyx*, *Haliclona*, and members of Suberitidae (e.g. *Suberites*, *Pseudosuberites*, *Plicatellopsis*) and Niphatidae (e.g. *Dasychalina*, *Haliclonissa*) (see Baldacconi et al. 2007; Maldonado and Riesgo 2009),

Table 4. Parental protection of embryonic development, either through body incubation or by producing protective egg capsules, from which larvae or juveniles may hatch. NO: indirect development via eggs released externally from the parent organism, with no parental care; YES: indirect or direct development involving some form of incubation or parental care; SD: no data.

Phylum	Class	NO	SD	YES	Total
Annelida	Polychaeta	2		5	7
Arthropoda	Malacostraca			11	11
	Pycnogonida			1	1
	Thecostraca			2	2
Brachiopoda	Rhynchonellata		1	2	3
Bryozoa	Gymnolaemata	1		5	6
	Stenolaemata			1	1
Chordata	Ascidiacea	2		3	5
Cnidaria	Hexacorallia	2		5	7
	Hydrozoa		9	2	11
	Octocorallia	1	1		2
Echinodermata	Asteroidea	5		5	10
	Crinoidea			1	1
	Echinoidea	4		1	5
	Holothuroidea	1		1	2
	Ophiuroidea	3		2	5
Mollusca	Bivalvia	4		1	5
	Gastropoda	1	1	17	19
Porifera	Calcarea		1		1
	Demospongiae		10	12	22
Total		26	23	77	126

all present in the study area. Species of the order Haplosclerida typically incubate embryos in the mesohyl or aquiferous canals. For example, *Haliclona bilamellata* showed oocytes and embryos in early developmental stages during winter in South Georgia Island (Isla San Pedro) (Burton 1932), and *H. penicillata* was reported to incubate 30-60 embryos inside internal chambers (Koutsouveli et al. 2018).

Summarizing, sponge larvae of the shelf-break front may be mainly lecithotrophic, short-lived, and undergo a planktonic or crawling phase lasting from a few hours up to three weeks. They usually use cilia for swimming in the water column, although some larvae glide or creep over the substrata. Once settled, they metamorphose into juvenile sponges (Maldonado 2006; Maldonado and Bergquist 2006).

Cnidaria

Cnidarians exhibit diverse reproductive strategies, especially among the subphylum Medusozoa, which often undergo metagenesis involving a benthic polyp stage and a planktonic medusa stage. Polyps reproduce asexually by budding, producing medusae that reproduce sexually, yielding a planula larva (Brusca and Brusca 2005). In most species, however, the medusa stage is reduced or absent,

Table 5. Presence of larval stages in the life cycles of the studied organisms. DD: direct development; ID: indirect development; LLE: lecithotrophic larva; LPL: planktotrophic larva; SD: no data; LLE-LPL: both possibilities.

			ID				
Phylum	Class	DD	LLE	LPL	SD	LLE-LPL	Total
Annelida	Polychaeta	1	1	5			7
Arthropoda	Malacostraca	4		7			11
	Pycnogonida			1			1
	Thecostraca		2				2
Brachiopoda	Rhynchonellata			1	2		3
Bryozoa	Gymnolaemata		5	1			6
	Stenolaemata		1				1
Chordata	Ascidiacea		5				5
Cnidaria	Hexacorallia	3	3	1			7
	Hydrozoa		11				11
	Octocorallia		1		1		2
Echinodermata	Asteroidea		7	3			10
	Crinoidea					1	1
	Echinoidea		1	4			5
	Holothuroidea		1	1			2
	Ophiuroidea	2		3			5
Mollusca	Bivalvia	1	2	2			5
	Gastropoda	10	1	7	1		19
Porifera	Calcarea		1				1
	Demospongiae		22				22
Total		21	64	36	4	1	126

with the larva being the only planktonic stage. On the contrary, in the subphylum Anthozoa, the medusa stage is entirely absent. Gametes are produced by adults, and fertilization can be external or internal, with larvae developing either in the water column or within the parent.

At least 25 cnidarian species were reported from the study area: 15 hydrozoans, at least 4 sea anemones, 5 corals, and 1 zoantharian (Bremec et al. 2003; Genzano et al. 2009; Schejter et al. 2015); 19 of them were included in this revision. Among hydrozoans, there was a trend of reduced medusa stages in deeper and colder waters. Most species retain sessile gonophores and directly release planula larvae (Bouillon et al. 2006). Examples include *Synthecium robustum*, *Symplectoschyphus subdichotomus*, *Sertularella mediterranea*, *S. striata*, *Halecium beanii*, *Lafoea dumosa*, *Filellum* spp., *Grammaria abietina*, and *Eudendrium ramosum*. Studies conducted in the intertidal zone of Mar del Plata showed that reproductive structures of *H. beani* were recorded only during the summer, whereas those of *S. mediterranea* began to appear in late summer and increased throughout autumn and winter (Genzano 1994). In *S. mediterranea*, larvae develop within a gelatinous brood cham-

Table 6. Information on the studied species. YES: at least partial information on reproductive aspects; SD: no species-level information available.

Phylum	Class	SD	YES	Total
Annelida	Polychaeta	7		7
Arthropoda	Malacostraca	4	7	11
	Pycnogonida	1		1
	Thecostraca	1	1	2
Brachiopoda	Rhynchonellata	1	2	3
Bryozoa	Gymnolaemata	4	2	6
	Stenolaemata	1		1
Chordata	Ascidiacea	2	3	5
Cnidaria	Hexacorallia	1	6	7
	Hydrozoa	9	2	11
	Octocorallia	2		2
Echinodermata	Asteroidea	1	9	10
	Crinoidea		1	1
	Echinoidea	2	3	5
	Holothuroidea		2	2
	Ophiuroidea	1	4	5
Mollusca	Bivalvia	2	3	5
	Gastropoda	12	7	19
Porifera	Calcarea	1		1
	Demospongiae	14	8	22
Total		66	60	126

ber (= acrocyst) outside the gonotheca. *Phialella chilensis* probably exhibits a full medusoid cycle (implying the existence of external fertilization), as recorded for other *Phialella* species (Blanco et al. 2000). Lecithotrophic planulae with limited swimming ability have been reported in other *Eudendrium* species, and their metamorphosis has been described in detail by Sommer (1990). Based on genus- and family-level life-history descriptions, *Phialella* and many Sertulariidae produce non-feeding planulae (lecithotrophic) (Boero 1987; Bouillon et al. 2004). However, no data were available on reproductive seasonality or larval duration in the region. Existing studies focused mainly on intertidal or shallow-water species in Argentina (e.g. Genzano 1994; Genzano et al. 2002; Jaubet and Genzano 2011). In general, planulae are lecithotrophic and swim, or they are transported by the currents, until settling and metamorphosing into polyps.

In hydrozoan species with free-living medusae, species dispersal depends not only on the larval stage but also on the medusa phase (Bouillion et al. 2006). However, other dispersal mechanisms, such as rafting, the production and release of frustules (type of asexual propagule that detaches from the colony), and the movement of free-living planktonic colonies by water currents, can also contribute to a species' broad geographic range (Jaubet and Genzano 2011 and reference therein). Asexual reproduction seems to be extremely important for maintaining populations of *Filellum* spp. The numerous colonies frequently recorded on the Argentine continental shelf were always immature, lacking gonothecae (pers. obs. G. N. Genzano)

Anthozoans, such as sea anemones, corals, and zoantharians, display only a polyp stage. *Actinostola crassicornis*, a common gonochoric sea anemone usually recorded in the shelf-break front benthic community, shows year-round gametogenesis, internal fertilization, and it is also a brooder, releasing juveniles with three tentacle cycles (Riemann-Zürneck 1978; Rodríguez and López-González 2013; Lauretta et al. 2020) (Figure 2). *Antholoba achates* also exhibits brooding, which has been reported as hermaphroditic or gonochoric (Fautin 1984; Häussermann and Försterra 2009), often associated with volutid gastropods in the studied area (Schejter and Escolar 2013).

