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Development patterns and oxidative metabolism of antarctic sea stars

Analía PÉREZ [1], Cintia FRAYSSE [2], Malena PFOH [3] & Claudia C. BOY [2]

[1] Centro de Ciencias Naturales, Ambientales y Antropológicas (CCNAA), Universidad Maimónides, Laboratorio de Invertebrados Marinos, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, Argentina. [2] Laboratorio de Ecología, Fisiología y Evolución de Organismos Acuáticos, Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ushuaia, Tierra del Fuego AeIAS, Argentina. [3] Laboratorio de Crustáceos, Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ushuaia, Tierra del Fuego AeIAS, Argentina

Abstract: Sea stars exhibit different development patterns that comprise indirect and direct development, including pelagic or benthic larvae, and planktotrophic or lecithotrophic nutrition. The purpose of our research was to study the general parameters of oxidative metabolism during female gonadal maturation in Antarctic sea stars with different development patterns. Summer sampling was performed in 2012 in Antarctica. Every asteroid was taxonomically identified, and its development pattern was established. Sex and the reproductive stage were determined through histological analyses. The general parameters of the oxidative metabolism were determined in mature ovaries by measuring reactive oxygen species (ROS) and total antioxidant capacity (TAC). The development patterns with internal or oral brooding presented a lower production of ROS than those with a broadcaster strategy. The free-living planktotrophic larvae pattern presented lower TAC values than both types of brooding patterns. The development patterns of free-living lecithotrophic larvae and facultative lecithotrophic larvae presented intermediate values of TAC but did not show significant differences. We concluded that species that offspring rapidly acquire the ability to feed during development (planktotrophic larvae) exhibit lower TAC and higher levels of ROS than the species that do not feed during their development, which will receive greater maternal supply of antioxidants, resulting in reduced ROS levels. The development patterns with brooding ensure better quality oocytes and higher fitness in offspring than those unprotected.

Key words: Sea star, Antioxidants, ROS, Antarctica, Brooding, Free-living larvae

Resumen: Patrones de desarrollo y metabolismo oxidativo en estrellas de mar antárticas. Las estrellas de mar presentan diferentes patrones de desarrollo, que comprenden desde desarrollo indirecto a directo, incluyendo la presencia de larvas pelágicas o bentónicas y nutrición planctotrófica o lecitotrófica. El objetivo de muestra investigación fue estudiar los parámetros generales del metabolismo oxidativo durante la maduración gonadal femenina en asteroideos antárticos con diferentes patrones de desarrollo. Se realizaron muestreos estivales durante 2012 en Antártica. Cada asteroideo fue identificado taxonómicamente y se estableció su patrón de desarrollo. Mediante histología determinamos el sexo y estadio reproductivo. En los ovarios maduros se determinaron los parámetros generales del metabolismo oxidativo midiendo especies reactivas del oxígeno (ERO) y capacidad antioxidante total (CAT). Los patrones de desarrollo que incluyen incubación interna u oral presentaron menor producción de ERO que aquellas con estrategias de desove libre. El patrón con larva planctotrófica libre presentó menor CAT que ambos patrones incubantes. Los patrones de desarrollo con larva lecitotrófica libre y larva lecitotrófica facultativa presentaron valores intermedios de CAT, pero no presentaron diferencias significativas. Concluimos que aquellas especies donde sus descendientes adquieren rápidamente la capacidad de alimentarse durante el desarrollo (larvas planctotróficas) presentan baja CAT y elevados ERO, respecto de las especies que no se alimentan durante su desarrollo. Estas últimas reciben un mayor aporte materno de antioxidantes reduciendo de esta forma los niveles de ERO. Los patrones de desarrollo que presentan incubación garantizan una mejor calidad de los ovocitos y una mayor aptitud de las crías que las no protegidas.

Palabras clave: Estrellas de mar, Antioxidantes, ERO, Antártida, Incubación, Larva de vida libre

INTRODUCTION

Sea stars exhibit different development patterns that involve indirect and direct development, which can include a larval stage that can be pelagic or benthic with planktotrophic or lecithotrophic feeding (Mileikovsky, 1971; Chia, 1974; McEdward & Miner, 2001). Most asteroids have pelagic planktotrophic or lecithotrophic larvae that spread widely (Hyman, 1955; Chia & Walker, 1991). Nevertheless, a few species include non-pelagic lecithotrophic larvae (benthic) brooded by the progenitors (retained larvae), and even the larval stage can be absent, in which case, the egg develops directly. These strategies have been widely discussed, especially regarding the importance of brooding and parental care (Gillespie & McClintock, 2007; Pérez *et al.*, 2015; 2024; Fraysse, 2021).

