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Institut de Ciències del Mar
EXCELENCIA SEVERO OCHOA

A todos los que me han acompañado en esta etapa

“Don’t be a drag, just be a queen”

Born this way, **Lady Gaga**

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Creo que todos los que estáis leyendo esto sabéis que esta tesis no ha sido un camino de rosas (¿cuál lo ha sido?). Pero si he llegado hasta aquí ha sido gracias a todos vosotros y vosotras que de alguna manera habéis hecho menos malos y más divertidos los días. Y también por qué no decirlo, gracias a mi empeño, que pocas veces nos lo reconocemos a nosotras mismas.

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Bueno, y ahora sin más dilación, comienzo con las menciones a los miembros de la secta Gilita. Una secta ya disuelta pero que de una manera u otra permanece en nuestros corasonsitos, por increíble que parezca. La verdad, no sé cómo empezar con vosotros, menudo grupo! Se me vienen a la cabeza las comidas y cafés en el despacho del jefe y alguna que otra birra o botella de cava/ratafía a altas horas de la tarde. Y como no mencionar esas reuniones de grupo que hacíamos en las que aún no entiendo cómo solo era el jefe quien se dormía, porque eran eternas. Madre mía, cuántos recuerdos y cómo pasa el tiempo! (comentario un tanto viejuno) Pero para viejuno del grupo, Jordi (además de los miembros anteriormente mencionados). Contigo comencé con *macrospina* y culminé cerrando con el GRAN Miticap. Mi primera salida de pesca fue contigo y con Salvador, menuda primera pesca jaja! Gracias por esas llamadas de tant en tant.

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Y dejando de banda la secta gilita, aunque digamos que las personitas de las que voy hablar ahora también fueron gilitos por un tiempo. Son mis tortilleros del alma. Ari, Claudia y Joan, con quienes compartí los últimos coletazos del Rescap y Miticap. Menudos meses más intensos vivimos juntos, todas terminamos hasta el coñísimo xD! Y como diría el gran sabio Jordi Puigvert, yo no sé como aguantaste, Joan, con menudas tres te fuiste a juntar (cambiando aquí totalmente el contexto de la frase jaja). Pienso en vosotros y solo se me vienen recuerdos llenos de risas, los cuales mencionaré muy escuetamente pero, creo que será más que suficiente para provocaros la misma alegría y cariño con los que os dedico estas palabras: #meahogo #hostiaputaquébuenaestá #peluquería #babytrump #canyonki #bebota #cómovasatiraresta…Joan, gracias por esta maravillosa portada y por las separatas!

Ahora sí que sí, comienzo con el resto de “malagente”. Tras abandonar el régimen estricto de los gilitos, amplié mis fronteras y me sumergí en el B12A, el mejor despacho EVER! Lo teníamos todo, nevera y acuario incluidos! Y también teníamos a los bioinformáticos más sexies del mundo, Aleix y Adri. La envidia de toda persona viviente, vamos jajaja! Aleix, el meu fidel company d’esdeveniment socials (tú aniràs?) i de berenars a les 17h en punt de la tarda. Gràcies per tenir sempre un somriure per mi, escoltar-me quan ho he necessitat i ajudar-me amb l’estadística i Indesign. He gaudit molt al teu costat aquests anys, però el més important és que m’en porto un gran àmic! Adri, la persona que em va ensenyar que juntar taules al campito pot ser molt divertit jajaja! Ho sento, aquesta anècdota havia de sortir. Que divertit va ser muntar un crim a la teva taula i enterrar l’Aleix a la seva! Mariona, tu també et mereixes unes paraules. Només diré, que fort tot plegat, soc bruixa! Jajaja! Quina alegría em dona sempre veure’t i quina il·lusió compartir aquest moment amb vosaltres! Que mai et faltin els pepinillos! Sara, la sureña del grupo, el nexo entre los viejales y los nuevos, ya no tan nuevos jeje! Y compi de contraltos en la coral. Qué gran idea la tuya de llevarnos de karaoke, tanto que repetimos jeje! No debo olvidar mencionar a Scatters, Houdini and Company. Joder, aún me sorprende cómo sobrevivieron tanto tiempo con aquella salinidad tan alta… Tanto sobrevivieron, que pudimos devolver a Scatters al mar que lo vio nacer. Buah, gran llorera la de aquel día. Lo recuerdo ahora y también lloro y el jodio de Joan grabándome jajaja! Gracias por acompañarme en ese momento tan especial, Joan! Andreu, menudas cosas hemos hecho eh! Ains!