Evidence of brooding was also reported for *Isotealia antarctica*, also frequently found on gastropod shells in the study area (Häussermann and Försterra 2009; Schejter and Escolar 2013). Among scleractinian corals, *Flabellum curvatum* and *F. thouarsii* are morphologically similar species with documented gonochorism and brooding (they retain eggs and larvae in their gastrovascular cavity) in Antarctic waters, where larvae are released. Females release year-round larvae with developed tentacle buds and an oral disc. Due to their limited swimming ability, coral larvae's dispersal distance was mostly determined by their longevity (i.e. maximum lifetime), settling ability, larval survival, and oceanographic conditions (e.g. water current speed and direction). *Flabellum*'s larvae remain in the environment for a short period and then settle in the vicinity of the adults and even on the theca of the adult coral (Squires 1962; Waller et al. 2008). Settlement on the parent coral's theca has also been observed by the authors of the present study in the shelf-break front (Figure 2). The cup coral *Desmophyllum dianthus* is a cosmopolitan species, rarely recorded at the shelf-break front (Schejter et al. 2015), although it is frequently recorded in deeper areas of the slope in Argentinian waters (Cairns and Polonio 2013; Schejter and Bremec 2019). It is a gonochoric species, and the reproduction was studied in the Chilean Patagonia, turning out to be highly seasonal, with a spawning at the end of austral winter (August) and beginning gamete production in early spring (September) (Feehan et al. 2019). These authors also recorded a high fecundity compared to other deep-sea scleractinians, ranging from 2,448 (± 5.13 SE) to 172,328 (± 103.67 SE) potential oocytes per polyp. In accordance with Addamo et al. (2012), it was concluded that *D. dianthus* may use the same reproductive techniques as other deep-water coral species, being a broadcast spawner with lecithotrophic larvae. Coral larvae are relatively poor swimmers; therefore, their dispersal distance is mostly dependent on their longevity (i.e. maximum lifetime), settlement competence, larval survival, and oceanographic conditions (e.g. speed and direction of currents) (see also Scheltema 1986).

Two octocoral species are common in the region. *Alcyonium antarcticum* (= *A. paessleri*) is frequently found on scallop shells but lacks reproductive data; reproductive modes within the genus vary widely (McFadden et al. 2001; Kahng et al. 2011; Quintanilla et al. 2013). No species-level reproductive data were found for *Convexella magelhaenica*. Based on family- and genus-level accounts for Primnoidae and Octocorallia, the most parsimonious inference was that *C. magelhaenica* produces a planktonic planula following broadcast spawning, and that larvae are likely lecithotrophic. Given documented variation in octocoral reproductive modes (brooding vs. spawning; gonochorism vs. hermaphroditism), this should be stated as an inference pending species-specific histological or rearing evidence (Waller et al. 2023). The zoantharian *Epizoanthus paguricula* was exclusively associated with the hermit crab *Sympagurus dimorphus* (Schejter and Mantelatto 2011). While reproductive data were scarce for zoanthids, related *Epizoanthus* spp. associated with hermit crabs were gonochoric, reproduce year-round, have and likely produce planktotrophic larvae (Muirhead and Tyler 1986).

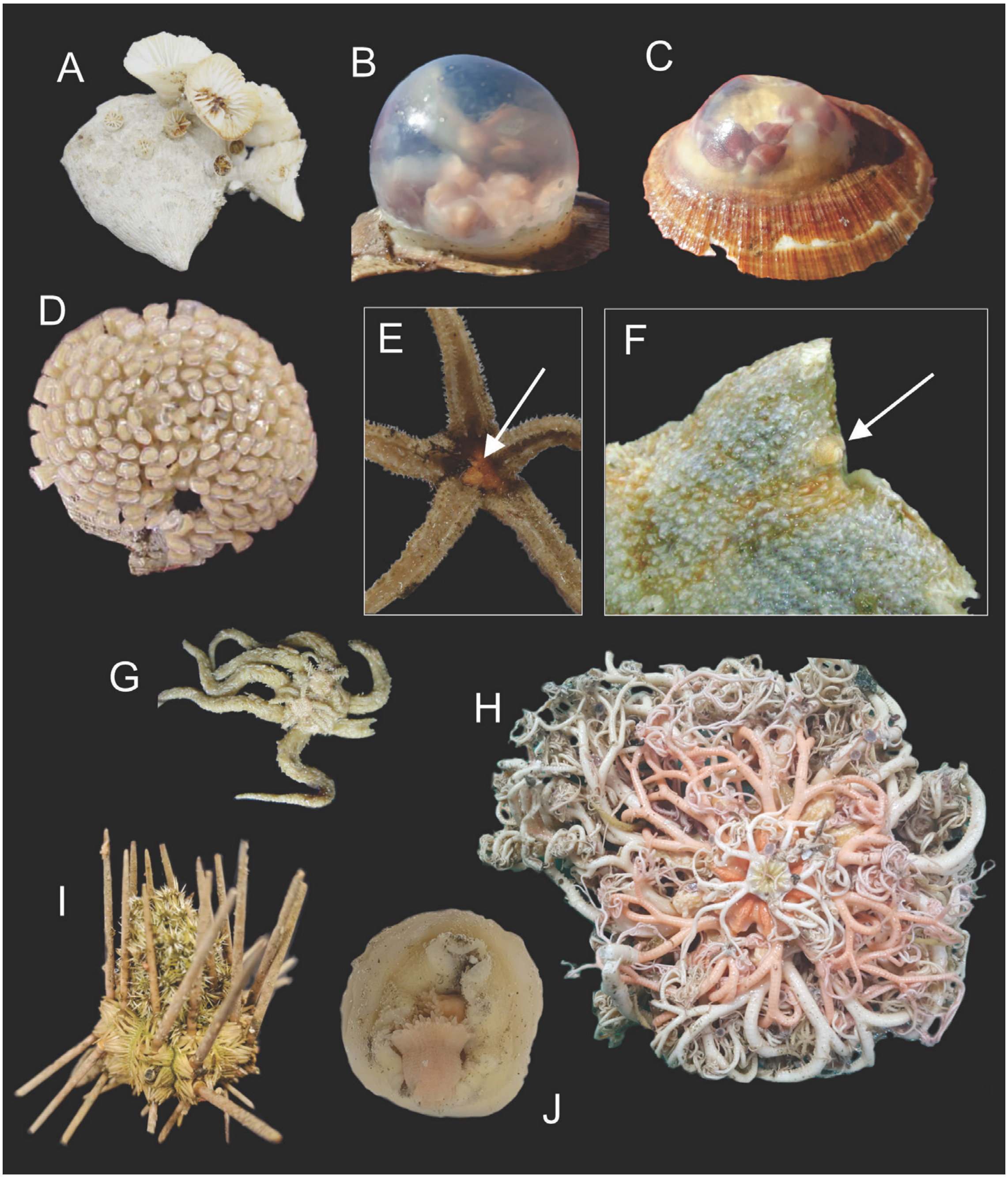

Figure 2. Parental care in some of the species recorded in the study area. A) Adult *Flabellum curvatum* with juveniles attached to the theca. B) Egg capsule of *Odontocymbiola magellanica*; C) Egg capsule of *Adelomelon ancilla*. D) Egg capsules of *Fusitriton magellanicus*. E) Oral incubation in *Diplasterias brandti*. F) Incubation within the body wall in *Diplopteraster clarki*. G) *Ophiosabine vivipara* with associated juveniles. H) *Gorgonocephalus chilensis* with an associated juvenile. I) Female *Austrocidaris canaliculata* carrying numerous juveniles on the aboral surface. J) *Actinostola crassicornis* brooding juveniles within the gastrovascular cavity.

Annelida

Polychaete annelids display diverse reproductive strategies among marine invertebrates (Wilson 1991; Giangrande 1997; Rouse and Pleijel 2001). Most reproduce sexually and are gonochoric, although hermaphroditism is also present. Gametes typically develop in specialized organs or coelomic cavities and are released via nephridia, gonoducts, or through body rupture. Larval development includes planktonic trochophore, metatrochophore, and nectochaeta stages before settling.