Reproductive effort in sea stars can vary based on their development patterns. For instance, in species with planktotrophic larvae, reproductive investment is generally equal between the sexes, and females produce numerous small oocytes. In contrast, in species that spawn lecithotrophic larvae or brood their young, the patterns of energy allocation to gonads between sexes provide strong evidence of a higher energy investment (per mass unit) to reproduction in females than in males. This results in fewer but larger oocytes, determining females to face the costs associated with incubating embryos (Thorson, 1950; Mileikovsky, 1971; Bosch & Slattery, 1999; Raymond *et al.,* 2004; 2007; Gillespie & McClintock, 2007).

The cost of reproduction plays a central role in evolutionary theory and oxidative stress is thought to play a significant role in explaining this cost. Researchers have reported a variety of associations between reproduction and oxidative stress. The “oxidative cost” hypothesis proposes that the energy and resources allocated to reproduction lead to increased oxidative stress. On the other hand, the “oxidative constraint” and “oxidative shielding” hypotheses offer alternative perspectives. The former suggests that mothers may limit their reproductive efforts to mitigate oxidative damage, while the latter posits that mothers proactively manage oxidative stress by minimizing potential damage before it occurs (Blount *et al.*, 2016; Meniri *et al.*, 2022).

During their evolution, aerobic organisms have adapted to the increase of oxygen in the environment, reaching metabolisms of high energetic efficiency and developing systems that protect them from the inherent damage of using oxygen (Fridovich, 1974). The mechanisms that protect against the damaging effects of oxygen consist of several antioxidant enzymatic and non-enzymatic defenses that facilitate the conservation of endemic reactive oxygen species (ROS) in concentrations that are compatible with life, reducing the damages related to their high reactivity (Wilhelm-Filho *et al.*, 2001). In a cellular state of redox homeostasis, these defenses manage to compensate for the levels of ROS produced. However, an imbalance between ROS production and antioxidant defenses, favoring the former, can lead to oxidative stress (Halliwell & Gutteridge (2015). This situation is reached at the cellular level either by an increase in ROS production rates or by a decrease in the activity of antioxidant defenses. The generation of ROS, such as the superoxide anion (O2•−), the hydrogen peroxide (H2O2), and hydroxyl radical (•OH), occur constantly in the cells, mainly as a result of cellular respiration during the reduction of molecular oxygen into water (Hermes Lima, 2004). Fluctuations in ROS production in aquatic organisms have been attributed to (a) exogenous factors such as hypoxia, hyperoxia, pollution, poisoning, UV radiation, and availability and quality of food (Abele-Oeschger *et al.*, 1994; Power & Sheedan, 1996; Wilhelm-Filho *et al.*, 2001; Geracitano *et al.*, 2004; Keller *et al.*, 2004; Malanga *et al.*, 2007); and (b) endogenous factors, such as feeding rate, growth, motion, age, sex, metabolic rate, oxygen consumption, and reproduction (Livingstone *et al.*, 1990; Winston & Di Giulio, 1991; Abele *et al.*, 1998; Pérez *et al.*, 2011).

Recent work on subantarctic asteroids reinforces the idea of differential energy allocation among contrasting developmental patterns (Fraysse 2021, Fraysse *et al.*, 2020b, 2024) and has made significant contributions regarding the fluctuations of oxidative metabolism concerning the reproduction of subantarctic echinoderms (Pérez, 2009; Pérez, *et al.*, 2011; 2015; Fraysse *et al.*, 2020a; Fraysse, 2021). However, little is known about ROS production and consumption of antioxidant defenses in Antarctic sea stars with contrasting developmental patterns.

We hypothesize that the general parameters of oxidative metabolism in mature females differ among contrasting developmental patterns in Antarctic sea stars. Species with lecithotrophic (free or retained) larvae or direct development may accumulate more antioxidants in mature ovaries than those with planktotrophic development, ensuring that offspring that do not feed during the early stages of development remain protected from the effects of ROS and ensure the fitness of the progeny. The present work aims to study general parameters of oxidative metabolism as reactive oxygen species (ROS) and total antioxidant capacity (TAC) during gonadal maturity in females of Antarctic sea stars with contrasting development patterns.

MATERIALS AND METHODS

Sampling sites

The present study was conducted during the 2012 Summer Antarctic Campaign (SAC) aboard the ARA “Puerto Deseado” oceanographic research vessel. The study area was located from South Orkney to the Palmer Archipelago (Antarctic Peninsula). Sea stars were obtained from 8 stations with different geographic localizations (Table 1) using bottom otter trawls. Temperature, salinity, and depth were registered at each station using a CTD oceanographic sounding line (electric conductivity, temperature, and saltwater pressure) (Table 1). The sampling of the individuals was qualitative.