Y sigo con mi sister de zumba y de conciertos, mi rubia del Besós. Da igual qué música nos pongan que allí estaremos meneando el culo, aunque una mejor que la otra, eso es innegable. Joder, qué habría hecho sin ti y sin nuestras terapias en tu despacho o en el gym. Lo mejor de todo es que da igual donde estemos y los kilómetros que nos separen, que seguimos contándonos nuestras mierdas y alegrías. Gracias por estar siempre ahí! Alex, el chuloplayas de la rubia, a ti también te tengo que incluir aquí. Gracias por prepararme la camita siempre que salimos de fiesta y dejarme tantas mantas porque ya me conoces y sabes que soy friolera. Y por todas esas visitas a Cadaqués con y sin gasolina! Sin duda ir contigo en coche es una experiencia religiosa jajaja! Anna, madre mia cuánto hace que acabaste la tesis? A mi me parece que fue ayer y eso que creo que fuiste la primera del grupo! Gracias por ser un gran soporte, especialmente los primeros años de esta locura. Esas visitas a vuestro despacho eran clave, me recargábais las pilas para continuar. Manu, la persona que nos arrastró a todos más allá de los muros del ICM. Quien nos sacaba de excursión y organizaba las mejores tardes de juegos que podíamos tener. Nunca olvidaré el día del simulacro de incendio en el que ibas con un vestido rosa, peluca y maquillado andando por los pasillos del ICM, que te llegaste a cruzar con Peters, brutal! Qué bien me lo pasé grabando tu vídeo de final de tesis, haciendo bailar Lady Gaga a todo dios y medio en pelotas jaja! Bueno, realmente he disfrutado tanto haciendo todos esos vídeos de final de tesis...son todos un pequeño recuerdo de vuestro paso del que me encanta haber podido formar parte. Miguel, mi actor favorito, qué gran honor escucharte cantar en la coral y qué honor que me dieras un cachito de tu pan siempre que tenías! Queralt (gran foto la del mes de abril en la biblioteca. Venga ánimo que ya casi lo tienes también!!!), Deju (estabas realmente sexy vestido de Lady Gaga jajaja! #brothersdefinaldetúnel), Dani (otro madrileño colgao por las gorgonias y por los gatos), Marta royo, (la mejor vidente ever), Ana Sotomayor, Carlota, Ana Trindade (si comes mejillones con Guillem, ojo, que te deja sin, aunque ya lo sabrás), Charlie, Elena, Sandra, Alan (gracias por resolver mis mil y una dudas en la recta final) y Guillaume. En este pequeño gran grupo quiero también mencionar a Marc. Tu paso por el instituto fue demasiado fugaz para lo que me habría gustado. Qué alegría me daba bajar a la ZAE sabiendo que estarías. Menudos dramas te comiste por mi parte, gracias por escucharlos siempre con un abrazo. Orlandi, qué poquito nos vemos para lo mucho que te aprecio y lo mucho que me haces reir siempre, siempre es un placer verte. Ahora sí, espero no dejarme a nadie, aunque seguro que alguien me dejo. Por cierto, que sepáis que guardo vuestros culitos con gran cariño, no negaré que me los miro de vez en cuando para echarme unas risas. Poco tiempo me disteis para tocarlos, sueño con la repetición jajaja! Se os quiere!

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Tampoco me olvido de mi familia adoptiva de Barcelona, los yayitos. Aunque ahora ya debería pasarse a llamar yayitos + hijitas. A este paso nos superarán en número, no puede ser. En fin, parece que ya voy a publicar mi trabajo en el TOT Sant Cugat jajaja! Gracias por vuestro apoyo e interés por este mundillo que os queda tan lejano y por todos los momentos compartidos, normalmente comiendo xD. Carles, a ti te tengo que dar las gracias por ser nuestro guía particular en las excursiones, solo puedo reprocharte tu pasión por las torres eléctricas. Gracias por aceptarme en vuestro selecto club y dar cabida a pizzushi jeje!

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A mis peludas, Kenya, Nala y Misha. Todas siempre encima a la mínima que me siento o me tumbo, dándome tanto amor. Quienes hacen que tenga que ponerme el despertador un poco antes para poder disfrutar de los mimos matutinos. Escribir la tesis sin vuestros ronquidos como banda sonora de fondo no habría sido lo mismo.

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Summary

The exploration of marine environments, especially the deep sea, has been an ongoing effort. With the majority of Earth's surface covered by oceans, the invention of SCUBA and subsequent deep-sea expeditions has expanded our understanding of marine ecosystems. However, much of the ocean remains underexplored due to its vast depths. Understanding the biodiversity and functioning of marine ecosystems is crucial for developing effective management plans to protect the oceans. In this regard, this thesis aims to understand biodiversity from various perspectives and how it can vary depending on biological or abiotic factors. Utilizing non-invasive methods with Remotely Operated Vehicles (ROVs), we investigated benthic communities in the area located in front of the Filchner-Ronne Ice-Shelf, in the southernmost part of the Weddell Sea, and in the easternmost part of the same sea, specifically at Maud Rise and Astrid Ridge, covering a depth range from 251 to 1989 meters.

Firstly, we examined the relationship between different demersal fish species and benthic communities comprised of various ecosystem engineers. The study demonstrated that the majority of observed fish species were positively associated with structurally complex ecosystems, with juvenile specimens predominantly found resting or hiding among the engineer organisms. Secondly, we described anthozoan communities on two seamounts and revealed significant biodiversity differences compared to the nearby plain and even between the two seamounts. The reason for these observed differences is partly due to the factor defined by the seamount itself, the region within it (summit vs. slope), the type of substrate and hydrodynamics. Lastly, with the aim of further understanding the biodiversity of one of these seamounts, a *Chrysogorgia* colony was sampled, revealing that the colony belonged to an undescribed species. After the recent review of this genus, it appears that this new species is the only representative of *Chrysogorgia* in the Southern Ocean. While only one sample of this species exists, its colonial morphology characteristics and proximity suggest potential sightings on two other occasions on the same seamount. However, the oceanographic peculiarities of seamounts raise the question of whether this species has an endemic distribution limited to a small region of seamounts or is more widely distributed. Overall, this thesis enhances ecological knowledge of different Antarctic benthic communities, highlighting that seemingly similar environments can exhibit significant different benthic communities and that even at small scales, notable community-level differences can be observed.

Resumen

La exploración marina, especialmente en las zonas más profundas, conlleva un esfuerzo continuo. Los océanos representan la mayoría de la superficie terrestre, y gracias a la invención del SCUBA y las expediciones al mar profundo hemos podido conocer los ecosistemas marinos. Sin embargo, muchos de estos ecosistemas permanecen inexplorados, debido a que gran parte se encuentran a muy elevada profundidad. El conocimiento de la biodiversidad y funcionamiento de los ecosistemas marinos es clave para desarrollar planes de gestión realmente efectivos para proteger los océanos. En este sentido, la presente tesis se plantea con el objetivo global de entender la biodiversidad desde diferentes perspectivas y cómo esta puede ser tan diferente o tan similar según los factores biológicos o abióticos que estudiemos. Para ello, nos hemos basado principalmente en una metodología no invasiva mediante el uso de vehículos operados por control remoto (ROVs), logrando así analizar las comunidades bentónicas presentes en el área marina localizada frente a Filchner-Ronne Ice-Shelf, en la parte más al sur del mar de Weddell y en la parte más al este del mismo mar, concretamente en las montañas submarinas de Maud Rise y Astrid Ridge. Cubriendo un rango batimétrico que va desde los 251 hasta 1989 m de profundidad.

