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Epizoic diatom communities on chitons (Mollusca: Polyplacophora) and southern king crabs (Crustacea: Decapoda) from central coastal waters of San Jorge Gulf (Patagonian Sea, South Atlantic Ocean)

Comunidades de diatomeas epizoicas sobre quitones (Mollusca: Polyplacophora) y centollas (Crustacea: Decapoda) de aguas costeras centrales del Golfo San Jorge (Mar Patagónico, Océano Atlántico Sur)

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Abstract

Diatoms constitute one of the most diverse groups of marine microalgae worldwide, both free-living as well as associated with different types of substrata. In particular, marine benthic macroinvertebrates represent surfaces to which diatoms can attach. The present study aims to characterize the diversity of diatom communities associated with chitons and southern king crabs from coastal waters of San Jorge Gulf (South Atlantic Ocean), and to analyze possible differences in diatom diversity among those communities according to the animal substrata, the environment and season of the year. For this purpose, we conduct-

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ed manual samplings to collect chitons from the intertidal, and sea diving samplings to collect southern king crabs from the subtidal at different sampling sites near Comodoro Rivadavia during winter 2018 and summer and winter 2024. Each specimen was carefully brushed and scraped to obtain microalgal material, which was subsequently processed using conventional methods and analyzed under both light microscopy (LM) and scanning electron microscopy (SEM). We estimated the relative abundance (%) of the identified diatom taxa as well as species richness (S), Shannon-Weaver diversity index (H´) and Pielou´s Evenness index (J) for each sample for comparison. Epizoic diatom communities included 43 taxa in Polyplacophorans and 62 in Decapods, mainly pennate diatoms with a scarce representation of centric diatoms. Solitary diatoms were the most frequent, with adnate, erect and motile forms recognized; various various morphological types of colonies were also recorded. We observed significant differences (α=0.05) in diatom diversity between the 2024 summer and winter for each invertebrate; however, no significant differences were found between the 2018 and 2024 winter samples. Polyplacophorans were studied for the first time as diatom hosts, and direct evidence of diatom attachment to the surface of both hosts is provided. This research study represents an important contribution to the knowledge of marine epizoic diatoms.

Keywords: Diatoms diversity; epibiosis; marine benthic macroinvertebrates; Patagonian Sea.

Resumen

Las diatomeas constituyen uno de los grupos de microalgas marinas más diverso a nivel mundial, tanto de vida libre como asociadas a diferentes tipos de sustratos. En particular, los macroinvertebrados bentónicos marinos representan superficies a las cuales las diatomeas se pueden adherir. Los objetivos del presente estudio son caracterizar la diversidad de las comunidades de diatomeas asociadas a quitones y centollas de aguas costeras del Golfo San Jorge (Océano Atlántico Sur) y analizar posibles diferencias en la diversidad de diatomeas entre dichas comunidades según el sustrato animal, el ambiente y la estación del año. Se realizaron muestreos manuales para colectar quitones del intermareal y muestreos mediante buceo autónomo para colectar centollas del submareal de sitios cercanos a Comodoro Rivadavia en Invierno de 2018 y Verano e Invierno de 2024. Cada ejemplar fue cepillado y raspado cuidadosamente para obtener el material microalgal que fue posteriormente tratado por métodos convencionales y analizado con microscopía de luz y electrónica de barrido. En cada muestra se estimó la Abundancia Relativa (%) de los taxa de diatomeas identificados así como la Riqueza Específica (S), Índice de Shannon-Weaver (H´) y el Índice de Equitatividad de Pielou (J) para su comparación. Las comunidades de diatomeas epizoicas incluyeron 43 taxa en quitones y 62 taxa en centollas, siendo la mayoría diatomeas pennadas con escasa representación de diatomeas centrales. Las formas solitarias fueron las más frecuentes, reconociéndose formas adnatas, erectas y móviles; asimismo se registraron colonias de diversa morfología. Se observaron diferencias significativas (α=0.05) entre la diversidad de diatomeas de verano e invierno de 2024 para cada invertebrado, no así entre los inviernos de 2018 y 2024. Los quitones fueron estudiados por primera vez como hospedadores de diatomeas y se proporciona evidencia directa de la adhesión de diatomeas a la superficie de ambos hospedadores. Este trabajo representa una contribución al conocimiento de las diatomeas epizoicas marinas.

Palabras clave: Diversidad de diatomeas; epibiosis; macroinvertebrados bentónicos marinos; Mar Patagónico.

INTRODUCTION

Diatoms constitute one of the major and most diverse components of marine communities worldwide, contributing substantially to the marine primary productivity. In benthic environments they may live freely or associated with different types of substrata such as sand, rocks or even other organisms like algae (epiphytic diatoms) or animals (epizoic diatoms) (Round, 1971; Round *et al.*, 1990). Epibiont diatoms usually present highly silicified frustules and exhibit multiple mechanisms for attachment: some diatoms are adnate and attach strongly to their host´s surface while other produce abundant mucilage that allow them to form mucilage stalks or pads for adhesion (Tiffany, 2011). Diatoms may be solitary or colonial or even constitute monospecific or polyspecific aggregations. When analyzing the diatom-animal association, diatoms may benefit by gaining protection against grazing, by accessing to higher nutrients and carbon dioxide concentrations produced by the animal metabolism and also by avoiding resuspension in sediments. Animals may benefit by capturing higher amounts of oxygen produced by photosynthesis, gaining camouflage against predators or, in some cases, they may be affected by a high density of diatoms that might reduce considerably their motility or even interfere with their reproduction (Totti *et al.*, 2011; Gómez *et al.*, 2018). The diatom-animal association may have a degree of specificity that allows the identification of generalist and specialist diatoms that may live in many or a few animal hosts, respectively. In order to characterize the species diversity, spatial distribution, abundance and ecological aspects of the epizoic diatoms, it is important to consider the hardness and chemical composition of the animal substrata as well as environmental conditions (Tiffany, 2011).

Studies on epizoic diatoms have increased in the past decades, with records of diatoms associated to marine copepods (Hiromi *et al.*, 1985; Gómez *et al.*, 2018; Purushothaman *et al.*, 2024), sessile marine invertebrates such as sponges and cnidarians (Totti *et al.*, 2005, 2011; Romagnoli *et al.*, 2007), hard-shelled mollusks and crustaceans (Round, 1971; Gillan & Cadée, 2000; D´Alelio *et al.*, 2011; Madkour *et al.*, 2012) and also in vertebrates such as