Sample treatment

Every collected sea star (N= 60) was photographed and dissected. The major radius was measured (mm), the macroscopic characteristics of the gonads of each individual were registered, and the presence of embryos was examined. Subsequently, taxonomic identification was made, and a development pattern was established. Finally, the gonads were extracted, one subsample was kept in Bouin’s solution to perform the histological analysis, and another was maintained at -80°C to determine the general parameters of the oxidative metabolism.

Taxonomy

Taxonomic determinations were performed based on Bernasconi (1962), Bernasconi (1970), Clark & Downey (1992), Fisher (1940), Koehler (1912), Mah *et al.* (2014), Mah (2020), Sladen (1889), Tablado (1982), and Verril (1914), and subsequently checked with the Census of Antarctic Marine Life (Clarke & Johnston, 2003; De Broyer *et al.*, 2022), and Global Biodiversity Information Facility [GBIF] (2022) to ensure that synonymies or misspellings were removed.

Development pattern

The developmental pattern for each species collected was reviewed based on Pérez *et al.* (2024) according to the bibliographic background (Hyman, 1955; Bernasconi, 1970; McClary & Mladenov, 1990; Pearse & Bosch, 1994; Janies, 1995).

Histological analysis

To determine the sex and reproductive stage of each individual (N= 60), a gonad of each sample was used. After Bouin’s solution fixation, dehydration and inclusion in paraffin, the gonads were cut into sections of 5-7 μm using a microtome. The histological sections were stained with hematoxylin and eosin, following the protocol described by Pérez *et al.* (2010). The histological preparations were examined and photographed using an Olympus BX40 optical microscope with a digital camera attached. Mature females were identified and used to determine general parameters of oxidative metabolism.

Determination of the general parameters of oxidative metabolism

The remaining ovaries of mature females were used to measure the general parameters of oxidative metabolism. Total antioxidant capacity (TAC) against peroxyl radicals was determined through the production of ROS, according to the method of Amado *et al.* (2009), with modifications (Pérez *et al.*, 2015). To quantify ROS production, the reaction buffer (30 mM HEPES at pH 7.2, 200 mM KCl, and 1 mM MgCl2) and 10 μL of the supernatant were added to a 96-well microplate. Two wells were used per sample: 4 mM 2,2′-azobis(2-methylpropionamidine) dihydrochloride (ABAP) was added to one well and the same volume of ultrapure water to the other well, reaching a final volume of 145 μL in each well. Fluorescence was determined at 37°C using a spectrofluorometer microplate reader (Fluoroskan Ascent FL 2.6 equipped with Ascent Software Version 2.6). Before reading, 10 μL of the fluorogenic probe 40 μM 2′,7′ dichlorofluorescein diacetate (H2DCF-DA) were added to each well. The fluorophore DCF was detected at λex = 488 nm and λem = 525 nm. Total fluorescence production was calculated by integrating the fluorescence units (FU) over the time of measurement. The results were expressed as the difference between the areas of FU/min/wet weight in the same sample with and without ABAP and standardized to the ROS area without ABAP (background area). The gonads total antioxidant capacity was calculated as follows: TAC= 1/ [(ROS area ABAP – ROS area background) / (ROS area background)].

Table 1. Geographic localization of the sampling stations in Antarctica, physical parameters of seawater (temperature and salinity), and the maximum depth.

Station	Latitude	Longitude	Superficial temperature (°C)	Superficial salinity (%)	Depth (m)
1	64°24.740	66°5.420	2.34	33.59	320
7	64°9.947	64°27.288	3.00	33.67	562
8	63°36.182	64°21.809	3.13	33.72	361
11	63°43.092	61°7.402	1.94	34.08	131
13	62°59.310	59°57.246	2.42	34.11	977
35	60°40.992	46°19.560	3.07	34.14	110
36	60°42.331	46°1.342	3.12	34.07	98
37	60°47.561	45°36.854	1.50	34.08	120

Statistical analysis

Reactive oxygen species (ROS) production among contrasting development patterns was analyzed with one-factor ANOVAs followed by Tukey's multiple comparisons. The assumptions of homogeneity of variance (Bartlett test) and normality (Kolmogorov-Smirnov test) were verified after transforming the data by using the logarithmic function. The total antioxidant capacity (TAC) among contrasting development patterns was analyzed with the non-parametric Kruskal-Wallis test followed by Dunn's multiple comparisons since the parametric test assumptions were not met, even transforming the data. The statistical analyses were performed using GraphPad Prism 8.0.1 (GraphPad Software, San Diego, CA).