En primer lugar, hemos estudiado la relación que guardan las especies de peces demersales con las diferentes comunidades bentónicas conformadas por distintos tipos de especies ingenieras. Este estudio probó que la gran parte de las especies de peces observadas estaban positivamente relacionadas con los ecosistemas más complejos estructuralmente y que son los especímenes juveniles los que mayoritariamente encontramos reposando o escondiéndose entre los organismos ingenieros. En segundo lugar, hemos descrito las comunidades de antozoos presentes en dos montañas submarinas y hemos visto que la biodiversidad encontrada es realmente diferente a la que encontramos en la planicie más próxima a dichas montañas. Y no solo eso, sino que las comunidades observadas mostraron grandes diferencias incluso comparando las dos montañas submarinas. La razón de estas diferencias observadas se debe en parte al factor definido por la montaña submarina en sí misma, la zona dentro de esta (cima vs. pendiente), el tipo de sustrato y el hidrodinamismo. Y, por último, con la intención de conocer con mayor detalle la biodiversidad de una de estas montañas submarinas, se muestreó una colonia de *Chrysogorgia*, resultando ser una especie no descrita. Además, tras una reciente revisión del género, se ha comprobado que la especie nueva es la única representante de *Chrysogorgia* en el océano Austral. Únicamente se tiene una muestra de dicha especie y, por las características morfológicas de la colonia y proximidad espacial, podríamos decir que se ha observado en dos ocasiones más en la misma montaña submarina. Sin embargo, las peculiaridades oceanográficas de las montañas submarinas nos plantean la incógnita de si es una especie con una distribución endémica de una pequeña región de montañas o se distribuye de una manera más amplia. En general, esta tesis amplia el conocimiento ecológico de diferentes comunidades bentónicas antárticas, resaltando que los entornos aparentemente similares pueden exhibir comunidades bentónicas significativamente diferentes y que incluso a pequeña escala se pueden observar diferencias notables a nivel de comunidad.

Resum

L'exploració marina, especialment en les zones més profundes, implica un esforç continu. Els oceans representen la major part de la superfície terrestre, i gràcies a la invenció del SCUBA i les expedicions al mar profund hem pogut conèixer els ecosistemes marins. No obstant això, gran part d'aquests ecosistemes romanen inexplorats, ja que es troben a molta profunditat. El coneixement de la biodiversitat i el funcionament dels ecosistemes marins és clau per desenvolupar plans de gestió realment efectius per protegir els oceans. En aquest sentit, la present tesi es planteja amb l'objectiu global d'entendre la biodiversitat des de diferents perspectives i com aquesta pot ser tan diferent o tan semblant segons quins factors biològics o abiòtics estudiem. Per això, ens hem basat principalment en una metodologia no invasiva mitjançant l'ús de vehicles operats per control remot (ROVs), aconseguint així analitzar les comunitats bentòniques presents a l'àrea marina localitzada davant del Filchner-Ronne Ice-Shelf, a la part més meridional del Mar de Weddell i a l'est del mateix mar, concretament a Maud Rise i Astrid Ridge. Cobrint un rang batimètric que va des dels 251 fins als 1989 m de profunditat.

En primer lloc, hem estudiat la relació que guarden les espècies de peixos demersals amb les diverses comunitats bentòniques conformades per diferents tipus d'espècies enginyeres. Aquest estudi va demostrar que la major part de les espècies de peixos observades estaven positivament relacionades amb els ecosistemes més complexos estructuralment i que són els espècimens juvenils els que majoritàriament trobem reposant o amagant-se en aquest tipus d'ecosistemes. En segon lloc, hem descrit les comunitats d'antozous presents a dues muntanyes submarines i hem vist que la biodiversitat trobada és realment diferent a la que es troba a la plana més pro-pera a aquestes muntanyes. I no només això, sinó que les comunitats observades mostraven grans diferències, fins i tot comparant les dues muntanyes submarines. La raó d'aquestes diferències observades es deguda en part al factor definit per la muntanya submarina en si mateixa, la zona d'aquesta (cim vs. pendent), el tipus de substrat i l'hidrodinamisme. I, finalment, amb la intenció de conèixer amb més detall la biodiversitat d'una d'aquestes muntanyes submarines, es va mostrejar una colònia de *Chrysogorgia*, resultant ser una espècie no descrita. A més, després d'una recent revisió del gènere, s'ha comprovat que l'espècie nova és l'única representant de *Chrysogorgia* a l'oceà Austral. Només disposem d'una mostra d'aquesta espècie i, per les característiques morfològiques de la colònia i la proximitat espaial, podríem dir que s'ha observat en dues ocasions més a la mateixa muntanya submarina. No obstant això, les peculiaritats oceanogràfiques de les muntanyes submarines ens plantegen l'incògnita de si és una espècie amb una distribució endèmica d'una petita regió de muntanyes o es distribueix de manera més àmplia. En general, aquesta tesi amplia el coneixement ecològic de diferents comunitats bentòniques antàrtiques, ressaltant que els entorns aparentment semblants poden exhibir comunitats bentòniques significativament diferents i que fins i tot a petita escala es poden observar diferències notables a nivell de comunitat.

