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Ecological role of the sea urchin *Austrocidaris canaliculata* (Cidaroida: Cidaridae) as a basibiont: Epibiont assemblages in the Marine Protected Area Namuncurá – Burdwood Bank and adjacent deep areas

Jonathan N. FLORES[1, *], Nicolás FLAIBANI[3, 4], M. Gabriela PALOMO[2] & Martín I. BROGGER[1]

[1] Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos, Instituto de Biología de Organismos Marinos, CCT CONICET-CENPAT, Bvd. Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina. [2] Laboratorio de Ecosistemas Marinos, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET, Av. Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina. [3] Grupo Bioestadística Aplicada, Departamento de Ecología, Genética y Evolución, Instituto de Cálculo, Universidad de Buenos Aires, Intendente Güiraldes 2160, C1428EGA, Ciudad Autónoma de Buenos Aires, Argentina. [4] Instituto de Ecología, Genética y Evolución de Buenos Aires, Universidad de Buenos Aires, CONICET, Intendente Güiraldes 2160, C1428EGA, Ciudad Autónoma de Buenos Aires, Argentina.
* Corresponding author: jflores@cenpat-conicet.gob.ar, flores.jonathan@gmail.com

Abstract: Organisms that provide settlement sites for sessile fauna play a key role in shaping the structure of benthic communities. Sea urchins of the order Cidaroida can offer these sites for settlement on their primary spines, which lack antifouling protection. In this study, the ecological role of *Austrocidaris canaliculata* (Cidaroida: Cidaridae) as a basibiont at the MPA Namuncurá – Burdwood Bank (MPA NBB) and adjacent deep-sea areas was evaluated. For this, we described the composition and the diversity of the epibiont assemblages within the MPA NBB and external deep-sea sites. Additionally, we analyzed the relationship between the size of *A. canaliculata* and the epibionts richness in these zones using generalized additive models. From the 120 specimens of *A. canaliculata* studied, epibiosis was recorded in 96.67%. A total of 39 epibiont taxa were identified, representing two kingdoms, 10 phyla, 13 classes, and 27 families, including new records of species in the study area. The highest epibiont species diversity observed was Bryozoa, followed by Cnidaria. The epibiont assemblages showed no significant differences in the estimated diversity within each zone, and the estimated epibiont richness was slightly higher in deep-sea areas. Finally, our modelling suggests that the epibiont richness is correlated with the horizontal diameter of the test, showing an opposite variation between shallow and deep-sea zones. This study provides detailed faunistic information on the epibionts associated with *A. canaliculata* from the MPA NBB and adjacent deep-sea areas, reinforcing the ecological role of cidaroids as basibionts in benthic ecosystems.

Key words: Echinoderms, symbiosis, epibiota, benthos, Argentine continental shelf, generalized additive models (GAM)

Resumen: Rol ecológico del erizo de mar *Austrocidaris canaliculata* (Cidaroida: Cidaridae) como basibionte: Ensamblejes de epibiontes en el Área Marina Protegida Namuncurá – Banco Burdwood y áreas profundas aledañas. Los organismos que proporcionan sitios de asentamiento para la fauna sésil desempeñan un papel clave en la conformación de la estructura de las comunidades bentónicas. Los erizos de mar del orden Cidaroida pueden ofrecer estos sitios de asentamiento en sus espinas primarias, ya que carecen de protección anti incrustante. En este estudio, se evaluó el rol ecológico de *Austrocidaris canaliculata* (Cidaroida: Cidaridae) como basibionte en el AMP Namuncurá – Banco Burdwood (AMP NBB) y en áreas profundas adyacentes. Para ello, se describió la composición y la diversidad de los ensamblajes de epibiontes dentro del AMP NBB y sitios profundos externos. Además, se analizó la relación entre el tamaño de *A. canaliculata* y la riqueza de epibiontes en estas zonas utilizando modelos aditivos generalizados. De los 120 ejemplares estudiados de *A. canaliculata*, se registró epibiosis en el 96,67%. Se identificaron un total de 39 taxones de epibiontes, representando dos reinos, 10 phyla, 13 clases y 27 familias, incluyendo nuevos registros de especies en el área de estudio. La mayor diversidad de epibiontes observada correspondió a Bryozoa, seguida por Cnidaria. Los ensamblajes de epibiontes no mostraron diferencias significativas en la diversidad estimada dentro de cada zona, y la riqueza estimada de epibiontes fue ligeramente mayor en áreas profundas. Finalmente, nuestros modelos sugieren que la riqueza de epibiontes está correlacionada con el diámetro horizontal de la testa, mostrando una variación opuesta entre las zonas poco profundas y las profundas. Este estudio proporciona información faunística detallada sobre los epibiontes asociados a *A. canaliculata* en el AMP NBB y áreas profundas aledañas, reforzando el rol ecológico de los cidaroideos como basibiontes en los ecosistemas bentónicos.

Palabras clave: Equinodermos, simbiosis, epibiota, bentos, plataforma continental Argentina, modelos aditivos generalizados (GAM)

INTRODUCTION

Interactions between organisms play a crucial role in shaping community structure by influencing species abundance and distribution. While competition and predation have historically been central topics of interest for ecologists studying these interactions, symbiosis represents another important interaction type. Symbiosis is a widespread phenomenon that can significantly regulate the presence, abundance, and identity of species within a community (Hatcher *et al.*, 2006; Hétérier *et al.*, 2008). In marine environments, many phyla exhibit a sessile lifestyle at least one ontogenetic stage. These organisms depend on hard substrates for survival, making their limited availability a critical resource. The competition for a hard substrate for settlement may have been a driving force in the evolution of epibiosis, a lifestyle commonly observed in marine benthic environments. Epibiosis refers to a spatially close association in which one living organism (epibiont) lives on the external surface of another living organism (basibiont), either of the same or a different species, regardless of the nature of this relationship (Harder, 2009; Wahl, 2009). In environments where hard substrates are scarce, competition for these surfaces becomes a major factor influencing the distribution and diversity of sessile and low-motile fauna. This phenomenon has been well-documented in Antarctica, where epibiosis plays a critical role in structuring benthic communities, by reducing competition for the limited availability of hard substrates (Gutt & Schickan,1998; Hardy *et al.*, 2011; Hétérier *et al.*, 2008).

The ecological role of sea urchins in structuring marine communities has been widely recognized as ecosystem engineers, agents of biological disturbance, and drivers of the ecosystem structure and functions across a variety of ecosystems (Steneck, 2020). Sea urchins of the order Cidaroida can offer sites for sessile and low-motile organisms to settle, as their primary spines lack epithelial covering (Märkel & Röser, 1983). This characteristic turns the primary spines of cidaroids into bare calcium carbonate rods devoid of any antifouling protection, and the microstructure of their shafts facilitates epibiont settlement (David *et al.*, 2009). Epibiosis has been reported in various cidaroid species across different oceanic regions, revealing a wide diversity of associated epibionts (Brey *et al.*, 1993; Cerrano *et al.*, 2009; Gutt & Schickan,1998; Hardy *et al.*, 2011; Hétérier *et al.*, 2008; Linse *et al.*, 2008). Notably, some of these epibionts have been identified as new species (Aguirre *et al.*, 2011; Massin & Hétérier, 2004).