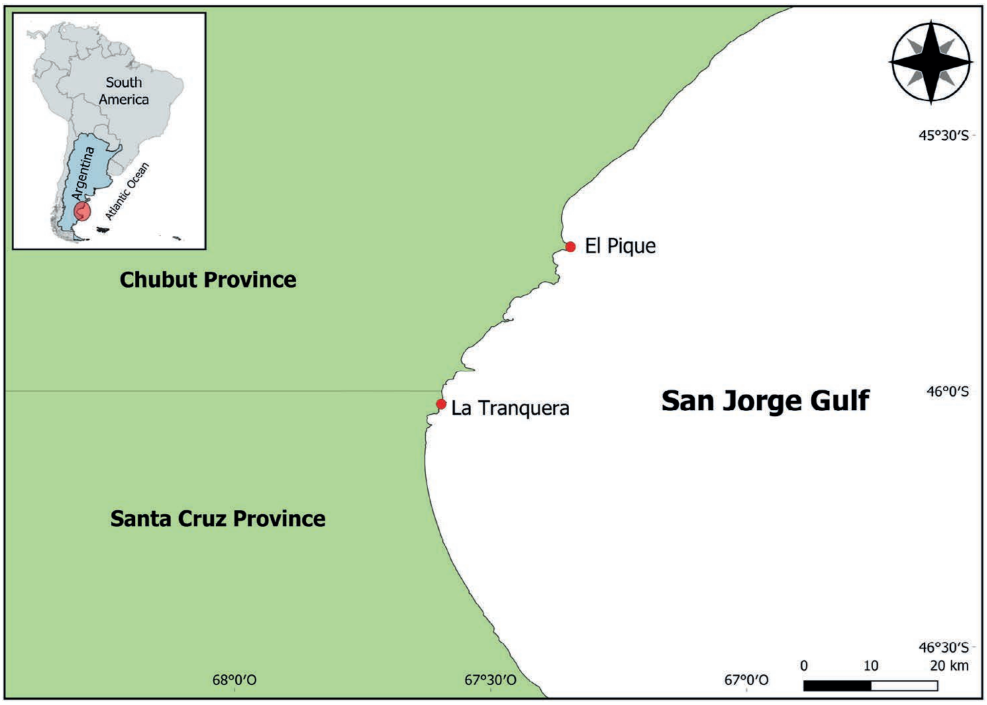

Fig. 1. Map of the San Jorge Gulf indicating the sampling sites (red dots).
Fig. 1. Mapa del Golfo San Jorge indicando los sitios de muestreo (puntos rojos).

sea turtles carapaces (Majewska *et al.*, 2015, 2021), seabird feathers (Holmes & Croll, 1984) and the skin of cetaceans (Nemoto 1958; Nemoto *et al.*, 1977; Holmes, 1985; Ferrario *et al.*, 2019; Ten *et al.*, 2022). In Argentina, Dr. Joaquín Frenguelli was a pioneer in the study of freshwater and marine diatom diversity, having described and characterized benthic diatoms along the Argentine Sea (Frenguelli 1930, 1938, 1939a, b). He analyzed samples obtained from the scrapping or washing of both marine macroalgae and macroinvertebrates, such as sponges, gastropod mollusks, bryozooans, ascidians, echinoderms and crustaceans, alongside marine sediments, which can be considered nowadays as early records of marine epibiont diatoms in Argentine waters. Later on, Sar and Sunesen (2014), Sunesen *et al.* (2015), Ferrario *et al.* (2019) and Cefarelli *et al.* (2024) recorded and described epizoic taxa, but this topic still remains as an unexplored subject with potential future prospects in the region.

This is a preliminary study of epizoic diatom diversity in San Jorge Gulf whose aim is to characterize the diatom flora associated to two benthic macroinvertebrates in the area, particularly chitons and the southern king crab. Additionally, possible differences according to the animal substrata, their environment and season of the year are evaluated. This will lead to a better understanding of the diversity and structure of epizoic diatoms communities on the study area.

MATERIAL AND METHODS

San Jorge Gulf is located in the mid-Atlantic Patagonian waters, between approximately 45°S and 47°S, covering about 40,000 km^2 with the predominance of coarse sediments in coastal areas (Reta, 1986; Fernández *et al*., 2005). This gulf is considered one of the Southern Hemisphere's most productive ecosystems and its benthic environment supports a great diversity of living organisms (Longhurst, 2007; Dans *et al*., 2020).

The macroinvertebrates collected in this study included Polyplacophoran Mollusks *Plaxiphora aurata* Spalowsky 1795 (Chiton) and the Decapod Crustacean *Lithodes santolla* Molina 1782 (Southern King Crab, SKC). They were collected in La Tranquera sampling site (46º01'31" S, 67º35'47" W, San Jorge Gulf) during summer (20 and 21-XII-2023) and winter (28-VII-2024 and 08-VIII-2024) of 2024. Additionally, exploratory SKC samples were collected during 2018 winter (01-VII-2018) at the same sampling site (Fig. 1). Chitons were collected by manual samplings in the intertidal zone during low tides whereas SKC were collected by sea diving in the subtidal zone at a depth between 12-15 m. Given the scarce and random distribution of SKC in the subtidal environment, at least three specimens of each invertebrate species under study were collected during each seasonal sampling (Fig. 2).

Sampled macroinvertebrates specimens were carefully brushed, scrapped and finally rinsed with filtered sea water *in situ*. This same proceeding was applied to a similar area of the rocky surface located in the proximities of the sampled invertebrates and constitute the corresponding environmental samples (except for 2018 winter when no environmental sample was taken).

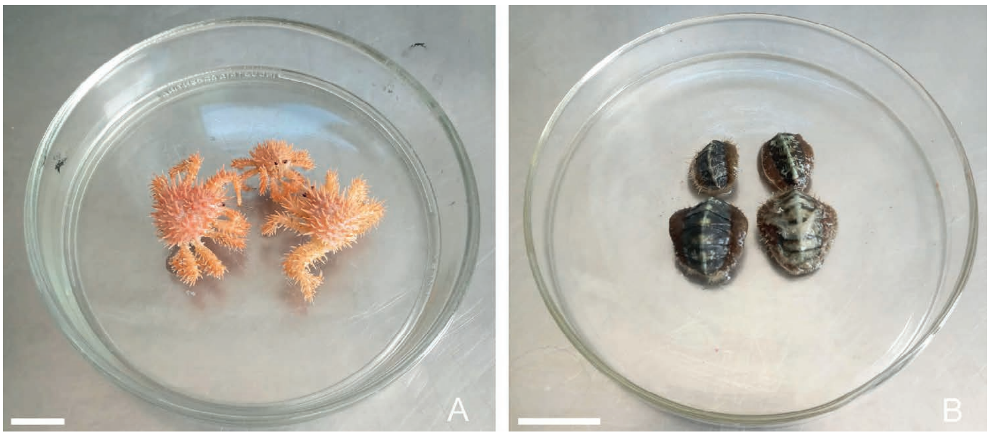

Fig. 2. Specimens of analyzed macroinvertebrates. A) *Lithodes santolla.* B) *Plaxiphora aurata*.

Fig. 2. Especímenes de los macroinvertebrados analizados. A) *Lithodes santolla.* B) *Plaxiphora aurata*.

All samples were fixed *in situ*, the 2018 winter and 2024 summer samples were fixed with 4% formaldehyde solution (due to processing later in time) while 2024 winter samples were fixed with 70% ethanol (due to processing briefly after sampling). In each case, the obtained microalgal material was treated to remove the organic matter according to Prygiel & Coste (2000). The cleaned material was mounted for light (LM) and scanning electron microscopy (SEM) according to Ferrario *et al*. (1995). Permanent slides were made with Naphrax medium. Permanent slides, SEM material as well as the remaining treated microalgal material fixed with 4% formaldehyde solution (preserved in appropriately labeled Eppendorf tubes) are stored at Instituto de Desarrollo Costero (IDC – Universidad Nacional de la Patagonia San Juan Bosco, UNPSJB) as a part of the "Colección de Diatomeas Epizoicas del Golfo San Jorge" for further studies.

