SUPPLEMENT

#### REVISTA DE Biología Tropical

https://doi.org/10.15517/rev.biol.trop..v72iS1.58676

# Noble hosts: effects of internal parasites on the physiology of an intertidal brooding Sea-star

Cintia Pamela Fraysse<sup>1\*</sup>; https://orcid.org/0000-0002-0254-2263 Claudia Clementina Boy<sup>1</sup>; https://orcid.org/0000-0002-0819-8205 Marianela Veyñ <sup>1</sup>; https://orcid.org/0009-0006-0465-314X Ayelen Farias <sup>1</sup>; https://orcid.org/0009-0007-6798-0671 Analía Fernanda Pérez <sup>2</sup>; https://orcid.org/0000-0001-5945-7468

- 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; fraysse.cintia@gmail.com (\*Correspondence), ccboy@conicet.gov.ar, marianela.veyn@gmail. com, ayelenfarias11790@gmail.com
- 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; analiafperez1@gmail.com

Received 23-I-2023. Corrected 14-IX-2023. Accepted 27-IX-2023.

#### ABSTRACT

**Introduction:** The endoparasite *Dendrogaster argentinensis* infects the intertidal brooder sea star *Anasterias antarctica*. This sea-star species is in the highest trophic level in the Beagle Channel.

**Objective:** To study the effects of parasitism by *D. argentinensis* on the fitness and reproduction of *A. antarctica.* **Methods:** Adults from the brooder sea-star were collected from the rocky intertidal of Ensenada Zaratiegui bay (54°51' S & 68°29' W), Argentina. Eight seasonal samplings were performed (four seasons in two years) in the upper and low intertidal. During dissection, parasites were removed, and all organs were extracted and weighed separately.

**Results:** *Dendrogaster argentinensis* prevalence was the highest for the region (20.4 %). Parasitized individuals were more frequent in the low intertidal in all seasons, with a higher difference in summer, where it is likely that the higher temperatures and strong winds could make the upper intertidal more challenging for a parasitized individual. Five parasitized individuals were castrated. Generally, the gonadal (GI) and somatic (pyloric caeca, PCI; stomach, SI; body wall, WI) indexes were lower in parasitized than non-parasitized individuals.

**Conclusions:** Parasitism by *D. argentinensis* negatively affects *A. antarctica* condition. It affects reproduction because it reduces the GI, and can also produce castration. The parasite competes for the sea-stars' energetic resources, also decreasing the individual's capacity for feeding (reduced stomach) and growth (reduced body wall).

Key words: Asteroidea; Ascothoracida; parasite; gonadal index; somatic indexes; prevalence; Beagle Channel.

#### RESUMEN Huéspedes nobles: los efectos de parásitos internos en la fisiología de una estrella de mar incubadora del intermareal

Introducción: El endoparásito *Dendrogaster argentinensis* infecta a la estrella de mar *Anasterias antarctica*, especie que se encuentra en el nivel trófico más alto del Canal Beagle.

(i) (i)

**Objetivo:** Estudiar los efectos del parasitismo de *D. argentinensis* en la condición fisiológica y reproducción de *A. antarctica.* 

**Métodos:** Adultos de la estrella de mar incubadora fueron recogidos del intermareal rocoso de la bahía Ensenada Zaratiegui (54°51' S & 68°29' W). Se realizaron ocho muestreos estacionales (cuatro temporadas en dos años) en el intermareal superior y bajo. Durante la disección, se removieron los parásitos, y todos los órganos, los cuales fueron pesados por separado.

**Resultados:** La prevalencia de *D. argentinensis* fue la más alta de la región (20.4 %). Los individuos parasitados fueron más frecuentes en el intermareal bajo en todas las estaciones, siendo la mayor diferencia en verano, donde es probable que las temperaturas más altas y los fuertes vientos puedan hacer que el intermareal superior sea más desafiante para un individuo parasitado. Se observaron cinco individuos parasitados que estaban castrados. Generalmente, los índices gonadales (GI) y somáticos (ciego pilórico, estómago, y pared del cuerpo) fueron menores en los individuos parasitados que no parasitados.

**Conclusiones:** El parasitismo de *D. argentinensis* afecta negativamente la condición fisiológica de *A. antarctica.* Afecta a la reproducción en términos de bajo GI y puede causar castración. El parásito compite por los recursos energéticos de las estrellas de mar, disminuyendo también la capacidad del individuo para alimentarse (reducción del estómago) y crecer (reducción de la pared del cuerpo).

Palabras clave: Asteroidea; Ascothoracida; parásito; índice gonadal; índices somáticos; prevalencia; Canal Beagle.