RESULTS

Taxonomy and development patterns

- From the histological study of the gonads, 38 mature females were determined. Seven species were identified and utilized in this study:
- *Pteraster stellifer* (Sladen, 1882) ($N=4$) = internal brooding
- *Diplasterias brucei* (Koehler, 1907) ($N=4$) = oral brooding
- *Glabraster antarctica* (Smith, 1876) ($N=9$) = free-living facultative lecithotrophic larvae
- *Bathybiaster loripes* (Sladen, 1889) ($N=4$) = free-living lecithotrophic larvae
- *Cycethra verrucosa mawsoni* (Clark, 1962) ($N=5$) = free-living lecithotrophic larvae
- *Psilaster charcoti* (Koehler, 1906) ($N=7$) = free-living lecithotrophic larvae
- *Odontaster meridionalis* (Smith, 1876) ($N=5$) = free-living planktotrophic larvae

Production of reactive oxygen species and total antioxidant capacity among species

ROS values of the ovaries varied from 56357 to 758310 FU/min/wet weight, with a mean value of 539592 FU/min/wet weight, with *P. stellifer* having the lowest (56357 FU/min/wet weight) and *O. meridionalis* the highest ROS (758310 FU/min/wet weight) (Table 1). The mean TAC of female gonads was 1.02 relative FU, being *O. meridionalis* the lowest (0.3728 relative FU) and *D. brucei* the highest (1.938 relative FU) (Table 2).

ROS and TAC among contrasting development patterns

The production of ROS in mature ovaries presented significant differences among the contrasting development patterns (ANOVA 1F; $F=10.97$, $P<0.0001$). The internal and oral brooding patterns did not show significant differences; however, both patterns exhibited a lower production of ROS compared to the free-living larvae, regardless of their feeding strategy (Tukey's multiple comparison test $p<0.05$) (Fig. 1).

The TAC values in the mature ovaries presented significant differences among contrasting development patterns (Kruskal Wallis $H=13.92$, $P=0.0076$). The free-living planktotrophic larvae presented lower TAC than the internal and oral brooding ones (Dunn's multiple comparison test $P<0.05$). The free-living lecithotrophic larvae and the facultative lecithotrophic larvae patterns exhibited intermediate values of TAC but no significant differences were observed (Dunn's multiple comparison test $P>0.05$) (Fig. 2).

DISCUSSION

In the present work, seven species of Antarctic sea stars were studied, *Pteraster stellifer*, *Diplasterias brucei*, *Cycethra verrucosa*

Table 2. Taxonomy, developmental patterns, production of reactive oxygen species (ROS) and total antioxidant capacity (TAC) of mature ovaries for seven representative species of Antarctic Sea stars. ROS and TAC were expressed as FU/min/wet weight and relative FU, respectively; Mean ± SD FU = fluorescence units.

Family	**Species**	**Development Patterns**	**ROS**	**TAC**
Asteriidae	*Diplasterias brucei*	Oral brooding	152988±174487	1.9380±1,28
Asterinidae	*Cycethra verrucosa mawsoni*	Free-living lecitotrophic larvae	334710±63916	0.6422±0,22
Astropectinidae	*Bathibiaster loripes*	Free-living lecitotrophic larvae	184689±72207	1.6450±0,65
	Psilaster charcoti	Free-living lecitotrophic larvae	633479±479706	0.6729±0,47
Odontasteridae	*Odontaster meridionalis*	Free-living planktotrophic larvae	758310±311221	0.3728±0,14
Poraniidae	*Glabraster antarctica*	Free-living facultative lecitotrophic larvae	396610±335890	0.7344±0,26
Pterasteridae	*Pteraster stellifer*	Internal brooding	56357±24460	1.1350±0,24

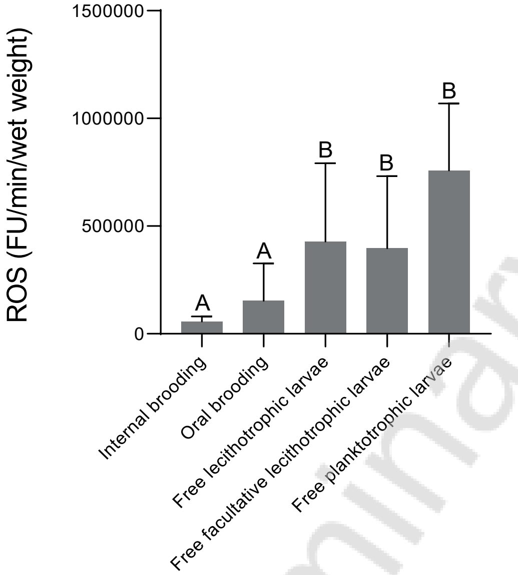

Fig. 1. Production of reactive oxygen species (ROS) in mature ovaries among contrasting development patterns of Antarctic sea stars. Different uppercase letters above bars show significant differences between groups. Mean ± standard deviation. FU fluorescence units.