Epibiosis in cidaroids suggests that these sea urchins could play a crucial role in benthic communities by enhancing the availability of hard substrate for settlement. Several studies have highlighted the role of cidaroids as basibionts and the significant contribution of epibiosis to Antarctic benthic communities associated with them (Hardy *et al.*, 2011; Hétérier *et al.*, 2008; Linse *et al.*, 2008). For instance, Linse *et al.* (2008) pointed out that while sea urchins and their epibionts may represent minor components of the deep benthic biomass, they significantly contribute to the biodiversity of the Southern Ocean biodiversity. Hétérier *et al.* (2008) compared the epibiont assemblages on cidaroids and rocks from deep waters of the Weddell Sea. They observed that whereas rocks are often colonized by more generalist species, cidaroids tend to be colonized by relatively specialist sessile species. In addition, the presence of cidaroids generally promotes greater local species richness, allowing some of the sessile species already present to become dominant by increasing their abundance, as cidaroids provide more favorable niches compared to rocks. Similarly, Hardy *et al.* (2011) compared the epibiont assemblages present on cidaroids and rocks at three different localities in the Weddell Sea. They demonstrated that epibiosis on cidaroids reflects species-specific relationships, while rock-associated epibionts are primarily influenced by local environmental factors. Additionally, they further proposed that cidaroid ectosymbioses significantly contribute to benthic colonization in Larsen embayments. Together, these studies highlight the key ecological role of cidaroids in shaping benthic biodiversity and ecosystem complexity.

Cidaroids are recognized as Indicator Taxa (ITs) of Vulnerable Marine Ecosystems (VMEs), alongside other macro-invertebrates such as several species of corals, sponges, ascidiaceans, and crinoids (CCAMLR, 2023; FAO, 2009). The Food and Agriculture Organization (FAO) has outlined the functional roles of ITs, emphasizing their significant contributions to creating complex three-dimensional structures, enhancing surface complexity through high-density clustering, modifying substrate structure, providing a substrate for other organisms, and representing rare or unique organisms (CCAMLR, 2023; FAO, 2009; Jones & Lockhart, 2011).

Austrocidaris canaliculata (A. Agassiz, 1863) (Cidaroida: Cidaridae) is the most widely distributed cidaroid species in the Magellanic Province. In the Southwestern Atlantic Ocean, it is reported from southern Brazil to the southern tip of Argentina (32-55° S) at depths up to 1,400 m (Flores *et al.*, 2019). This species is also found in the Straits of Magellan at 53-54° S between 104-214 m (Larraín *et al.*, 1999), around Isla de los Estados, the Malvinas (Falkland) Islands, and the Burdwood Bank (Flores *et al.*, 2019). Although the epibiosis in *A. canaliculata* has been previously documented in the literature (Bernasconi, 1953; Doti *et al.*, 2008; Romero *et al.*, 2017), the ecological role of this species in benthic communities remains poorly understood.

The Burdwood Bank (BB), part of the westernmost section of the North Scotia Ridge, is a submarine plateau situated between 54-55° S and 56-62° W in the Southwestern Atlantic Ocean. It lies approximately 135 km east of Isla de los Estados and 160 km south of the Malvinas (Falkland) Islands (COPLA, 2017). The plateau has an elongated W-E orientation, covering an area of 25,000 km^2 circumscribed by the 200 m isobaths, with minimum depths of around 75 m (COPLA, 2017). To the north, it is separated from the Argentine continental shelf by the Malvinas (Falkland) Trough, reaching depths of up to 500 m, while its southern side descends steeply to depths of 3,000 m. The BB was designated as Argentina's first offshore Marine Protected Area (MPA) in 2013, aiming to protect benthic invertebrates that are long-lived, slow-growing, sessile, and function as ecosystem engineers, such as sponges, ascidians, bryozoans, corals, among others ITs (CCAMLR, 2023; Schejter *et al.*, 2016; Tombesi *et al.*, 2020). In 2018, the MPA was expanded to include the adjacent southern slope, extending protection to depths of 4,000 m, and was renamed the Marine Protected Area Namuncurá – Burdwood Bank (hereafter MPA NBB). This extension was the result of many scientific research and expeditions that identified the slope as a critical area for marine biodiversity and key oceanographic and ecological processes (Tombesi *et al.*, 2020). Notably, the benthic communities on the slope host diverse associated fauna, with some deep-sea environments exhibiting characteristics of VMEs (Schejter *et al.*, 2018, 2020a).

This study aimed to evaluate the ecological role of *Austrocidaris canaliculata* as a basibiont at the Marine Protected Area Namuncurá – Burdwood Bank and its adjacent deep-sea regions. To achieve this, we described the composition and the diversity of the epibiont assemblages located on the primary spines of *A. canaliculata* across these sites. Additionally, we analyzed the relationship between the size of sea urchins and the richness of the epibionts associated with this species.

MATERIALS AND METHODS

The study area includes the MPA NBB and surrounding deep-sea areas in the Southwestern Atlantic Ocean. The specimens of *A. canaliculata* were collected during three scientific expeditions conducted by the RV *Puerto Deseado*: 1) *AMP Namuncurá – Banco Burdwood: Bentos* (2016), 2) *Banco Burdwood - Buque Oceanográfico ARA "Puerto Deseado" - PD BB Abr 17* (2017), and 3) *AMP Namuncurá – Banco Burdwood: Ingenieros Ecosistémicos* (2018) (Table 1). Data from 19 stations where *A. canaliculata* was collected were used, selected from all stations sampled during the three expeditions. Samples were collected using a bottom trawl net (6 m in total length, 50 mm mesh size, and 10 mm mesh size in the cod end), and the specimens of *A. canaliculata* were fixed and conserved in 96% ethanol.

Since trawling may lead to damage in different ways to the collected specimens (i.e., parts of the test or primary spines partially broken or absent), only those specimens with more than 90% of their primary spines intact were considered for this study, to minimize the potential impact of the capture method on the incidence of epibiosis. Additionally, only specimens of *A. canaliculata* with a horizontal test diameter greater than 5 mm were included, as individuals above this size are considered to have reached the free juvenile developmental stage (Flores *et al.*, 2019). From the eligible specimens, a random sub-sample of 120 *A. canaliculata* was analyzed, including 113 specimens from 17 stations within the MPA NBB and 7 specimens from 2 stations at external deep-sea sites (Fig. 1).