# INTRODUCTION

Parasites infect animals ranging from invertebrates to fish and even whales (Poulin & Hamilton, 1997). Parasitic associations have been casually reported in the literature between echinoderms and polychaetes, tardigrades, barnacles, amphipods, tanaidaceans, acarians, pycnogonids and insects (Jangoux, 1987). Parasitism is a typical life form among crustaceans (Bowman et al., 1982) and it has emerged independently on several occasions in their phylogenetic history. Generally, parasites impact marine organisms by decreasing fertility, increasing mortality and altering the growth and normal behavior of their hosts. These direct effects may also indirectly increase the possibility of predation on parasitized organisms (Dunne et al., 2013; Lafferty et al., 2006; Mouritsen & Poulin, 2002). Ascothoracida is an infraclass with six recognized families within the Crustacea subphylum that comprises a few more than 100 species with the ability to parasitize echinoderms or/and cnidarians (Grygier & Høeg, 2005; Saito et al., 2020). There are over thirty species of the genus Dendrogaster described from various sea stars around the world, which inhabit from the intertidal to 4 000 m deep (Grygier, 1985; Grygier & Høeg, 2005). This genus consist of endoparasites

species that occupy part of their host's perivisceral coelom (Grygier, 1985). Females have a reduced abdomen and thorax with simplification or loss of limbs (Webber et al., 2010). The carapace is enlarged and completely distorted, forming branches unrecognizable as a crustacean (Webber et al. 2010). Males are tiny, with a typical crustacean larvae-like morphology and are found within the mantle cavity of females (Boxshall et al., 2005; Grygier, 1985; Grygier & Høeg, 2005; Grygier & Salvat, 1984; Webber et al. 2010). Their feeding is poorly known. A primitive feature of the ascothoracid parasites is that they feed by the piercing-sucking mouth apparatus (Grygier & Høeg, 2005). However, the ultrastructure of the cuticle of the best-known genus of ascothoracid parasite, Ulophysema, suggests absorptive feeding as rhizocephalan barnacles, it is unclear if it is their primary mode of food intake (Boxshall et al., 2005; Grygier & Høeg, 2005). The complete life cycle, the host infection or the copulation has not been studied for any ascothoracidan (Boxshall et al., 2005).

The endoparasite, *Dendrogaster argentinensis* was first noted to infect *Anasterias minuta* [junior synonym of *Anasterias antarctica* (Mah, 2023; Romanelli-Michel, 2014)] by Grygier and Salvat (1984). Salvat (1985) reported an infection rate of 1.5 % in *A. minuta* 

2

from Ría de Puerto Deseado (Santa Cruz, Argentina); all parasites were found in the celomic cavity during dissection. Pérez et al. (2017) found a high prevalence of 11 % in A. antarctica from the Beagle Channel, the region of highest prevalence so far. Anasterias antarctica is a brooder species inhabiting the intertidal zone to 185 m depth (Bernasconi, 1964; Romanelli-Michel, 2014). This species exhibits a wide distribution, from about 40° S to the south of Isla Grande de Tierra del Fuego and the north of the Antarctic Peninsula. They are within the highest trophic level in the Beagle Channel (Adami & Gordillo, 1999) and are top predators of intertidal and sub-tidal communities (Curelovich, 2012). Females brood the lecithotrophic embryos on the oral surface over the mouth for eight months, from April to November. (Fraysse et al., 2021; Pérez et al., 2015; Pérez et al., 2017), and do not feed during this period (Gil & Zaixso, 2008; Gil et al., 2011). A recent study on their reproductive cycle showed that females undergo two consecutive and different annual cycles (Fraysse et al., 2021). The first cycle corresponds to the production of large oocytes (approx. 1 080 µm) that, once fertilized, will develop into a modified lecithotrophic brachiolaria larva, which will be retained and brooded (Fraysse et al., 2021). In the second consecutive cycle, the gonadal maturation produces many smaller oocytes (approx. 219.30 µm) while the females are still brooding. Although the female reproductive effort is 25 % higher than males (Pérez et al., 2015), males' gametes production is greater (Pérez et al., 2017).

The Beagle Channel (55°S, 68° W) has two semidiurnal tides, which define daily two low tides and two high tides. The intertidal habitat is a stressful environment in which species are exposed to highly variable atmospheric and oceanographic conditions (Davenport & Davenport, 2005; Helmuth & Hofmann, 2001). Stresses resulting from varying environmental conditions or internal constraints are important factors causing a decrease in the reproductive output (Lawrence & Herrera, 2000). In this context, the main objective of this work was to study the physiological constraints that may produce the presence of the endoparasite *D. argentinensis* in the brooder sea-star, *A. antarc-tica*, which inhabits a stressful environment as the rocky Fuegian intertidal.