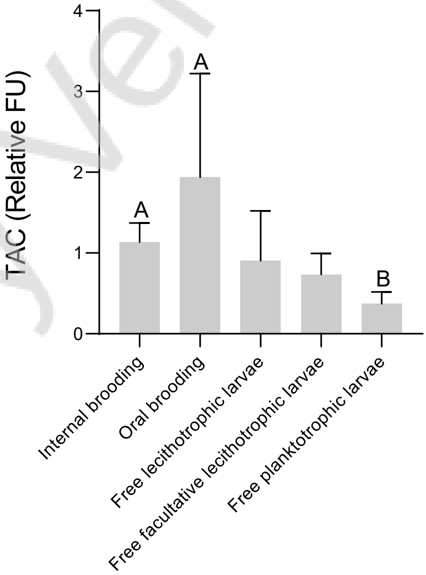

Fig. 2. Total antioxidant capacity (TAC) in mature ovaries among contrasting development patterns of Antarctic sea stars. Different uppercase letters above bars show significant differences between groups. Mean ± standard deviation. FU fluorescence units.

mawsoni, *Bathybiaster loripes*, *Psilaster charcoti*, *Glabraster antarctica,* and *Odontaster meridionalis*. These species present different development patterns such as internal and oral brooding, free-living lecithotrophic larvae, facultative lecithotrophic larvae, and free-living planktotrophic larvae (Table 2). Moreover, general parameters of oxidative metabolism (ROS and TAC) were established in mature ovaries of species with contrasting development patterns. Our results, in agreement with previous studies, reinforce an association among reproduction, development and oxidative metabolism (Pérez *et al.*, 2011; 2015; Fraysse *et al.*, 2020a; Fraysse, 2021). These previous studies were the first to confirm the relationship between the reproductive condition (reproductive stages) and the oxidative metabolism in echinoderms, emphasizing the strong relationship between the reproductive cycle, the total antioxidant capacity (TAC) and its antioxidant content, the production of reactive oxygen species (ROS), the lipid radical content and the lipid damage (Pérez, 2009; Pérez *et al.*, 2011; Fraysse *et al.*, 2020a; Fraysse, 2021).

Our results indicate that species with internal and oral brooding development patterns exhibit lower levels of ROS and higher TAC in their mature ovaries. This suggests an oxidative stress-free scenario, compared to species with planktotrophic development patterns. These findings are consistent with previous studies of subantarctic echinoderms although they did not address interspecific comparisons, where a greater reproductive effort, energetic investment, and antioxidant assignation during the maturing of the ovary were reported in species with parental care, both with internal or oral brooding, in contrast to species that presented planktotrophic development (Pérez *et al.*, 2008; 2010; 2011; 2015; Pérez, 2009; Fraysse *et al.*, 2020a; Fraysse, 2021). In the sea star *Diplopteraster verrucosus* (internal brooder) it has been found that the mature females, both brooding and non-brooding, present higher levels of TAC than males (Fraysse *et al.*, 2020a). Likewise, in *Anasterias antarctica* (oral brooder) the production of ROS in mature females (maturity I, according to Fraysse *et al.*, 2021) was lower and presented higher TAC levels (also, α-tocopherol, β-carotene, and echinenone antioxidants) than non-mature females (Pérez *et al.*, 2015; Fraysse, 2021). On the contrary, during development, *D. verrucosus* embryos increased the production of ROS while TAC was constant (Fraysse *et al.*, 2020a). In *A. antarctica*, there was also a progressive and significant increase of ROS during the development of embryos (Pérez *et al.*, 2015) and TAC remained constant (Fraysse, 2021), suggesting in both cases that the non-favourable oxidative condition towards the end of the brooding period could trigger the release of embryos (Fraysse *et al.*, 2025). In the echinoid *Loxechinus albus* (free-living planktotrophic development pattern) Pérez *et al.* (2011) corroborated that the content of antioxidants (α-tocopherol, β-carotene and echinenone) decreases during the gametogenesis while the lipid oxidation and the content of lipid radicals increases, reaching gonad maturity with oxidative imbalance.