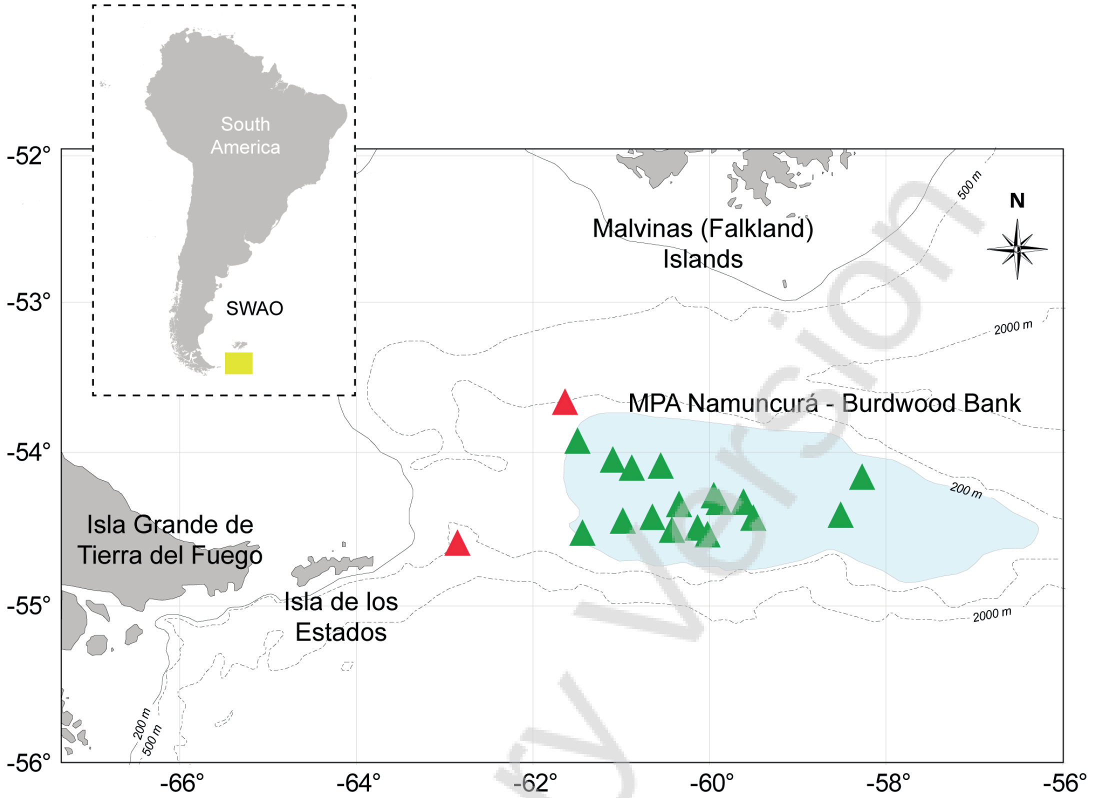

Fig. 1. Map of the study area showing the sampling stations. Green triangles represent internal sites, while red triangles indicate external deep-sea sites surrounding the MPA Namuncurá – Burdwood Bank. The plateau of the MPA NBB is highlighted in light blue. The inset (dashed box) displays a map of South America with the study area marked (yellow box) in the Southwestern Atlantic Ocean (SWAO).

In the laboratory, the horizontal and vertical diameters of the test at the ambitus (VD and HD, respectively) of each specimen of *A. canaliculata* were measured using a digital caliper with ± 0.01 mm accuracy. Each primary spine of every specimen of *A. canaliculata* was thoroughly examined for epibionts, and individuals with at least one organism on at least one primary spine were considered colonized. The specific identification of epibionts was done under a stereoscopic microscope (Leica MZ95) or an optical microscope (Zeiss Axio Imager Z1), as appropriate. Epibionts were determined at the lowest taxonomic level possible, using the following bibliography for each taxon: Brachiopoda (Cooper, 1973; Gordillo *et al.*, 2019), Bryozoa (Hayward, 1992; Liuzzi *et al.*, 2018; López-Gappa & Lichtschein, 1990; López Gappa, 1975), Isopoda (Doti *et al.*, 2008), Folliculinidae (Andrews, 1941; Fauré-Fremiet, 1936; Ringuelet, 1953), Hydrozoa (Blanco, 1967; Marques *et al.*, 2011; Peña Cantero, 2008; Schejter *et al.*, 2020b; Soto Àngel & Peña Cantero, 2019), Polychaeta (Vine, 1977), and Porifera (Boury-Esnault & Rützler, 1977; Hooper & van Soest, 2002). In addition, some epibiont organisms were sent to specialists for verification of identification (see Acknowledgements). Complete specimens of *A. canaliculata* were photographed using a Nikon D800 camera with a Micro-Nikkor 60 mm f/2.8 lens. Images of the epibionts were taken with a Leica IC80 HD camera coupled to a Leica MZ95 and with a Zeiss SteREO Discovery. V20 stereoscopic microscope. All images were digitally processed.

For each specimen of *A. canaliculata*, the presence or absence of each observed epibiont species was recorded to form a species-by-sample incidence matrix, where “1” indicates presence and “0” indicates absence. The specimens of *A. canaliculata* were categorized into two zones based on whether the sampling stations were located, within the MPA NBB or outside, in the seep-sea sites, defined as “Internal” (17 sampling stations, 113 specimens) and “External” (2 sampling stations, 7 specimens) (Table 1 and Fig. 1). For the statistical analyses, each specimen of *A. canaliculata* was treated as a replicate, as suggested by Shaw and Dobson (1995) for the host-parasite relationship, and also by Hétérier *et al.* (2008). Due to the difference in sampling effort between zones, analyses of observed and expected diversity and richness were performed separately within each zone. The analysis of the epibiont assemblages was performed using a diversity profile estimator as suggested by Chao and Jost (2015) for incidence data, and richness was estimated by the Chao2 index (Chao, 1987; Chao & Chiu, 2016). All analyses were performed using the online version of the software SpadeR (Chao *et al.*, 2015) available via the link: https://chao.shinyapps.io/SpadeR, with a bootstrap of 1,000 replications for the estimation of its associated standard error, following recommendations from the software user guide for the choice of indices (Chao *et al.*, 2016).

Additionally, a linear regression analysis was conducted to assess co-variability between the HD and the VD. The variation in the observed species richness of the epibiont assemblages was evaluated according to the HD, Zone (Internal, within the MPA NBB, and External, deep-sea sites), and their interaction (HD*Zone), controlling for Year (years of the expeditions: 2016, 2017, and 2018), with all these factors being considered as fixed. The analysis was carried out using generalized additive models (GAM). For the richness model, a negative binomial distribution was assumed to account for the over-dispersion observed when implementing the model with a Poisson distribution. We performed a model without this interaction to evaluate the significance of the interaction between Zone and HD. We considered a difference greater than 4 units of AIC (ΔAIC > 4) between the models as having significance since these would not have similar statistical support (Burnham & Anderson, 2002). GAMs were conducted using the *mgcv* package (Wood & Wood, 2015) and their performance was evaluated using the Dharma package (Hartig, 2022). All analyses were performed in R software (R Development Core Team, 2017).

RESULTS

The size of the specimens of *A. canaliculata* analyzed ranged from 5.42 to 48.30 mm in horizontal diameter of the test (HD) (N = 120, mean ± SD = 19.78 ± 8.83 mm), and from 2.71 to 28.16 mm in vertical diameter of the test (VD) (N = 120, mean ± SD = 10.45 ± 5.49 mm) (Fig. 2A).