### MATERIALS AND METHODS

Area of study: The Beagle Channel (55°S, 68° W) connects the Pacific and Atlantic oceans at their southernmost extreme. Its waters are characterized by their low salinity due to the profuse drainage in both margins; small streams and rivers that descend from melting and glaciers towards the sea keep surface values of salinity below 32 UPS (Fraysse et al., 2021; Iturraspe et al., 1989; Pérez et al., 2008). Anasterias antarctica individuals were collected from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel, Fig. 1), in Parque Nacional Tierra del Fuego (54°51' S & 68°29' W; Tierra del Fuego AIAS, Argentina), where tides are semidiurnal, defined by two high tides and two low tides with a marked (0.1-2.3 m) difference in amplitude (Balestrini et al., 1998; Curelovich, 2012). Eight seasonal samplings (February, May, August, and November) were carried out in both 2017 and 2018 from two tidal levels: low (0.2 m) and upper (1.2 m).

**Sampling:** A total of 510 adults of *A. antarctica* [(> 1.5 cm radius, (Gil et al., 2011, Pérez et al., 2017)] were collected. They were transported to the Centro Austral de Investigaciones Científicas (CADIC) in 3l plastic containers with portable aerators and seawater from the sampling site. Before dissection, each individual was superficially dried with tissue paper, weighed (total weight  $\pm$  0.01 g), and photographed.

All individuals were anaesthetized by immersion in MS-222 (ethyl 3-aminobenzoate methanesulfonate acid salt, 98 %, Sigma-Aldrich) 1 % in seawater, for 45 min (O'Neill, 1994), before dissection (Fraysse et al., 2021). During dissection, the following variables were registered: sex (if possible), brooding or nonbrooding condition in females, castration (if gonads were no present), and presence of the



Fig. 1. Location of the sampling site in Beagle Channel. The Beagle Channel, Ushuaia City, Tierra del Fuego National Park, Route 3, and sampling area in Ensenada Zaratiegui bay (red dot) are shown.

coelomic parasites, *D. argentinensis* (Fig. 2). Subsequently, gonads, pyloric caeca, stomach and body wall were weighed.

**Population prevalence and gonadosomatic indexes:** Population prevalence (parasitized frequencies) was calculated as the quotient between the number of parasitized individuals and the total number of individuals collected for each intertidal level and season.

Whereas the prevalence by sex (proportion of parasitized individuals) was constructed by season. Castrated individuals were treated separately.



**Fig. 2. A.** Oral view of a parasitized individual of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel) during dissection. **B.** *Dendrogaster argentinensis* parasite extracted from A. References: coelomic cavity (CC), parasite (P), pyloric caeca (PC), main branch (MB), middle piece (MP), and dissection cut (dotted line) to expose the coelomic cavity.

Gonadal, somatic and parasite load indexes: Were calculated as follows:

$$\frac{Wbc}{Tw} \times 100$$

Where Wbc stands for the wet weight of the body component and Tw is the total wet weight of the individual before dissection.

Statistical analyses: To evaluate the sex ratio of the total of parasitized individuals, in all seasons a Chi-square test was performed. Also, to evaluate differences in the gonadal and somatic indexes between parasitized and non-parasitized individuals T-test were performed for each sex or reproductive condition (males, brooding and non-brooding females). This analysis was performed separately for each body component (gonads, pyloric caeca, stomach and body wall). The assumptions of normality (Shapiro-Wilk) and homoscedasticity (Levene) were tested (Sokal & Rohlf, 1995). When assumptions were not met, nonparametric statistical method was used (Wilcoxon-Mann-Whitney). For the parasite load index by season a Kruskal-Wallis test was performed, followed by Dunn post hoc comparisons. Statistical analyses and graphs were

performed using Rstatix package from R software (Kassambara, 2023).

### RESULTS

**Population prevalence:** Of the 510 individuals collected, 104 were parasitized, resulting in a prevalence of 20.4 %. Parasitized individuals were more frequent in the low intertidal for all seasons (autumn, spring, summer and winter). However, the greatest difference between the frequency of parasitized and non-parasitized individuals was found in summer (Fig. 3).

**Prevalence by sex:** On the total of parasitized individuals, in almost all seasons, the sex ratio was 1:1, showing no preference of the parasite for either sex (Chi-square test, p = 0.27, p = 0.62 and p = 0.12, for autumn, spring and summer, respectively), in winter sex ratio was biased towards males (Chi-square test, p = 0.04). In spring and summer there were a few parasitized individuals castrated (n=2 and n=3, respectively) where the gonads were absent. Although the number of castrated individuals was low, all of them were parasitized (Fig. 4).



Fig. 3. Population prevalence of *Dendrogaster argentinesis* in *Anasterias antarctica*, from both rocky intertidal levels (upper and low) of Ensenada Zaratiegui bay (Beagle Channel) by season.