The nutrients and antioxidants stored in mature oocytes are transferred to the larvae and embryos, where they are used during development (Plank *et al.*, 2002). In this sense, those species where their offspring rapidly acquire the capacity to feed during development, such as free-living planktotrophic larvae (Pearse *et al.*, 1991), present low antioxidant protection (TAC) and high ROS, such as *O. meridionalis* and the sea urchin *L. albus* (Pérez *et al.*, 2011). In contrast, species that do not feed during their development will receive a higher maternal contribution of antioxidants (Pérez *et al.*, 2015) or will present a higher TAC (Fraysse, 2021) thus preserving low levels of ROS, as corroborated in *P. stellifer* and *D. verrucosus* (Fraysse *et al.*, 2020a), where the embryos are incubated or retained for extended periods. In these cases, a higher assignation of antioxidants to mature ovaries could ensure the production of good-quality oocytes thus increasing the fitness of the offspring. The translocation and the accumulation of antioxidants suggest an oxidative damage prevention strategy, both by the end of oogenesis and in the earliest stages of embryonic development (Perez *et al.*, 2011; Fraysse, 2021).

We conclude that brooding Antarctic sea stars may preventively lower oxidative stress levels prior to reproduction, to protect themselves and their physiologically dependent offspring from the negative intergenerational consequences of oxidative stress during reproduction ("oxidative shielding" hypothesis). In contrast, species with a planktotrophic development pattern are consistent with the "oxidative cost" hypothesis suggests that the reproductive investment can result in an elevated metabolic rate and consequently elevated ROS production. However, individuals may have adjusted the output of offspring to their conditions to avoid excessively high oxidative costs of reproduction that could negatively impact fitness. While the relationship between reproduction, development and oxidative metabolism requires further exploration, the present work lays the groundwork for studying these aspects in Antarctic sea stars.

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REFERENCES

Abele, D., Burlando, B., Viarengo, A., & Pörtner, H. O. 1998. Exposure to elevated temperatures and hydrogen peroxide elicits oxidative stress and antioxidant response in the Antarctic intertidal limpet *Nacella concinna*. *Comparative Biochemistry and Physiology Part B* 120, 425-435.

Abele-Oeschger, D., Oeschger, R., & Theede, H. 1994. Biochemical adaptations of *Nereis diversicolor* (Polychaeta) to temporarily increased hydrogen peroxide levels in intertidal sandflats. *Marine Ecology Progress Series* 106, 101-110.

Amado, L. L., Garcia, M. L., Ramos, P. B., Freitas, R. F., Zafalon, B., Ferreira, J. L., Yunes J. S., & Monserrat, J. M. 2009. A method to measure total antioxidant capacity against peroxyl radicals in aquatic organisms: application to evaluate microcystin toxicity. *Science of the Total Environment* 407*,* 2115-2123.

Bernasconi, I. 1962. Asteroideos Argentinos III. Familia Odontasteridae. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 9*,* 1-25.

Bernasconi, I. 1970. Equinodermos antárticos. II. Asteroideos. 3. Asteroideos de la extremidad norte de la Península Antártica. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 9, 211-281.

Blount, J. D., Vitikainen, E. I. K., Stott, I., & Cant, M. A. 2016. Oxidative shielding and the cost of reproduction. *Biological Reviews of the Cambridge Philosophical Society* 91, 483–497.

Bosch, I., & Slattery, M. 1999. Costs of extended brood protection in the Antarctic sea star, *Neosmilaster georgianus* (Echinodermata: Asteroidea). *Marine Biology* 134, 449-459.

Chia, F.S. (1974). Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugoslavica* 10, 121-130.

Chia, F. S., & Walker, C. W. 1991. Echinodermata: Asteroidea. In A. C. Giese, J. S. Pearse, V.B. Pearse, (Ed.), Reproduction of Marine Invertebrates, Echinoderms and Lophophorates (Vol. 6, pp. 301-353). Pacific Grove: Boxwood Press.

Clark, A. M., & Downey, M. E. 1990. *Starfishes of the Atlantic*. England: Chapman & Hall.

Clarke, A., & Johnston, N. M. 2003. Antarctic marine benthic diversity. In Oceanography and marine biology (pp. 55-57). CRC Press.

De Broyer, C., Clarke, A., Koubbi, P., Pakhomov, E., Scott, F., Vanden Berghe, E., & Danis, B. 2024. Register of Antarctic Marine Species (RAMS). http://www.marinespecies.org/rams.

Fisher, W. K. 1940. Asteroidea. *Discover Report 20,* 69-306.

Fraysse, C. P., Boy, C. C., Becker, J., Calcagno, J., & Pérez, A. 2020a. Brooding in the Southern Ocean: The Case of the Pterasterid Sea Star *Diplopteraster verrucosus* (Sladen, 1882). *Biological bulletin* 239, 1-12.