Also, we had access to three chiton specimens from El Pique sampling site (45º43'06" S, 67º20'38" W, San Jorge Gulf) (Fig. 1) from 2023 winter (25-VII-2023) and a SKC moult from La Tranquera sampling site (August 2023) in order to determine the presence of diatoms directly attached to Polyplacophoran´s spines and Decapod´s carapace with LM and SEM.

The slides were examined using a Differential Interference Contrast (DIC) Leica DM2500 LM equipped with a Leica DFC420 digital camera and a DIC Olympus BX51 LM equipped with an Olympus DP71 digital camera. The SEM material was examined in different microscope services from Argentina including a Jeol JSM-6510 LV SEM from UNPSJB, a C. Zeiss Gemini 1 SEM from "Bernardino Rivadavia Museum" (MACN) microscopy service, a C.Zeiss Crossbeam 340 SEM from LANAIS-MIE (UBA-CONICET), a C. Zeiss (FE-SEM) Supra 40 from "Centro de Microscopías Avanzadas " (FCEN-UBA) and a C. Zeiss Sigma SEM from "Laboratorio de Análisis Materiales por Espectrometría de Rayos X" (LAMARX, UNC).

The Relative Abundance (RA) of diatoms on macroinvertebrates samples from 2018 winter and 2024 summer and winter were estimated by counting a minimum of 400 valves per permanent slide at a magnification of 1000x using a DIC Olympus BX51 LM and oil immersion, the results being expressed in percentages (Prygiel & Coste, 2000; Cefarelli *et al*., 2024). It is important to remark that we could not estimate the relative abundance of environmental samples due to the impossibility of reaching the minimum amount of 400 valves thus we only indicate the presence of diatom taxa on those samples. We also estimated different diversity indexes such as Specific Richness (S), the Shannon-Weaver diversity index (H´) and Pielou´ s Evenness index (J) in order to characterize each diatom community. Finally, Hutcheson´s *t*-tests were applied to compare the H' indexes estimated for each seasonal sample and determine possible differences between them (Zar, 2010):

$$t = \frac{H'_1 - H'_2}{s_{H'_1} - s_{H'_2}}$$

where:

$$s_{H'_1} - s_{H'_2} = \sqrt{s^2_{H'_1} + s^2_{H'_2}}$$

and the variance of each *H'* was approximated by:

$$s^2_{H'} = \frac{\sum fi \,.\log^2 fi - \left(\sum fi \,.log\, fi\right)^2 / n}{n^2}$$

where: *n*, sample size
f_i, number of observations in category *i*.

Indexes and *t*-tests were calculated using Microsoft Excel (Windows 10, 2024) with a significance level (α) of 0.05.

The estimated indexes constitute a preliminary effort to study possible similarities and differences in between the diatom communities associated to the macroinvertebrates here studied. Further samples will need to be analyzed in future studies in order to conduct a more thorough analysis.

The nomenclatural status of all taxa referred to in the study was consulted in AlgaeBase (Guiry & Guiry, 2024) and DiatomBase (Kociolek *et al*., 2024).

Epizoic diatoms morphology and determination follows Round *et al*. (1990), Witkowski *et al*. (2000).

RESULTS AND DISCUSSION

Diatom flora associated with marine macroinvertebrates

As a result of the analysis of the epizoic diatoms of both macroinvertebrates from La Tranquera we recorded 83 diatom taxa, 43 and 62 of them being recorded on chitons and SKC, respectively (Table 1).

Most of the diatoms observed on both invertebrates were mainly pennate and included within *Amphora* (8 taxa), *Cocconeis* (10 taxa), *Navicula* (6 taxa), *Nitzschia* (11 taxa) and *Tabularia* (2 taxa). Centric diatoms were generally scarce, mostly represented by *Odontella* spp. and *Paralia sulcata sensu lato*. Both invertebrate hosts shared 21 taxa.

We identified differences regarding diatom diversity associated to the hosts analyzed. Some taxa such as *Caloneis* sp., *Campylopyxis garkeana*, *Planothidium* spp., *Psammothidium* sp. and *Rhoicosphenia* spp. were only observed on chitons whereas *Amphiprora lata*, *Delphineis surirella*, *Grammatophora macilenta*, *G. angulosa var. islandica*, *Hyalodiscus radiatus*, *Licmophora flabellata*, *L. hyalina*, *L.* aff. *ehrenbergii*, *L. gracilis*, *Plagiotropis lepidoptera* and *Pleurosigma* spp. were only observed on SKC.

Table 1 (part 1 of 3)**.** Diatom taxa recorded for chitons and southern king crabs from La Tranquera sampling site, indicating their presence (P) and percentual relative abundances (only when RA % > 3%) for each sampling season. Env.: environmental samples.

Tabla 1 (parte 1 de 3)**.** Taxa de diatomeas registradas en quitones y centollas de La Tranquera indicando su presencia (P) y las abundancias relativas porcentuales (sólo cuando AR % > 3%). Amb.: muestra ambiental.

Invertebrate Host	Chitons				Southern King Crabs				
Diatom taxa/Season	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024	Winter 2018	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024
Achnanthes spp.			P	P					
Achnanthes cf. *adnata* Bory		P	P	P		P			
Achnanthidium spp.	P	P	P	P	P			P	
Amphiprora lata Greville								P	
Amphora aff. *crassa* W.Gregory								P	
Amphora aff. *proteus* Ehrenberg ex Kutzing	P	P	P		P			P	P
Amphora aff. *pusio* Cleve	P				P				
Amphora sp.I	P (14%)	P	P (5.5%)	P	P	P		P	
Amphora sp. II	P	P							
Amphora sp. III			P						
Amphora sp. IV			P						
Amphora sp. V						P			
Bacillaria socialis var. *kariana* (Grunow) Grunow	P				P (3%)	P	P	P (3%)	
Bacillaria sp. I								P	
Caloneis spp.			P	P					
Campylopyxis garkeana (Grunow) Medlin	P								
Centric spp.				P	P				
Cocconeis convexa Giffen						P			
Cocconeis cf. *disculus* (Schumman) Cleve					P				
Cocconeis cf. *patagonica* Riaux-Gobin & Cefarelli				P		P (4.5%)			
Cocconeis scutellum Ehrenberg	P (11.5%)	P	P (20.5%)	P	P (5.4%)	P (4.75%)	P	P (18.75%)	P
Cocconeis stauroneiformis H.Okuno					P				
Cocconeis sp.I		P			P (10.4%)	P (10%)		P (10.4%)	
Cocconeis sp.II		P						P (18.25%)	
Cocconeis sp.III		P						P	
Cocconeis sp.IV		P	P						
Cocconeis sp.V	P								
Delphineis surirella (Ehrenberg) G.W. Andrews				P			P	P	
Donkinia carinata (Donkin) Ralfs				P					
Diploneis vacillans var. *delicatula* Cleve			P			P			P

Table 1 (part 2 of 3)**.** Diatom taxa recorded for chitons and southern king crabs from La Tranquera sampling site, indicating their presence (P) and percentual relative abundances (only when RA % > 3%) for each sampling season. Env.: environmental samples.

Tabla 1 (parte 2 de 3)**.** Taxa de diatomeas registradas en quitones y centollas de La Tranquera indicando su presencia (P) y las abundancias relativas porcentuales (sólo cuando AR % > 3%). Amb.: muestra ambiental.