Fig. 4. Prevalence of *Dendrogaster argentinensis* in *Anasterias antarctica* by sex, from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel) showed by (castrated, females, and males) and season.

Gonadal indexes: In females, there were significant differences between the gonadal indexes (GI) of parasitized and non-parasitized individuals, showing lower values (thus reduced resource allocation to reproduction) in the parasitized females than non-parasitized, regardless of the reproductive condition, brooding and non-brooding (Wilcoxon-Mann-Whitney test, p = 0.04 and p = 0.02, respectively, Fig. 5). Differences in the GI between brooding and non-brooding females are due to the fact that their gonads are in different condition, while non-brooding females might be ongoing gametogenesis, brooding females gonads are mainly post spawned (Fraysse et al. 2021). There were no significant differences between the GI of parasitized and non-parasitized males (Wilcoxon-Mann-Whitney test, p = 0.49).

**Somatic indexes:** Females in the nonbrooding reproductive condition and males showed significant differences (t-test, p = 0.04and Wilcoxon–Mann–Whitney test, p = 0.04, respectively) between the pyloric caeca index (PCI) of parasitized and non-parasitized individuals (Fig. 6), showing lower values those that were parasitized. However, females in the brooding reproductive condition did not show significant differences (t-test, p = 0.06).

There were significant differences between the stomach index (SI) of parasitized and nonparasitized individuals. Parasitized females showed lower values than non-parasitized (Fig. 7), regardless of the reproductive condition (Wilcoxon–Mann–Whitney test, p = 0.04and p < 0.01, for brooding and non-brooding females, respectively). Also, males showed significant differences between parasitized and non-parasitized individuals (t-test, p < 0.01), being the SI lower in those parasitized.

Significant differences between the body wall index (WI) of parasitized and non-parasitized individuals were found. Parasitized females exhibited lower values than non-parasitized individuals (Fig. 8), regardless of the reproductive condition (t-test, p = 0.04 and p = 0.04, for



Fig. 5. Gonadal indexes (GI) expressed in percentages from females in different reproductive condition (brooding and non-brooding) and males of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel), compared by parasitized and non-parasitized. Significant differences between parasitized and non-parasitized are indicated with an asterisk. The horizontal line in the middle of the boxes represents the median and the edges of the boxes the first and third quartiles. Outliers are shown as points, and a white square indicates the mean.



**Fig. 6.** Pyloric caeca indexes (PCI) expressed in percentages from females in different reproductive conditions (brooding and non-brooding) and males of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel), compared by parasitized and non-parasitized. Significant differences between parasitized and non-parasitized are indicated with an asterisk. The horizontal line in the middle of the boxes represents the median and the edges of the boxes the first and third quartiles. Outliers are shown as points, and a white square indicates the mean.



**Fig. 7.** Stomach indexes (SI) expressed in percentages from females in different reproductive conditions (brooding and non-brooding) and males of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel), compared by parasitized and non-parasitized. Significant differences between parasitized and non-parasitized are indicated with an asterisk. The horizontal line in the middle of the boxes represents the median and the edges of the boxes the first and third quartiles. Outliers are shown as points, and a white square indicates the mean.



**Fig. 8.** Body wall indexes (WI) expressed in percentages from females in different reproductive conditions (brooding and non-brooding) and males of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel), compared by parasitized and non-parasitized. Significant differences between parasitized and non-parasitized are indicated with an asterisk. The horizontal line in the middle of the boxes represents the median and the edges of the boxes the first and third quartiles. Outliers are shown as points, and a white square indicates the mean.



**Fig. 9.** Parasite load index (PI) expressed in percentages from individuals of *Anasterias antarctica* from the rocky intertidal of Ensenada Zaratiegui bay (Beagle Channel), compared by season. Different letters denote significant differences, the horizontal line in the middle of the boxes represents the median and the edges of the boxes the first and third quartiles. Outliers are shown as points, and a white square indicates the mean.

brooding and non-brooding females, respectively). Also, males presented significant differences between parasitized and non-parasitized individuals (t-test, p < 0.01), showing the lower values of WI, those that were parasitized.

**Parasite load index:** There were significant differences among the parasite load index (PI) of individuals from different season (Kruskal-Wallis, p < 0.01, Fig. 9). The PI values in summer were lower than autumn (Dunn-test, p < 0.01), spring (Dunn-test, p < 0.01), and winter (Dunn-test, p = 0.04).

# DISCUSSION

This study gathers information on the physiologic constraints of the brooding sea-star *Anasterias antarctica*, when it is parasitized by *Dendrogaster argentinensis* (Fig. 2). This sea-star plays an essential role as a top predator of

the intertidal and subtidal zone in the coasts of the Beagle Channel.