Contents

INTRODUCTION

Introduction

Commence at the onset

The marine benthic environment constitutes an ecosystem of considerably greater magnitude than its terrestrial counterpart, only about 5% adequately mapped so, there is still much to discover (Wölfl et al., 2019). It is within the depths of the marine seabed that we encounter what are referred to as benthos, encompassing all species engaged in direct associations with the seabed (Haeckel, 1981)

To comprehend everything, we currently know about benthic communities, numerous technological advancements have been indispensable throughout the course of time. The study of benthic organisms is a challenging endeavour, as it involves investigating an environment distinct from our own, the aquatic realm. Additionally, the complexity is compounded by the challenges associated with depth exploration. Humans have been practicing freediving since the Stone Age, whether in search of food resources or goods like red corals and bath sponges (Tescione, 1973; Voultsiadou et al., 2011; Cattaneo-Vietti and Mojetta, 2021). This age-old costume of underwater exploration laid the foundation for early research on benthic communities. In the initial phases of this research, sampling methods such as trawls and dredges were employed (Rhoads et al., 2001; Anderson and Rice, 2006). Centuries passed before significant advancements in underwater exploration unfolded.

The 16th century saw the invention of the diving bell and later, initial diving suits connected to the surface by a tube for air supply, made their debut (Cattaneo-Vietti and Mojetta, 2021). However, it wasn't until 1942–43 that Jacques-Yves Cousteau and Emile Gagnan introduced the revolutionary invention of the self-contained underwater breathing apparatus (SCUBA) (Olmstead, 2008; Lang et al., 2013). The SCUBA facilitated the study of the marine ecosystem, reaching depths up to 50–60 meters. Direct observation gave rise to significant discoveries, particularly regarding the ecology of benthic communities (Lang et al., 2013; Sayer, 2007). In this context, in 1975, Dayton coined the term of "foundation species", a concept now acknowledged as ecosystem engineer species (Jones et al., 1994). The three-dimensional structure of most macrobenthic sessile organisms, such as sponges, gorgonians and bryozoans increase the heterogeneity of habitats. That reduces current velocity facilitating food availability, provides shelter against predators and serves as nursery grounds for a multitude of associated species, thereby promoting ecosystem biodiversity (Gili and Coma, 1998; Buhl-Mortensen et al., 2010; Rossi et al., 2017). It was also during the 20th century when taxonomy ceased to be the primary focus in marine research, giving rise to a significant interest in understanding the relationship between species and the environment (Solan et al., 2003).

Throughout this century, a high number of publications were dedicated to ecological studies (e.g. Sanders, 1968; Johnson, 1971; Kiørboe, 1979)

Deep-sea exploration

The SCUBA represented a milestone in marine research; however, its usage only allows the study of a tiny fraction of the marine environment, given that the average depth of the ocean is around 3,688 meters (Eakins and Sharman, 2010). The deep sea is the largest biome in Earth.

The record of the first sample from the deep sea dates back to 1818, featuring an ophiuroid species collected by Sir John Ross while dredging at 1,600 meters depth (Menzies et al., 1973). In spite of this, it was in 1844 when Forbes coined the Azoic theory, which posited that marine life diminished progressively with increasing depth, ultimately disappearing entirely by 600 meters (Forbes, 1944). Decades later, numerous findings substantiated the theory's invalidity (Ramirez-Llodra et al., 2010). Nevertheless, it was through deep-sea expeditions in the British Isles and the Mediterranean Sea between 1868 and 1870 that Wyville-Thomson, a Scottish naturalist, and Carpenter, a former vice president of the Royal Academy, ultimately refuted the azoic theory (Anderson and Rice, 2006). Two years later, from 1872 to 1876, the circumglobal Challenger expedition took place, signifying a transformative moment in deep-sea research. In fact, this oceanographic cruise is considered as the birth of modern oceanography (Menzies et al., 1973; Ramirez-Llodra et al., 2010).

In the same century of the SCUBA invention, precisely in 1930, *Beebe's* bathysphere was created, the first vehicle that enabled exploration to a depth of approximately 800 meters (Lang et al., 2013). During the first expedition, photographs of the seabed were captured through the porthole (Solan et al., 2003). Three decades later, advancements in underwater photography allowed the documentation of deep-sea megafauna through the use of two cameras positioned at the front of the manned submersible *Alvin* (Grassle et al., 1975). At the same time, different sampling tools were also developed, including the epibenthic sled and the box corer (Hessler and Sanders, 1967; Grassle et al., 1979). Even though it had been quite some time, back in the 18th century, Müller had already invented the first dredge for scientific purposes (Anderson and Rice, 2006). Furthermore, statistics began to emerge as a methodology for studying marine ecosystems, particularly in the context for benthic ensample comparison (Sanders, 1968).

Not long after the fabrication of *Beebe's* bathysphere, technological advances enabled a leap in exploration to one of the planet's deepest areas, the Mariana Trench. It was in the bathyscaphe *Trieste* in 1960 that Jacques Piccard and Don Walsh set the exploration record, investigating benthic communities at 10,916 m depth (Kohnen, 2009). In spite of this significant accomplishment and all the aforementioned advancements, exploration into the depths remained rather infrequent and so much expensive (Wüst, 1964). It has been during the recent decades, facilitated by the development of Remotely Operated Vehicles (ROVs) and Autonomous Underwater Vehicles (AUVs), that marine exploration has made notable strides, concurrently increasing the accessibility to the study of the deep sea by reducing costs and risks (Macreadie et al., 2018; McLean et al., 2020). Consequently, this has led to an exponential increase in the number of scientific publications on deep-sea ecosystems, however numerous undisclosed facets persist, awaiting discovery (Boos et al., 2019; Levin et al., 2019) (**Fig.1**).

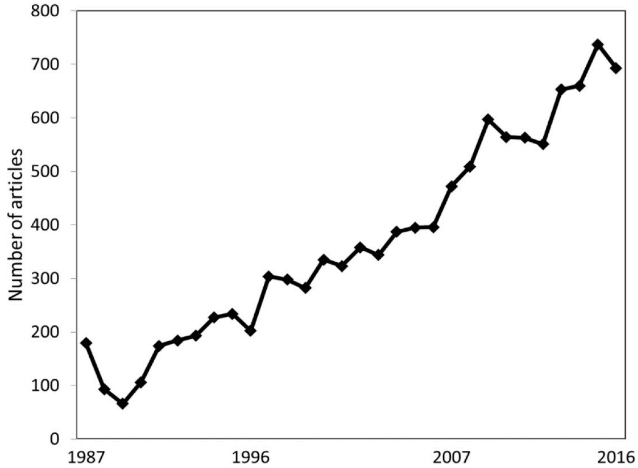

Figure 1. Evolution of the number of scientific articles published on deep-sea studies from 1987 to 2016 according to Web of Science data (Boos et al., 2019).