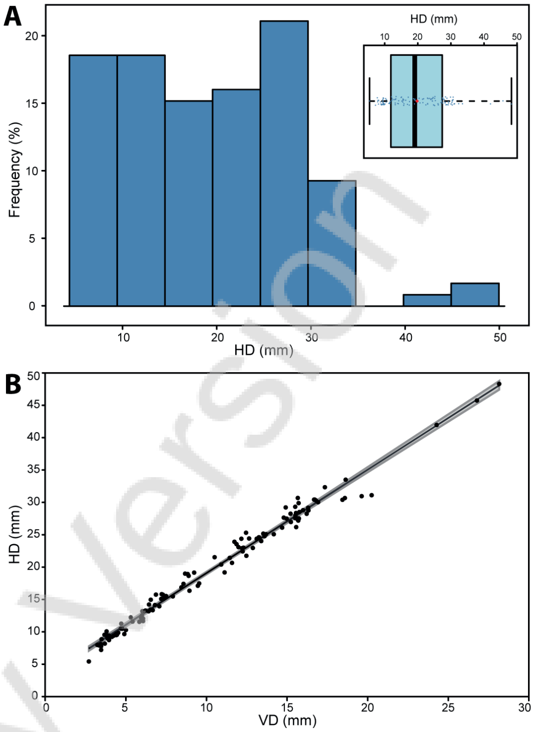

Fig. 2. Biometric of *Austrocidaris canaliculata*. (A) Size distribution of the specimens of *Austrocidaris canaliculata* analyzed. In the box plot, the black square indicates the mean, the rectangle boundaries represent the mean with standard deviation, and the whiskers show the minimum and maximum values estimated (N = 120), and (B) linear regression of the horizontal and vertical diameter of the test (HD and VD, respectively) (N = 120, $R^2 = 0.98$, $p < 0.001$).

Epibiosis and epibiont diversity

Epibiosis was recorded in 96.67% of *A. canaliculata* specimens analyzed, only 4 out of 120 specimens lacked epibiont species. The average epibiont richness per individual was 4.82 ± 2.94 species, and a maximum of 15 epibiont species was recorded on a single individual of *A. canaliculata* (Fig. 3).

The taxonomic diversity of the recorded epibionts includes 39 taxa spanning two kingdoms, 10 phyla, 13 classes, and 27 families, with 17 out of the 39 identified to the species level (Figs. 4A-L, 5). Additionally, two organisms despite being found on the spines of *A. canaliculata*, were not considered epibionts due to their free-living and non-sessile lifestyle (*Pseudidothea miersi* and Ammotheidae indet.). The highest diversity was observed in Bryozoa, represented by 12 taxa distributed across 2 classes and 7 families, followed by Cnidaria with 10 taxa grouped in 1

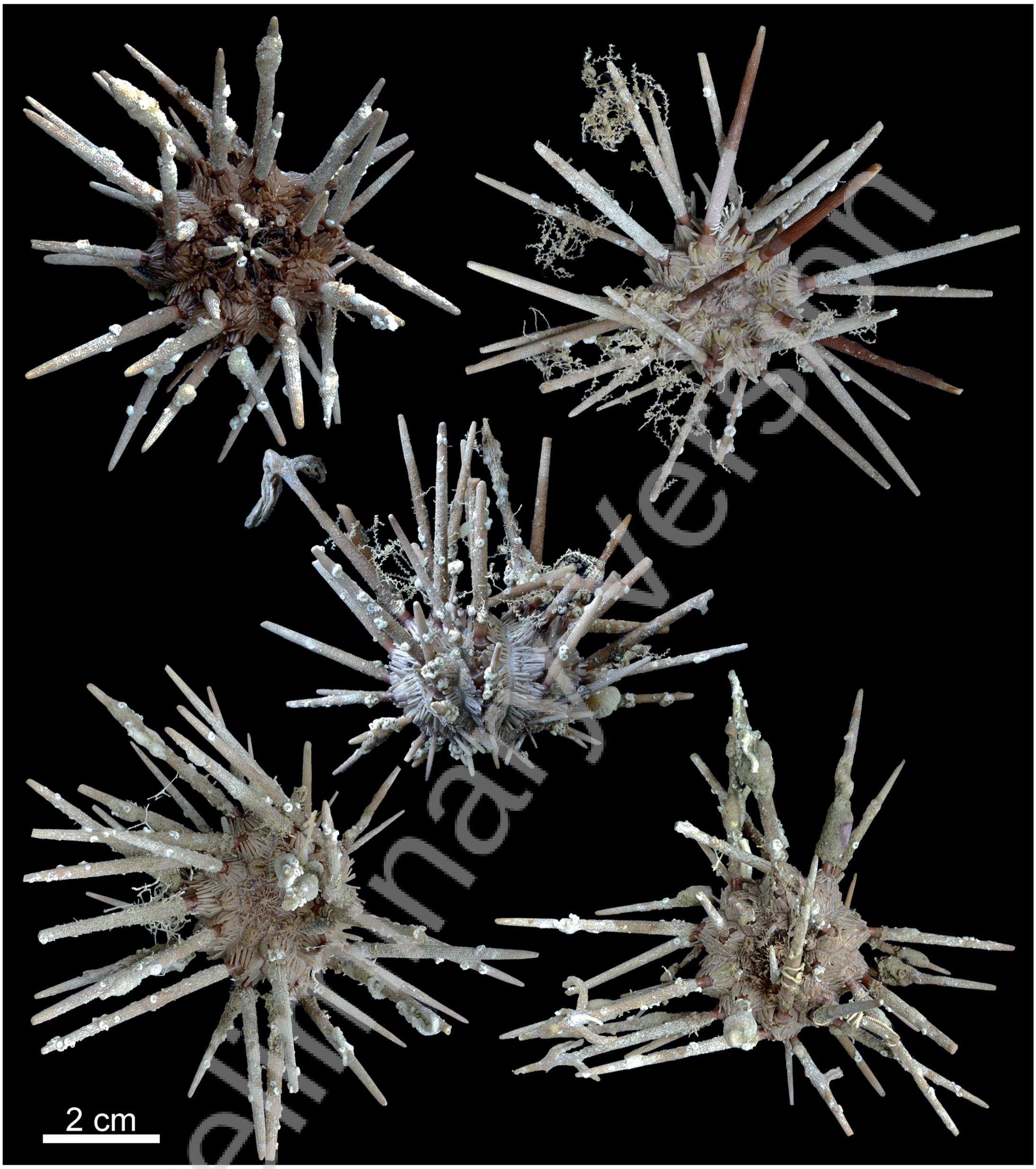

Fig. 3. Individuals of *Austrocidaris canaliculata* from the MPA Namuncurá – Burdwood Bank and surrounding deep-sea sites, showing primary spines fouled with epibionts.

class and 7 families. In contrast, the lowest diversity was recorded in Chordata and Mollusca, each represented by a single species. At the species level, the most recurrent epibiont was *Filellum* sp. 1 (Hydrozoa: Lafoeidae), found in 91 out of 120 specimens of *A. canaliculata* analyzed. This was followed by the ciliate *Lagotia* sp. (Ciliophora: Folliculinidae), which was recorded 70 times (Fig. 5). A total of 14 epibiont taxa were recorded only once: *Pista corrientis* (Polychaeta: Terebellidae), Ammotheidae indet. (Arthropoda: Pycnogonida), *Weltnerium gibberum* (Arthropoda: Scalpellidae), *Philobrya brattstromi* (Mollusca: Philobryidae), *Magellania venosa* (Brachiopoda: Terebratellidae), *Andreella uncifera* (Bryozoa: Microporidae), *Arachnopusia* sp. (Bryozoa: Arachnopusiidae), *Ellisina incrustans* (Bryozoa: Ellisinidae), *Tricellaria aculea-*