The overall prevalence of D. argentinesis was 20.4 %, twice the percentage reported in 2009 by Pérez et al. (2015) in the same region. While the objective of the study was not to conduct an interannual comparison, this increase in prevalence after almost ten years could be due to a gradual rise in the average annual temperature or a high eventual contagion rate favoring D. argentinensis infection. However, further studies in this line should be conducted. By definition, any parasite will harm its host to a certain degree, from minor metabolic changes to severe tissue damage (Mouritsen & Poulin, 2002). Regarding the population prevalence by intertidal zone (upper and low intertidal), it is evident, in all seasons, that parasitized individuals are more frequent to find in the low intertidal (Fig. 3). Furthermore, the difference between zones becomes more evident

10

in summer when it is likely that the higher temperatures and strong winds (Iturraspe et al., 1989) could make the upper intertidal more challenging for a parasitized individual to survive. Whether this is caused by the parasitized individuals moving towards a more comfortable environment or a higher mortality of parasitized individuals from the upper intertidal remains unknown. Under usual environmental conditions, the infection may not be mortal, but when conditions approach the host adaptation limits, a reduced survival may be expected, particularly in intertidal species that inhabit the edge of their thermal, osmotic and oxygen conditions (Mouritsen & Poulin, 2002). For instance, several species of intertidal or estuarine gastropods show decreased resistance to extreme conditions when infected by trematodes (Lauckner, 1987; McDaniel, 1969). In long-term field experiments the higher mortality among infected snails was observed in winter and summer, when the abiotic factors also reach their extremes (Huxham et al., 1993; Mouritsen & Poulin, 2002). Compromised survival of infected individuals is not restricted to gastropods. This was also reported in bivalves, such as Mytilus edulis, that acts either as first or second intermediate host of trematodes, and experience reduced condition, byssus thread production, and may be easier to open by predators (Calvo-Ugarteburu & McQuaid, 1998; Zwarts, 1991). A third plausible hypothesis could be that the dispersal or survival of the parasite is lower in the upper intertidal, but more biological studies of the species are needed to confirm this.

When analyzing the prevalence by sex in each season, the parasite only shows a preference for male individuals in winter (Fig. 4). The difference in prevalence between males and females in this season could be either because females are committed to brooding in winter, or a higher mortality of brooding females during this season. The first hypotheses lays on the fact that during brooding females carry their offspring on the oral area and do not feed (Gil et al., 2011); they may be less active and thus, less exposed to *D. argentinensis* infection. Males may also be more susceptible to infection since they are more active during this period because they dynamically search for food and refuge. The second hypothesis of the higher mortality of brooding females in winter is founded upon the idea that in this season they have already faced half of the brooding period. Also, the cost of the incubation effort must be added to the extreme winter conditions that may hinder the survival of the females. In addition, the parasitic load in winter remains high (Fig. 9). Salvat (1985) reported five parasitized individuals, two were females, two males and one had no gonads. In this work, although the number of castrated individuals was low, they were all parasitized (present only in spring and summer). This is an important observation since this parasite is known to castrate their host (Hamel & Mercier, 1994; Jangoux, 1987; Tyler & Pain, 1982). The presence of castrated individuals with endoparasite in the celomic cavity was also noticed by Pérez et al. (2015). According to Brattström (1947), castration results from competition for resources between gonads and the ascothoracid parasites, Ulophysema oeresundense, in Spatangoids (heart sea urchins). This competition leading to castration was also noted by Wagin (1976) in Ophiocten sericeum (Ophiuroid host) infested by Ascothorax ophioctenis.

Several works on parasitism of different ascothoracid parasites mention adverse effects on reproduction and fecundity in sea-stars (Grygier, 1985; Grygier, 1986; Grygier & Salvat, 1984; Hamel & Mercier, 1994; Jangoux, 1987; Tyler & Pain, 1982). D. argentinensis negatively affects the reproduction in A. antarctica. Concerning the gonadal indexes (GI, Fig. 5), parasitized females showed lower GI than non-parasitized individuals, regardless of the reproductive condition (brooding and nonbrooding). In the case of non-brooding females, this will result in the reduction of fecundity, given either by fewer oocytes and then fewer embryos of equal quality to those not parasitized females or same number of oocytes of lower quality than the non- parasitized females that could led to decreased survival. Reproduction it is metabolically more expensive for

females of *A. antarctica* (Fraysse et al., 2021; Pérez et al., 2017) than males, therefore, being parasitized will help increase that cost resulting in reduced gonadal index and fecundity. In contrast, males do not go through starvation periods, and their reproductive expenses are also lower than females, so the costs of parasitism may not be reflected in the gonadal index. Gonad's atrophy was observed in *Hippasteria phrygiana* individuals compared with other unparasitized sea-stars (Hamel & Mercier, 1994). This gonad decrease was explained as being probably induced by interference with nutrient translocation to the gonads (Hamel & Mercier, 1994).