While employing catch sampling as a method can lead to a disordered collection of animals, and often even the death of the specimens, the use of manned submarines, ROVs and AUVs enables the direct observation of marine ecosystems. This approach represents a conservative method that significantly minimizes impacts on organisms and also can cover vast extensions and depths in a relatively short period of time (Ninio et al., 2003; Solan et al., 2003). These technological instruments are equipped with cameras that facilitates the analysis of the video or photo transects and that can be applied in studies about animal behaviour (La Mesa et al., 2019; Baena et al., 2023), demography, and spatial distribution of benthic (Grinyó et al., 2016; Santín et al., 2018; Corbera et al., 2019) and motile species (Ambroso et al., 2016; Amsler et al., 2015; Ekau, 1990). Furthermore, they are also useful for mapping tasks and sampling, whether it be sediment, water or even specimens for later laboratory research (Marsh et al., 2013; Yoshida et al., 2009).

The development of different types of submersibles, coupled with technological advancements in underwater cameras, have facilitated the exploration of previously unknown habitats, revealing some distinctly peculiar and different ones (Solan et al., 2003). Examples include ecosystems found in hydrothermal vents, seamounts and beneath sea ice (Marsh et al., 2013; Clague et al., 2017; Katlein et al., 2017). However, despite being a realm still rich in undiscovered mysteries, an integral part of planet Earth, and offering numerous resources, the deep sea fails to arouse significant interest among non-scientific society (**Fig. 2**). It shares significant parallels with the field of astronomy in terms of research scope, yet it lacks the same attraction (Jamieson et al., 2021). While many people recall the year when humans first set foot on the moon, far fewer are aware that just nine years prior, mankind reached a depth of 10,916 meters.

Figure 2. Charles Saxon's publication in The New Yorker magazine in 1983, in which the cartoonist humorously asks, 'Why aren't people interested in the deep sea?

Seamount exploration

In 1869, the first seamount, Josephine Bank, was identified and located west of Gibraltar in the North Atlantic Ocean (Ankarcrona, 1969). However, before this discovery, fishermen, merchants and explorers of new lands had already noted increased fish concentrations in specific areas, many of which were later identified as seamounts (Pitcher et al., 2007). Additionally, as early as 1842, Charles Darwin posited the potential existence of seamounts through the hypothesis of the subsidence of volcanic islands and coral reefs (Brewin et al., 2007). Certainly, a significant advancement for the study of marine topography and, consequently, for the identification of seamounts was the development of sonar technology in the mid-1800s (Brewin et al., 2007). This technology was employed during World War II to detect submarines and in preceding inspections for the construction of transatlantic telegraph cable-laying, enabling the discovery of a considerable number of seamounts. In 1952, Marie Tharp commenced the compilation of all echo soundings conducted up to that date, enabling the creation of the first bathymetric map of the Atlantic Ocean, thereby unveiling the V-shaped formation of the Mid-Atlantic Ridge valley (Barton, 2002). This discovery has proven to be a crucial contribution to the theory of plate tectonics and unveil numerous seamounts (Kunzig, 2000).

Despite awareness of the existence of seamounts, they were often referred to by various terms such as “bank,” “ridge,” or “shoal”. It wasn’t until 1938 that the term “seamount” was officially coined (US Board of Geographic Names, 1938). Interestingly, even today, some seamounts still retain these terms as part of their names, as exemplified by Astrid Ridge in the Eastern Weddell Sea. Historically, underwater features exceeding 1000 m have been regarded as seamounts (Menard, 1964). However, this perspective has evolved, and the current concept adopts a more ecological standpoint, considering formations as seamounts regardless of their height (Epp and Smoot, 1989; Smith and Cann, 1990; Staudigel et al., 2010).

The environmental characteristics of seamounts are significantly different from their nearest surroundings, typically represented by vast plains (Auster et al., 2005). These marine rises stand out for their high and complex hydrodynamics, favouring the presence of hard substrate, which is generally uncommon in the surrounding plains (Lundsten et al., 2009; Lavelle and Mohn, 2010; Vlasenko et al., 2018). These features prompted the scientific community to rethink theories related to species biogeography. One of the early theories that emerged is the one that regards seamounts as “stepping-stones”, enabling transoceanic dispersal of species (Hamilton, 1956). Another one that arose together with the existence of seamounts is “isolation theory” which posits that these are isolated habitats fostering the evolution of new species and promoting unique communities (Hubbs, 1959). Part of this isolation is due to the closed recirculating currents (Roden, 1987; Mullineaux and Mills, 1997; Dower and Ian Perry, 2001). Both theories stand in contrast although it does not imply that either one is exclusively true (Clark and Bowden, 2015). In addition, it is also believed that seamounts could have served as a refuge for many species during past climatic changes (Hubbs, 1959; Bowden et al., 2011) and periods of anoxia during interglacial periods (Galil and Zibrowius, 1998; Samedi et al., 2007). Indeed, they could also be crucial for benthic fauna in a warming ocean in the present-future (Rowden et al., 2010).

