REVIEW

Reproductive investment in marine fish: regional patterns across species from the southwestern Atlantic Ocean

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ABSTRACT. The reproductive investment strategy of 19 species inhabiting different ecosystems in the Southwest Atlantic Ocean was analyzed. It was observed that fish with a short reproductive period, as those inhabiting Antarctic waters, showed lower annual reproductive investment (RI). This was associated with a determinate fecundity pattern of oocyte development and, presumably, a pre-reproductive energy accumulation strategy (capital breeding). In contrast, fish with longer reproductive periods and many spawning opportunities are likely to rely on energy acquired during reproduction (income breeding). Some batch spawners, such as red porgy, sea salmon and flatfish, combined low relative fecundity with a high frequency of spawning. Rocky reef fish (grouper and sea salmon) and black drum were characterized by long-lived and slow growing, with a long reproductive life span, and generally low RI. In small pelagic species (anchovy) growth rate was high, and RI was focused on oocyte number rather than quality, resulting in the production of less developed larvae. The extent of the spawning area is proposed as a trait relevant to recruitment, on the hypothesis that a larger spawning area may favour larval survival by attenuating density-dependent mortality, a mechanism supported by evidence for Argentine hake and Argentine anchovy but not tested here for the full set of species.

Key words: Reproductive strategy, spawning, growth, Argentine Sea, austral waters.

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Inversión reproductiva en peces marinos: patrones regionales entre especies del Océano Atlántico Sudoccidental

RESUMEN. Se analizó la estrategia de inversión reproductiva de 19 especies que habitan en diferentes ecosistemas del Atlántico Sudoccidental. Se observó que los peces con un período reproductivo breve, como aquellos que habitan en aguas antárticas, presentaban una menor inversión reproductiva (IR) anual. Esto se asoció con un patrón de fecundidad determinada en el desarrollo de los ovocitos y, presumiblemente, con una estrategia de acumulación de energía previa a la reproducción (*capital breeding*). Por el contrario, es probable que los peces con períodos reproductivos más prolongados y múltiples oportunidades de desove dependan de la energía adquirida durante la propia etapa reproductiva (*income breeding*). Algunas especies de desove fraccionado, como el besugo, el salmón de mar y los peces planos, combinaban una baja fecundidad relativa con una alta frecuencia de desove. Los peces de arrecifes rocosos (meros y salmones de mar) y la corvina negra se caracterizaron por ser longevos y de crecimiento lento, con una vida reproductiva prolongada y, por lo general, una IR

baja. En las especies pelágicas pequeñas como la anchoíta, la tasa de crecimiento fue elevada y la IR estuvo centraba más en el número de ovocitos que en su calidad, lo que daba lugar a la producción de larvas menos desarrolladas. Se propone la extensión del área de desove como un rasgo relevante para el reclutamiento, bajo la hipótesis de que una mayor área de desove podría favorecer la supervivencia larvaria al atenuar la mortalidad dependiente de la densidad; este mecanismo cuenta con evidencia en el caso de la merluza argentina y la anchoíta argentina, aunque no ha sido evaluado aquí para el conjunto total de las especies.

Palabras clave: Estrategia reproductiva, desove, crecimiento, Mar Argentino, aguas australes.

INTRODUCTION

During the life cycle, fish allocate energy primarily to maintenance, growth and reproduction (Ware, 1982). In the early stages of life, most of the acquired energy is directed towards somatic growth, reducing the mortality associated with small size, which increases vulnerability to competition or predation (Roff 1982). As fish reach gonadal maturation, a greater proportion of available energy is diverted towards reproduction, which requires a significant expenditure throughout the life cycle (Nielsen et al. 2012). The energy used for this process, depending on the reproductive strategy of fish, is distributed both for gamete production and for accessory activities like migration to spawning areas, courtship and parental care (McBride et al. 2015). These activities collectively constitute what is often referred to as 'reproductive effort', while the energy devoted exclusively for the formation of gametes or offspring development, in the case of a viviparous species, is more accurately defined as 'reproductive investment' (McBride et al. 2015). In species with external fertilization, where parental care is absent or performed by males, the energy investment of the mother for the development of offspring is reflected in the number and quality of the eggs produced during the reproductive season.

Building on this distinction, three nested levels of reproductive allocation should be distinguished. Total reproductive effort encompasses all resources, in terms of energy, time and survival risk that an individual diverts to reproduction, including gamete production, mate acquisition and courtship, spawning migrations, parental care by either sex, and the costs of gonadal maintenance. Maternal reproductive investment is the female component of that effort, comprising oocyte production together with any additional maternal contribution to offspring, such as provisioning during gestation in matrotrophic viviparous species. Female oocyte allocation is the narrowest level, namely the annual quantity of resources channeled into oocyte production through fecundity, spawning frequency, oocyte quality and the duration of the spawning season. The index quantified here corresponds exclusively to this last level; it is therefore not a measure of maternal investment or of total reproductive effort, and its values should not be interpreted as such.

The way in which the available energy is invested in reproduction throughout the reproductive cycle is also a key feature of fish reproductive strategy to maximize offspring survival. For example, the production of eggs (both in quantity and quality) in fish species that spawn once a year (total spawners) depends on the energy reserves accumulated in the ovaries prior to the onset of spawning. Fish with this energy allocation strategy are called 'capital breeders' and are usually found in environments where the optimal reproductive conditions are temporally restricted, such as high latitudes (Stephens et al. 2009). At the other end of the spectrum are species that have multiple spawning events (batch spawners) over a relatively long reproductive season, which are mainly found in tropical areas. These fish species feed and continuously store ovarian energy during the spawning period and are referred to as 'income

breeders'. Fish inhabiting temperate-cold waters often adopt an intermediate strategy between these two categories, characterized by the accumulation of reserves both prior and during the reproductive period. Capital and income breeding are the ends of a continuum rather than discrete categories, and their assignment ideally requires direct evidence on feeding, energy reserves or condition. Such evidence is available for some of the species considered here, whereas for others the assignment is inferred from spawning pattern and the duration of the reproductive season and should be regarded as a hypothesis.

Ultimately, the energy investment results in the production of eggs, larvae and offspring, whose quantity, quality and survival capacity largely depend on the maternal contribution during the maturation process (Trippel 1999). This phenomenon, known as maternal effect, generates variability in the Stock-Recruitment (S-R) models, which establish the relationship between the abundance of parents (SSB) and their offspring (Marshall et al. 1998). Therefore, to improve the accuracy of these models, it is essential to determine the precise contribution of the mother to the reproductive potential of the stock, which is closely linked to the energy invested in the production of gametes.

A wide spectrum of reproductive strategies has been recorded in marine fishes from the Southwestern Atlantic Ocean (SWA), covering almost all the categories described in terms of fertilization type, reproductive behavior, gender roles, oocyte growth type, spawning pattern, embryonic development, etc. (Saborido-Rey and Macchi 2021). Among chondrichthyans, all of which have internal fertilization, a variety of strategies can be found, including oviparous to viviparous species with both embryo nutrition modes, either lecithotrophic or matrotrophic (Awruch, 2015; Lessa et al. 2021). Bony fishes also display a variety of reproductive modalities, although most commercially important species are typically oviparous with external fertilization, producing a large quantity of small eggs (about 1 mm in diameter or smaller) throughout the reproductive season, which are fertilized by males in the marine environment. This reproductive mechanism is prevalent in demersal, pelagic, and benthic species inhabiting both coastal and offshore areas (Macchi et al. 2021a). Beyond this general pattern, important variations in reproductive strategies have also been documented. For example, some species exhibit certain reproductive behaviors, such as parental care or mate selection, which have evolved to increase the chances of offspring survival. On the other hand, the environmental variability associated with the spatial distribution of organisms has also generated different tactics that affect the way in which energy is distributed or invested in the reproductive process. This includes variations in the number of spawning events, reproductive frequency, fecundity, and oocyte size.

In order to compare these strategies and evaluate how marine bony fishes in the SWA region allocate energy in reproduction, we selected 19 species that inhabit diverse ecosystems in the Argentine Sea, and also in the Antarctic-Subantarctic waters (Figure 1), with variable life cycles in terms of their extension, reproductive modalities and growth rates. Most of the selected species are economically important fish resources for the SWA region. The main objective of this study was to review the parameters that define female oocyte allocation in these species (fecundity, spawning frequency, oocyte quality and extension of the reproductive period) and to integrate them into a reproductive index (RI). Parameters were compiled from published literature and, in some species, derived from the reanalysis of historical datasets. In addition, these above data were analyzed in relation to different aspects of the life cycle of each species, in particular information on length and age at maturity, extension of the reproductive life span and reproductive area, longevity and growth rate. Finally, the results were interpreted in terms of other population aspects relevant to fisheries, such as abundance, recruitment and survival rates that characterize these species.