Regarding the somatic indexes, the pyloric caeca (PCI, Fig.6), the stomach (SI, Fig. 7), and body wall (WI, Fig. 8) indexes of parasitized individuals were significantly lower than nonparasitized from each sex, except in brooding parasitized females, where the PCI showed the same pattern, but without significant difference. Thus, evidence is presented on how the parasite restricts the feeding ability, the nutrients storage, and the growth, which led to a decrease of the overall condition. In Ría de Puerto Deseado (Santa Cruz, Argentina) an infected individual of A. antarctica presented atrophied pyloric caeca which was explained by the lack of available space in the celomic cavity (Grygier & Salvat, 1984; Salvat, 1985). In heavy infestation of Ophionotus victoriae by Ascothorax gigas, the stomach volume was observed to be reduced. but there was no demonstrable reduction in the volume of stomach contents (Grygier & Fratt, 1986). The reduction of the stomach volume, also noted in this study, can be related to the endoparasite feeding on the celomic fluids of the host as Brattström (1947) determined for Ulophysema oeresundense parasite and its echinoid host. Wagin (1976) proposed that the main diet of Dendrogaster sp could be encapsulating coelomocytes. This same competition from nutrients between the host and the endoparasite could lead to a decrease in the body wall index since it could be affecting growth in A. antarctica. Contrary, the parasites found in Hippasteria phrygiana did not seem to affect the

host's pyloric caeca nor the body wall (Hamel & Mercier, 1994). The decreased parasite load index in summer (Fig. 9) could be because the endoparasite females mature throughout the year and, in summer, release the cypris larvae. Consequently, on one hand, this will place new hosts and begin their maturation, and on the other hand will leave the mature female spawned, thus exhibiting lower parasite load indexes in the host. Nevertheless, D. argentinensis reproduction cycle is not yet described (Boxshall et al., 2005). This work suggests that the ascothoracid parasite D. argentinensis would affect the physiological condition and reproduction of A. Antarctica from the Beagle Channel. We provide evidence of how the endoparasite adversely affects its host and its overall condition. It affects reproduction by decreasing fecundity and fitness, it enhances the reduction of the feeding capacity, nutrient storage, and growth by consuming and competing for the host resources (nutrients), and it is also probably related to the castration of individuals. Nevertheless, it is important to note that the biology of D. argentinensis and its interaction with A. antarctica can be influenced by various environmental and biological factors, and more studies are needed to fully understand the dynamics of this parasite-host relationship.

**Ethical statement:** the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

#### ACKNOWLEDGMENTS

We are grateful to Sonia Rimbau and Daniel Aureliano, technicians of Laboratorio de Ecología, Fisiología y Evolución de Organismos Acuáticos (CADIC-CONICET), Ing. Maximiliano Rubel, and Dr. Pablo Di Salvatore for their technical assistance during the samplings. We

also thank Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Felipe Fiorellino Foundation.

#### REFERENCES

- Adami, M. L., & Gordillo, S. (1999). Structure and dynamics of the biota associated with *Macrocystis pyrifera* (Phaeophyta) from the Beagle Channel, Tierra del Fuego. *Scientia Marina*, 63(S1), 183–191. https://doi. org/10.3989/scimar.1999.63s1183
- Balestrini, C., Manzella G., & Lovrich, G. (1998). Simulación de corrientes en el Canal Beagle y Bahía Ushuaia, mediante un modelo bidimensional. Servicio de Hidrografía Naval, 98, 1–58.
- Bernasconi, I. (1964). Distribución geográfica de los Equinoideos y Asteroideos de la extremidad austral de Sudamérica [Technical inform]. Boletín del Instituto de Biología Marina.
- Bowman, T. E., Abele, L. G., & Bliss, D. E. (1982). Classification of the recent Crustacea. In D. E. Bless (Ed.), *The Biology of Crustacea* (pp. 1–27). Academic Press.
- Boxshall, G., Lester, R., Grygier, M. J., Hoeg, J. T., Glenner, H., Shields, J. D., & Lützen, J. (2005). Crustacean parasites. In K. Rohde (Ed.), *Marine Parasitology* (pp. 123–169). CSIRO Publishing.
- Brattström, H. (1947). On the ecology of the Ascothoracid Ulophysema öresundense. In H. Brattström (Ed.), Studies on Ulophysema Öresundsense (pp. 1–75). Undersökningar över Öresund XXXII.
- Calvo-Ugarteburu, G., & McQuaid, C. (1998). Parasitism and invasive species: effects of digenetic trematodes on mussels. *Marine Ecology Progress Series*, 169, 149–163. https://doi.org/10.3354/meps169149
- Curelovich, J. N. (2012). Mecanismos reguladores de la estructura y dinámica de la comunidad intermareal rocosa de Ensenada Zaratiegui, Tierra del Fuego [Unpublished doctoral dissertation]. Universidad de Buenos Aires.
- Davenport, J. & Davenport, J. L. (2005). Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series*, 292, 41–50. https://doi.org/10.3354/ meps292041
- Dunne, J. A., Lafferty, K. D., Dobson, A. P., Hechinger, R. F., Kuris, A. M., Martinez, N. D., McLaughlin, J. P., Mouritsen, K. N., Poulin, R., Reise, K., Stouffer, D. B., Thieltges, D. W., Williams, R. J., & Zander, C. D. (2013). Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology*, 11, e1001579. https://doi.org/10.1371/journal.pbio.1001579