Asexual reproduction via budding, fission, or fragmentation is also common, with regeneration of lost segments. In the shelf-break front region, several tube-dwelling polychaetes live on biogenic substrates like mollusk shells and crabs (i.e. Bremec et al. 2003; Schejter and Bremec 2007). The Serpulidae (*Serpula narconensis*, Spirorbinae spp.) and Sabellidae (*Potamilla antarctica*) construct calcareous or translucent tubes and are indicators of Vulnerable Marine Ecosystems (CCAMLR 2009). Hermaphroditism, asexual reproduction, and regeneration are reported in both families, with alternation between reproductive modes. Sexual reproduction involves external fertilization, either within the tube water or the surrounding environment (Giangrande 1997; Gambi et al. 2000; Rouse and Pleijel 2001). Embryos are often incubated on radioles (Sabellidae) or modified opercula (Spirorbinae) (Knight-Jones and Bowden 1984; Giangrande 1997). Planktonic development with feeding trochophores is well known in some genera such as *Serpula*, while Spirorbinae has lecithotrophic larvae that are competent to settle when released from the brood chamber, and the duration of swimming lasts up to several hours (Kupriyanova et al. 2019). Smaller sabellids typically brood embryos, whereas larger species release gametes for external fertilization (Rouse and Fitzhugh 1994).

Another tubiculous polychaete species that settles abundantly on Patagonian scallop shells is *Idanthyrsus macropaleus*, a member of the family Sabellariidae. This species constructs rigid tubes made of cemented sand grains, which may occasionally cover the entire upper valve and extend beyond its margin (Bremec et al. 2003; Schejter and Bremec 2007). Members of this family are dioecious and broadcast their gametes into the water column, where external fertilization occurs. The resulting larvae are planktotrophic (Pawlik 1992; Kirtley 1994), with a prolonged planktonic stage and a high dispersal potential (Giangrande 1997). Successful settlement and development into sessile adults depend on finding suitable substrates, a process mediated by chemical cues detected through sensory organs located in the anterior region of the body (Kirtley 1994; Helm et al. 2018). *Chaetopterus antarcticus* is also a conspicuous tubiculous polychaete species recorded in the study area. Although primarily infaunal, it has occasionally been reported as an epibiont on the Patagonian scallop (Bremec and Schejter 2019). Members of this family (Chaetopteridae) are gonochoric; males and females can be distinguished by the color of the gamete-containing posterior body segments (white in males and yellow in females) (Rouse and Pleijel 2001). Some species of this genus have also been observed to reproduce asexually and exhibit regenerative capabilities (Nishi 1996; Giangrande 1997).

Less frequently, tubiculous polychaetes of the genus *Phyllochaetopterus* have been recorded in samples collected from the shelf-break front (Bremec et al. 2003). Studies conducted on other species of this genus suggest that they are gonochoric and capable of sexual reproduction, as well as regeneration. Additionally, the presence of eggs inside the tubes has been documented in some individuals (Bloom 1976).

Finally, some polychaete species exhibit a boring lifestyle and may be found inhabiting mollusk shells. This group includes species of the genus *Polydora*, belonging to the family Spionidae. These worms are generally gonochoric and brood their offspring; some species release planktotrophic larvae, while others release juveniles (Wilson 1991). *Polydora* species –or traces left by them on different substrates– have been sporadically detected in the study area (see Schejter and Bremec 2007).

Mollusks

More than 20 mollusk species are frequently recorded in the study area. However, the Patagonian scallop *Zygochlamys patagonica* is the dominant and keystone species in the benthic community associated with the Argentine shelf-break front. Although its distribution extends beyond this region, it is in this area where dense aggregations are found, supporting the development of an industrial fishery since 1996 (Schejter et al. 2017a; Campodónico et al. 2019). This species is gonochoric, with a marked seasonal reproductive cycle and partial spawning events occurring between September and March (Campodónico et al. 2004, 2008), which are associated with food availability (Schejter et al. 2002). Fertilization is external. Under laboratory conditions, the trochophore larva appears approximately 80 hours post-fertilization (Schwartz and Campodónico 2019), followed by a free-swimming, planktotrophic veliger larva, which reaches the pre-umbonate stage within 50 days and remains in the water column for up to 70 days (Schejter et al. 2010; Schwartz and Campodónico 2019). Primary settlement substrates in this community include hydroids, mainly *Symplectoscyphus subdichotomus* and *Grammaria abietina* (= *Grammaria magellanica*) (Bremec et al. 2008).

Although less abundant in terms of biomass and density, several bivalve species occur frequently in this benthic community. *Hiatella umbonata* (= *Hiatella meridionalis*, see Zelaya and Güller 2023) is among the most common, and is morphologically and ecologically distinguishable from other bivalves in the region by its sessile lifestyle and the presence of byssus. Reproductive information for this species is scarce; however, like *Z. patagonica*, it has been observed to possess a planktotrophic veliger larva capable of recruiting onto hydroids within the benthic community (Schejter et al. 2010). *Limea pygmaea* is another frequently recorded species. Studies based on specimens from sub-Antarctic areas (Marion Islands) have concluded that this species undergoes direct development, brooding its larvae within the mantle and releasing fully developed juveniles (Linse and Page 2003). For *Limopsis hirtella*, Martin et al. (1995) based on samples collected between 40 and 240 m (partially overlapping the study area) proposed a year-round reproductive period, although seasonal peaks in recruitment may occur. Other studies on the genus *Limopsis* suggest that most species are gonochoric and release lecithotrophic larvae without brooding (Tanabe 1990; Nakaoka and Ohta 1998; Malchus and Warén 2005), although in the Japanese species *L. azumana*, brooding and juvenile release have been observed (Tanabe 1990). Additionally, organisms identified as *Entodesma* sp. have been recorded in the study area. Reproductive studies on other species of this genus indicate that they are functional hermaphrodites; external fertilization produces short-lived lecithotrophic larvae in the plankton (Campos and Ramorino 1981).

Among gastropods inhabiting this benthic community, the main reproductive strategy involves the deposition of egg capsules containing fertilized eggs onto the seafloor or a suitable substrate. The volutid snails *Odontocymbiola magellanica* and *Adelomelon ancilla* are frequently found in this region. Both are gonochoric and deposit their egg capsules on loose mollusk shells, empty skate capsules, and other biogenic substrates (Bremec et al. 2003) (Figure 2). Although their reproductive cycles have only been studied in Patagonian gulfs, they exhibit seasonality, with egg-laying occurring primarily in spring (associated with increasing photoperiod) and extending through late summer (Bigatti et al. 2008; Penchaszadeh et al. 2009). Juveniles emerge directly from the capsules, having developed by feeding on intracapsular fluid (Penchaszadeh et al. 1999).

Another conspicuous and abundant gastropod in the shelf-break front is *Fusitriton magellanicus*, which also produces distinctive egg capsules (Figure 2), typically associated with biogenic substrates (often mollusk shells) in this region, although in other parts of its distributional range, egg masses have been observed on rocky substrates. Studies from the Strait of Magellan have described a seasonal reproductive strategy, with spawning occurring in spring. Unlike volutids, *F. magellanicus* releases long-lived, swimming, planktotrophic veliger larvae, thus favoring the potential of dispersion of the species. The complete intracapsular development lasts between 55 and 67 days (Cañete et al. 2012). Each female may deposit 20 to 290 capsules per spawning event, with each capsule containing between 2,800 and 4,200 eggs (Penchaszadeh and De Mahieu 1975).

Among muricids, *Coronium acanthodes* has been occasionally recorded. It produces distinctively lenticular egg masses from which juveniles emerge directly (Pastorino and Penchaszadeh 2009). Another muricid, *Fuegotrophon pallidus*, is also recorded in the region, although no data are available on its egg mass morphology or embryonic development (Pastorino et al. 2014), as is also the case for *Trophon ohlini*. *Trochita pileus* is a common species in the area, mostly associated with *Z. patagonica* shells. It is a protandric hermaphrodite, a trait common to many members of the family Calyptraeidae, which also exhibits parental care. Torroglosa and Giménez (2012) reported that each *T. pileus* female lays between 7 and 8 capsules, each containing 4 to 14 embryos, from which juveniles emerge directly. Teso and Penchaszadeh (2019) later provided evidence for the presence of nutritive cells within the capsules.