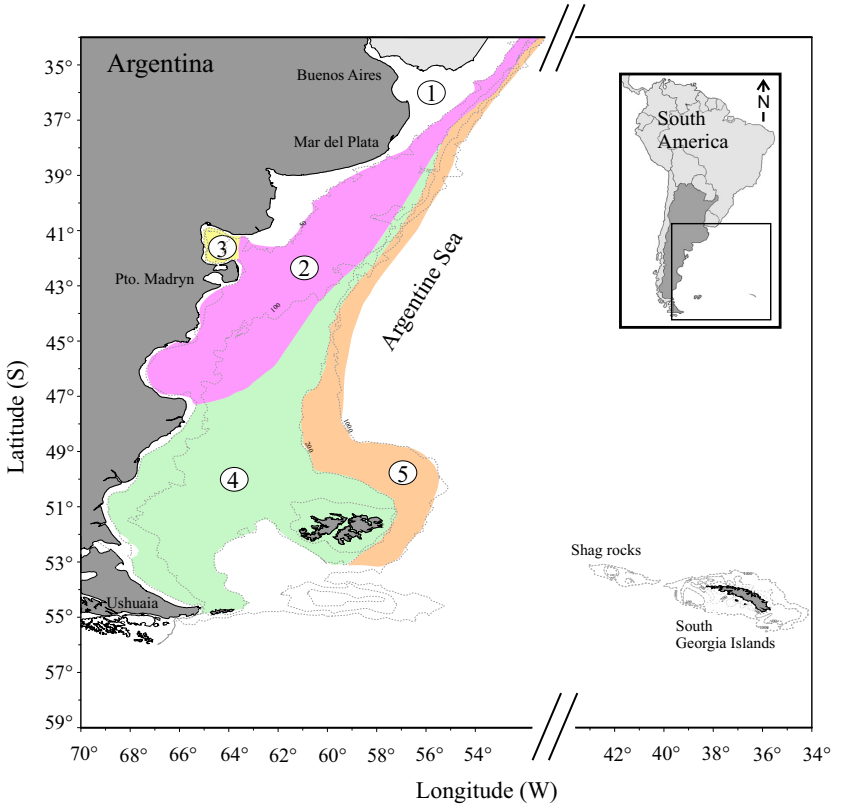


Figure 1. Main fish assemblages associated with the five ecosystem units of the Argentine Sea according to Angelescu and Prensky (1987): 1) Bonaerense coastal area; 2) Mid and northern Patagonian shelf; 3) Patagonian gulfs; 4) Southern Patagonian shelf; 5) Shelf break and deep waters. The inset shows the South Georgia and Shag Rocks area, in the Subantarctic sector, from which the three icefish species were obtained; this sector lies outside the classification of Angelescu and Prensky (1987) and is shown separately, not as a sixth numbered unit.

METHODS OF THE REVIEW

Scope species selection and evidence base

This study included *Merluccius hubbsi* (Argentine hake), which is the most important demersal fish for the SWA. We focus on Patagonian stock since it is the most abundant (Table 1). The Argentine hake is an oviparous species with external fertilization, batch spawning, and 'asynchronous ovaries' that show a continuous recruitment of oocytes during the reproductive season (indeterminate annual fecundity). The Patagonian stock of this species spawns mainly during the austral spring and summer, with a main peak in January.

Another species of economic importance from the austral area, but which is mostly associated with subantarctic waters, is *Micromesistius australis* (southern blue whiting) (Table 1). This species is a batch spawner, but unlike the Argentine hake, it has 'group synchronous ovaries' with determined annual fecundity (Macchi et al. 2005). Thus, the stock of oocytes to be spawned in *M. australis* during its reproductive season is defined at the beginning of spawning (Hunter et al. 1992). For this reason, the reproductive period in the Argentine waters is shorter than *M. hubbsi*, limited mainly to September during the austral spring.

In the coastal waters of the SWA, Sciaenidae constitutes one of the most important fish families for fisheries. It is characterized by a broad latitudinal distribution and includes several key species, such as *Micropogonias furnieri* (whitemouth croaker), *Cynoscion guatucupa* (stripped weakfish), *Macrodon ancylodon* (king weakfish) and *Pogonias cromis* (black drum) stand out (Table 1). Within this group, *M. furnieri* and *C. guatucupa* are the most abundant and relevant for the fisheries of Argentina and Uruguay. These species are batch spawners with indeterminate annual fecundity, and a reproductive period that covers the spring and summer months. Another demersal species from the coastal waters of Buenos Aires considered in this analysis was *Percophis brasiliensis* (Brazilian flathead) (Table 1). It is also a batch spawner with indeterminate annual fecundity that reproduces during the spring months.

The study also included information on fish species that inhabit the rocky reefs of the Buenos Aires and north Patagonian waters, such as *Acanthistius patachonicus* (grouper), *Pseudopercis semifasciata* (sea salmon) and *Pagrus pagrus* (red porgy) (Table 1). These fish are characterized by being long-lived species, that reproduce mostly during spring, with low annual catches. They are also batch spawners with indeterminate annual fecundity and gonochorism; however, the existence of hermaphroditism in *P. pagrus* has been recorded during the juvenile stage. In addition, *P. semifasciata* is a species that shows sexual dimorphism in coloration and size, with males reaching a maximum length larger than females (González 1998, 2006). These characteristics suggest that the species would have a particular reproductive behavior, such as courtship or male competition during egg fertilization.

As for benthic fish, two species of flatfish were included, one from the coastal area of Buenos Aires *Paralichthys patagonicus* and the other from deeper waters with a spatial distribution that includes the north-Patagonian region called *Xystreuris rasile* (Cousseau and Perrotta, 1998) (Table 1). *Paralichthys patagonicus* is the flatfish of greatest economic importance for Argentine fisheries (Diaz de Astarloa 2002). The reproductive activity of both species occurs mostly during the spring, and the type of spawning is by batches with indeterminate annual fecundity.

The most abundant small pelagic fish in the SWA is *Engraulis anchoita* (Argentine anchovy), which plays a key trophic role in the Buenos Aires and Patagonian ecosystem, since it is the main food item for larger fish such as Argentine hake, marine mammals and birds (Hansen 2004) (Table 1). In Argentina, the northern stock (Bonaerense) is the most relevant, with a biomass that oscillate annually between 1 and 5 million t (Orlando et al. 2024). This is a batch spawner with indeterminate annual fecundity, whose main reproductive activity in the Buenos Aires region occurs during the spring. Another pelagic species incorporated into this study was *Brevoortia aurea* (Brazilian menhaden), that is particularly abundant in Samborombón Bay (35° 27′S-36° 22′S), an estuarine zone (Acha and Macchi 2000). It is a batch spawner with indeterminate annual fecundity that reproduces mainly during the summer. *Ramnogaster arcuata* is another small pelagic fish with a short life cycle that inhabits the coastal region, mainly in estuaries. This species has low commercial value but reproduces in winter near the Río de la Plata (35° S-37° S) (Rodrigues et al. 2008), unlike most cold-temperate SWA marine fishes.

We included information on some icefish from the Antarctic-Subantarctic region, such as *Champsocephalus gunnari*, *Chaenocephalus aceratus* and *Pseudochaenichthys georgianus*, which are total spawners with a synchronous development of oocytes and a shorter reproductive period compared to fish of the temperate zone (Table 1). These species are distributed in the Scotia Arc region, and in the area surrounding the South Georgia Islands (SG) (Figure 1) is where the largest abundances have been usually recorded, mainly of *C. gunnari* (Kock and Everson 1997). Currently, the fishing activity of this species focuses on the northwest of SG, with a catch limit between 1,000 and 5,000 t (CCAMLR 2023). Most of the icefish are characterized by car-

Table 1. Main reproductive traits of the species analyzed. PC, parental care; LV, lecithotrophic viviparity. *Protogynous hermaphrodite during the immature phase. **Mecom (2025).

Species (common name)	Latitudinal distribution	Depth range (m)	Gender	Fecundity type	Fertilization	Spawning period (months)	Annual catch (t)	References
Merluccius hubbsi (Argentine hake) Southern stock – Patagonian	41° S to 55° S Atlantic	50-500	Gonochoric	Indeterminate	External	November-March	292,000	Macchi et al. (2004, 2007)
Micromesistius australis (southern blue whiting)	South 38° S Atlantic-Pacific	100-800	Gonochoric	Determinate	External	September	11,000	Otero (1976); Pájaro and Macchi (2001); Macchi et al. (2005)
Micropogonias furnieri (whitemouth croaker)	25° N (Gulf of Mexico) to 41° S (Argentina)	< 50	Gonochoric	Indeterminate	External	October- March	37,000	Nieland and Wilson, (1993); Isaac-Nahum, (1988); Macchi et al. (2003); Militelli et al. (2013)
Pogonias cromis (black drum)	25° N (Gulf of Mexico) to 41° S (Argentina)	< 50	Gonochoric	Indeterminate	External	October-December	630	Nieland and Wilson (1993); Isaac-Nahum (1988); Macchi et al. (2002)
Macrodon ancylodon (king weakfish)	10° S to 40° S Atlantic	< 50	Gonochoric	Indeterminate	External	October- March	330	Militelli et al. (2013)
Cynoscion guatucupa (stripped weakfish)	23° S to 41° S Atlantic	< 100	Gonochoric	Indeterminate	External	October- March	7,600	Militelli et al. (2013)
Percophis brasiliensis (Brazilian flathead)	23° S to 48° S Atlantic	< 100	Gonochoric	Indeterminate	External	October- March	4,800	Militelli and Macchi (2001); Rodrigues (2012)
Pagrus pagrus (red porgy)	34° S to 42° 57′ S Atlantic		Gonochoric*	Indeterminate	External	October- February	3,500	Militelli et al. (2017); López (2023)
Acanthistius patachonicus (grouper)	23° S to 48° S Atlantic	< 100	Gonochoric	Indeterminate	External	September-December	1,000	López (2023)

Table 1. Continued.