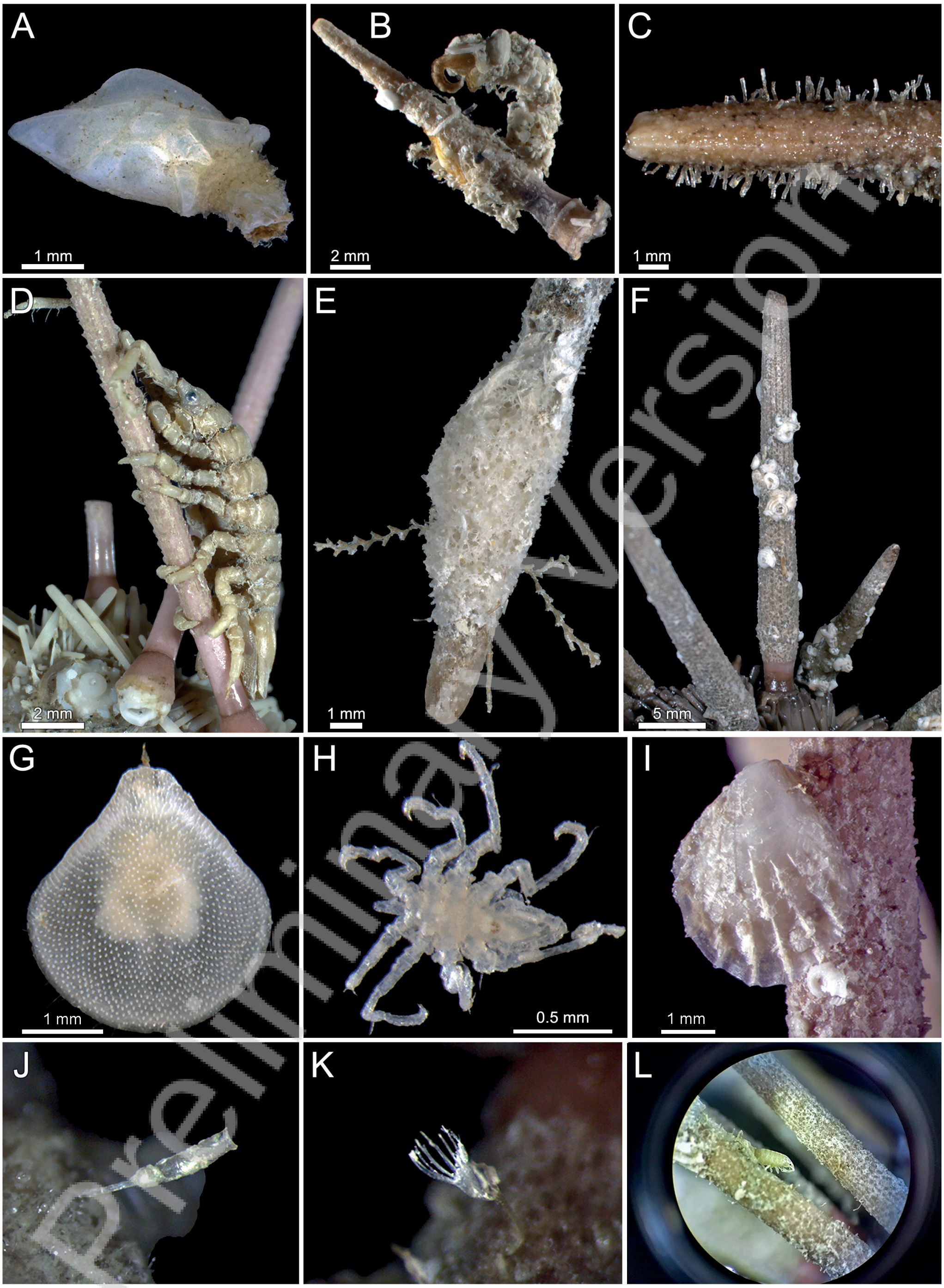

Fig. 4. Taxa recorded on the primary spines of *Austrocidaris canaliculata* at the MPA Namuncurá – Burdwood Bank and surrounding deep-sea area. (A) *Weltnerium gibberum* (Arthropoda: Scalpellidae); (B) *Pista corrientis* (Polychaeta: Terebellidae); (C) *Filellum* sp. 1 (Cnidaria: Lafoeidae); (D) *Pseudidothea miersi* (Arthropoda: Pseudidotheidae); (E) bryozoan colony and *Sertularella* sp. (Cnidaria: Sertularellidae); (F) aggregation of polychaetes tubes of the family Serpullidae; (G) *Liothyrella uva* (Brachiopoda: Terebratellidae); (H) pycnogonid indet. (Arthropoda: Ammotheidae); (I) *Philobrya brattstromi* (Mollusca: Philobryidae); (J) *Lafoea* sp. (Cnidaria: Lafoeidae); (K) bryozoan ancestrula; and (L) *P. miersi* (Arthropoda: Pseudidotheidae).