Fissurellidea megatrema, commonly known as the keyhole limpet, is also a gonochoric species found in this region. Unlike the previously mentioned gastropods, fertilization is external and produces a swimming larva without any parental care (Yuvero et al. 2022). No specific reproductive information is available for the calliostomatid species found in this area (*Calliostoma* spp., *Falsimargarita iris*, *Photinula coerulescens*). However, based on data from related taxa, these species are likely to be gonochoric, have external fertilization, with larval development occurring within the egg capsule and emerge as crawling juveniles without a free-swimming planktonic stage (Clench and Turner 1960), although planktonic larvae were also reported for some species of the genus *Calliostoma* (i.e. Holyoak 1989). In some species studied elsewhere, the eggs are released embedded in gelatinous ribbons (Ramón 1990; Holmes 1997).

For *Capulus compressus*, a rare species in the study area, protandric hermaphroditism and egg incubation have been reported. This species produces a unique larval form called 'echinospira' which is a planktotrophic larva that enables a long pelagic dispersal; it has a double shell, a trait also found in the genus *Lamellaria* (Lebour 1935; Orr 1962; Fassio et al. 2015). In *Pareuthria* spp. collected in Argentine Patagonia, reproductive observations indicate that the egg masses consist of multiple capsules, each containing up to five embryos. All larval development occurs within the capsules, and juveniles emerge directly (Pastorino and Penchaszadeh 2002). No specific reproductive data are available for other frequently recorded gastropods in the area belonging to the genera *Admete* and *Volvarina* (Families Cancellariidae and Marginellidae), but based on general patterns (i.e. Coovert 1986; Pawlik et al. 1988), they might be gonochoric, with internal fertilization and planktonic (possibly planktotrophic) larvae, although in the studied species of Marginellidae, larvae development remains intracapsular and emerge juveniles from egg capsules. No specific information on the reproduction of *Cirsotrema magellanicum* (= *Epitonium magellanicum*) is currently available. Nevertheless, based on data from other epitoniid species, this species is likely gonochoric, with females depositing egg capsules from which planktotrophic larvae emerge (e.g. Pastorino and Penchaszadeh 1999; Collin 2000).

Nudibranchs have occasionally been reported in the benthic community of the shelf-break front. At least two nudibranch species are mentioned to be recorded up to 100 m depth in Argentina: *Doris fontainii* (= *Anisodoris fontainei*) and *Marionia cucullata* (Castellanos 1967). Most members of this group are hermaphrodites with complex genital systems of high taxonomic value. Following reciprocal copulation, these organisms lay egg masses in the form of spiral ribbons (i.e. in *D. fontainii*), coiled bands, or gelatinous aggregations depending on the species. After 2 to 3 weeks, swimming veliger larvae emerge, which may be either planktotrophic or lecithotrophic (Muniain et al. 1992; Häussermann and Försterra 2009). In the case of *D. fontainii*, planktotrophic larvae emerged after a 14 days' incubation period at 14.5 °C in a laboratory study (Muniain et al. 2007). There is no specific information available for *M. cucullata* or other members of the genus, and therefore it is not possible to assign a larval developmental mode for this species. Evidence indicates that within the family Tritoniidae, to which this species belongs, both planktotrophic and lecithotrophic larval developments occur (Kempf and Willows 1977; Kempf and Todd 1989).

Crustacea

Among the most conspicuous and frequent crustaceans in this region are the spider crabs *Libidoclaea granaria* and *Eurypodius latreillii* (Bremec et al. 2003; Schejter and Spivak 2005). In these species, fertilization is internal, involving copulation, and females incubate the eggs on their pleopods. Eggs hatch into planktotrophic larvae (zoeae) which, under laboratory conditions at 15-20 °C, completed metamorphosis to the first benthic crab stage, passing through zoea I, zoea II, and megalopa stages in approximately 50 days (Fagetti 1969; Campodónico and Guzmán 1972). Another crab inhabiting the slope front is *Peltarion spinosulus*, which also produces planktotrophic larvae. Larval stages (four zoeae and one megalopa) were described by Iorio (1983) from plankton samples collected in various sectors of the continental shelf. Larvae were recorded between July and December, with megalopae being particularly abundant in November and December. Ovigerous females were only recorded in March. The larval distribution matched that reported for adults of *P. spinosulus*, and the evidence suggests this is likely an annual-cycle species.

Among hermit crabs, two species are particularly common: *Pagurus comptus* and *Sympagurus dimorphus*. The reproductive cycle of *P. comptus* has been studied in specimens from the Beagle Channel by Lovrich and Thatje (2006). In that environment, almost 90% of ovigerous females were recorded between April and September, while fewer than 10% were recorded in March and November. Embryonic development within the egg was estimated to take 5-6 months under environmental conditions (4-6 °C). The number of eggs carried by a female ranged from 138 to 848, depending on female size. Larval development consists of four zoeal stages and one megalopa stage, with a duration of approximately four months in the laboratory. *Sympagurus dimorphus* is another relatively frequent hermit crab in the shelf-break front, showing a patchy distribution and mostly living in symbiosis with a zoanthid (Schejter and Mantelatto 2011, 2015). According to data from Schejter et al. (2017b), most females likely hatch their eggs between spring and summer, as females collected in September already carried eggs at an advanced stage of development. Females can carry between 800 and 2,200 eggs, depending on size. Lemaitre and McLaughlin (1992) described the megalopa stage and juveniles of this species. However, there is currently no information on the duration of its larval cycle or early larval stages. A third hermit crab species, *Propagurus gaudichaudi*, also occurs in the shelf-break front region, although it is much less frequent (Bremec et al. 2003), and no specific information is available on its reproductive habits or larval development, although it should follow the generalities reported for Paguridae.

The gregarious squat lobster *Grimothea gregaria*, another anomuran like the hermit crabs, forms large concentrations in more coastal or shelf areas, where it plays an important role in the ecosystem (e.g. Romero et al. 2004), but is also found in the shelf-break front (Bremec et al. 2003). Several studies have addressed its reproductive strategies in different regions of the Argentine Sea. This dioecious species has seasonal reproduction that varies geographically. According to Dellatorre and Barón (2008), studies conducted in northern Patagonian gulfs showed that brooding females of *G. gregaria* were present from June to December and that embryonic development lasted 26-29 days at 11 °C; the synchrony between ovarian re-maturation and embryogenesis suggests the capacity for more than three consecutive egg clutches per reproductive season. Also, more than 10,750 eggs have been recorded in a single female (Tapella et al. 2002). The planktotrophic larvae (six zoeal stages and one megalopa stage) have a high dispersal capacity (e.g. Tapella et al. 2002; Pérez-Barros et al. 2007; Vinuesa 2007).

Among Cirripedia, the lepadomorph barnacle *Weltnerium gibberum* is a common epibiont of the Patagonian scallop but has also been recorded on other organisms in this benthic community (Schejter and Bremec 2007). Descriptions of its developmental stages were provided by Nilsson-Cantell (1930). In general, lepadomorph barnacles may be hermaphroditic or have separate sexes, with dwarf males permanently associated with the female and unable to feed. Copulation occurs between sessile mating pairs. Eggs are fertilized within the mantle cavity (brood chamber) and remain there until hatching (Buhl-Mortensen and Høeg 2006). Depending on the species, either nauplius or cypris larvae may be released, and either planktotrophic or lecithotrophic larval modes may occur, with the latter being more common in deep or shelf environments. Nilsson-Cantell (1930) described for *W. gibberum* a free-living stage called ‘pupa without plates’, equivalent to a cypris larva, which remains within the female’s mantle cavity. Cypris larval release has been observed in other species of *Weltnerium*, as well as in members of *Ornatoscalpellum* and *Verum* (Buhl-Mortensen and Høeg 2006, 2013). Dispersal capacity in these species is presumably limited, as cypris larvae are lecithotrophic and are estimated to settle within 3-4 days after release, which is a developmental strategy likely advantageous in deep-sea organisms dependent on rare and/or patchily distributed habitats (Buhl-Mortensen and Høeg 2013). Only general data was previously reported for *Balanus laevis*, a cirriped distributed up to 275 m, although larval settlement was reported to occur more frequently in spring in Chubut, Argentina (Rico et al. 2001; Häussermann and Forsterra 2009). The life cycle of *Balanus laevis*, could resemble that of other congeners, including a sessile adult phase and a planktonic larval phase. As reported for other *Balanus*, this should be a simultaneous hermaphrodite, exhibiting internal cross-fertilization typical of balanid barnacles (Desai et al. 2006); fertilization is internal and embryos are brooded until hatching into planktotrophic nauplii, which pass through six stages before reaching the non-feeding cypris stage. The cypris settles on a suitable substrate and metamorphoses into a juvenile barnacle (Anderson 1994).