Species (common name)	Latitudinal distribution	Depth range (m)	Gender	Fecundity type	Fertilization	Spawning period (months)	Annual catch (t)	References
Pseudopercis semifasciata (sea salmon)	23° S to 47° S Atlantic	< 100	Gonochoric	Indeterminate	External	September-February	300	López (2023)
Paralichthys patagonicus (flatfish)	22° S to 43° S Atlantic	< 120	Gonochoric	Indeterminate	External	October- February	2,700	Macchi and Astarloa (1996a)
Xystreuris rasile (flatfish)	Coastal area of Buenos Aires and north-Patagonian region, up to 47° S	< 150	Gonochoric	Indeterminate	External	October - February		Cousseau and Perrotta (1998)
Engraulis anchoita Argentine anchovy Northern stock – Bonaerense)	34° S to 41° S Atlantic	< 200	Gonochoric	Indeterminate	External	October-January	3,600	Sánchez (1995)
Brevoortia aurea (Brazilian menhaden)	13° S to 41° S Atlantic	< 15	Gonochoric	Indeterminate	External	September-January	120	Cousseau and Perrotta (1998); Acha and Macchi (2000)
Ramnogaster arcuata (Jenyns's sprat)	34° S to 52° S Atlantic	10-100	Gonochoric	Indeterminate	External	June-August		Rodrigues et al. (2008)
Champsocephalus gunnari (mackerel icefish)	Subantarctic-Antarctic	100-350	Gonochoric	Determinate	External	February-June		Kock and Everson (1997); Militelli et al. (2015)
Chaenocephalus aceratus (blackfin icefish)	Antarctic shelf	450-770	Gonochoric	Determinate	External. PC	February-June		Militelli et al. (2015); Novillo et al. (2019)
Pseudochaenichthys georgianus (South Georgia icefish)	Subantarctic	100-300	Gonochoric	Determinate	External	February-June		Militelli et al. (2015)
Sebastes oculatus (Patagonian redfish)	38° S to 56° S Atlantic	20-200	Gonochoric	Determinate	Internal. LV	October-January	7	Sánchez and Acha (1988); Rodrigues et al. (2024)

rying out a single spawning event during the breeding season, producing larger eggs with diameters between 2 and 4 mm (Militelli et al. 2015; Novillo et al. 2019). Also, in the case of *C. aceratus*, the existence of parental care has been recorded, with nest formation during rearing (Detrich et al. 2005).

Finally, the analysis included information on a viviparous species (with internal fertilization), *Sebastes oculatus* (Patagonian redfish), characterized by a lecithotrophic viviparity (embryos development depends on the yolk sac for nutrition) (Table 1). The genus *Sebastes* sp. is economically important in Northern Hemisphere fisheries, especially in the Pacific (Saborido-Rey 1994), whereas *S. oculatus* has low commercial value in Argentina. Two morphotypes are distinguished along its distribution, one more coastal (mostly < 30 m depth) and another inhabiting deeper waters > 80 m depth (Rodrigues et al. 2024). Regardless of the morphotype, this species corresponds to the group of spawners with determined annual fecundity, with a single event of larval release during spring.

The review is organized around three questions; Q1: how do relative fecundity, spawning frequency and oocyte provisioning combine to determine annual female allocation across taxa inhabiting contrasting environments of the same regional system?, Q2: how do the resulting patterns covary with life-history traits such as growth rate, age at maturity and the extent of the reproductive life span?, Q3: what hypotheses relevant to stock assessment and management follow from those patterns, particularly in relation to the spatial extent of spawning grounds? This synthesis is not intended as a general model of fish reproduction: the patterns described here characterize the 19 species considered, selected for the consistency and comparability of the reproductive data available for them, and should not be extrapolated to bony fish without testing.

Reproductive variables and derived indices

Annual reproductive investment (RI) in bony fishes was estimated with data of relative fecundity (number of eggs produced per unit of female total weight), spawning frequency, expressed as the average time (days) between successive spawning events (Kjesbu 2009) and oocyte dry weight (ODW), as a measure of maternal provisioning per oocyte. Throughout this study, terms such as 'egg quality' or 'oocyte quality' are used as shorthand for this provisioning trait; ODW is not a universal measure of egg quality or offspring survival but has been widely used as an indicator of egg quality and larval survival potential, since heavier oocytes often produce larger, better-developed larvae with greater starvation resistance (Hinckley 1990; Rijnsdorp and Vingerhoed 1994). In all cases, fecundity and oocyte weight were determined using females with hydrated oocytes (close to spawning) obtained during the reproductive peak of each species (Macchi et al. 2004, 2006). The spawning frequency was estimated by the proportion of females with postovulatory follicles, following the criterion of Hunter and Goldberg (1980). For species with several years of data available (*M. hubbsi*, *E. anchoita*, *M. furnieri*, *C. guatucupa* and *P. brasiliensis*), these variables were estimated by analyzing all available historical information in order to obtain values representing the most robust average condition (Table 2). For the rest of the species considered, data on reproductive parameters were obtained from the bibliographic information (Table 3). When species-specific values were unavailable, estimates from closely related taxa were used as proxies, following standard practice in comparative fisheries biology for filling gaps in life-history datasets (Froese and Binohlan 2000; Thorson et al. 2017) (Table 3). The RI was then estimated as the percentage relationship between the dry weight of the total oocytes produced during the reproductive season and the weight of the females, according to the following equation:

$$RI\ (\%) = [(RF \times NS \times ODW) / 1{,}000] \times 100$$

where, RF is relative fecundity (number of oocytes per gram of female total weight, in grams), NS (number of spawning events per year) is the ra-

Table 2. Mean values of the variables considered to estimate the annual reproductive investment (RI) in those fishes that counted with data from many years. RF, relative fecundity (number of oocytes/female gram); F, spawning frequency (days); NS, number of spawning events in the year; ODW, oocyte dry weight (mg); SD, standard deviation, n, number of specimens. BS, Bonaerense stock; PS, Patagonian stock.

Species	RF (SD, n)	F (n)	NS	ODW (SD, n)	Sampling period (years)
Merluccius (PS) *hubbsi*	528 (191, 1,324)	6 (11,467)	25	0.029 (0.003, 1,068)	2001, 2004-2014, 2017, 2018, 2021
Micropogonias furnieri	192 (74, 178)	4.7 (997)	38	0.026 (0.005, 100)	1994, 1995, 2000, 2001, 2003, 2011-2013
Cynoscion guatucupa	184 (104, 127)	5.4 (413)	33	0.025 (0.007, 109)	1994, 2000, 2001, 2003, 2005, 2008, 2011-2013
Percophis brasiliensis	272 (113, 359)	5.7 (811)	32	0.019 (0.003, 415)	1998, 1999, 2003, 2005, 2008, 2011-2013, 2019, 2021
Engraulis anchoita (BS)	493 (156, 991)	8 (6,061)	15	0.021 (0.006, 206)	1993, 1995, 1996, 1999, 2001-2004, 2006, 2008, 2013, 2019, 2021

Table 3. Mean values of the variables considered to estimate the annual reproductive investment (RI) of the species analyzed, obtained from bibliographic information. RF, relative fecundity (number of oocytes/female gram); F, spawning frequency (days); NS, number of spawning events in the year; ODW, oocyte dry weight (mg); SD, standard deviation. *Taken from *Paralichthys orbignyanus* (Radonic 2011). **Taken from *Ramnogaster arcuata* (Rodrigues et al. 2008).

Species	RF (SD)	F	NS	ODW (SD)	References
Micromesistius australis	122 (43)	4	7	0.09 (0.008)	Macchi et al. (2005)
Pogonias cromis	75 (31)	3.6	25	0.042 (0.004)	Macchi et al. (2002)
Macrodon ancylodon	285 (25)	6	30	0.033 (0.001)	Militelli and Macchi (2004)
Pagrus pagrus	83 (11)	2	75	0.025 (0.0008)	López (2023)
Acanthistius patachonicus	155 (49)	3	40	0.021 (0.002)	López (2023)
Pseudopercis semifasciata	53 (9)	3	60	0.034 (0.003)	López et al. (2020); López (2023)
Paralichthys patagonicus	71 (11)	3*	50	0.013 (0.0006)	Militelli (2011)
Xystreuris rasile	66 (21)	3*	50	0.02	Aubone (2006)
Brevoortia aurea	135 (34)	8	19	0.049**	Macchi and Acha (2000)
Ramnogaster arcuata	235 (59)	6	15	0.049	Rodrigues et al. (2008)
Champsocephalus gunnari	21 (5)	-	1	1.2 (0.5)	Militelli et al. (2015)
Chaenocephalus aceratus	7 (1)	-	1	7.0 (2.2)	Militelli et al. (2015)
Pseudochaenichthys georgianus	7 (0.7)	-	1	7.7 (1.2)	Militelli et al. (2015)
Sebastes oculatus	250	-	1	0.06	Rodrigues et al. (2024)

tio between the length of the reproductive season (days) and the spawning frequency (F), and ODW is the mean dry weight of an oocyte (mg) (Tables 2 and 3). The factor 1/1,000 converts the product from milligrams of oocyte per gram of female to grams per gram, so that RI is expressed as a percentage. Hence, the RI value gives an idea of the energy investment made by females for egg production during the spawning season, determined as the percentage of weight of the mother invested in dry weight of oocytes.

In addition to the RI of the females, the reproductive life span of each species (RL) was estimated from the time difference between maximum recorded age and estimated age at maturity (Table 4). The proportion of time in which sexual maturity occurs within the total life cycle of each species (SM), was also estimated as follows:

$$SM = (AM/MA) \times 100$$

where, AM is the age at maturity, and MA is the maximum age of each species (Table 4).