Invertebrate Host Diatom taxa/Season	Chitons				Southern King Crabs				
	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024	Winter 2018	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024
Fallacia spp.							P		
Gomphonemoid sp. I	P (3.75%)								
Gomphonemoid sp. II	P (10%)					P			
Grammatophora marina (Lyngbye) Kutzing	P		P		P (12.5%)	P		P	
Grammatophora angulosa var. *islandica* (Ehrenberg) Grunow								P	
Grammatophora macilenta W.Smith					P			P	
Gyrosigma spp.					P				
Halamphora aff. *granulata* W.Gregory					P	P			
Homoeocladia angularis (W.Smith) Kuntze	P		P (3.5%)						
Hyalodiscus radiatus (O`Meara) Grunow								P	
Licmophora flabellata (Greville) C.Agardh					P (12.6%)	P		P	
Licmophora aff. *ehrenbergii* (Kutzing) Grunow								P	
Licmophora gracilis (Ehrenberg) Grunow								P	
Licmophora hyalina (Kutzing) Grunow						P			
Licmophora lyngbyei (Kutzing) Grunow					P				
Navicula cf. *directa* (W.Smith) Brébbison		P	P (3%)		P	P	P	P (3.25%)	P
Navicula aff. *perminuta* Grunow				P					P
Navicula oscitans var.*curvipunctata* (Leuduger-Fortmorel) Frenguelli					P	P			
Navicula sp.I	P (6.75%)	P	P (7.25%)	P	P	P (5%)	P	P (5.25%)	P
Navicula sp. II	P								
Navicula sp. III						P			
Nitzschia spp.					P				
Nitzschia aff. *dissipata* (Kutzing) Rabenhorst			P						
Nitzschia aff. *frustulum* (Kutzing) Grunow	P (12.5%)	P	P (18.25%)	P		P		P	P
Nitzschia aff. *hybrida* Grunow						P		P	
Nitzschia aff. *inconspicua* Grunow	P (15.5%)	P	P (6.25%)	P	P	P		P	P
Nitzschia aff. *media* Hantzsch		P	P			P			
Nitzschia sigma aff. var. *sigmatella* Grunow			P	P		P		P	
Nitzschia aff. *valida* Cleve & Grunow						P			
Nitzschia sp. I	P	P		P					P

Table 1 (part 3 of 3)**.** Diatom taxa recorded for chitons and southern king crabs from La Tranquera sampling site, indicating their presence (P) and percentual relative abundances (only when RA % > 3%) for each sampling season. Env.: environmental samples.

Tabla 1 (parte 3 de 3)**.** Taxa de diatomeas registradas en quitones y centollas de La Tranquera indicando su presencia (P) y las abundancias relativas porcentuales (sólo cuando AR % > 3%). Amb.: muestra ambiental.

Invertebrate Host	Chitons				Southern King Crabs				
Diatom taxa/Season	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024	Winter 2018	Summer 2024	Env. Summer 2024	Winter 2024	Env. Winter 2024
Nitzschia sp. II			P (3.25%)						P
Nitzschia sp. III						P			
Odontella spp.	P		P						
Odontella aff. *aurita* C. Agardh					P				
Odontella obtusa Kutzing						P		P	
Paralia sulcata s.l. (Ehrenberg) Cleve		P	P			P		P	
Parlibellus sp.	P	P	P		P	P	P		
Pinnularia spp.					P				
Plagiotropis lepidoptera (W.Gregory) Kuntze						P			
Planothidium spp.	P	P		P					P
Pleurosigma spp.				P	P	P			
Psammodictyon spp.			P					P	
Psammothidium aff. *marginulatum* (Grunow) Bukhtiyarova			P						
Pseudostaurosira cf.*perminuta* (Grunow) Sabbe & Vyverman			P						
Pseudogomphonema kamtschaticum (Grunow) Medlin		P							
Rhoicosphenia spp.					P				
Rhoicosphenia genuflexa (Kutzing) Medlin			P						
Rhopalodia spp.					P				
Synedra spp.	P		P		P				
Synedra aff. *gaillonii* (Bory) Ehrenberg							P		
Synedrosphenia fulgens (Greville) Lobban & Ashworth								P	
Tabularia investiens (W.Smith) D.M.Williams & Round	P (13%)	P	P (5.5%)	P	P (39.7%)	P (54.25%)		P (33%)	
Tabularia parva (Kutzing) D.M.Williams & Round	P		P (4.75%)		P	P		P	
Trachyneis aspera (Ehrenberg) Cleve	P		P		P			P	
Pennate sp. I			P						
Pennate sp. II								P	
Pennate sp. III					P				
Pennate sp. IV		P							
Pennate sp. V		P							
Total taxa	**25**	**23**	**33**	**19**	**32**	**32**	**8**	**33**	**11**

Cefarelli *et al.* (2024) commented on the variation of diatom epibiosis in between different macroinvertebrate hosts, within a same host and among sampling sites of the San Jorge Gulf. Also, the authors had recorded a lower diatom epibiosis on the same host taxa analyzed in deeper waters within the gulf than in coastal shallow waters of the subtidal zone near Comodoro Rivadavia city. This difference between intertidal and subtidal samples highlights the importance of depth and light conditions of each area as key factors (Gómez *et al.*, 2018).

Regarding the presence of centric diatoms, Madkour *et al.* (2012) proposes that they are mainly planktonic but they are often found associated to invertebrates such as Decapod Crustaceans because they are tangled up to different morphological structures of the animal body and thus, they appear in some benthic-epizoic samples. Centric diatoms were not abundant in our epizoic material but the recurrent presence of some yet unidentified centric taxa indicates that these kinds of diatoms were not accidentally found and therefore could be epizoic.

Round (1981) and Totti *et al*. (2011) propose that the degree of epibiosis is inversely related to the motility of the animal host, concluding that active animals will be less colonized by diatoms than sessile animals. Chitons have reduced motility and may represent a more stable and easily colonizable surface for diatoms than SKC do given their motility. Cefarelli *et al*. (2024) reported SKC with and without epibiosis in different sites along the gulf and recorded *Amphora*, *Cocconeis*, *Grammatophora*, *Licmophora*, *Navicula*, *Nitzschia* and *Tabularia* as the more abundant diatom taxa as we also observed in our samples.

Diatoms life mode and growth forms

Most of the diatom taxa found were solitary forms and other taxa may form colonies of diverse morphologies such as "ribbon-like" colonies (*Bacillaria socialis var. kariana* and *Trachyneis aspera*), "fan-shape" colonies (*Licmophora flabellata* and *Tabularia investiens*, Fig. 3 A-B), "zig-zag" colonies (*Grammatophora marina* and *Odontella obtusa*, Fig. 3 C), "chain-like" colonies (*Paralia sulcata* s.l., Fig. 3 D) and "tube-like" colonies (*Parlibellus* spp. and undetetermined naviculoids, Fig. 3 E-F). *Cocconeis* spp. specimens were observed gathered along the surface of chitons spines and SKC carapaces surface constituting polyspecific aggregations but not true colonies (Fig. 4 A-D).