Among peracarid crustaceans, several species of isopods and amphipods have been recorded in this region (Bremec et al. 2003; Sánchez et al. 2011; Schejter et al. 2012). The most conspicuous species are the isopods *Acanthoserolis schytei* and *A. polaris*, while some spheromatids are frequently recorded as well. Although no species-specific information is available on reproduction and development, in general, serolid isopods are gonochoric with direct development, and females brood their developing young in a ventral marsupium formed by overlapping oostegites, from which juveniles emerge (Johnson et al. 2001). For Antarctic serolid isopods, incubation has been suggested to last 8-20 months, with juvenile release coinciding with the peak in primary production (Luxmoore 1982). The number of eggs/embryos per female is related to female size and likely also to nutritional condition. Observations on *A. polaris* described the copulatory behavior and suggested that females do not ingest food during breeding (Moreira 1973).

Pycnogonida

Pycnogonids, commonly known as sea spiders, are dioecious arthropods that exhibit an unusual reproductive strategy within the group, as males provide parental care for eggs and early post-embryonic stages. When sexually mature adults meet, the female positions herself over the male and releases eggs into the water simultaneously as the male releases sperm, resulting in external fertilization. Subsequently, the male collects and attaches eggs onto his ovigerous appendages, which is the modified third legs specialized for this purpose. Eggs hatch into free-swimming protonymph larvae, which may sometimes act as symbionts of cnidarians, mollusks, or echinoderms. Through successive molts, the larvae add segments and appendages until they develop into juveniles. Depending on the species' developmental pattern, embryos may remain protected by the male until they reach stages resembling adults (Bain 2003; Brusca and Brusca 2005; Fornshell 2015). In other species, endoparasitic larvae can also occur on the gastrozooids of hydroid colonies (Genzano et al. 2002).

Brachiopoda

Three brachiopod species have been recorded on the shelf-break front: *Magellania venosa*, *Terebratella dorsata*, and *Liothyrella uva* (McCammon 1973, Bremec et al. 2003). Studies on *M. venosa* in the Magellanic region showed that its distribution is mainly associated with the type of available settlement substrate and current velocity. This species is gonochoric and viviparous, with a marked reproductive season, although some individuals with mature gonads were observed year-round. Sperm is released in mucous masses, and fertilization occurs internally within the female's nephridia (McCammon 1973).

In *L. uva*, larval development and reproduction were studied in specimens from Antarctic waters. This species is also gonochoric, with a possibly seasonal reproductive cycle and internal fertilization. Gamete release mainly occurs between September and November. Females brood eggs on their lophophores and primarily release a ciliated gastrula-stage larva in January (Peck and Robinson 1994). However, Peck et al. (2001) found that females may release larvae at different developmental stages, ranging from early gastrulas to competent larvae ready to settle. Competent larvae were observed to prefer settling on live brachiopods. The estimated time from gamete release to larval settlement ranges between 115 and 160 days, although metamorphosis may be delayed in the absence of suitable settlement substrate. Meidlinger et al. (1998) proposed that *L. uva* might reproduce asynchronously throughout the year under certain conditions as an adaptive response to interannual resource variability.

There is no specific information available for *T. dorsata*, the third brachiopod species frequently recorded in the study area. However, it is reasonable to assume that it shares similar characteristics with the other two species mentioned, given that they belong to the same group (Articulata), occupy the same habitat, and have been recorded in coexistence.

Echinodermata

Echinoderms are an important component of the benthic community in the shelf-break front region, where mainly nine species of the class Asteroidea, five of Ophiuroidea, five of Echinoidea, three of Holothuroidea, and one of Crinoidea have been recorded (Escolar and Bremec 2015; Schejter et al. 2026). Additionally, some other less common species are occasionally found. Among sea stars (Asteroidea), various reproductive strategies are observed, ranging from species with free-living larvae (bipinnaria and brachiolaria, which can have pelagic, benthic, planktotrophic, or lecithotrophic development) to species with direct development (Bosch and Pearse 1990; Byrne 2006). Brooding of offspring on different parts of the female's body is common among some species distributed on the shelf-break front. For example, *Ctenodiscus australis*, one of the most abundant and frequent species (see Escolar et al. 2011), was observed by Lieberkind (1926) incubating embryos beneath the paxillae on the aboral surface. The developmental stages were later described by Rivadeneira et al. (2017) in specimens collected from deep waters of the slope. These authors also noted that females may brood embryos at different developmental stages simultaneously. The maximum number of offspring recorded per female was 73, with one stage comparable to a brachiolaria larva but lacking larval arms and possessing an adhesive disc at the center of the preoral lobe. Development in this species is lecithotrophic, and reproduction may occur continuously throughout the year, as females with mature oocytes and embryos were observed in different months of the year, with no particular pattern (Rivadeneira et al. 2017).

Other brooding species in the shelf-break front include *Diplopteraster clarki*, *Pteraster affinis lebruni* (Figure 2), *Diplasterias brandti* and *Anasterias antarctica* (= *Anasterias minuta*). The first two retain lecithotrophic larvae in brood chambers. Bernasconi (1937) reported 18 juveniles under the supradorsal membrane of one arm in *Pteraster affinis lebruni*. Fraysse et al. (2020a) documented year-round reproduction in *Diplopteraster verrucosus*, a congeneric species occasionally recorded near the Burdwood Bank. *Diplasterias brandti* and *A. antarctica* brood their offspring in oral brood chambers, which causes females not to feed during incubation. Populations of *A. antarctica* in coastal Patagonia showed a seasonal reproductive pattern with an incubation period of 7 to 8 months (Gil et al. 2011; Pérez et al. 2015), spawning between April and May, and juvenile release in August-September (Gil et al. 2011). Eight developmental stages were recorded, including a lecithotrophic larva and a modified brachiolaria (Gil et al. 2011).

Among species that possess indirect development and external fertilization in the study area are *Henricia obesa* and *Acodontaster elongatus*, both with lecithotrophic larvae, and *Odontaster penicillatus*, with planktotrophic larvae (Janosik et al. 2008; Fraysse et al. 2020b). A particular case is *Glabraster antarctica*, which has external fertilization but releases nutrient-rich eggs and a facultatively planktotrophic larva (Bosch 1989; Fraysse et al. 2020b). There is no species-specific information on the reproduction or larval development of the sun star *Labidiaster radiosus*, also common in the region (Escolar and Bremec 2015). However, for its Antarctic congener *Labidiaster annulatus*, indirect development with release of planktotrophic bipinnaria larvae has been reported, which metamorphose into juveniles after passing through a brachiolaria stage (Janosik et al. 2008).