Information on growth rate was considered in this analysis, including the growth coefficient (K) reported for each species (Table 4), and also by estimating a proxy of the average annual energy investment in growth made by females during their reproductive life span. This last variable was estimated as the average annual weight gain (AWG) as follows:

$$AWG = (TWMax - TWMat)/RL$$

where, TWMax is the total weight at maximum length and TWMat is the total weight at the length at maturity. TWMax and TWMat were determined from the values of length at maturity, maximum length and the total length (TL) versus total weight (TW) models estimated for each species (Table 4).

Since the species considered in this analysis have very different size and total weight ranges, to standardize the AWG values, they were relativized to the TWMax estimated for each species. Thus, we obtained a relative growth index that represents the percentage of annual growth during the reproductive life span (RG), as follows:

$$RG\ (\%) = (AWG/TWMax) \times 100$$

We also included information on the average gonadosomatic index (GSI) of the species analyzed (Table 4), estimated during the mature phase (with hydrated oocytes) of the females, as follows:

$$GSI\ (\%) = (GW/TW) \times 100$$

where, GW is the gonad weight of each female sampled.

On the other hand, as the size of the spawning area is a relevant trait for the reproductive resilience of fish populations (Lowerre-Barbieri et al. 2016), information of this variable was considered into the analyzes. This variable was estimated as the area (nm^2) covered by the spatial distribution of the mature females close to spawning or in ovulation (with hydrated oocytes) observed during the research surveys carried out during the reproductive peak of each species in different years, between 1993 and 2021. According to the available data, the spatial distribution of the spawning females was analyzed in the following species: *E. anchoita*, *M. hubbsi*, *P. patagonicus*, *P. brasiliensis*, *M. furnieri*, *C. guatucupa*, *P. pagrus*, *P. semifasciata*, *A. patachonicus* and *B. aurea*.

In order to estimate the extent of the spawning area for each selected species, a polygon that included the sampling stations where spawning females appeared during the period considered was drawn, and its surface was calculated using Surfer® (Golden Software, LLC, https://www.goldensoftware.com). This estimate represents the maximum reproductive area for each species, including the inter-annual variability normally recorded in the spatial distribution of the spawning females. In addition to the size of the spawning area, the proportion occupied for this area with respect to the total spatial distribution reported for each species or

Table 4. Main life cycle parameters of the analyzed species. AM, age at maturity (years); MA, maximum age (years); LM, length at maturity (cm); ML, maximum length (cm); *a* and *b*, coefficients of the relationship $TW = a\ TL^b$; TW, total weight; TL, total length; K, coefficient of growth; GSI, mean gonadosomatic index; n, number of specimens. *Estimated in this paper. **Taken from *S. fasciatus* (Saborido-Rey 1994). BS, Bonaerense stock; PS, Patagonian stock.

Species	AM	MA	LM	ML	a	b	K	GSI* (n)	References
Merluccius hubbsi (PS)	2.5	15	33	95	0.0104*	2.9*	0.17	15.52 (1,331)	Irusta et al. (2016)
Micromesistius australis	4.2	23	39	66	0.006	2.95	0.12	13.52 (62)	Ruocco et al. (2017)
Micropogonias furnieri	5	30	34	63	0.0198*	2.85*	0.2	8.94 (125)	Carozza et al. (2004)
Pogonias cromis	3	41	33	120	0.03	2.78	0.18	9.47 (45)	Urteaga and Perrotta (2001)
Macrodon ancylodon	2	7	23	42	0.00048	3.11	0.42	14.79 (116)	Haimovici (1988)
Cynoscion guatucupa	3	20	32	65	0.0244*	2.73*	0.39	7.27 (127)	Ruarte and Sáenz (2008)
Percophis brasiliensis	2.7	16	36.8	70	0.0036*	3.04*	0.29	9.53 (358)	Barretto et al. (2011)
Pagrus pagrus	2.06	16	24.7	54	0.00575	3.17	0.15	5.70 (111)	Cotrina (1989); Cousseau et al. (1998); López (2023)
Acanthistius patachonicus	6.93	45	26.04	68	0.02	2.91	0.07	7.10 (51)	Cousseau and Perrotta (1998); Riestra et al. (2020); López (2023)
Pseudopercis semifasciata	3	30	7	125	0.012	3.02	0.08	4.93 (26)	Elías and Burgos (1988); González (1998); López (2023); Rosset (2023)
Paralichthys patagonicus	3	19	32	67	0.0055	3.18	0.17	5.14 (77)	Perier and Di Giacomo (2002); Riestra (2010)
Xystreuris rasile	2	8	21	43	0.0017	3.54	0.43	6.50 (35)	Fabré (1992); Cousseau and Perrotta (1998)
Engraulis anchoita (BS)	1	8	9.3	21	0.003*	3.29*	0.62	13.9 (332)	Hansen (1994); Cousseau and Perrotta (1998)
Brevoortia aurea	3	11	25	41	0.263	2.11	0.27	15.03 (125)	López Cazorla (1985)
Ramnogaster arcuata	1	3.5	7.7	13.1	0.00064	3.05	0.57	17.22 (41)	López Cazorla and Sidorkewicj (2009)
Champsocephalus gunnari	3	15	27	60	0.0016	2.95	0.16	6.53 (98)	CCAMLR (2022)
Chaenocephalus aceratus	13	17	57.7	75	0.00047	3.69	0.15	12.39 (21)	Reid et al. (2007); Riginella et al. (2016)
Pseudochaenichthys georgianus	4	6	47.5	59.0	0.00007	3.43	0.26	10.07 (7)	Clarke et al. (2008)
Sebastes oculatus	8**	25**	27**	47**	0.0031	2.9	0.096**	10.84 (8)	Saborido-Rey (1994); Buratti (2020)

fishing stock was calculated (Ospina-Álvarez et al. 2022). The information on the spatial distribution of the species was obtained from the bibliography (Cousseau and Perrotta 1998).

Quantitative comparative methods

The quantitative component evaluates the reproductive investment index and its constituent variables, life-history covariation using correlation and principal component analyses, and the spatial extent of spawning grounds using survey-derived polygons. Because the synthesis combines heterogeneous sources, the analyses should be interpreted as exploratory comparisons rather than as a formal systematic meta-analysis.

To evaluate the strength and direction of the association between RI and its parameters (RF, NS and ODW) across the species studied, a correlation matrix was constructed including all four variables. Given the non-normal distribution of the data, Spearman's rank correlation coefficient was used. Two-tailed tests were used for statistical significance of each correlation, and p-values were adjusted using the Holm method to account for multiple comparisons.

Also, to characterize how the analyzed species allocate their energy resources throughout their life cycle, both for reproduction and growth, a Principal Component Analysis (PCA) was performed, including key reproductive context variables: reproductive life span (RL); the proportion of time in which sexual maturity occurs within the total life cycle of each species (SM); annual reproductive investment (RI); relative annual weight gain during the reproductive life span (RG); growth coefficient (K). The information generated from this multivariate analysis was used to determine potential groupings of species based on the similarities or differences that define their reproductive strategies. The PCA was performed on standardized variables (correlation matrix). Components with eigenvalues > 1 were retained (PC1 and PC2), which together explained 80% of the total variance. The analysis is used here as a descriptive tool; groupings are exploratory and no inferential tests were applied.

Results were considered statistically significant at $p < 0.05$. Statistical analyses were performed using Infostat® (Di Rienzo et al. 2020) for the PCA and R version 4.3.1 (R Foundation for Statistical Computing, Vienna, Austria) software for the other assessment.

To explore the relationship between GSI and reproductive traits across species, we fitted two simple regressions using species-level values (n = 14): GSI against RF and F. A logarithmic model ($GSI = a \ln(RF) + b$) was used, and a linear model ($GSI = a F + b$) for F. Models were fitted by ordinary least squares and goodness of fit is reported as R^2. Species were treated as independent data points; phylogenetic relatedness was not accounted for, so these regressions are exploratory.

RESULTS AND DISCUSSION

Reproductive investment

Among the components of RI, the only significant association was the inverse relationship between NS and ODW (Spearman's coefficient = -0.77, adjusted $p < 0.001$): species with fewer spawning events per year produced heavier oocytes. RF was not correlated with NS (Spearman's coefficient = 0.05) and showed a negative, non-significant association with ODW (Figure 2). Because NS and ODW vary inversely, their contributions to RI partly cancel, and RI was significantly correlated only with RF. Since RI is calculated from these three variables, the correlations between RI and each of them are partly structural and are reported descriptively. This is particularly evident in the icefish species, whose mature oocytes reach weights close to 7-8 mg, between 200 and 300 times heavier than the other bony fish. In these species, the low number of oocytes is accompanied by greater provisioning per oocyte, which gives rise to larger larvae.