We recognized three types of diatom growth forms according to their mechanisms of attachment to the invertebrate substrata: adnate diatoms which adhere strongly to the surface by means of their raphe valve (Figs. 4 A-D and Fig. 6 B), erect diatoms which form mucilaginous structures of adhesion such as "pads" and "stalks" (Figs. 3 A-C, Figs. 4 D, Figs. 5 A-C, Fig. 6 A) and, motile diatoms which have the capability to slide along the invertebrate surface (Figs 3 E-F, Fig. 6 A). D´Alelio *et al*. (2011) pro-

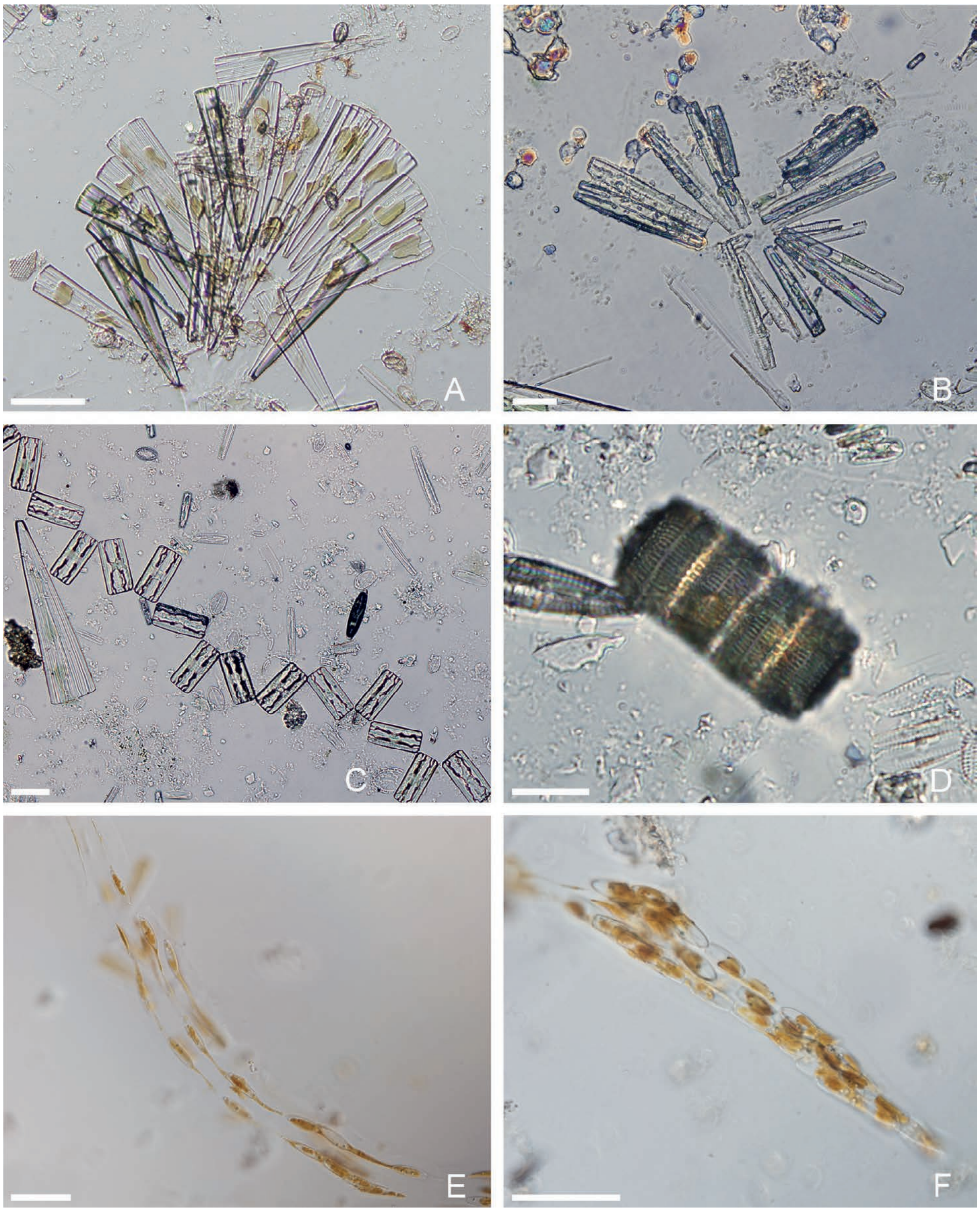

Fig. 3. LM. Diatom colonies of diverse morphologies. A-B) "Fan-shaped" colonies of (A) *Licmophora flabellata* and (B) *Tabularia investiens*. C) "Zig-Zag" colony of *Grammatophora marina*. D) "Chain-like" colony of *Paralia sulcata* s.l. E-F) "Tube-like" colonies of undetermined pennate diatoms. Scale bars 10 µm (A-D) and 50 µm (E-F).

Fig. 3. MO. Diatomeas formando colonias de diversa morfología. A-B) "Colonias en abanico" de (A) *Licmophora flabellata* y (B) *Tabularia investiens*. C) "Colonias en Zig-Zag" de *Grammatophora marina*. D) "Colonia en cadena" de *Paralia sulcat*a s.l. E-F) "Colonias tubícolas" de diatomeas pennadas indeterminadas. Escala de 10 µm (A-D) y 50 µm (E-F).

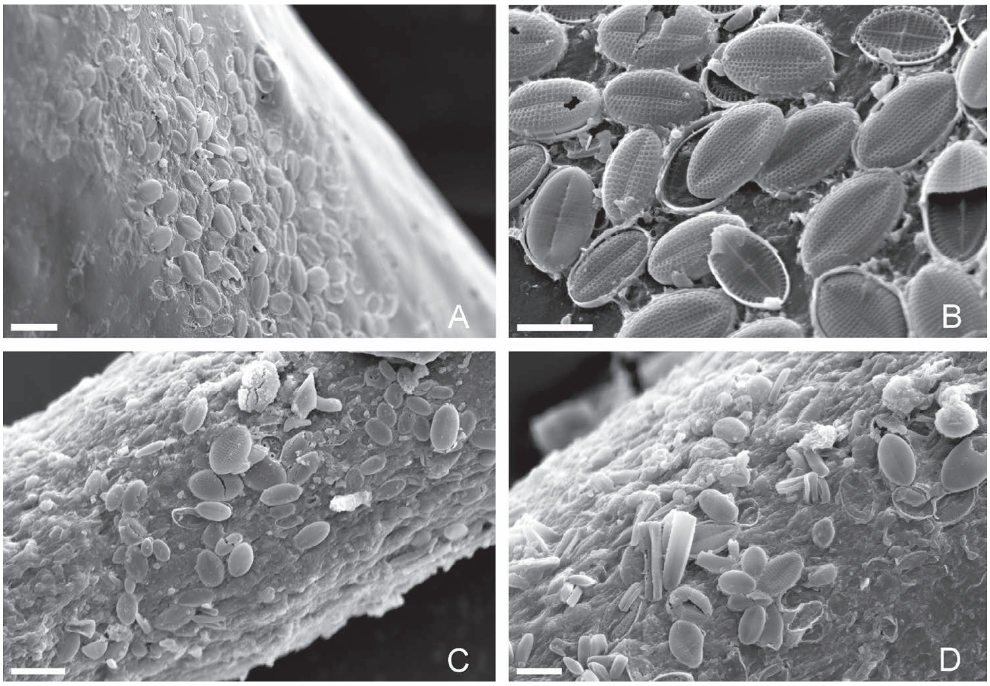

Fig. 4. SEM. Diatoms directly attached to chitons and southern king crabs surface. A) General view of diatoms attached to southern king crabs carapace. B) Detail of *Cocconeis* polyspecific aggregations, note the adnate diatom adhesion through the raphe valve. C) General view of diatoms attached to chitons spines. D) Detail of *Cocconeis* polyspecific aggregations alongside *Tabularia investiens* and *Nitzschia* specimens. Scale bars: 20 μm (A, C) and 10 μm (B, D).