Most brittle stars (class Ophiuroidea) are dioecious, with external fertilization and indirect development. Mature gametes are released into bursae and expelled to the outside. Two larval types occur: planktotrophic ophiopluteus and lecithotrophic pelagic vitellaria. Some species brood their young within bursae, ovaries, or coelom. Metamorphosis occurs while larvae are still swimming (Hendler 1991; McEdward and Miner 2001; Pérez et al. 2014). Some ophiuroids also reproduce asexually by fission and regeneration (Hyman 1955). The largest species in the study region is *Gorgonocephalus chilensis* (‘basket star’), which likely has indirect development with release of pelagic larvae capable of dispersal (Barboza et al. 2010). Juveniles of other *Gorgonocephalus* species associate with corals in other regions (Neves et al. 2020). In the shelf-break front and Burdwood Bank, juveniles were observed closely associated with adults (personal observations, Figure 2), suggesting adults may be important for population maintenance. Other abundant but smaller brittle star species include *Ophiosabine vivipara* (= *Ophiacantha vivipara*), *Ophiuroglypha lymani*, *Ophiactis asperula*, and *Ophiomixa vivipara*. As their names suggest, the first and last are viviparous, retaining eggs in bursae until juveniles emerge (Mortensen 1936; Hyman 1955). *Ophiosabine vivipara* shows an annual reproductive cycle, with smallest individuals recorded in adult genital slits between March and October (Sánchez 2011; Escolar et al. 2013). Huenten et al. (2025) reported a high genetic connectivity between several populations of *O. asperula* in Argentina facilitated by a planktotrophic larvae. Other *Ophiactis* species have planktonic larval stages (Mortensen 1913; Selvakumaraswamy and Byrne 2000). *Ophiactis resiliens* from Australia shows an annual reproductive cycle with peak spawning in winter (Falkner and Byrne 2003), possibly similar in *O. asperula*. No specific studies exist for *O.*

lymani, but isolated observations confirm separate sexes and many small eggs (Mortensen 1936).

Among sea urchins (class Echinoidea), reproductive strategies vary. Most are dioecious with external fertilization and indirect development, but some cold-water incubators have direct development (Pérez et al. 2014). The planktonic larva, called echinopluteus, has six pairs of elongated arms and metamorphoses rapidly to juvenile, unlike asteroids with a fixed larval stage (Ruppert and Barnes 1996). In temperate sea urchins, reproductive cycles are annual or semiannual, influenced by photoperiod, lunar phase, water temperature, and nutrition (Brogger et al. 2010). Five main sea urchin species occur on the shelf-break front. *Austrocidaris canaliculata*, a frequent and easily recognized species (Bremec et al. 2003), is dioecious and unique among Cidaroidea urchins for brooding offspring on its aboral surface, protected by spines (Figure 2). Development is direct and lecithotrophic, with a female observed brooding up to 536 offspring (Flores et al. 2019). *Pseudechinus magellanicus*' reproductive cycle has been studied in South American populations (Orler 1992; Marzinelli et al. 2006; Kino 2010; Gil et al. 2020; Pfoh et al. 2025). It is dioecious with planktotrophic larvae, exhibiting an annual reproductive cycle with main spawning in spring and a smaller, asynchronous spawning late in summer. Reproductive success is attributed to synchronization with environmental factors like temperature, photoperiod, and chlorophyll increases (Gil et al. 2020). Recently, a small proportion of hermaphrodite specimens of *P. magellanicus* was reported by Pfoh et al. (2025) in the Beagle Channel. The green urchin *Arbacia dufresnii*, occasionally recorded on the shelf-break front ca. 80 m depth, follows the annual pattern with spawning peaks in spring and summer (Brogger et al. 2010). There is evidence that in this species the embryonic and larval development are conditioned by water temperature and maternal origin of eggs (Pía-Fernández et al. 2021). *Sterechinus agassizii*, another frequent urchin in the region, lacks reproduction data, but the Antarctic congener *Sterechinus neumayeri* shows annual cycles, slow development rates, and planktotrophic larvae released coinciding with phytoplankton blooms (Bosch et al. 1987). Little is known about the irregular urchin *Tripylaster philippii*, the fifth most commonly recorded species. Genera *Tripylaster* and *Brisaster* species are the only Schizasteridae known not to brood their young, exhibiting indirect development with planktotrophic larvae (Pearse et al. 2008).

Sea cucumbers (class Holothuroidea) have a single gonad (unlike other radially symmetrical echinoderms). Generally, they have external fertilization and indirect development through an auricularia larva (Hickman et al. 2001). *Psolus patagonicus*, a frequent and conspicuous species often associated with the Patagonian scallop, is dioecious and brooding (Bernasconi 1941; Hernández 1981; Giménez and Penchaszadeh 2010; Martínez et al. 2011). It reproduces during the austral summer, spawning in February-March, with females brooding under their bodies from February to September. The doliolaria larval stage was observed in June, pentactula in late July, and juveniles were released in September-October (~ 2 mm size) (Giménez and Penchaszadeh 2010). *Pentactella leonina* (= *Pseudocnus dubiosus leoninus*) is also a frequent species and has been suggested to have indirect development with external fertilization (Martínez et al. 2020).

Within Crinoidea (sea lilies), there are two species described for the Southwest Atlantic Ocean *Isometra vivipara* and *Phrixometra nutrix*, both of which are brooding species (Clark and Clark 1967; Pertossi et al. 2019, 2021; Pertossi and Martinez 2022). The reproduction and development of both species was studied near Burdwood Bank (Pertossi et al. 2019; Pertossi and Martinez 2022). However, only *I. vivipara* was recorded in the study area until present. It is dioecious with internal fertilization and uniquely presents two brooding stages: lecithotrophic embryos in a marsupium, followed by cystidean larvae adhering to the mother's cirri. The next stage is the feeding pentacrinoid larva (Mortensen 1920). Oocytes in various developmental stages were recorded simultaneously, suggesting year-round reproduction. The larva attaches to the substrate via a specialized adhesive pit, where metamorphosis into a sessile juvenile crinoid occurs. Crinoids have high regenerative capacity similar to asteroids and ophiuroids, using asexual reproduction in adverse conditions or after predation (Ruppert and Barnes 1996).

Bryozoa

Bryozoans are organisms capable of reproducing both sexually and asexually. In the shelf-break front, many bryozoan species occur, most of them recorded as epibionts (e.g. López Gappa and Landoni 2009; Schejter et al. 2014). Asexual reproduction is used to increase colony size, whereas sexual reproduction involves free-swimming larvae, which may be either planktotrophic or lecithotrophic, with the ability to disperse and colonize new habitats. In general, individuals are hermaphroditic, although some dioecious species have been also recorded among cheilostomes. Some groups can brood the early developmental stages; there are viviparous species, and in some cases, species develop a structure functionally similar to a placenta (Brusca and Brusca 2005; Ostrovsky et al. 2008, 2009). Most of the species reported in the shelf-break front belong to the order Cheilostomatida (see López Gappa and Landoni 2009; Schejter et al. 2014), which is characterized by a variety of methods for embryonic incubation. Embryos may be brooded in external membranous sacs, skeletal (calcified) chambers, or internal incubation sacs formed by uncalcified zooidal walls, or they may develop intracelomically in viviparous species. In some cases, extraembryonic nutrition has been recorded. Most cheilostomes brood their offspring in skeletal chambers called ovicells. The presence or absence of ovicells, as well as their morphology, are considered important traits in the taxonomy of the group (Ostrovsky 2008). However, the species-specific information on reproduction for the bryozoans recorded in this area is very scarce. As exceptions, Ristedt (1991) reported a size of the ancestrula (the size of the ancestrula corresponds closely to the maximum dimension of a cyphonautes larva) of 300 × 350 µm for *Andreella uncifera.* Among the Cyclostomatida bryozoans, the genus *Tubulipora* is recorded in the shelf-break front, and the presence of non-feeding larvae, viviparity, placentation and polyembryony is common in this order (Nekliudova al. 2021). Lastly, Porter and Hayward (2004) reported that *Alcyonidium australe* (Order Ctenostomatida) may release gametes and produce planktotrophic larvae.