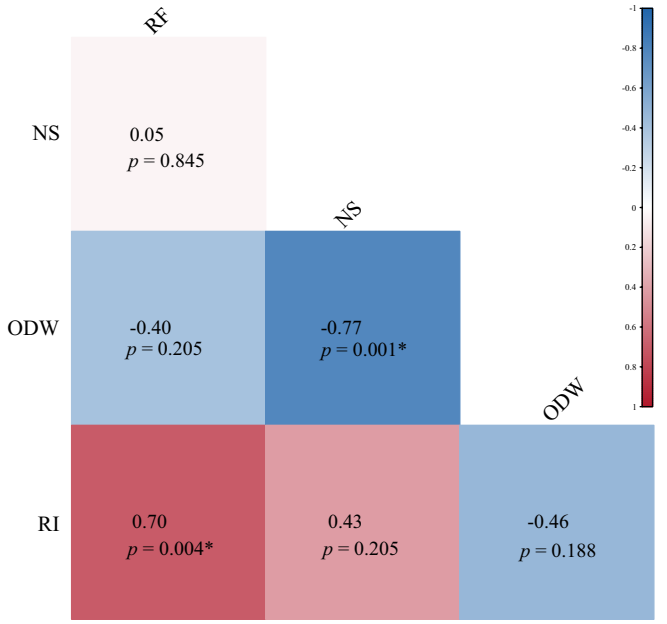


Figure 2. Spearman correlation matrix between annual reproductive investment (RI) and the variables relative fecundity (RF), number of spawning events per year (NS) and oocyte dry weight (ODW), estimated for the analyzed bony fish species. Correlation coefficients and p values adjusted using the Holm method are indicated. *Indicates significant correlation. The scale corresponds to Spearman's coefficient value.

The RF values estimated for batch spawning species showed lower values (< 100 oocytes g^{-1}) in the black drum, rocky-reef fish, such as *P. semifasciata and P. pagrus*, and flatfishes. In contrast, Argentine hake and anchovy were the species with the highest RF within the group of fish analyzed, with average values near 500 oocytes g^{-1}. The number of days between spawning events (F) evidences an increasing trend in those species with the higher RF (Figure 3), suggesting that, within this group, low relative fecundity is associated with frequent spawning, although this pattern was not tested statistically; across all 19 species RF and NS were not correlated (Spearman's coefficient = 0.05).

Reproductive strategies across environmental domains

The PCA showed a grouping of species based on the variables of the reproductive context considered in the analysis, which reflects different strategies according to the way in which the energy expenditure is distributed during reproduction and growing of the fish (Figure 4; Table 5). For example, the species with low annual reproductive investment (RI) were those from the Antarctic-Subantarctic ecosystem (*C. gunnari*, *C. aceratus* and *P. georgianus*) or that inhabit at high latitudes (*M. australis*), the viviparous fish (*S. oculatus*) and the flatfish *P. patagonicus*.

Reproductive investment captures only female oocyte allocation, thus, parental care, courtship, maternal protection of embryos and larval survival lie outside it. These components may offset low RI in fitness terms, but they are not commensurable with it and were not quantified here. The low RI of Antarctic and austral species may be partly related to the limited reproductive period characterizing these fishes, which provides a short time window for spawning. These species have determined annual fecundity; thus, the number of oocytes produced during the reproductive season is defined at the

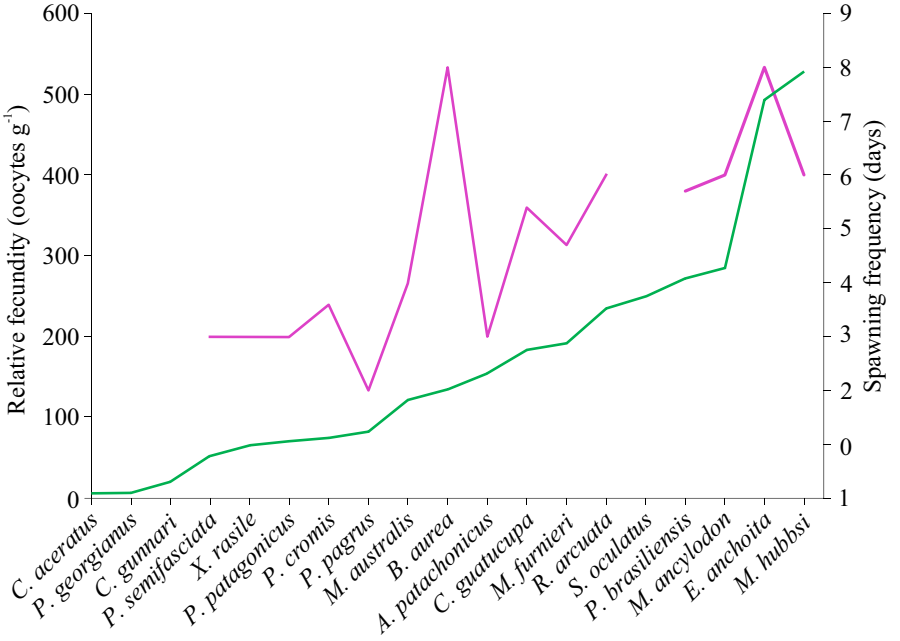


Figure 3. Mean values of relative fecundity (green line) and spawning frequency (magenta line) estimated for the analyzed bony fish species.

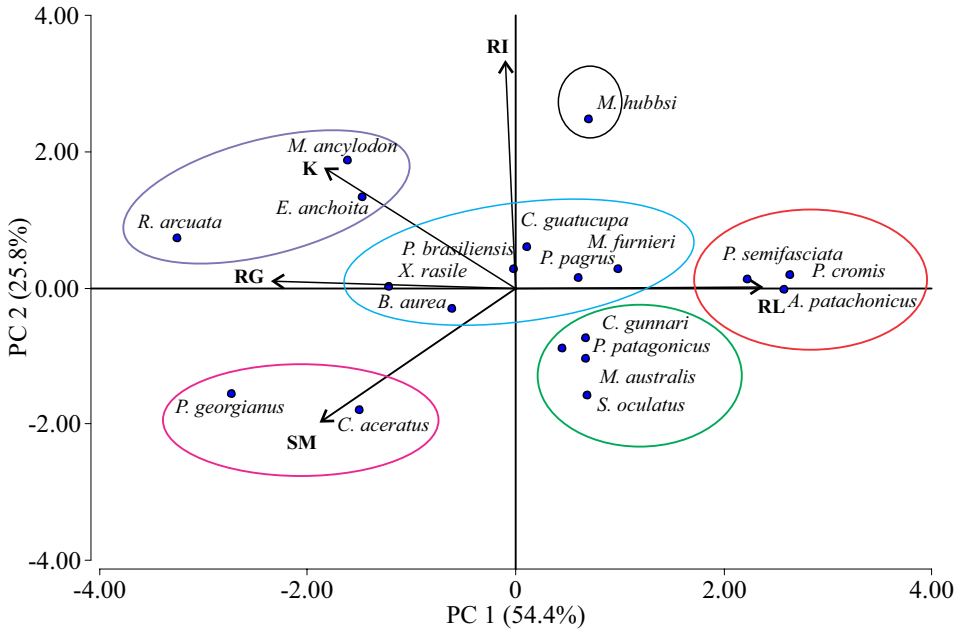


Figure 4. Biplot of the first two principal components (PC) obtained using key reproductive context variables: reproductive life span (RL); the proportion of time in which sexual maturity occurs within the total life cycle of each species (SM); annual reproductive investment (RI); relative annual weight growth during the reproductive life span (RG); growth coefficient (K). The ellipses qualitatively indicate the clustering of the analyzed species.

Table 5. Results of the principal component analysis (PCA) carried out with the variables of the reproductive context estimated for the species analyzed. Reproductive life span (RL); the proportion of time in which sexual maturity occurs within the total life cycle of each species (SM); reproductive investment (RI); relative annual weight growth during the reproductive life span (RG); growth coefficient (K). PC: principal component.

	Eigenvectors					
Variables	PC1	PC2	PC	Eigenvalue	Proportion of variance	Cumulative proportion
RL	0.56	0.05	1	2.72	0.54	0.54
SM	-0.44	-0.46	2	1.29	0.26	0.80
RI	-0.02	0.78	3	0.57	0.11	0.92
RG	-0.55	0.02	4	0.24	0.05	0.96
K	-0.43	0.41	5	0.18	0.04	1.00

beginning of the spawning period, and fecundity would be expected to depend mainly on the energy invested prior to the onset of spawning. Parental care has also been recorded in some of these species, such as *C. aceratus*, which builds nests (Detrich et al. 2005). This behavior suggests an additional component of reproductive effort, beyond oocyte production, associated with the protection of spawned eggs, which may increase larval survival. In addition, these species produce larger oocytes, which has been proposed to increase egg quality through greater maternal provisioning (Hinckley 1990; Rijnsdorp and Vingerhoed 1994) and, in turn, to reduce early mortality, for example due to predation (Green 2008). In *S. oculatus*, a lecithotrophic species, the lower annual RI could be consistent with additional maternal provisioning during larval development (Rodrigues et al. 2024), although this was not tested here. These links between investment, provisioning and offspring survival are hypotheses supported by the literature; they were not assessed in our synthesis, and oocyte mass alone cannot be taken as evidence of survival.

The flatfish, like other species with a high number of spawning events during the reproductive season, such as those inhabiting the rocky reefs (*P. semifasciata*, *A. patachonicus* and *P. pagrus*), were characterized by lower RF and ODW, in particular *P. patagonicus*. The low number of hydrated oocytes produced during the mature phase, before spawning, is reflected in a lower GSI compared to the other fish evaluated to be with a similar reproductive mode, i.e. batch spawning and indeterminate annual fecundity (Figures 5 and 6 A). In this group of species, the low number of eggs per batch is accompanied by a high number of spawning events during the season (Figure 6 B), however the total number of eggs produced per year would remain relatively low compared to other batch spawning species.