Fig. 4. MEB. Diatomeas directamente adheridas a la superficie de quitones y centollas. A) Vista general de diatomeas adheridas al caparazón de las centollas. B) Detalle de agregaciones poliespecíficas de *Cocconeis*, nótese la adhesión de las diatomeas mediante la valva con rafe. C) Vista general de diatomeas adheridas a las espinas de quitones. D) Detalle de agregaciones poliespecíficas de *Cocconeis* junto a ejemplares de *Tabularia investiens* y *Nitzschia*. Escala de 20 μm (A, C) y 10 μm (B, D).

poses that, in terms of an ecological succession, the presence of all three diatom growth forms (adnate, erect and motile) is typical of a mature and well-structured diatom community. Thus, adnate forms are the first ones to colonize an animal substrate strongly adhering to their surface and then erect and motile forms partially adhere to the same surface. The macroinvertebrates here analyzed exhibited the three types of growth forms, hosting a possibly well-structured and mature diatom community.

From the analysis of Chitons' spines and SKC' carapace moults, we were able to record the presence of diatoms directly attached to both hosts' surfaces. Particularly, numerous *Cocconeis* spp. specimens forming conspicuous polyspecific aggregations alongside *T. investiens, Nitzschia* sp. and *Amphora* sp. (Fig. 4 A-D). Several authors have also previously indicated *Cocconeis* as an epibiont constituting mono or polyspecific aggregations on diverse living surfaces. For instance, De Stefano *et al.* (2000), Tiffany (2011) and Majewska *et al.* (2013) reported aggregations of diverse *Cocconeis* taxa on different marine macroalgae. Similarly, Romagnoli *et al.* (2007) and Totti

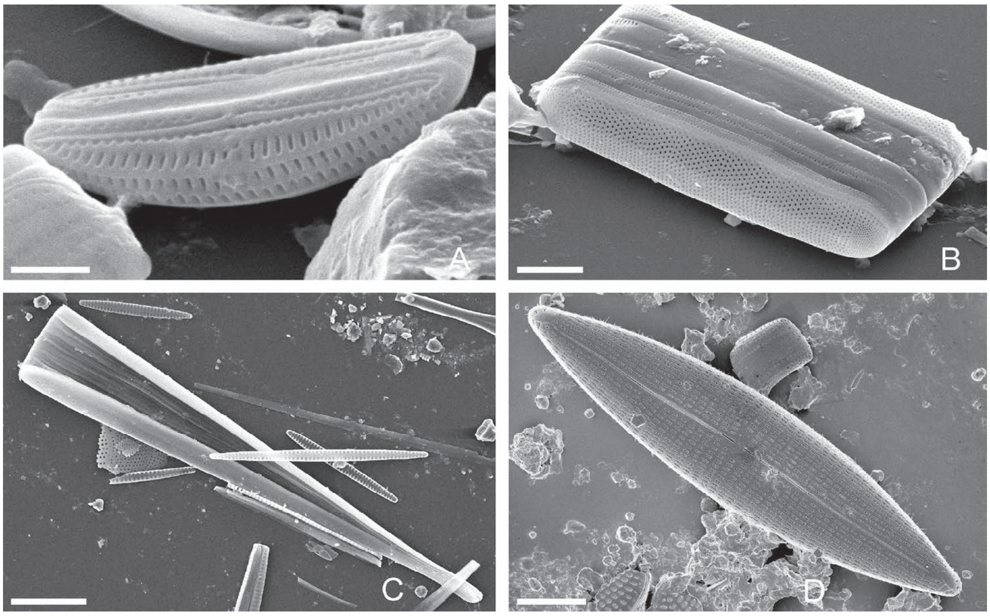

Fig. 5. SEM. Epizoic diatoms on chitons and southern king crabs. Frustules of (A) *Amphora*, (B) *Grammatophora marina* and (C) *Licmophora flabellata*. (D) External valve view of *Navicula* aff. *directa*. Scale bars: 2 µm (A), 5 µm (B, D) and 20 µm (C).

Fig. 5. MEB. Diatomeas epizoicas de quitones y centollas. Frústulos de (A) *Amphora*, (B) *Grammatophora marina* y (C) *Licmophora flabellata*. (D) Vista valvar externa de *Navicula* aff. *directa* (D). Escala: 2 µm (A), 5 µm (B, D) y 20 µm (C).

et al. (2011) reported epizoic communities integrated by *Amphora*, *Cocconeis* and *Tabularia*, among other taxa, growing on Hydroid Cnidarians. Recently, Cefarelli *et al.* (2024) described *Cocconeis patagonica* and *T. investiens* on Squad Lobsters (*Grimothea gregaria*) from San Jorge Gulf and provided LM evidence of the specimens directly attached to the carapaces surface.

Macroinvertebrates and environmental samples

When comparing the diatom flora associated to chitons and SKC with their respective environmental samples from 2024, each host shared 19 and 11 diatom species with them, respectively. Although the brushed surface of the invertebrates and environmental samples had similar dimensions, the scarce microalgal material obtained from the latter allows us to suggest that the host´s surface may represent an optimal microhabitat for diatoms to attach to (Totti *et al.*, 2011) (Table 1).

Diatoms associated with chitons are likely to be similar to those benthic diatoms living in the surrounding rocky surfaces considering the host has reduced movement and represents an easily colonizable surface for diatoms (Round, 1971; Tiffany, 2011). Also, the chiton body is flat, and its entire body surface is quite close to the rocky intertidal substrata on which it lives so similarities with benthic diatom flora are to be expected. The 19 diatom taxa shared between chitons and environmental samples