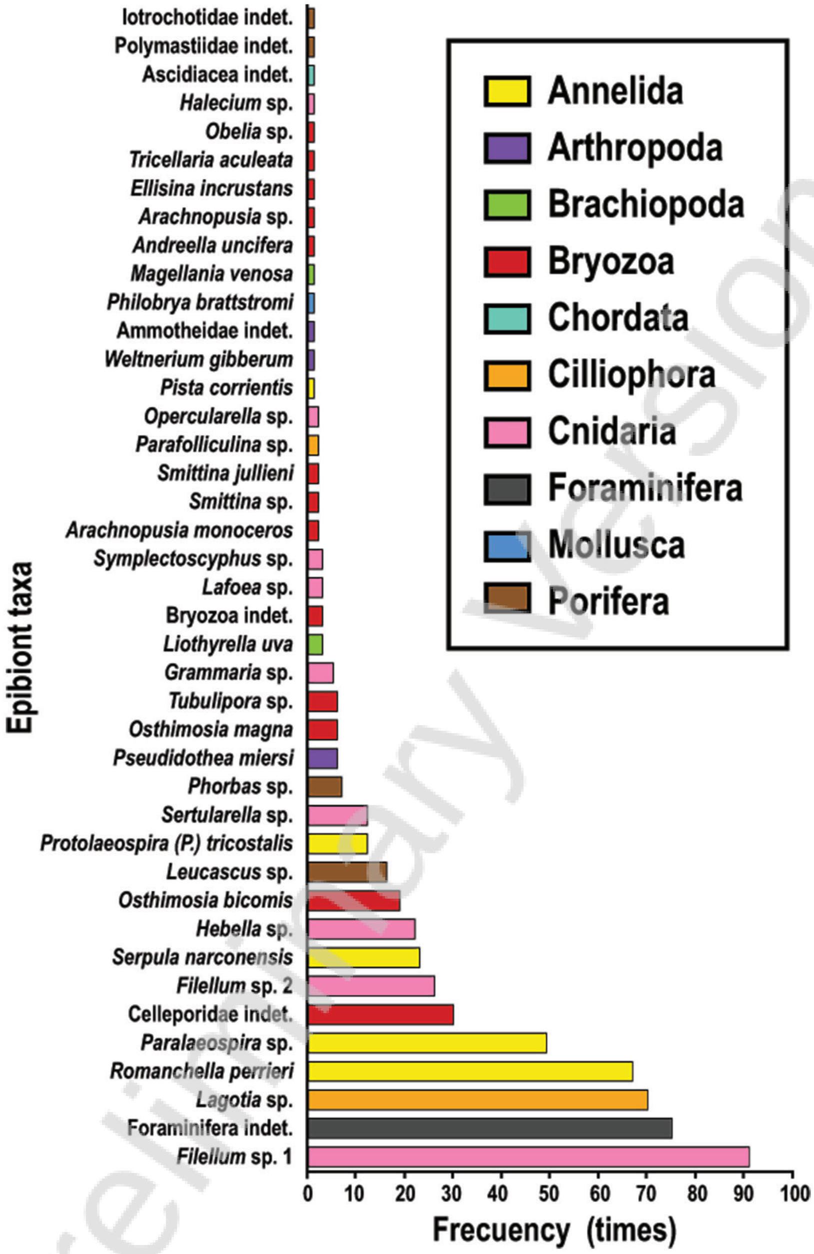

Fig. 5. Frequency distribution of the taxa recorded on the primary spines of *Austrocidaris canaliculata* at the MPA Namuncurá – Burdwood Bank and surrounding deep-sea sites.

ta (Bryozoa: Candidae), *Obelia* sp. (Cnidaria: Campanulariidae), *Halecium* sp. (Cnidaria: Haleciidae), Ascidiacea indet. (Chordata), Polymastiidae indet. (Porifera), and Iotrochotidae indet. (Porifera) (Figs. 4 A-L, 5).

Analysis of the epibiont assemblages

No significant differences were found in the estimated diversity within each zone, as evidenced by the overlapping diversity profiles obtained for the Internal and External zones (Fig. 6A-B). In all cases, the curve for the estimated diversity as a function of the parameter q was consistently higher than the curve for the observed diversity, reflecting a bias related to the underestimating species richness, mainly due to

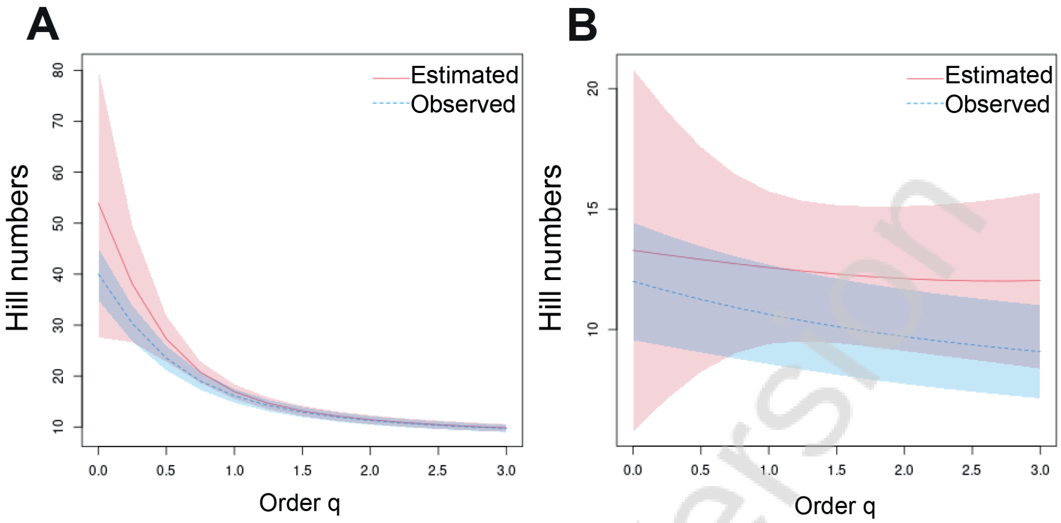

Fig. 6. Diversity profiles of the epibiont assemblages: (A) Internal zone; and (B) External zone of the MPA Namuncurá – Burdwood Bank. Shaded areas indicate 95% confidence intervals.

the presence of infrequent species that are often excluded from the samples. Similarly, no significant differences were observed in the estimated species richness of the epibiont assemblages for the Internal zone, whereas the estimated richness for the External zone was slightly higher (Table 2).

The linear regression revealed a strong positive correlation between the horizontal and vertical diameter of the test (HD and VD respectively) (N = 120, $R^2 = 0.98$, $p < 0.001$) (Fig. 2B). Due to the high correlation between HD and VD, we choose HD as the predictor variable to avoid multicollinearity in the posterior analyses. The observed richness of epibionts in the Internal and External zones of the MPA NBB showed a contrasting pattern, with different trends according to the HD, while controlling for the covariate Year. Specifically, we observed an increasing tendency with the HD within the Internal zone, whereas, in the External zone, the tendency was decreasing (Fig. 7). The significance of the interaction HD*Zone was quantified by a decrease of 5.5 units of AIC between the model with the interaction and the model without it, with the former resulting in a lower AIC value (Table 3). Additionally, no significant effect of Year on the richness was detected (*p*-value 0.248).

DISCUSSION

Epibiosis and epibiont diversity

The results indicate that epibiosis in *Austrocidaris canaliculata* from the MPA Namuncurá – Burdwood Bank and adjacent deep areas. areas is highly frequent, occurring in 96.67% of the specimens analyzed. This ecological association involves a remarkable diversity of epibiont species, including 39 (+2) taxa distributed across two kingdoms, 10 phyla, 13 classes, and 27 families. In some cases, specific identification was not possible due to the deteriorated condition of the epibiont organisms (i.e., worn bryozoan colonies) or the absence of diagnostic features (i.e., lack of reproductive structures in hydrozoans), so a higher taxonomic level was used. Linse *et al.* (2008) reported similar patterns of epibiosis in cidaroid species on sea urchins from the Scotia Arc, collected at depths of 90 to 1,045 meters. Among the 23 sea urchin species identified, epibionts were observed on nine species, all within the family Cidaridae, and a total of 51 epibiont species, grouped into 10 classes, were associated with these cidaroids. These findings, along with our study, highlight the ecological role of cidaroids as basibionts for diverse epibiont assemblages across different oceanic regions.