The black drum (*P. cromis*) is another species characterized by a relatively low RI which is partly offset over its lifetime by an extended reproductive life span. This strategy is similar to that of *P. semifasciata* and *A. patachonicus*, which are coastal species whose reproductive habitat is associated with rocky reefs. It should be noted that species that depend on this type of ecosystem for reproduction, usually have particular sexual features or behaviours, such as sexual dimorphism, spawning in caves, or male competition, and their parents are expected to derive part of their reproductive effort to sexual courtship and the protection of their offspring (González 1998; López 2023, López et al. 2025). All these species are also characterized by relatively low body growth both in terms of K index and average annual growth after sexual maturity.

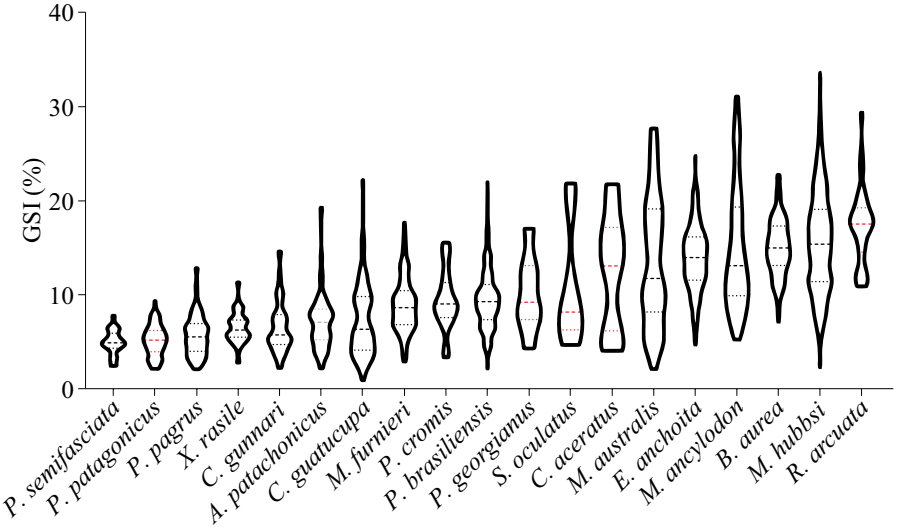


Figure 5. Mean values and dispersion of the gonadosomatic index (GSI) estimated for the analyzed bony fish species.

The Argentine hake (*M. hubbsi*) was the species that stood out in this study for its high RI, evidenced by the production of eggs during the reproductive season. Females of Argentine hake showed the highest values in terms of percentage of weight destined for reproduction, evidenced mainly by a high RF, with a relatively early sexual maturity and a medium growth rate. The sciaenid *M. ancylodon* is another species with high RI, but with a shorter reproductive life span and greater energy invested in body growth. At this point, this species resembles the small pelagic fish of the SWA as *E. anchoita*, with a short life cycle and a medium reproductive investment. The anchovy presents higher RF values, similar to those estimated for Argentine hake, but with a relatively low number of spawning events during the reproductive season and a lower oocyte dry weight. Like anchovy, *R arcuata* has also a short reproductive life span, although its growth rate is higher, the fastest compared to other species. Annual reproductive investment in *R. arcuata* is similar to that estimated for *E. anchoita*, but its fecundity is much lower with hydrated oocytes up to two times heavier than that estimated for anchovy.

The fish group composed of the most abundant coastal species in the SWA region, such as *M. furnieri*, *C. guatucupa*, *P. brasiliensis* and *P. pagrus*, was characterized by average values of the main reproductive effort traits, as annual reproductive investment, reproductive life span and growth rate after maturation. Therefore, summarizing the above information for all the species analyzed according to the reproductive and growth variables considered, the following strategies can be distinguished:

- Low annual investment in reproduction (RI) and growth, with an average reproductive life span, (*C. gunnari*, *M. australis*, *P. patagonicus*, *S. oculatus*).
- Low RI, but with a short reproductive life span, late maturity and high growth after maturity (*C. aceratus*, *P. georgianus*).
- Average or low RI, with early maturity, slow growth and a long reproductive life span (*P. cromis*, *P. semifasciata*, *A. patachonicus*).
- Average or high RI with high growth rate and short reproductive life span (*R. arcuata*, *E. anchoita*, *M. ancylodon*)
- High RI, with early maturation and an average growth rate and reproductive life span (*M. hubbsi*).

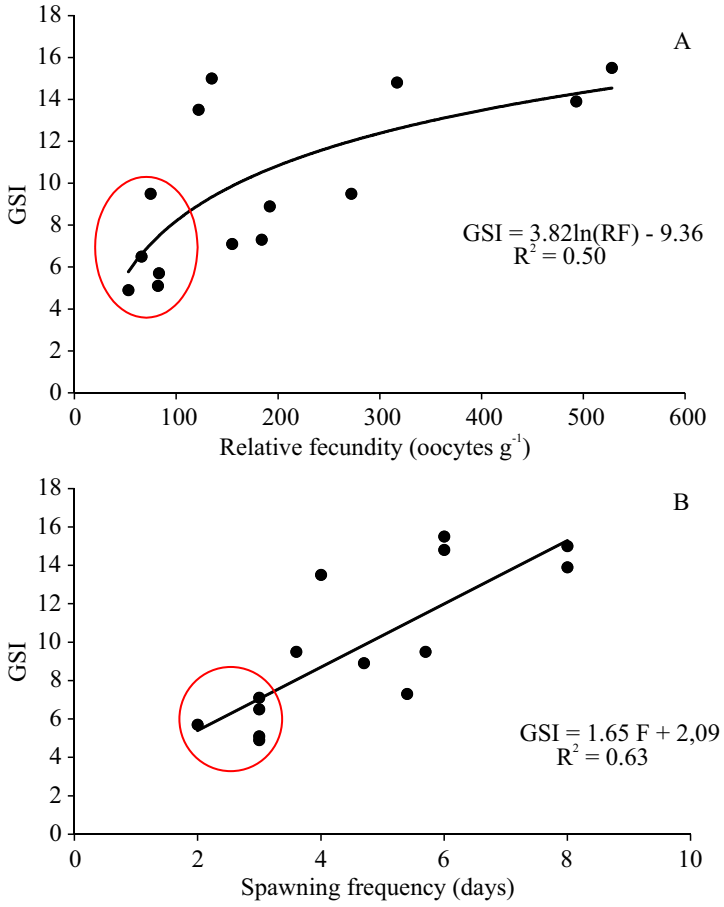


Figure 6. Relationships between the gonadosomatic index (GSI) and the variables relative fecundity (a) and spawning frequency (b), estimated for the bony fish species that spawn in batches. RF: relative fecundity; F: spawning frequency. The red ellipse highlights values corresponding to rocky reef fish and flatfish. Lines show the fitted regressions (a: logarithmic; b: linear; ordinary least squares); equations and R^2 are shown in each panel.

- Average RI and reproductive life span, with slow/average (*M. furnieri*, *C. guatucupa*, *P. brasiliensis*, *P. pagrus*) or average/high growth rates (*X. rasile*, *B. aurea*)

Life history covariation and fisheries implications

The species considered in this analysis cover a wide spectrum, not only in terms of their reproductive and growth strategies, but also in terms of other population characteristics, such as abundance, spatial distribution, stock size structure, recruitment, and larval survival. The Argentine hake from the Patagonian stock and the anchovy from the Bonaerense stock are the most relevant fish populations in terms of their abundance in the Argentine waters, with biomass values close to 1,200,000 t (Santos and Villarino 2022) and 2,300,000 t (Orlando et al. 2024) estimated in 2022 and 2023, respectively. Hence, these two species deserve particular attention. Both species mature early in their life cycle but differ in their growth rates and energy invested during reproduction. Anchovy has a higher growth rate with a shorter reproductive life span and a lower annual investment in reproduction,

although its relative fecundity is similar to that estimated for hake. The difference in RI between both species is mainly due to the fact that Argentine hake females spawn more frequently during the reproductive season and also produce heavier eggs (Leonarduzzi et al. 2014). The lower oocyte weight in anchovy results in a larval morphology at hatching much simpler in comparison to Argentine hake (Ciechomski 1965; Diaz et al. 2011). Nevertheless, in terms of recruitment success, it is possible that the lower annual RI of anchovy compared to hake may be partly offset by a higher larval survival rate. In this sense, the anchovy has much less specific environmental requirements for larval development than other species, allowing it to have a larger breeding area that would attenuate mortality rate driven by density-dependent process. Indeed, the nutritional condition of larvae appears to be significantly affected by the density-dependent effects in both *E. anchoita* (Diaz et al. 2009, 2016) and *M. hubbsi* (Diaz et al. 2020; Rodriguez et al. 2025). However, this effect is difficult to quantify, and these processes are still under investigation. Based on the spatial distribution of the spawning females of main species analyzed during their reproductive season from historical fishery research surveys carried out by Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) (Figure 7), the size of the spawning area for each species corresponding to the maximum area covered by spawning females in all the years assessed was estimated (Table 6). The Bonaerense stock of anchovy showed the wider reproductive area in comparison to other species, near to 30,000 nm^2, covering a large extent of its distribution range. Recent studies have shown that *E. anchoita* larvae exhibit a more diverse diet and greater trophic flexibility than previously thought (Do Souto et al. 2025). Moreover, they have been observed to adjust their trophic position in response to environmental conditions. Female anchovies spawn over a broad area, and this trophic flexibility may enhance larval adaptability, increasing their chances of survival during early ontogeny. This contrasts with hake larvae, which have a much more selective diet (Temperoni et al. 2014). The spawning area of the Patagonian hake stock is smaller in surface than that estimated for the Bonaerense population of anchovy (Table 6). However, reproduction of hake is linked to the North Patagonian Frontal System, where a large quantity of eggs is spawned in a more limited area, with a high plankton productivity (Macchi et al. 2023), so a higher mortality rate due to competition or predation is to be expected. Hake's larval success resulted strongly associated with a combination of physical and biological processes within the frontal system (Diaz et al. 2020). A recent study showed that the years with the highest egg production in hake are associated with poor nutritional condition of its larvae, suggesting an increase in their mortality (Rodriguez et al. 2025). This pattern can be partly explained by density-dependent processes and seems to be consistent with the increase in larval survival and recruitment of the species when the size of its optimal reproductive area is increased, as suggested by Macchi et al. (2021b). The northern Patagonian region is also characterized by showing in some years a high density of gelatinous organisms during the summer, which spatially coincide with fish larvae. Recent studies have precisely demonstrated the existence of a negative relationship between the abundance of the ctenophore *Mnemiopsis leidyi* and hake and anchovy larvae, which could be associated both with predation on larvae and competition between species (Sobrero et al. 2023).