Generally, seamounts are considered biodiversity hotspots at times (Hubbs, 1959; Genin et al., 1986; Rogers, 1994). However, there exist both scientific works supporting these theories and some that refute them (Wilson and Kaufmann, 1987; Parker and Tunnicliffe, 1994; Richer de Forges et al., 2000; Hall-Spencer and Rogers, 2007). In this regard, when seeking to comprehend the distribution of any species and the connectivity between populations, factors such as evolutionary history and biological traits, such as the reproduction cycle and dispersal abilities, must be considered (Dayton et al., 1974; Connell and Slatyer, 1977; Gili et al., 2006; Fukami, 2015). Additionally, environmental factors such as substrate and current regimes should also be considered (Gutt, 2007; Baena et al., 2023). However, information about the distribution and bathymetry of a species is sometimes based on a single or very few observations (e.g. Cairns, 2002; Xu et al., 2021; Baena et al., 2024). Seamounts continue to be undersampled, so the knowledge of species present in these underwater features, as well as their known biogeography, is quite incomplete. Although exploration of the deep sea in general has increased in recent decades and many deep-sea species has discovered, the effort remains insufficient (Clark et al., 2012). Access to research vessels is limited, and often samples are left forgotten in storage due to the lack of funding and taxonomic expertise (Bouchet et al., 2023). All these knowledge gaps contribute to the fact that many paradigms related to the distribution and biodiversity concerning seamounts are still unresolved.

As previously mentioned, one of the characteristics of seamounts, and one of the earliest discoveries related to them, is the high abundance of fish around these underwater formations (Hubbs, 1959; Morato et al., 2010). This phenomenon is particularly notable in seamounts with summits at depths of less than 1500 m, where both pelagic and benthopelagic species are found in high densities (Dower and Ian Perry, 2001; Rogers, 1994). Squids, turtles, sharks, mammals, and even seabirds are also frequently observed in large aggregations (Pitcher et al., 2007). Various theories attempt to explain the high abundance around seamounts. Initially, it was believed that the elevated primary production was transferred to higher trophic levels (Hubbs, 1959; Roden, 1987). Later, the “topographic blockage” theory emerged, explaining that micronecton is captured as it becomes trapped by the seamount’s topography as it moves downwards (Genin, 2004). Others posit that seamounts serve as navigational waypoints for migratory species (Holland and Grubbs, 2007; Kaschner, 2007) as well as breeding grounds (Pankhurst et al., 1987; Tsukamoto, 2006; Litvinov, 2007).

This led to the exploitation of many seamounts through fisheries, with the Azores and Madeira serving as examples of regions where such exploitation began in the 1960s (Heydorn 1969; Da Silva and Pinho, 2007). Seamount fisheries are characterized by sequences of boom and bust exploitation patterns (Clark and Koslow, 2007). This type of practice involves a significant risk to the sustainability of fish stocks (Roberts, 2002; Morato et al., 2006). In this regard, there is a growing concern that a substantial portion of seamounts is currently being overexploited (Clark, 2009; Clark et al., 2012). Moreover, one of the commonly employed fishing methods in seamounts is trawling, leading to severe impacts on benthic communities (Clark and Rowden, 2009). Many benthic organisms in seamounts are considered vulnerable species, such as a significant proportion of anthozoans, characterized by slow growth and low recruitment rates (Sherwood and Edinger, 2009; Watling et al., 2011; Clark et al., 2016). Consequently, the recovery of these organisms following any kind of impact is very slow (Williams et al., 2010). This situation prompted the inclusion of seamounts as part of Vulnerable Marine Ecosystems (VMEs) in the United Nations General Assembly (UNGA) Resolutions 61/105 and 64/72 in 2007 and 2009, respectively, as a conservation measure.

Antarctic exploration

The Southern Ocean encompasses a total area of approximately 35 million km^2, representing 10% of the Earth's oceans (Clarke and Johnston, 2003; Brandt et al., 2007a). It is characterized by a continental shelf unusually deep, with an average depth of 450–500 meters, although at certain points, it exceeds 1000 m. Around 80% of the Southern Ocean seabed exceeds depths of 3000 m, encompassing a substantial portion of Antarctic marine ecosystems within what is referred to as the deep sea (Clarke and Johnston, 2003).

The exploitation of Antarctic resources, such as sealing and whaling, dates back to the last years of the 18th century (Bonner, 1987; Hempel, 2007). However, it was not until the mid 19th century that the Erebus and Terror expeditions (1839-1843), led by James Clark Ross, resulted in the publication of the first studies on diatoms in pack ice (Ehrenberg, 1844; Hooker 1847). It was during the circumglobal expedition of the Challenger (1872–1876) that a total of 4714 species were sampled and described, many of which were of Antarctic origin (Dater, 1975; Gutt et al., 2010). This expedition along with others such as Belgica (1897–1898), Valdivia (1898–1899) and Pourquoi pas? (1908–1910) contributed to the backbone of Antarctic marine taxonomy (Hempel, 2007). In 1925, the Discovery and Meteor expeditions were initiated, aiming to comprehend the factors determining the distribution of whales. Consequently, the study of krill became a primary objective of these campaigns (Bonner, 1987; Hempel, 2007). In the mid to late 20th century, a significant economic interest in the fishing of fish and krill emerged, leading to the subsequent and necessary establishment of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) (Hempel, 2007). It was in the late 20th and early 21st centuries, notably with the RV Polarstern, that the understanding of the Antarctic ecosystem experienced a substantial leap, particularly concerning benthic ecology (Arntz et al., 1994; Hempel, 2007).

Nonetheless, studying in Antarctica presented a greater challenge compared to other regions due to the extreme cold conditions. Despite the earlier invention of SCUBA, the extreme cold conditions limit diving times and safety conditions. Coupled with sea-ice constraints, this has restricted research in the Southern Ocean (Katlein et al., 2017). The development of ROVs, along with other submersible devices, has marked a significant turning point in general marine exploration, as mentioned previously. But in Antarctic exploration, this advance had a greater impact by breaking the limitations imposed by the freezing climatology (Clarke, 1996; Kaiser et al., 2013).