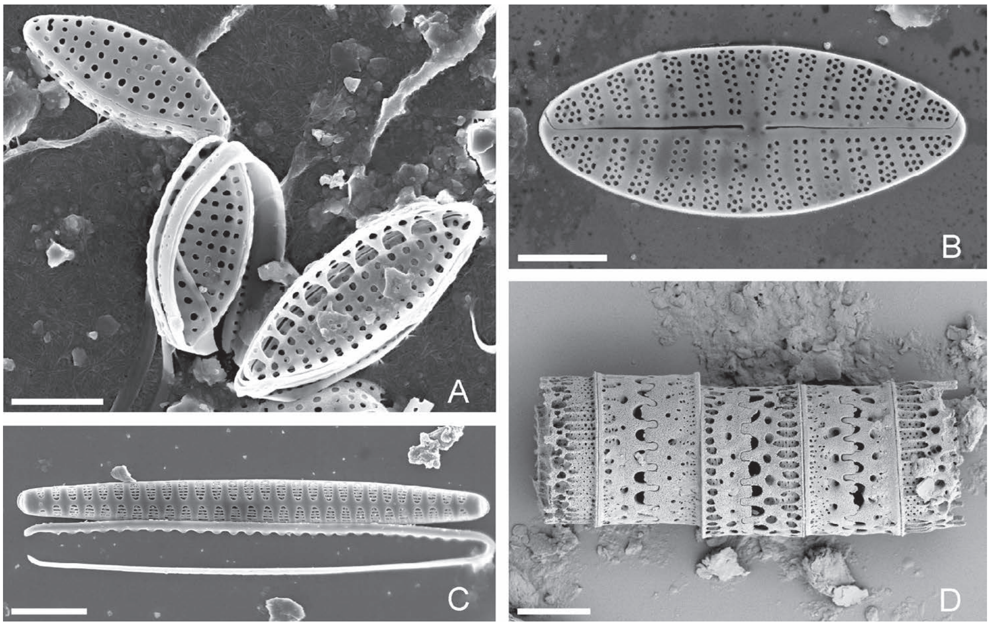

Fig. 6. SEM. Epizoic diatoms of chitons and southern king crabs. A) External and internal views of *Nitzschia* aff. *Inconspicua* valves. B) External valve view of *Planothidium* sp. R-valve. C) External valve view of *Tabularia investiens* with the detail of a girdle band alongside. D) *Paralia sulcata* s.l. frustules forming a "chain-like" colony. Scale bars: 2 µm (A, B) and 5 µm (C, D).

Fig. 6. MEB. Diatomeas epizoicas de quitones y centollas. A) Valvas en vistas externas e internas de *Nitzschia* aff. *inconspicua*. B) Vista valvar externa de valva-R de *Planothidium* sp. C) Vista valvar externa de *Tabularia investiens* con detalle de una banda de la cintura a su lado. D) Frústulos de *Paralia sulcata* s.l. formando una colonia "en cadena". Escala: 2 µm (A, B) y 5 µm (C, D).

are particularly very abundant on chitons suggesting a similarity between both surfaces' diatom flora. These taxa are mainly pennate and exhibited the three attachment mechanisms previously recorded for chitons.

Southern king crabs shared less diatom taxa (11) with their environmental samples suggesting that both samples may not be comparable considering the decapod motility. In this particular case, the common diatom taxa are mainly adnate and erect taxa.

Totti *et al*. (2011) proposes that colonized animals offer an extension of the available surface for the benthic diatoms in the surrounding areas to colonize. Hence, diatoms found on animal hosts are in fact mostly benthic diatoms who developed a particular closeness to hosts as can be the case of some diatom taxa on the chitons here analyzed. In particular, Brandani *et al*. (1974) reported *P. aurata* living over intertidal environments of the South Atlantic Ocean exposed to sunlight, constituting a microhabitat potentially colonizable by diatoms. Madkour *et al*. (2012) studied the Spider Crab *Schizophrys dahlak* (Decapod Crustacean) from Suez Canal and concluded that diatoms found on this particular host are in fact the same as those found on the proximities. This appears not to be the case of the SKC given the fact it did not share many diatom taxa with its environment.

Seasonal Epizoic diatom communities diversity comparison

A comparative analysis for the diatom communities associated to intertidal chitons and subtidal SKC from La Tranquera for 2024 summer and winter, and for an additional sample of SKC from 2018 winter is presented below.

Chitons.— Diatom´s Species Richness (S) on chitons was higher in winter (33) than in summer samples (25). The comparison of Shannon-Weaver index (H´) showed significant differences (α=0.05) in between seasons with a higher diatom diversity in winter samples. Pielou´s Eveness Index (J) were quite similar, indicating that there is no clear dominance of certain species over the rest (Table 2).

Table 2. Diversity indexes estimated for diatom communities from both invertebrate host during summer and winter (2018-2024).

Tabla 2. Índices de diversidad estimados para las comunidades de diatomeas obtenidas de ambos invertebrados durante el verano e invierno (2018-2024).

Invertebrate Host Index / Season	Chitons		Southern King Crabs		
	Summer 2024	Winter 2024	Winter 2018	Summer 2024	Winter 2024
S	25	33	32	32	33
H'	2.48	2.76	2.14	1.98	2.23
J	0.77	0.79	0.62	0.56	0.64

When comparing the diatom communities composition, summer and winter samples shared 34.8% of the taxa, the rest of them being different in between both seasons. *Amphora*, *Cocconeis*, *Navicula*, *Nitzschia* and *Tabularia* were the most representative genera in terms of relative abundance and species richness. *Cocconeis*, *Navicula* and *Nitzschia* were slightly more abundant in Winter whereas *Amphora* and *Tabularia* were more abundant in summer (Table 1; Fig. 7).

Mollusks have been previously studied as possible diatom hosts, particularly Bivalves and Gastropods given the nature of their hard shells and low motility which make them a potential surface for diatoms to colonize (Round, 1971; Totti *et al*., 2011). Gillan & Cadée (2000) found *Cocconeis placentula* and *Achnanthes lemmermanii* forming biofilms on shells of marine gastropods. Also, D`Alelio *et al.* (2011) recorded *Amphora* and *Cocconeis* as the more abundant diatom genera on gastropod shell communities followed by *Grammatophora*, *Licmophora*, *Navicula*, *Nitzschia* and *Tabularia*. These taxa were also recorded in our material and suggest possible similarities in the composition of the epibiotic communities in different types of mollusks. However, this is the first ever study on Polyplacophoran mollusks as potential diatom host and further studies on these particular animal substrata will be conducted in the same area in the future.

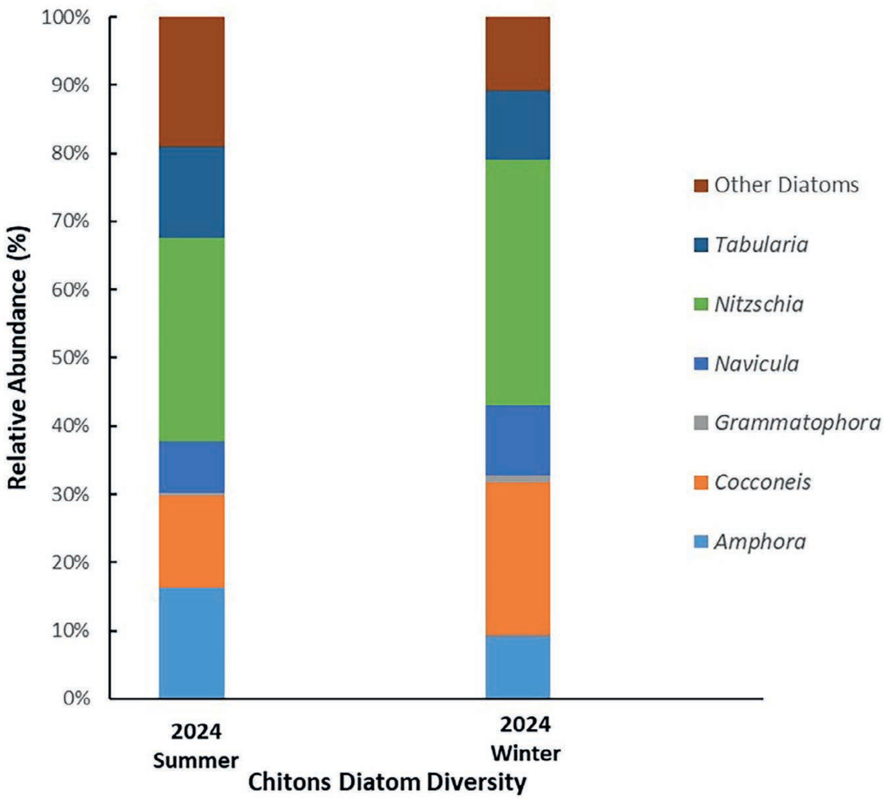

Fig. 7. Relative abundance (%) of the most abundant diatom genera for chitons 2024 summer and winter samples.