The other bony fish species included in this study reach much lower abundances in the Argentine Sea than those estimated for the Bonaerense population of anchovy and the Patagonian stock of hake. In turn, these species have smaller spawning areas (Table 6), because they are generally restricted to specific habitats with particular environmental conditions during reproduction. For example, in species from the coastal environment, such as *M. furnieri*, *P. cromis*, *M. ancylodon* and *B. aurea*, spawning is linked to estuarine waters (Acha and Macchi 2000; Militelli et al. 2013). Reproduction

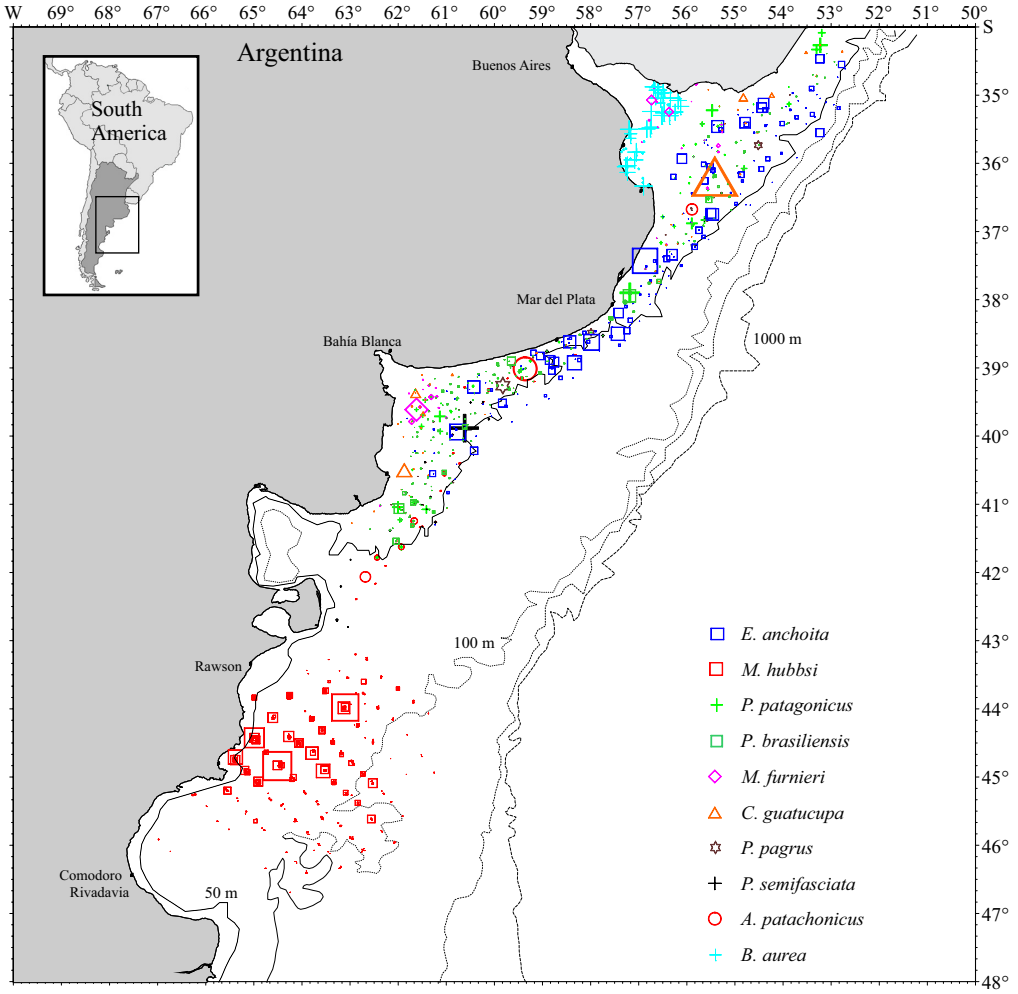


Figure 7. Spatial distribution of spawning females (with hydrated oocytes) of the analyzed species, based on research surveys conducted during the reproductive season between 1993 and 2021.

and larval breeding of *M. furnieri* occurs mainly in coincidence with the bottom saline front of the Río de la Plata generated by the confluence of the river water with the sea, where a retention mechanism has been described (Macchi et al. 1996b; Acha et al. 1999). This front would favor the feeding and subsequent migration of the larvae to the recruitment areas (Acha et al. 1999). A similar mechanism has been adopted by *M. ancylodon*, another sciaenid that inhabits the Rio de La Plata estuary (Militelli et al. 2013), while *P. cromis* spawns mostly in the shallow waters of Samborombón Bay, which is also within this estuarine system (Macchi et al. 2002). The survival conditions of these species during the early life stages would depend largely on the freshwater input from the Río de la Plata, which is strongly influenced by rainfall and wind regimes (Lucas et al. 2005), and this fact affects significantly the magnitude and variability of annual recruitment (Acha et al. 2011). Within the Sciaenidae family, the black drum, *P. cromis*, is the longest-lived species characterized by slow growth and low annual RI, with a reduced reproductive area, favoring the formation of denser spawning

Table 6. Size of the spawning (SA) and total (TA) distribution areas of the species analyzed in the Argentine Sea. N, number of trawl stations with spawning females. BS, Bonaerense stock; PS, Patagonian stock.

Species	Spawning area (nm^2)	Total distribution area (nm^2)	SA/TA	N
Engraulis anchoita (BS)	29,520	88,308	0.33	105
Merluccius hubbsi (PS)	20,988	226,800	0.10	473
Paralichthys patagonicus	15,804	127,656	0.12	92
Percophis brasiliensis	14,004	54,936	0.25	254
Micropogonias furnieri	12,924	48,996	0.26	37
Cynoscion guatucupa	11,520	56,736	0.20	61
Pagrus pagrus	8,568	40,716	0.21	66
Pseudopercis semifasciata	5,904	162,900	0.03	32
Acanthistius patachonicus	5,256	176,400	0.03	35
Brevoortia aurea	1,440	48,960	0.03	55

aggregations (Tellechea et al. 2010), which makes the species extremely vulnerable to fishing during reproduction.

Within the coastal waters of the SWA at < 50 m depths, the sciaenids *M. furnieri* and *C. guatucupa*, and the perchophid *P. brasiliensis*, are among the species with wider spatial distributions. The spawning grounds of these species are similar in size (Table 6), although they differ in location. In this sense, the reproductive activity of *M. furnieri* is associated with the estuarine environments, as mentioned above, whereas the other two species reproduce in more oceanic waters. Both the RI and the spawning ground size of these species are larger than the majority of the coastal fish evaluated in this study, and for many years they were the most landed fish in the coastal fisheries of Argentina and Uruguay (Elías et al. 2011). Thus, we hypothesize that the larger size of spawning areas could be associated with their higher biomasses. Within the flatfish group, *P. patagonicus* is the most relevant species in Argentine waters, with an extended spatial distribution in the Buenos Aires and nor-Patagonian coastal waters, and a relatively wide spawning area (Figure 7; Table 6). The other flatfish included in this study, *X. rasile*, covers a wider distribution area to the south, but the recorded catches are lower, and little information is known about the location and extent of its reproductive areas (Aubone 2006).

Fish that reproduce on rocky reefs ecosystems, such as grouper and sea salmon, had much more spatially restricted and less abundant populations, with annual catches close or lower than 1,000 t (Mecom 2024). The spawning females of these species are generally limited to specific habitats, usually close to the 50 m depth isobath associated with rocky reefs (Figure 7). The extension of their reproductive area shows low surface values compared to other species (Table 6). Like the black drum, these are long-lived and slow-growing species that are highly vulnerable to overexploitation. The red porgy (*P. pagrus*) is another species usually associated with rocky reefs. This species also has a slow growth rate and an average RI similar to salmon and grouper, but its reproductive habitat is less dependent on reefs, as evidenced by the larger spawning area in the coastal waters of Buenos Aires province (Table 6). This larger spawning area estimated for *P. pagrus*, compared to that for other rocky reef species, is likely to favor its reproductive opportunities and explain its higher population abundance (López 2023). In addition, this author suggests that *P. pagrus* displays an ‘income breed-

er' strategy, which would allow it to have a long reproductive season, compared for instance with the grouper, which has a shorter reproductive period and depends on the stored energy before the spawning season.