Ascidiacea

There is a high diversity of reproductive strategies within Ascidiacea (Tunicata), which are related to their organizational type: colonial species (with both sexual and asexual reproduction) and solitary species (with exclusively sexual reproduction). These differences can be observed from order to species taxonomic level. All ascidians are hermaphroditic, although some species are protandrous (Lambert 2005). Sexual reproduction involves the production of lecithotrophic larvae (with a head and tail bearing chordate structures such as a notochord, nerve cord, and pharynx). Larvae swim or float passively (as in some Molgulidae) for a short period before settling on the substrate where the sessile adult individual (or zooid) will remain, formed after larval metamorphosis (Tatián and Lagger 2009). At least twelve different modes of asexual reproduction have been described in colonial ascidians (Monniot et al. 1991), involving the formation of buds from various zooid organs and the regeneration of a new individual, genetically identical to the parent.

Most solitary species produce numerous oocytes that are released into the water for external fertilization; in colonial ascidians (and in some solitary ones), oocytes produced in lower numbers are fertilized in the atrial cavity, within the colony matrix, or in brooding pouches, where larvae develop before being released (Monniot et al. 1991). Information on the sexual reproductive cycles of ascidian species inhabiting the shelf-break front is scarce. In most descriptions, the presence of larvae in brooding (colonial) species is reported at different times of the year. The reproductive cycles of solitary, non-brooding species can only be inferred through observations, and preferably by histological examination of gonadal development. Diehl (1977) briefly described the larva of *Alloeocarpa incrustans*, a colonial species with internal fecundation that broods inside the atrial cavity (Rocha et al. 2012). Tatián and Lagger (2009) provided information on the months during which mature gonads have been found for some species in Chile, such as *Paramolgula gregaria* (mature gonads in November) and *Cnemidocarpa nordenskjoldi* (mature gonads from December to February). For the genus *Cnemidocarpa*, Rocha et al. (2012) also mentioned the release of gametes without brooding or parental care. In colonies of *Sycozoa sigillinoides* studied in Chile, larvae were recorded in March (Tatián and Lagger 2009); these authors also noted that in the colonial species *Didemnum studeri* sexual reproduction takes place during most of the year, with larvae located beneath the colony surface, as in other members of the family Didemnidae.

DISCUSSION

In the present study, the reproductive modes of 126 benthic invertebrate species (> 1 cm) inhabiting the shelf-break front of the Argentine Sea were investigated, focusing mainly on the most commonly recorded species. Echinodermata resulted in the most studied taxonomic group, while the less studied are Annelida (Polychaeta) and Bryozoa. Within the set of species here studied, a wide range of reproductive strategies coexist. However, species-specific information is available for less than 50% of the species, and only for 5 (4%) of these species does the information originate from studies conducted in the study area. The limited availability of reproductive information derived directly from the study area underscores the need for targeted, species-level reproductive studies in the shelf-break environment, particularly because reproductive traits may vary within species across their geographical ranges. Consequently, patterns inferred from populations studied elsewhere may not fully reflect local reproductive strategies under the environmental conditions prevailing in the studied area. Nevertheless, the present study represents a valuable starting point, as it provides, for the first time, a comprehensive overview of reproductive modes across the main benthic invertebrate species composing the community as a whole, rather than focusing on single species, families, or higher taxonomic levels. This integrative approach offers a baseline framework upon which future, region-specific reproductive studies can build to refine and validate observed patterns.

Approximately 84% of the species exhibit an indirect life cycle with some type of larva. Dispersal potential to other habitats is enhanced in species with indirect life cycles and longer larval periods, as in some mollusks such as the Patagonian scallop *Zygochlamys patagonica* (Schejter et al. 2010) and the hairy snail *Fusitriton magellanicus* (Cañete et al. 2012), decapod crustaceans such as all the crabs (e.g. Campodónico and Guzmán 1972; Iorio 1983; Lovrich and Thatje 2006) and certain echinoderms such as the basket star *Gorgonocephalus chilensis* (Barboza et al. 2010) and the red ophiuroid *Ophiactis asperula* (Huenten et al. 2025). However, many species are probably capable of increasing their dispersal capabilities by means of strategies such as the existence of a medusa phase in certain hydroids (such as in *Phialella* species, see Blanco et al. 2000), or asexual dispersive stages such as frustules, or through fragmentation as a result of mechanical impact, for example, with the resulting fragments potentially being transported by local currents, as reported for hydroids (Jaubet and Genzano 2011) and sponges in reproductive stages (Maldonado and Uriz 1999) in other regions of the world. The Malvinas Current and the oceanographic processes occurring along the shelf-break front (Franco et al. 2017) may facilitate the general dispersion of the organisms, as demonstrated for some species (e.g. Torres Alberto et al. 2025). The Patagonian scallop (*Z. patagonica*), one of the most extensively studied species in the shelf-break front, provides an illustrative example in which available genetic evidence suggests that, although planktotrophic larvae may be transported along the front, additional processes interact with larval dispersal to shape gene flow and biogeographic patterns across scallop beds (Trucco and Lasta 2008).

A biogeographical perspective is relevant because benthic faunas in the Argentine Sea are structured by large-scale oceanographic and hydrographic patterns. A transition between distinct biogeographic provinces is recognized along the Argentine shelf-break front, where benthic assemblages reflect the boundary between the subantarctic Magellanic (Patagonian) Province and the temperate Argentine Province. The Magellanic Province is characterized by benthic communities dominated by subantarctic taxa, strongly influenced by cold waters transported northward by the Malvinas Current, whereas the Argentine Province supports predominantly temperate benthic assemblages, with subantarctic elements largely confined to its southern boundary and to frontal environments (Balech and Ehrlich 2008). These water mass dynamics contribute to differences in faunal composition along both latitudinal and depth gradients, affecting the distribution of benthic invertebrates across the continental margin and probably their reproductive strategies as well. Moreover, previous work on benthic communities in the Argentine Sea has highlighted how depth, substrate type and oceanographic conditions shape species distribution and community structure across the coastal areas, shelf and upper slope (Bastida et al. 2007; Bremec and Giberto 2017). The present study area covers soft bottoms at 80-120 m depth between 37° S and 45° S and showed the presence of most of the conspicuous invertebrates distributed along the Magellanic Province according to a generalized scheme based on an extensive review of georeferenced data (Souto 2014).

It is interesting to note that more than half of the species provide some form of parental care. This may involve incubating offspring within their bodies or producing protective egg capsules, from which larvae or juveniles are later released. Such strategies protect most of the developmental stages but often result in juveniles with very limited or no dispersal capacity. Examples include the coral *Flabellum curvatum* (Waller et al. 2008), the anemone *Actinostola crassicornis* (Lauretta et al. 2020), the sea urchin *Austracidaris canaliculata* (Flores et al. 2019), and gastropods of the families Volutidae and Muricidae (Penchaszadeh et al. 1999, 2009; Bigatti et al. 2008; Pastorino and Penchaszadeh 2009). Consequently, these species are likely to occur in more restricted and noticeable patches.

There is no uniformity regarding the reproductive period of the studied species, while some species have a specific reproductive period, others seem to do so throughout the year, without distinction between seasons. However, much of the reliable information for most species comes from populations in other areas of their distribution, as previously mentioned.

This work represents the first comprehensive compilation of reproductive traits of benthic invertebrates from the shelf-break front of the Argentine Sea, integrating information scattered across numerous sources. Although in some cases the data had to be extrapolated from populations from other regions, higher taxonomic levels, or related species due to the lack of species-specific studies in the area, the general overview provided here is novel and highly valuable. By synthesizing these dispersed data, this study offers for the first time a broad picture of the predominant reproductive strategies among benthic invertebrates in this ecologically and economically important region. The information presented here is not only of scientific relevance but also provides essential baseline knowledge to be considered in ecosystem-based fisheries management plans. Understanding reproductive modes and dispersal capacities of the species is fundamental to predicting population connectivity, resilience, and vulnerability to fishing pressure, hydrocarbon exploitation or environmental changes. Consequently, this contribution fills a critical knowledge gap and represents a significant step toward the sustainable management of benthic communities in the shelf-break front of the Argentine Sea.

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Data availability

Data generated during this study are available in the CONICET Scientist Repository at http://hdl.handle.net/11336/273915.