Fraysse, C., Pérez, A. F., Calcagno, J., & Boy, C. C. 2020b. Energetics and development mode of the Asteroidea (Echinodermata) from the Southwestern Atlantic Ocean including Burdwood Bank/ MPA Namuncurá. *Polar Biology* 43, 175-186.

Fraysse, C. 2021. *Distribución, recursos energéticos y metabolismo oxidativo de Asteroideos subantárticos con diferentes estrategias reproductivas. Estudio particular de la incubación:* Argentina: UBA, Facultad de Ciencias Exactas y Naturales. Tesis Doctoral en Ciencias Biológicas.

Fraysse, C.P., Boy, C.C., & Pérez, A.F. 2021. Reproductive traits of the intertidal sea star *Anasterias antarctica* (Echinodermata: Asteroidea) from the Beagle Channel, Argentina. *Marine Biology 168,* 1-19.

Fraysse, C., Boy, C. C., Veyñ, M., Farias, A., & Pérez, A. F. 2024. Noble hosts: effects of internal parasites on the physiology of an intertidal brooding Sea-star. *Revista de Biología Tropical* 72.

Fraysse, C.; Pérez, A., Mattenet, A., Pfoh, M., Boy, C.C. 2025. Oral brooding (*Anasterias antarctica*) vs. internal brooding (*Diplopteraster verrucosus*): Contrasting strategies of the brooded juveniles for full development. *Revista del Museo Argentino de Ciencias Naturales* Under revision.

Fridovich, I. 1974. Superoxide and evolution. *Horizont Biochemistry Biophysics 1,* 1-37.

GBIF 2022 Occurrence Download. https://www.gbif.org/occurrence/Global Biodiversity Information Facility 2022.

Geracitano, L. A., Monserrat, J. M., & Bianchini, A. 2004. Oxidative stress in *Laeonereis acuta* (Polychaeta Nereididae): environmental and seasonal effects. *Marine Environmental Research* 58, 625-630.

Gillespie, J. M., & McClintock, J. B. 2007. Brooding in echinoderms: how can modern experimental techniques add to our historical perspective?. *Journal of Experimental Marine Biology and Ecology* 342, 191–201.

Halliwell, B., & Gutteridge, J. M. (2015). Free radicals in biology and medicine. Oxford university press, USA.

Hermes Lima, M. 2004. Oxygen in Biology and Biochemistry: Role of free radical. In K. B. Storey (Ed), Funcional Metabolism: Regulation and Adaptation (pp. 319-368). Hoboken: John Wiley & Sons, Inc.

Hyman, L. H. 1955. *The invertebrates: echinodermata, the coelomate bilateria (Vol. 4)*. New York: McGraw-Hill.

Janies D. A. 1995. *Reconstructing the evolution of morphogenesis and dispersal among velatid asteroids*: United Stated: UF. PhD Thesis.

Keller, M., Sommer, A., Pörtner, H. O., & Abele, D. 2004. Seasonality of energetic functioning and reactive oxygen species production by mitochondria of the lugworm *Arenicola marina*, exposed to acute temperature changes. *Journal of Experimental Biology* 207, 2529-2538.

Koehler, R. 1912. Échinodermes *(astéries, ophiures et* échinides*). Deuxième ExpéditionAntarctique Française (1908-1910).* Paris: Masson.

Livingstone, D. R., Garcia Martinez, P., Michel, X., Narbonne, J. F., O'Hara, S., Ribera, D., & Winston, G. W. 1990. Oxyradical production as a pollution mediated mechanism of toxicity in the common mussel, *Mytilus edulis* L., and other molluscs. *Functional Ecology* 4 (3), 415-424.

Mah, C. L. 2020. World Asteroidea Database. [Online]. http://www.marinespecies.org/asteroidea.

Mah, C., Neill, K., Eléaume M., & Foltz, D. 2014. New species and global revision of Hippasteria (Hippasterinae: Goniasteridae; Asteroidea; Echinodermata): Hippasteria revision. *Zoological Journal of the Linnean Society* 171, 422-456.

Malanga, G., Estevez, M., Calvo, J., Abele, D., & Puntarulo, S. 2007. The effect of seasonality on oxidative metabolism in *Nacella (Patinigera) magellanica*. *Comparative Biochemistry and Physiology Part B* 146, 551-558.

McClary, D. J., & Mladenov, P. V. 1990. Brooding biology of the sea star *Pteraster militaris* (O.F. Müller): energetic and histological evidence for nutrient translocation to brooded juveniles. *Journal of Experimental Marine Biology and Ecology* 142, 183-199.

McEdward, L. R., & Miner, B. G. 2001. Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology 79,* 1125-1170.