Brevoortia aurea and *R. arcuata* are two coastal species with pelagic habits whose spatial distribution is limited to shallow waters, and both have little commercial value in Argentina. The former reaches higher abundances, especially in Samborombón Bay during spring, when the reproductive activity takes place (Macchi and Acha 2000). As with *M. furnieri*, the spawning in this species is strongly influenced by the bottom saline front of the Río de La Plata estuary, where the greatest abundance of eggs and larvae in the plankton has been recorded (Acha and Macchi 2000). In this sense, the dependence of the reproductive activity of this species on the saline front largely limits the extension of its spawning area compared to other coastal fish (Figure 7; Table 6). The *Brevoortia* genus is also found in other latitudes of the American Atlantic coast, in the northern hemisphere, where it reproduces in marine waters under different salinity and temperature conditions to that described for *B. aurea*, reaching higher biomasses than in Argentina (Vaughan 1991; Powell 1994). On the other hand, *R. arcuata* also spawns in estuarine waters and coastal lagoons, but its reproductive season varies according to its latitudinal distribution (López Cazorla and Sidorkewicj 2009). In the Rio de La Plata area, *R. arcuata* spawns in winter, when the greatest abundance is reported (Rodrigues et al. 2008). The maximum size of this species is much smaller than that of *B. aurea*, its reproductive life span is very short (2 years) and, interestingly, its growth rate is the highest of all the species considered in this study.

Among the species inhabiting Antarctic and sub-Antarctic waters, *C. gunnari* is one of the most abundant in the Scotia Arc region, where at least three stocks have been identified (Kock and Everson 1997). The largest of these stocks is located around the South Georgia islands (Sub-area 48.3), with an estimated biomass of 22,000 t in 2021 (CCAMLR 2023). The other species inhabiting this region, *C. aceratus* and *P. georgianus*, in general are bycatch of the *C. gunnari* fishery (Kock et al. 2004). The extent of the reproductive area of these fishes is unknown, but at least in the sub-Antarctic Islands, it has been reported that some species migrate towards the coast where spawning takes place (Everson et al. 2001; Militelli et al. 2015). In the case of *C. aceratus*, Novillo et al. (2019) suggested that this species spawns in late summer in some inland areas of the South Shetland, such as Potter Cove. As previously mentioned, Antarctic fish are characterized by spawning a main batch of large eggs (2-4 mm diameter) during the reproductive season, giving rise to highly developed larvae, with greater chance of survival. For example, the larva of *C. gunnari* hatches between July and September with a total length of ~ 12.5 mm (Kock and Everson 1997). In particular, this fish has the highest fecundity values of the three species analyzed, but the size of its eggs is much smaller than those estimated for *C. aceratus* and *P. georgianus*. Another important aspect is parental care, as in the case of *C. aceratus*. During spawning, the female of this species deposits the egg mass on a substrate and the male then cares for them for an extended period until they hatch, thereby increasing their chances of survival (Detrich et al. 2005). This reproductive strategy would involve small spawning areas, probably associated with certain environments, which would partly reduce the chances of reproductive success because there are fewer opportunities to reproduce. In this sense, of the three species considered, *C. gunnari* which produces the largest number of eggs in a pelagic environment, is the most abundant. The development of oocytes during maturation in Antarctic fish depends largely on the accumulation of reserves prior to the spawning period, a strategy typical of 'capital breeders' in which the total fecundity is strongly influenced by the condition of the females before reproduction. Therefore, unfavorable food availability during the energy storage period could lead to a generalized atresia process, such as those described for *C. gunnari* (Macchi and

Barrera-Oro 1995). It has been suggested that the reproductive potential of this species is largely dependent on the abundance of krill, the main food item in Antarctic waters, during the energy accumulation period (Everson et al. 1991).

Micromesistius australis is a species of the cold austral waters, whose spawning in the SWA is associated with the slope front (Pájaro and Macchi 2001), where high concentrations of chlorophyll 'a' have been recorded (Acha et al. 2015). The RI and annual growth of this species are low and its reproductive period in the SWA is limited to 1-2 months during the austral spring (Macchi et al. 2005). The size of its reproductive area is unknown, but it is a mesopelagic fish with a relatively wide spatial distribution, and spawning associated with a highly productive frontal system that extends along the entire slope. These characteristics would favor larval survival and support the high biomass values estimated for the species, which ranged between 530,000 and 634,000 t in 2021 (Zavatteri and Giussi 2022).

The viviparous species considered in this study, *S. oculatus*, is of little commercial importance in the SWA and is mostly caught as by-catch in other fisheries. In Argentina, this species has been reported to live mainly on rocky bottoms particularly in the Patagonian waters (Venerus et al. 2013), but there are currently no estimates of its abundance or the size of its reproductive area. Rodrigues et al. (2024) suggested that this species has a determined annual fecundity, producing only one main batch of larvae during the reproductive season. These authors mention that once the eggs in the ovarian cavity are fertilized, the rest of the growing oocytes would undergo atresia, so it is very likely that the energy distribution strategy of this species corresponds to that of a 'capital breeder', similar to that reported for other fish of the same genus in the North Atlantic (Saborido Rey 1994). In fact, a recent study analyzing the proximal composition and energy density in different tissues throughout an annual cycle showed that *S. oculatus* stores energy prior to the beginning of reproduction (Rodrigues et al. 2025).

CONCLUSIONS

The analysis of the species from the SWA revealed that bony fishes characterized by a low annual reproductive investment (RI) were the viviparous (lecithotrophic) and those inhabiting the Antarctic and austral region, where the optimal conditions for reproduction are limited to a short period. In most of these species, low oocyte allocation coexists with additional components of reproductive effort, such as parental care or other reproductive behaviors, which lie outside RI, may offset it in fitness terms, and were not quantified here. Further work is needed to test whether the regularities described throughout this synthesis hold, using comparable reproductive data as they become available for additional taxa of the region.

In some batch spawning species with low relative fecundity, such as flatfish and some rocky reef fish, annual egg production is increased, comparatively to others, by a higher frequency of spawning during the reproductive season. As the increase in ovary weight would mainly depend on the number of oocytes produced per batch, these species have relatively low maximum GSI values.

The compilation of spawning-ground extent presented here is descriptive: it reports the maximum area covered by spawning females over the survey series available for each species, and no relationship between that area and recruitment or larval survival was fitted in this synthesis. We advance the hypothesis that a larger spawning area favors reproductive success by attenuating the density-dependent component of larval mortality, consistent with evidence reported elsewhere in this Review for Argentine hake and Argentine anchovy. Testing this hypothesis across the wider species set would require spawning-area time series matched to recruitment estimates, which are not currently available for most of the species considered here.

In species with external fertilization that require less strict conditions for early development, such as

anchovy, the spawning area is larger, which also favors the dispersion of individuals and recruitment.

In small pelagic species, as Argentine anchovy, reproductive investment is focused mainly on the number of eggs, rather than on quality (low ODW), which results in the generation of less developed larvae. On the contrary, in total spawners with a shorter reproductive period, as icefish, the RI is mainly directed at the size/weight of the eggs produced, giving rise to more developed larvae.

Similar to the size of the spawning area, longer reproductive periods in fish enhance the reproductive opportunities and increase the chances of eggs hatching in an environmental context more favorable to larval survival. Species with this characteristic require greater RI, and therefore energy needs to be incorporated during the reproductive season (income breeding).

In fish with limited reproductive periods, such as those living at high latitudes, the strategy of energy accumulation before reproduction (capital breeding) is more common.

Taken together, these results address the three questions posed at the outset. Across the 19 species considered, the main regularity among the components of annual female oocyte allocation is the inverse relationship between the number of spawning events and oocyte provisioning, while variation in RI largely tracks relative fecundity (Q1). This balance covaries with life-history strategy: species with longer reproductive life spans and slower growth, such as those associated with rocky reefs, sustain reproduction through repeated low-fecundity batches, whereas short-lived pelagic and some demersal species as hake rely on relative high fecundity; viviparous and high-latitude species may offset in fitness terms low oocyte allocation with parental care or extended incubation (Q2). These patterns generate testable hypotheses for stock assessment and management, in particular the proposition that the spatial extent of spawning grounds contributes to buffering density-dependent larval mortality, a mechanism supported for Argentine hake and Argentine anchovy but not yet examined in most of the species considered here (Q3).

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Data availability statement

Data can be made available upon request.

Conflict of interest statement

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (OpenAI, GPT-5) to assist in lan-

guage editing and improvement of grammar and fluency. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the publication.

Author contributions

Gustavo J. Macchi: conceived and designed the project; wrote the original manuscript and led the writing; performed the analysis and interpreted the results; provided critical feedback of the edited the manuscript; funding and supervision. Marina V. Diaz: wrote the original manuscript and led the writing; performed the analysis and interpreted the results; provided critical feedback of the edited the manuscript. Mariano Elisio: wrote the original manuscript and led the writing; performed the analysis and interpreted the results; provided critical feedback of the edited the manuscript. Ezequiel Leonarduzzi: performed the analysis and interpreted the results. Sofía López: performed the analysis and interpreted the results. María Inés Militelli: performed the analysis and interpreted the results. Karina A. Rodrigues: performed the analysis and interpreted the results. All authors approved the final version of the manuscript for publication.

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