Fig. 7. Abundancia relativa de los géneros de diatomeas más abundantes para las muestras de quitones de verano e invierno de 2024.

Southern King Crabs.— Diatoms´s Species Richness (S) on the SKC was slightly higher in 2024 winter (33) but the comparison of Shannon-Weaver indexes (H´) showed significant differences ($\alpha=0.05$) in between both 2024 seasons with a higher diatom diversity in winter samples. Pielou´s Eveness index (J) was also slightly higher in both winter samples showing intermediate values which may indicate the presence of some dominant diatom taxa. The diatom species richness, Shannon-Weaver and Pielou´s Eveness indexes of 2018 and 2024 winter were similar (Table 2).

The 2024 summer and winter samples shared 33.3% of the taxa while 2018 and 2024 winter samples shared 43.4% of the taxa, the rest of them being different in each case. When analyzing and comparing the diatom composition between the three sampled seasons, *Cocconeis, Grammatophora*, *Licmophora*, *Navicula* and *Tabularia* were the more representative genera although some differences as to their abundance and species richness can be recognized in each sample.

Cocconeis was clearly more abundant in 2024 winter. *Navicula* and *Nitzschia* were slightly more abundant and diversified in both 2024 samples and *Tabularia* was the more abundant genus in all three sampled seasons. *Grammatophora* and *Licmophora* were particularly more abundant in 2018 winter than in both 2024 samples (Table 1; Fig.8). *Tabularia* and *Cocconeis* can be regarded as dominant taxa in all seasons analyzed while *Grammatophora* and *Licmophora* were particularly dominant in 2018 winter as *Navicula* was in both 2024 samples.

Cefarelli *et al*. (2024) recorded *T. investiens* as the more abundant diatom species alongside *Cocconeis patagonica* and *Pseudogomphonema kamtschaticum* in a sample of SKC from San Jorge Gulf. We also found *T. investiens* to be the more abundant species on the analyzed hosts, *C. patagonica* was present but not as abundant and *P. kamtschaticum* was not found in the epizoic material but was recorded in environmental samples. *Cocconeis* has been already cited as an epizoic diatom genus on diverse animal substrata such as decapods (Cefarelli *et al*., 2024), bryozooans (Wuchter *et al*., 2003) and cnidarians (Di Camillo *et al*., 2005; Romagnoli *et al*., 2007; Totti *et al*., 2011). Among *Licmophora* species, commonly benthonic, *Licmophora flabellata* has been previously recorded in planktonic samples of the Bay of San Antonio (Argentine Sea) by Sar & Ferrario (1990) and also as an epiphyte species on marine seaweeds by Lobban *et al.* (2011) and Lobban & Santos (2022). Particularly, in this study the species is recorded for the first time as epizoic.

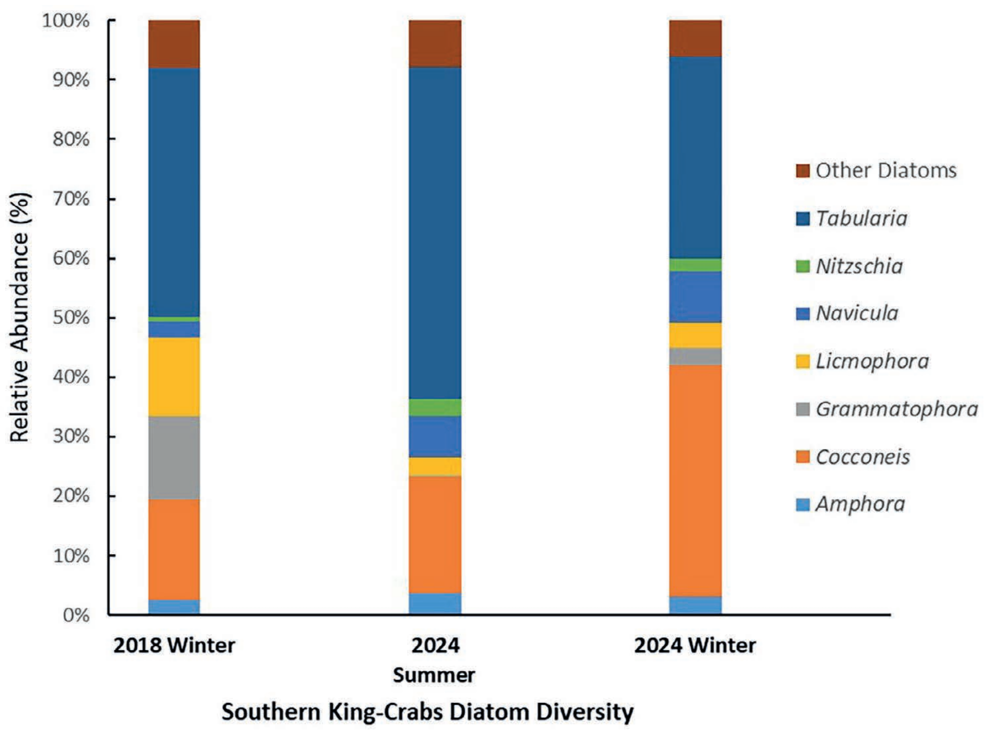

Fig. 8. Relative abundance (%) of the most abundant diatom genera for southern king crab samples from the 2018 austral winter and 2024 austral summer and winter.

Fig. 8. Abundancia relativa (%) de los géneros de diatomeas más abundantes para las muestras de centollas de invierno de 2018 y verano e invierno de 2024.

According to Carreto *et al*. (2007) and Dans *et al.* (2024), the phytoplankton abundance and productivity in San Jorge Gulf is lowest during winter and shows a clear peak in spring and towards summer when the environmental conditions are optimal for its proliferation. Overall and contrary to what we would have expected, diatoms were well represented and diversified during winter, exhibiting the capacity to proliferate and adapt to the winter´s environmental conditions. Similarly, Madkour *et al.* (2012) analyzed the variation of diatom diversity and abundance on decapods through time and also recorded a higher diatom diversity in winter although abundances were clearly smaller for that season. This matter will be addressed in future studies in the area.

CONCLUSIONS

This study constitutes the first characterization of epizoic diatom communities associated with Polyplacophoran Mollusks providing SEM evidence of the direct attachment to the host spines as well as to SKC´s carapace surface.

Diatom diversity and abundance indicate that these invertebrates represent suitable substrates for epizoic colonization and growth despite seasonal environmental differences.

The occurrence of three distinct diatom growth forms on both invertebrate hosts suggests the presence of well-structured epizoic diatom communities.

Amphora, *Cocconeis*, *Navicula*, *Nitzschia* and *Tabularia* are representative genera in terms of species richness and abundance for both invertebrate hosts. In this study, *L. flabellata* is recorded for the first time as an epizoic species.

Further studies need to be conducted in order to accomplish a more extensive and precise characterization of the structure and dynamics of epizoic diatom communities, the possible implications of this particular ecological interaction as well as to describe the diatom flora in the area.

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

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