Meniri, M., Evans, E., Thompson, F. J., Marshall, H. H., Nichols, H. J., Lewis, G., Holt, L., Davey, E., Mitchell, C., Johnstone, R. A., Cant, M. A., & Blount, J. D. (2022). Untangling the oxidative cost of reproduction: An analysis in wild banded mongooses. *Ecology and Evolution* 12(3), e8644. https://doi.org/10.1002/ece3.8644

Mileikovsky, S. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Marine Biology* 10, 193-213.

Pearse, J. S., McClintock, J. B., & Bosch, I. 1991. Reproduction of Antarctic benthic marine Invertebrates: tempos, modes, and timing. *American Zoology* 31, 65-80.

Pearse, J.S., & Bosch, I. 1994. Brooding in the Antarctic: Östergren had it nearly right. In B. David (Ed.), Echinoderms Through Time: Proceedings of the Eighth International Echinoderm Conference (pp. 111-120). Rotterdam: Balkema.

Pérez, A. F., Morriconi, E., Boy, C., & Calvo, J. 2008. Energetic variation of the sea urchin *Loxechinus albus* at the southernmost limit of their distribution range (Beagle Channel, Tierra del Fuego). *Polar Biology* 31, 443-449.

Pérez, A. F. 2009. *Reproducción, energética y metabolismo oxidativo del erizo comestible Loxechinus albus en el Canal Beagle, extremo sur de su distribución*. Argentina: UBA, Facultad de Ciencias Exactas y Naturales. Tesis Doctoral en Ciencias Biológicas.

Pérez, A. F., Boy, C., Morriconi, E., & Calvo, J. 2010. Reproductive cycle and reproductive output of the sea urchin *Loxechinus albus* (Echinodermata: Echinoidea) from Beagle Channel, Tierra del Fuego, Argentina. *Polar Biology* 33, 271-280.

Pérez, A. F., Malanga, G., & Puntarulo, S. 2011. Reproductive condition associate to changes in the liposoluble antioxidant capacity and the damage to lipids in the sea urchins *Loxechinus albus* (Echinodermata: Echinoidea). *Revista Ciencias Marinas y Costeras* 3, 183-194.

Pérez, A. F., Boy, C. C., Calcagno, J. A., & Malanga, G. 2015. Reproduction and oxidative metabolism in the brooding sea star *Anasterias antarctica* (Lütken, 1957). *Journal of Experimental Marine Biology and Ecology* 463, 150-157.

Pérez, A., Fraysse, C., & Ojeda, M. 2024. Distribución y patrones de desarrollo de asteroideos antárticos. *Revista de Biología tropical,* 72.

Plank, L. R., Lawrence, J. M., Lawrence, A. L., & Montoya Olvera, R. 2002. The effect of dietary carotenoids on gonad production and carotenoid profiles in the sea urchin *Lytechinus variegatus*. *Journal of the World Aquaculture Society* 33(2), 127-137.

Power, A., & Sheehan, D. 1996. Seasonal variations in the antioxidant defense systems of gill and digestive gland of the blue mussel, *Mytilus edulis*. *Comparative Biochemistry and Physiology Part C* 114, 99-103.

Raymond, J. F., Himmelman, J. H., & Guderley, H. E. 2004. Sex differences in biochemical composition, energy content and allocation to reproductive effort in the brooding sea star Leptasterias Polaris. *Marine Ecology Progress Series* 283, 179-190.

Raymond, J. F., Himmelman, J. H., & Guderley, H. E. 2007. Biochemical content, energy composition and reproductive effort in the broadcasting sea star *Asterias vulgaris* over the spawning period. *Journal of Experimental Marine Biology and Ecology* 341(1), 32-44.

Sladen, W. P. 1889. Report on the Asteroidea collected by HMS Challenger. *Zoology 30,* 893.

Tablado A. 1982. Asteroideos Argentinos Familia Poraniidae. Comunicaciones del Museo Argentino de Ciencias Naturales Bernardino Rivadavia. *Hidrobiología* 2, 87-106.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological reviews of the Cambridge Philosophical Society* 25, 1-45.

Verril, A. E. 1914. Monograph of the Shallow-water Starfishes of the North Pacific Coast from the Arctic Ocean to California. *Science* 40 (1032), 523-525.

Wilhelm-Filho, D., Tribess, T., Gáspari, C., Cláudio, F.D., Torres, M.A., & Magalhães, A.R.M. 2001. Seasonal changes in antioxidant defenses of the digestive gland of the brown mussel (*Perna perna*). *Aquaculture* 203, 149-158.

Winston, G.W., & Di Giulio, R.T. 1991. Prooxidant and antioxidant mechanisms in aquatic organisms. *Aquatic Toxicology* 19, 137-161.

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