Author contributions

Laura Schejter: conceptualization; investigation; data curation; writing original; review and editing; visualization; validation; supervision. Claudia S. Bremec: investigation; data curation; validation; writing original and review. Mariana Escolar: investigation; data curation; validation; writing original and review. Gabriel N. Genzano: investigation; data curation; validation; writing original and review. Diego A. Giberto: data curation; validation; formal analysis; writing original and review. Mariela Pavón Novarin: investigation; data curation; validation; writing original and review. Marcos Tatián: investigation; data curation; validation; writing original and review.

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APPENDIX

Table A1. Studied taxa.

Phylum Annelida	
Class Polychaeta	*Chaetopterus antarcticus* Kinberg, 1867
	Idanthyrsus macropaleus (Schmarda, 1861)
	Phyllochaetopterus sp.
	Polydora sp.
	Potamilla antarctica (Kinberg, 1866)
	Serpula narconensis Baird, 1864
	Spirorbinae
Phylum Arthropoda	
Class Malacostraca	*Acanthoserolis polaris* (Richardson, 1911)
	Acanthoserolis schythei (Lütken, 1858)
	Antarcturidae
	Eurypodius latreillii Guérin, 1828
	Grimothea gregaria (Fabricius, 1793)
	Libidoclaea granaria H. Milne Edwards and Lucas, 1842
	Pagurus comptus White, 1847
	Peltarion spinosulus (White, 1843)
	Propagurus gaudichaudii (H. Milne Edwards, 1836)
	Sphaeromatidae
	Sympagurus dimorphus (Studer, 1883)
Class Thecostraca	*Balanus laevis* Bruguière, 1789
	Weltnerium gibberum (Aurivillius, 1898)
Class Pycnogonida	Pantopoda
Phylum Brachiopoda	
Class Rhynchonellata	*Liothyrella uva* (Broderip, 1833)
	Magellania venosa (Dixon, 1789)
	Terebratella dorsata (Gmelin, 1791)
Phylum Bryozoa	
Class Gymnolaemata	*Osthimosia eatonensis* (Busk, 1881)
	Alcyonidium australe d'Hondt and Moyano, 1979
	Andreella uncifera
	Arachnopusia monoceros (Busk, 1854)
	Neothoa cf. *chiloensis*
	Smittina leptodentata Hayward and Thorpe, 1990

Table A1. Continued.

	Tubulipora sp.
Phylum Chordata	
Class Ascidiacea	*Alloeocarpa incrustans* (Herdman, 1886)
	Cnemidocarpa nordenskjoldi (Michaelsen, 1898)
	Didemnum sp.
	Paramolgula gregaria (Lesson, 1830)
	Sycozoa sigillinoides Lesson, 1830
Phylum Cnidaria	
Class Hexacorallia	*Actinostola crassicornis* (Hertwig, 1882)
	Antholoba achates (Drayton in Dana, 1846)
	Desmophyllum dianthus (Esper, 1794)
	Epizoanthus paguricola Roule, 1900
	Flabellum (Flabellum) curvatum Moseley, 1880
	Flabellum (Flabellum) thouarsii Milne Edwards and Haime, 1848
	Isotealia antarctica Carlgren, 1899
Class Hydrozoa	*Eudendrium ramosum* (Linnaeus, 1758)
	Halecium beanii (Johnston, 1838)
	Grammaria abietina (Sars, 1851)
	Filellum serratum (Clarke, 1879)
	Lafoea dumosa (Fleming, 1820)
	Phialella chilensis (Hartlaub, 1905)
	Synthecium protectum Jäderholm, 1903
	Sertularella mediterranea Hartlaub, 1901
	Sertularella patagonica (D'Orbigny, 1846)
	Symplectoscyphus subdichotomus (Kirchenpauer, 1884)
	Symplectoscyphus sp.
Class Octocorallia	*Alcyonium antarcticum* Wright and Studer, 1889
	Convexella magelhaenica (Studer, 1879)
Phylum Echinodermata	
Class Asteroidea	*Diplasterias brandti* (Bell, 1881)
	Acodontaster elongatus (Sladen, 1889)
	Anasterias antarctica (Lütken, 1857)
	Ctenodiscus australis Loven in Lütken, 1871
	Diplopteraster clarki Bernasconi, 1937
	Glabraster antarctica (E. A. Smith, 1876)
	Henricia obesa (Perrier, 1891)
	Labidiaster radiosus Loven in Lütken, 1871

Table A1. Continued.

	Odontaster penicillatus (Philippi, 1870)
	Pteraster affinis lebruni Perrier, 1891
Class Crinoidea	*Isometra vivipara* Mortensen, 1917
Class Echinoidea	*Arbacia dufresnii* (Blainville, 1825)
	Austrocidaris canaliculata (A. Agassiz, 1863)
	Pseudechinus magellanicus (Philippi, 1857)
	Sterechinus agassizii Mortensen, 1910
	Trypilaster philippii (Gray 1851)
Class Holothuroidea	*Pentactella leonina* (Semper, 1867)
	Psolus patagonicus Ekman, 1925
Class Ophiuroidea	*Gorgonocephalus chilensis* (Philippi, 1858)
	Ophiactis asperula (Philippi, 1858)
	Ophiomyxa vivipara Studer, 1876
	Ophiosabine vivipara (Ljungman, 1871)
	Ophiuroglypha lymani (Ljungman, 1871)
Phylum Mollusca	
Class Bivalvia	*Hiatella umbonata* Zelaya and Güller, 2023
	Entodesma sp.
	Limea pygmaea (R. A. Philippi, 1845)
	Limopsis hirtella Mabille and Rochebrune, 1889
	Zygochlamys patagonica (P. P. King, 1832)
Class Gastropoda	*Adelomelon ancilla* ([Lightfoot], 1786)
	Admete magellanica (Strebel, 1905)
	Calliostoma sp.
	Capulus compressus Smith, 1891
	Cirsotrema magellanicum (R. A. Philippi, 1845)
	Coronium acanthodes (R. B. Watson, 1882)
	Doris fontainii A. d'Orbigny, 1836
	Falsimargarita iris (E. A. Smith, 1915)
	Fissurellidea megatrema A. d'Orbigny, 1839
	Fuegotrophon pallidus (Broderip, 1833)
	Fusitriton magellanicus (Röding, 1798)
	Lamellaria sp.
	Marionia cucullata (Couthouy, 1852)
	Odontocymbiola magellanica (Gmelin, 1791)
	Paraeuthria sp.
	Photinula coerulescens (P. P. King, 1832)
	Trochita pileus (Lamarck, 1822)
	Trophon ohlini Strebel, 1904

Table A1. Continued.

	Volvarina warrenii (Marrat, 1876)
Phylum Porifera	
Class Calcarea	*Sycon* sp.
Class Demospongiae	*Callyspongia (Callyspongia) nuda* (Ridley, 1884)
	Calyx kerguelensis (Hentschel, 1914)
	Clathria (Clathria) discreta (Thiele 1905)
	Clathria (Clathria) microxa Desqueyroux 1972
	Clathria (Microciona) antarctica (Topsent, 1916)
	Dasychalina validissima (Thiele, 1905)
	Haliclona bilamellata Burton, 1932
	Hymedesmia (Hymedesmia) antarctica Hentschel 1914
	Hymedesmia (Hymedesmia) leptochela Hentschel, 1914
	Iophon proximum (Ridley, 1881)
	Isodictya setifera (Topsent, 1901)
	Isodictya verrucosa (Topsent, 1913)
	Mycale (Aegogropila) magellanica (Ridley, 1881)
	Mycale (Mycale) doellojuradoi Burton, 1940
	Myxilla (Myxilla) mollis Ridley and Dendy, 1886
	Pseudosuberites sp.
	Spongia (Spongia) magellanica Thiele, 1905
	Stelodoryx argentinae Bertolino *et al.* 2007
	Tedania (Tedaniopsis) charcoti Topsent, 1907
	Tedania (Tedaniopsis) massa Ridley and Dendy, 1886
	Tedania (Tedaniopsis) mucosa Thiele, 1905
	Tedania (Tedaniopsis) sarai Bertolino, Schejter, Calcinai, Cerrano and Bremec, 2007