- 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, 178. https://doi. org/10.1007/s00227-021-03987-9
- Gil, D. G., Escudero, G., & Zaixso, H. E. (2011). Brooding and development of Anasterias minuta (Asteroidea: Forcipulata) in Patagonia, Argentina. Marine Biology, 158, 2589–2602. https://doi.org/10.1007/ s00227-011-1760-1
- Gil, D. G., & Zaixso, H. E. (2008). Feeding ecology of the subantarctic sea star Anasterias minuta within tide pools in Patagonia, Argentina. Revista de Biología Tropical, 56(S3), 311–328.
- Grygier, M. J. (1985). Two species of *Dendrogaster* (Crustacea: Ascothoracida) parasitic in porcellanasterid starfishes. *Galathea*, 16, 113–120.
- Grygier, M. J. (1986). Dendrogaster (Crustacea: Ascothoracida) parasitic in Alaskan and eastern Canadian Leptasterias (Asteroidea). Canadian Journal of Zoology, 64, 1249–1253. https://doi.org/10.1139/z86-186
- Grygier, M. J., & Fratt, D. B. (1986). The ascothoracid crustacean Ascothorax gigas: redescription, larval development, and notes on its infestation of the Antarctic ophiuroid Ophionotus victoriae. In L. S. Kornicker (Ed.), Biology of the Antarctic Seas XVI (pp. 43–58). Wiley. https://doi.org/10.1002/9781118666579.ch2
- Grygier, M. J., & Høeg, J. T. (2005). Ascothoracida (ascothoracids). In R. Klaus (Ed.), *Marine Parasitology* (pp. 149–154). CSIRO Publishing and CABI Publishing.
- Grygier, M. J., & Salvat, M. B. (1984). Dendrogaster argentinensis, new species, a South American sea-star parasite (Crustacea: Ascothoracida). Proceedings of the Biological Society of Washington, 97(1), 43–48.
- Hamel, J. F., & Mercier, A. (1994). New distribution and host record for the starfish parasite *Dendrogaster* (Crustacea: Ascothoracida). *Journal of the Marine Biological Association of the United Kingdom*, 74, 419–425.
- Helmuth, B. S. T., & Hofmann, G. E. (2001). Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *The Biological Bulletin*, 201, 374–384.
- Huxham, M., Raffaelli D., & Pike, A. (1993). The influence of Cryptocotyle lingua (Digenea: Platyhelminthes) infections on the survival and fecundity of Littorina littorea (Gastropoda:Prosobranchia); an ecological approach. Journal of Experimental Marine Biology and Ecology, 168, 223–238. https://doi. org/10.1016/0022-0981(93)90262-M
- Iturraspe, R., Sottini, R., Schroeder, C., & Escobar, J. (1989). Hidrología y variables climáticas del Territorio de Tierra del Fuego [Technical inform]. Información

básica. Consejo Nacional de Investigaciones Científicas y Técnicas & Centro Austral de Investigaciones Científicas.