Bryozoa was one of the two phyla with the highest number of epibiont taxa associated with *A. canaliculata*. Additionally, bryozoans represent the group with the highest species richness among the benthic biodiversity within the MPA NBB (Schejter *et al.*, 2016). No differences were found between the species reported here as epionts of *A. canaliculata* and those previously recorded in the MPA NBB and adjacent deep-

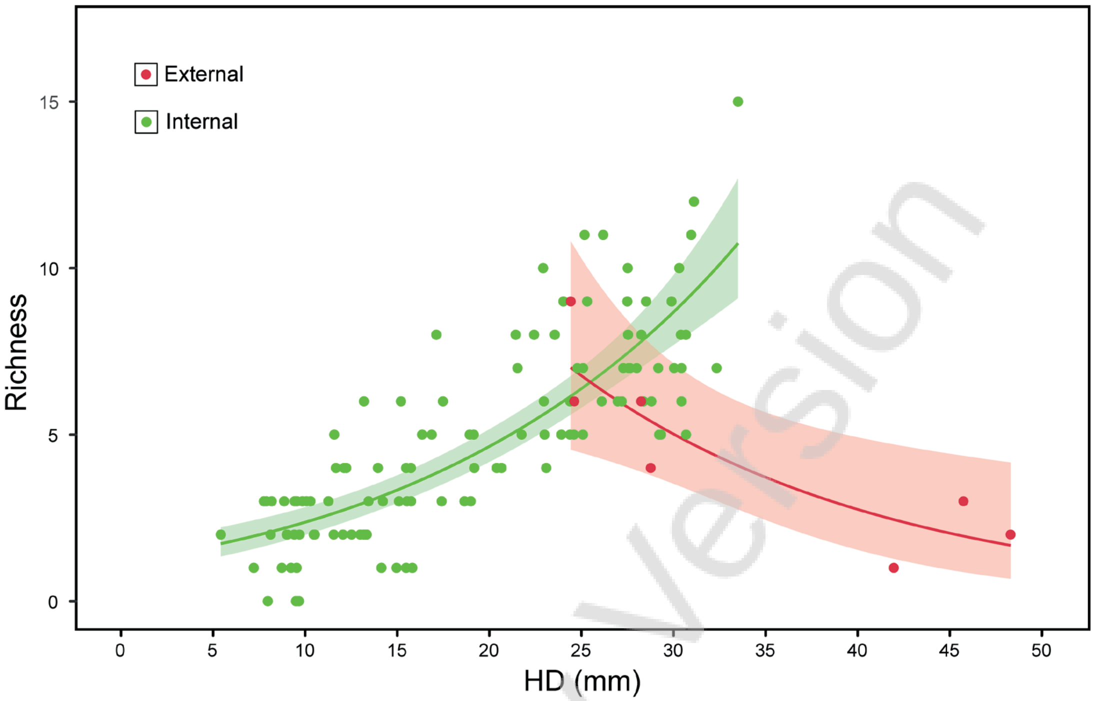

Fig. 7. Variations in the observed epibiont richness according to the horizontal diameter of the test (HD) of *Austrocidaris canaliculata*, categorized by zone, Internal (green) and External (red) of the MPA Namuncurá – Burdwood Bank.

sea areas (Schejter *et al.*, 2016; López-Gappa *et al.*, 2018). This phylum is also among the most recurrent and species-rich groups of epibionts on Antarctic cidaroids, as noted by Linse *et al.* (2008). Similarly, Cnidaria was the second most diverse phylum, with all species associated with *A. canaliculata* also previously recorded in the study area (Schejter *et al.*, 2020b).

Polychaeta diversity was represented by five taxa, four of which were recorded for the first time as epibionts of *A. canaliculata*: *Pista corrientis*, *Protolaeospira (Protolaeospira) tricostalis*, *Romanchella perrieri*, and *Serpula narconensis*. Additionally, for *P. (Protolaeospira) tricostalis*, *R. perrieri*, and *Paralaeospira* sp., also this study represents the first records of these species within the MPA NBB. The polychaete diversity of the MPA NBB and its adjacent slope has been extensively studied in two recent works. Schejter *et al.* (2016) reported a list of 19 polychaeta taxa, while Bremec *et al.* (2019) expanded the inventory to 39 species found within the MPA NBB and adjacent slope areas. Our findings represent 26% and 13% of the polychaetes species richness reported by Schejter *et al.* (2016) and Bremec *et al.* (2019), respectively. Both studies focused on identifying polychaetes collected at the same expeditions, using the same fishing gears, and included some of the sites analyzed in our study. The polychaete species recorded in these two studies likely were those that were larger or associated with larger fauna, such as corals and did not include the epibionts associated with *A. canaliculata*. Thus, our results not only demonstrate that *A. canaliculata* serves as a basibiont for these species but also suggest that it may function as a supplementary sampler for polychaete fauna and other sessile organisms, capturing a subset of sessile species that are often overlooked or not commonly encountered in final trawl catches.

Among the Arthropoda, we recorded the association with the isopod *Pseudidothea miersi*, as previously reported in the literature (Bernasconi, 1953; Doti *et al.*, 2008). Due to its low mobility and non-sessile nature, it was not classified as an epibiont. Another record of *P. miersi* (identified as *Pseudidothea bonnieri*) associated with cidaroid spines was reported by Sheppard (1957) at three stations around the Malvinas (Falkland) Islands. Although the sea urchin species were not identified, the most likely cidaroid sea urchin in question is either *A. canaliculata* or *Austrocidaris*

Table 1. Collection data of the specimens of *Austrocidaris canaliculata* analyzed. References: BB 2016, AMP Namuncurá – Banco Burdwood: Bentos; BB 2017, Banco Burdwood - Buque Oceanográfico ARA "Puerto Deseado" - PD BB Abr 1; BB 2018, AMP Namuncurá – Banco Burdwood: Ingenieros Ecosistémicos; Lat., latitude (S); Long., longitude (W); n, number of specimens.

Expedition - Station	Lat. (S)	Long. (W)	Depth (m)	Zone	n
BB 2016 - E30 L184	-54,288	-59,951	96	Internal	3
BB 2018 - E23 L110	-54,500	-60,134	96	Internal	7
BB 2018 - E22 L90	-54,332	-59,614	93	Internal	1
BB 2017 - E24 L184	-54,332	-59,896	97	Internal	12
BB 2017 - E25 L304	-54,346	-60,346	104	Internal	13
BB 2017 - E23 L173	-54,435	-59,504	91	Internal	8
BB 2018 - E26 L126	-54,095	-60,553	117	Internal	1
BB 2018 - E25 L120	-54,513	-60,426	100	Internal	4
BB 2016 - E34 L146	-54,454	-60,980	100	Internal	9
BB 2016 - E33 L159	-54,430	-60,648	101	Internal	8
BB 2016 - E32 L77	-54,543	-60,021	98	Internal	9
BB 2017 - E27 L326	-54,108	-60,880	128	Internal	8
BB 2016 - E36 L306	-53,930	-61,496	189	Internal	2
BB 2016 - E26 L27	-54,416	-58,515	137	Internal	1
BB 2016 - E35 L89	-54,532	-61,439	125	Internal	6
BB 2017 - E28 L287	-54,054	-61,095	140	Internal	11
BB 2016 - E27 L11	-54,168	-58,273	100	Internal	10
BB 2016 - E13 L172	-54,598	-62,855	608	External	4
BB 2017 - E31 L269	-53,673	-61,638	642	External	3

Table 2. Observed and estimated (Chao2 index) species richness, along with their standard errors and 95% confidence intervals, for the epibiont assemblages in the Internal and External zones of the MPA Namuncurá – Burdwood Bank.

		Richness				
Zone	n	Observed	Estimated	s.e.	95% Lower	95% Upper
Internal	113	40	53.96	10.31	43.83	90.90
External	7	12	13.29	2.01	12.15	23.37

spinulosa, as both species are frequently reported in this area (Flores *et al.*, 2019; Saucède *et al.*, 2020). Additionally, we report for the first time, the association of the pedunculate cirripede *Weltnerium gibberum* with cidaroids. This species (previously identified as *Ornatoscalpellum gibberum*) was also recorded attached to the stylasterid *Errina antarctica* (Hydrozoa) within the MPA NBB (Schejter *et al.*, 2016). Finally, the case of the pycnogonid (*Ammotheidae* indet.) is noteworthy. Pycnogonids are free-living organisms, so it is most likely that this single specimen was feeding on an organism present on the sea urchin spines, possibly bryozoan colonies, at the time of capture. For this reason, this species was not classified as an epibiont.