Bullivant and Dearborn (1967) were pioneers in employing photographic cameras for the study of benthic communities in the Ross Sea. While the investigation of benthic communities in the Weddell Sea did not transpire until 1988 (Voß, 1988). This sea is distinguished by its heavy sea-ice conditions, rendering access to the area challenging (Vernet et al., 2019). Technological advancements in photographic and video techniques facilitated the acquisition of quantitative and ecological data that were previously unattainable. Additionally, direct observation has revealed high diverse benthic communities (Arntz et al., 1994). Initial ecological research employing this methodology focused on the association of Antarctic benthic suspension feeders and motile deposit feeders with different types of substrate (e.g. Barthel and Gutt, 1992; Gutt, 1991; Gutt and Schickan, 1998; Gutt and Starmans, 1998). Besides, as early as 1990's, the analysis of underwater photographs and videos enabled the description of the habitat of high Antarctic notothenioid fish, along with some peculiarities in their behavior (Ekau, 1990; Ekau and Gutt, 1991).

Already in the 21st century, studies on the responses of Antarctic biodiversity to climate change have gained prominence (Kaiser and Barnes, 2008; Ingels et al., 2012; Zwerschke et al., 2021) and international collaborations have increased to understand the potential drivers of Antarctic biodiversity distribution (Kaiser et al., 2013). There has been a resurgence of interest in the study of biodiversity, leading to an increase in sampling intensity in the Southern Ocean, such as in the case of the eastern Weddell Sea (Clarke, 2008). This has resulted in the discovery of undescribed species and the recognition that Antarctic fauna can be highly diverse and abundant, even in abyssal depths, despite its patchy distribution (Brandt et al., 2007b; Kaiser et al., 2007). Moreover, approximately 80% of the Southern Ocean constitutes deep sea, suggesting a considerable reservoir of undiscovered fauna (Clarke and Johnston, 2003; Clarke, 2008). However, taxonomic expertise is unfortunately declining (De Broyer et al., 2011). For this reason, significant efforts are underway to facilitate identification through the improvement or development of new methods, such as online identification guides and interactive identification keys (David et al., 2005; Coleman et al., 2010).

In recent decades, molecular techniques have advanced significantly, which, along with morphological studies, has facilitated species identification (Kessel et al., 2023). However, many Antarctic samples were preserved in formaldehyde and, therefore, cannot be used for genetic approaches. It was not until the 1990s that the use of ethanol and freezing samples was established as protocols for subsequent genetic analysis (Kaiser et al., 2013). In recent times, taxonomy has evolved into an increasingly interdisciplinary field, with studies now incorporating genetic, morphological, ecological, and biogeographical analyses (Ivanova and Grebelnyi, 2021; López-González, 2022; López-González and Drewery, 2022; Peña Cantero, 2023). This shift is exemplified by a notable surge in integrative analyses of new octocoral species over the last decade (Kessel et al., 2023). Nevertheless, the prevalence of this broader approach varies by geographical region, with the Southern Ocean exhibiting a relatively lower percentage (~20 – 25%), while South Africa and Western Pacific seamounts boast the highest numbers, representing the majority of octocoral publications with an integrative focus.

AIMS AND OBJECTIVES

Aims and objectives

Marine exploration is crucial for understanding how we can protect marine ecosystems. However, only a small percentage of the ocean floor has been studied, with the deep sea and seamounts being clear examples of ecosystems that require greater research efforts. Thanks to technological advancements in recent decades, exploring these ecosystems at great depths has become more feasible, thus facilitating greater accessibility to previously inaccessible areas and enhacing our understanding of the biodiversity.

This thesis comprises three chapters aimed at studying Antarctic biodiversity from different perspectives, with the global aim of broading ecological knowledge for future management plans. The first chapter focuses on examining how the community of demersal fish varies depending on the type of benthic communities, and explores the specific relationship between the different fish species observed and the various engineer species. In the second chapter, we describe why we found different anthozoan communities in apparently similar ecosystems, specifically two seamounts, and how they differ from the surrounding plain. Finally, in the third chapter, we aim to deepen our understanding of the biodiversity on one of those seamounts by describing a newly discovered species of gorgonian.

The outline of the different chapters is further detailed by several tasks as follows:

Objective 1. **Are there distribution patterns and population structure differences among demersal fish species in relation to Antarctic benthic communities? A case study in the Weddell Sea.**

- Identification of demersal fish species, their density, spatial distribution and size-frequency distribution populations.
- Description of fish assemblages.
- Study of the relationship between benthic communities and the different fish species, including any behavioral patterns observed.

Objective 2. **Anthozoan communities of two Antarctic seamounts: a comparative study of Maud Rise and Astrid Ridge**

- Study the density and spatial and bathymetric distribution of anthozoans.
- Description of anthozoan assemblages.
- Analyse the relationship between these assemblages and the geomorphological features of the seamounts, type of substrate, and the co-occurring benthic fauna.
- Comparisons of anthozoan assemblages between seamounts and the adjacent plain.

Objective 3. **A new deep-sea species of golden gorgonian (Octocorallia: Scleralcyonacea: Chrysogorgiidae) from Antarctic waters.**

- Study of the colonial and sclerite morphology of the new species.
- Conduct molecular analyses through the sequencing of two mitochondrial markers (mtMutS and COI) and one ribosomal marker (28S) to reconstruct the phylogeny of the new species.
- Comparative study with other congeners regarding geographical and bathymetric distribution, as well as morphological and molecular characteristics.