- Jangoux, M. (1987). Diseases of Echinodermata. 111. Agents metazoans (Annelida to Pisces). Diseases of Aquatic Organisms, 3, 59–83.
- Kassambara, A. (2023). \_rstatix: Pipe-Friendly Framework for Basic Statistical Tests\_. R package version 0.7.2. https://CRAN.R-project.org/package=rstatix.
- Lafferty, K. D., Dobson, A. P., & Kuris, A. M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences*, 103(3), 11211–11216. https://doi.org/10.1073/pnas.0604755103
- Lauckner, G. (1987). Ecological effects of larval trematode infestation on littoral marine invertebrate populations. *International Journal for Parasitology*, 17, 391– 398. https://doi.org/10.1016/0020-7519(87)90114-7
- Lawrence, J. M., & Herrera, J. (2000). Stress and deviant reproduction in Echinoderms. Zoological Studies, 39(3), 151–171.
- Mah, C. L. (2023). World Asteroidea Database. Anasterias antarctica (Lütken, 1857). World Register of Marine Species. https://www.marinespecies.org/aphia. php?p=taxdetails&id=378829 on 2021-09-16
- McDaniel, S. J. (1969). Littorina littorea: Lowered heat tolerance due to Cryptocotyle lingua. Experimental Parasitology, 25, 13–15.
- Mouritsen, K. N., & Poulin, R. (2002). Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology*, 124, 101–117. https://doi. org/10.1017/S0031182002001476
- O'Neill, P. L. (1994). The effect of anaesthesia on spontaneous contraction of the body wall musculature in the asteroid *Coscinasterias calamaria*. *Marine Behaviour and Physiology*, 24, 137–150. https://doi. org/10.1080/10236249409378887
- Pérez, A. F., Boy, C. C., Calcagno, J., & 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. https://doi.org/10.1016/j. jembe.2014.11.009
- Pérez, A. F., Fraysse, C., Boy, C. C., Epherra, L. & Javier, C. (2017). Reproductive biology and energetics of the brooding sea star *Anasterias antarctica* (Echinodermata: Asteroidea) in the Beagle Channel, Tierra del Fuego, Argentina. *Revista de Biología Tropical*, 65(S1), 221–232.

- Pérez, A. F., Morriconi, E., Boy, C., & Calvo, J. (2008). Seasonal changes in energy allocation to somatic and reproductive body components of the common cold temperature sea urchin *Loxechinus albus* in a Sub-Antarctic environment. *Polar Biology*, 31, 443–449. https://doi.org/10.1007/s00300-007-0370-3
- Poulin, R., & Hamilton. W. J. (1997). Ecological correlates of body size and egg size in parasitic Ascothoracida and Rhizocephala (Crustacea). Acta Oecologica, 18, 621– 635. https://doi.org/10.1016/S1146-609X(97)80047-1
- Romanelli-Michel, M. V. (2014). Revisión taxonómica de las estrellas de mar de la familia Asteriidae Gray, 1840 (Asteroidea: Forcipulatida) del Atlántico Sudoccidental [Doctoral dissertation, Universidad de Buenos Aires]. Biblioteca Central. UBAEXACTAS. https://bibliotecadigital.exactas.uba.ar/download/tesis/tesis\_n5672\_ RomanelliMichel.pdf
- Saito, N., Wakabayashi, K., & Moritaki, T. (2020). Three new species of *Dendrogaster* (Crustacea: Ascothoracida) infecting goniasterid sea-stars (Echinodermata: Asteroidea) from Japan. *Species Diversity*, 25, 75–87. https://doi.org/10.12782/specdiv.25.75
- Salvat, M. B. (1985). Biología de la reproducción de Anasterias minuta Perrier (Echinodermata, Asteroidea): Especie incubadora de las costas patagónicas [Doctoral dissertation, Universidad de Buenos Aires]. Biblioteca Central. UBAEXACTAS. https://bibliotecadigital. exactas.uba.ar/download/tesis/tesis\_n1900\_Salvat. pdf
- Sokal, R. R., & Rohlf, J. (1995). *Biometry*. Freeman and Company.
- Tyler, P. A., & Pain., S. L. (1982). The reproductive biology of *Plutonaster bifrons*, *Dytaster insigns* and *Psilaster* andromeda (Asteroidea: Astropectinidae) from the Rockall Trough. Journal of the Marine Biological Association of the United Kingdom, 62, 869–887. https:// doi.org/10.1017/S0025315400070405

Wagin, V. L. (1976). Ascothoracida. Kazan University Press.

- Webber, W. R., Fenwick, G. D., Eagar, S. H., Buckeridge, J. S., Poore, G. C. B., Dawson, E. W., Watling, L., Brian, J., Wells, J. B. J., Bruce, N. L., Ahyong, S. T., Larsen, K., Chapman, M.A., Olesen, J., Green, J. D., Shiel, R. J., Rocha, C. E. F., Lörz, A.N., Bird, G.J., & Charleston., W. A. (2010). Phylum Arthropoda. Subphylum Crustacea. In D. P. Gordon (Ed.), *New Zealand Inventory of Biodiversity* (pp. 98–232). Canterbury University Press.
- Zwarts, L. (1991). Seasonal variation in body weight of the bivalves Macoma balthica, Scrobicularia plana, Mya arenaria and Cerastoderman edule in the Dutch Wadden sea. Netherlands Journal of Sea Research, 28, 231–245.