Regarding the ciliates, Ringuelet (1953) reported the presence of *Lagotia lutea* and *Parafolliculina amphora* (Ciliophora: Folliculinidae) on the spines of *A. canaliculata* from Puerto Deseado (Santa Cruz, Argentina). We confirm the presence of both genera as epibionts of *A. canaliculata* in the MPA NBB and surrounding deep-sea areas. However, due to the complexity of identifying these folliculinids, more exhaustive studies are needed to achieve accurate species identification. These folliculinids have been reported to associate with various basibiont species, such as macroalgae, bivalves, gastropods, and brachiopod shells, among others (Lopez Gappa *et al.*, 1982; Ringuelet, 1953), suggesting they could be considered generalist epibionts.

Among the less frequent epibiont species, brachiopods were represented by *Liothyrella uva* and *Magellania venosa* (Terebratellidae), with

Table 3. Results of Generalized Additive Models (GAM). References: Df degree of freedom; R^2 corresponds to the percentage of deviance explained.

Model	**Factors**	**Df**	**χ2**	**p(> | Chi (χ2)|)**
	Year	2	2.785	0.248
Richness ~ Year Zone + Zone: HD	Zone	1	4.605	0.032
	s(HD):Zone Ext.	1	5.587	0.015
AIC = 477.28	s(HD):Zone Int.	2.23	123.066	<0.001
$\mathbf{R^2}$ = 65.90%				
	Year	2	2.866	0.239
Richness ~ Year + Zone+HD	Zone	1	2.716	0.099
	s(HD)	4.38	121.4	<0.001
AIC = 482.792 $\mathbf{R^2}$ = 64%				

the former being one of the three most abundant species in the MPA NBB and the latter the least, according to Gordillo *et al.* (2019). Bivalvia was represented by a single specimen of *Phillobrya brattstromi* (Philobryidae), marking the first record of this species as a cidaroid epibiont.

As noted, for several species identified as epibionts of *A. canaliculata*, this study represents their first record in the study area. This may suggest some form of epibiont-basibiont specificity, as reported by Hétérier *et al.* (2008) and Hardy *et al.* (2011). Moreover, this could indicate that *A. canaliculata* provides a unique niche within the diverse range of available habitats. Consequently, any variation in the presence or abundance of the basibiont could lead to a significant change in local benthic diversity, particularly affecting those epibionts that exhibit specificity to the basibiont, potentially altering the species composition of the entire ecosystem. To test this hypothesis, further studies are needed to compare the diversity of epibionts on other substrates, biotic and abiotic, present in the study area.

Analysis of the epibiont assemblages

The high proportion of infrequent species may influence the estimation of the expected richness and diversity for each zone. Additionally, due to unequal sample sizes between the zones, meaningful comparisons of epibiont richness and diversity were not feasible. Despite this, when comparing the taxonomic composition of the epibiont assemblages, 12 epibiont species were shared between the MPA NBB and the deep-sea sites, while 29 epibiont species were found exclusively in the former, and only one species was recorded solely in the deep-sea sites. To clarify this aspect, it will likely be necessary to analyse a larger number of samples from surrounding deep-sea sites to better survey epibiont species richness and diversity.

As previously reported in other species of regular sea urchins (Cutress, 1965; Lawrence, 2020; McPherson, 1968), *A. canaliculata* also exhibits a positive linear correlation between the horizontal diameter (HD) and the vertical diameter of the test (VD). If we evaluate how these biometric variables are related to epibiont richness, we could assume that larger sea urchins have higher richness, as their probability of hosting epibionts increases due to a larger substrate surface. Although the surface area available for epibionts to settle on is determined by the sum of the surface areas of each primary spine, the greater HD of the sea urchin, the greater the VD will be, and this implies that the sea urchins will have more primary spines, and possibly these spines will also be larger, providing a greater total surface area for epibionts. In other words, we propose to use HD as a proxy for the increase in substrate surface area, simplifying the estimation of available substrate without the need to measure each spine individually.

Our study suggests a relationship between the size of the sea urchin and its capacity to host epibionts, due to the epibiont richness attached to *A. canaliculata* is correlated with the HD. Furthermore, this relationship varies depending on the zone where the sea urchins are found, showing contrasting tendencies: in the Internal zone (corresponding to the submarine plateau of the MPA NBB) species richness increases with HD, whereas in the External zone (surrounding deep-sea areas) richness decreases with HD. A possible explanation could be related to environmental conditions and the presence of a wide variety of organisms that could serve as a source of epibiont species, facilitating the likelihood of encounters between the epibionts and *A. cana-*

liculata within the MPA NBB. The bottom of the submarine plateau of the MPA NBB is covered by sandy sediments with gravel and may contain shell remains in some areas (COPLA, 2017). Images of the seabed landscape of this bottom were provided by Schejter *et al.* (2017), revealing a highly heterogeneous substratum across the bank, supporting a rich and diverse community of benthic species. Certain areas exhibited a complex three-dimensional architecture in rocky environments, interspersed with patches of both living and dead valves of brachiopods and tubeworms (Schejter *et al.*, 2017). These areas supported a diverse sessile community, dominated by bryozoans, hydrozoans, primnoid and stylasterid corals. Other areas, dominated by coarse biogenic sand, had less diverse assemblages, including sponge aggregations and other conspicuous organisms such as primnoid corals and colonial ascidians (Schejter *et al.*, 2017). The proximity of these organisms could facilitate the provision of epibiont larvae, aiding in colonization. The varied seabed landscape across the MPA NBB and its surrounding deep-sea areas could contribute to the variation in the epibiont richness observed on *A. canaliculata*. This highlights the intricate role of environmental factors in shaping the biodiversity and ecological interactions between shallow and deep-sea benthic ecosystems.

In conclusion, this study provides detailed faunistic information on the epibionts associated with *A. canaliculata* from the MPA NBB and adjacent deep areas, reinforcing the ecological importance of cidaroid species as basibionts in benthic ecosystems. The high frequency of epibiosis observed in this species, with a remarkable diversity of epibionts spanning numerous taxonomic groups, highlights its role in enhancing substrate availability for sessile and low-motile organisms, thereby contributing to the complexity and diversity of benthic communities. Notably, the richness of epibionts is correlated with the horizontal diameter of the test, with larger individuals providing more surface area for epibiont colonization. However, the relationship between epibiont richness and sea urchin size varies between shallow and deep-sea zones, suggesting that environmental factors, such as habitat heterogeneity and the presence of organisms serve as a source of epibiont species, could play a crucial role in shaping epibiont assemblages. This study not only reinforces the importance of *A. canaliculata* in supporting local biodiversity but also emphasizes the need for continued research to further unravel the complex interactions between basibionts and their epibionts, which are key to understanding the structure and functioning of benthic ecosystems in the region.

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