Sometimes I wonder if I should be medicated
If I would feel better just slightly sedated
A feeling comes so fast and I cannot control it
I'm on fire, but I'm trying not to show it
As it picks me up, puts me down

It picks me up, puts me down
Picks me up, puts me down
A hundred times a day
It picks me up, puts me down
It chews me up, spits me out
Picks me up, puts me down

I'm always running from something
I push it back, but it keeps on coming
And being clever never got me very far
Because it's all in my head
And "You're too sensitive", they said
I said, "Okay, but let's discuss this at the hospital"

As it picks me up, puts me down
It picks me up, puts me down
Picks me up, puts me down
A hundred times a day
It picks me up, puts me down
It chews me up, spits me out
Picks me up, puts me down

But I hear the music
I feel the beat
And for a moment
When I'm dancing, I am free
I hear the music
I feel the beat (ahh)
And for a moment
When I'm dancing, I am free, I am free

Ooh, ooh

Is this how it is?
Is this how it's always been?
To exist in the face of suffering and death
And somehow still keep singing
Oh like Christ up on a cross
Who died for us? Who died for what?
Oh, don't you wanna call it off?
But there's nothing else that I know how to do
But to open up my arms and give it all to you

'Cause I hear the music, I feel the beat
And for a moment, when I'm dancing
I am free, I am free
I am free, I am free

Free, **Florence + The Machine**

CHAPTER 1

CHAPTER 1

Are there distribution patterns and population structure differences among demersal fish species in relation to Antarctic benthic communities? A case study in the Weddell Sea

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Abstract

Despite the general belief that the Southern Ocean harbors low fish biodiversity, the Weddell Sea hosts one of the richest fish communities in the region. Parallelly, the Weddell Sea is also known for the presence of dense and diverse macrobenthos. Most macrobenthic invertebrates, such as gorgonians, sponges and bryozoans, are considered ecosystem engineers as they generate a three-dimensional structure that increases habitat heterogeneity. This structural complexity serves as a refuge against predators as well as a nursery ground for many organisms, including fish species. By analyzing video transects recorded by a Remotely Operated Vehicle, we investigated density, spatial distribution and size-frequency of populations of the demersal fish species inhabiting macrobenthic communities in the southernmost part of the Weddell Sea. We also attempted to unveil whether there is any relationship between benthic and fish communities and substrate, as well as some fish behavioral patterns. The dominance of juveniles in the surveyed fish assemblages provides evidence that, at this life stage, some fish species appear to be positively associated with complex benthic communities conformed by bryozoans, sponges and gorgonians which are more common in sand matrix with sparse rocks substrates. Moreover, about 37% of all specimens recorded were resting on benthic invertebrates or were using them to hide, implying that Antarctic benthic communities might offer suitable habitat. As such, it can be concluded that there was an apparent relationship between certain species of fish and the different benthic communities, yet the exact triggers and/or factors behind such an association remain partially elusive.

1. Introduction

The Southern Ocean is the water body occupying a total area of 34.8 million km^2 comprised between the coast of the Antarctic continent and the Antarctic Polar Front (also known as Antarctic Convergence, located at about 50°S in the Atlantic and Indian sectors and 60°S in the Pacific sector) (Hofmann, 1985). It is characterized by low water temperature and seasonal primary production due to seasonal ice cover, which has remained practically unaltered over the last 20 million years (Clarke and Crame, 1989). Yet, despite its large dimension and long evolutionary history, fish biodiversity is less diverse than expected (Eastman, 2005).

Fish species with benthic habits are the most diverse and abundant fish group in Antarctic waters, representing more than 60% of all Antarctic fish species, with the Notothenioidei suborder being the major component in terms of biomass and number of demersal species (Dewitt 1971; Eastman and Hubold, 1999; Eastman et al., 2013). In fact, most of the notothenioid species are endemic to the Southern Ocean (Andriashev, 1965; Kock, 1992). This high endemism has occurred due to the Antarctic Polar Front, which acts as a zoogeographic boundary, as well as the constant and severe conditions of the Southern Ocean waters (Eastman and Clarke, 1998; Peck, 2018). The Notothenioidei currently includes 9 families and 140 species, from which 5 families and 110 species are exclusively present in Antarctic waters, while only 4 families and 30 species are non-Antarctic (Eastman and Eakin, 2021; Daane and Detrich, 2022).

Despite the aforementioned generalization that the Southern Ocean presents lower fish diversity than expected, the Weddell Sea stands out as a hotspot of fish diversity within the area, harboring the highest number of fish species within the Southern Ocean (Hubold, 1991). Within the High-Antarctic Zone (*sensu* Kock, 1992), the Weddell Sea is characterized by a wide shelf as deep as more than 1000 m (Ekau, 1990; Anderson, 1999). It also shows the most durable sea-ice coverage, which plays a fundamental role in physical and biological processes, such as the formation of the coldest water masses and productivity (Clarke and Ackley, 1984; Peck, 2018). Furthermore, the bottom of the High-Antarctic Zone stands out due to the presence of diverse and dense macrobenthic communities, known as the Antarctic Marine Animal Forests (AMAF) (Arntz et al., 1994; Gutt et al., 2004; Gili et al., 2006). Most of the macrobenthic sessile organisms in these communities, such as gorgonians, sponges and bryozoans, are considered ecosystem engineers since they generate a three-dimensional structure that increases habitat heterogeneity (Jones et al., 1994; Gili and Coma, 1998; Rossi et al., 2017). This increase in structural complexity provides a wide array of niches in the areas those species occur, which in turn might serve as a refuge against predators or as nursery grounds for many other species, including fish species (Gutt et al., 1994; Gratwicke and Speight, 2005; Buhl-Mortensen et al., 2010; La Mesa et al., 2019). In this regard, previous studies have noted that some fish species settle on elevated benthic structures such as sponges, a behavior considered characteristic for certain species (Ekau and Gutt, 1991; Gutt and Ekau, 1996). Yet, while macrobenthic sessile organisms might increase the diversity and density of other taxa, their presence does not always lead to an increase in diversity, as the degree of habitat modification depends on the density and size of the engineer species (Jones et al., 1994; Cerrano et al., 2010).

In the past, it was only possible to study marine ecosystems through destructive methods but, thanks to technological advances, that has changed. Technological advances and the development of remotely operated vehicles (ROVs), manned submersibles, autonomous underwater vehicles (AUVs) and ocean floor observation systems (OFOS) have made it possible to go further in understanding the marine environment, enabling an in situ overview of the ecosystem (Gutt and Ekau, 1996; Santín et al., 2018; La Mesa et al., 2022). While catch sampling is a destructive technique that normally results in a disordered sampling of animals, underwater photography and video are conservative methods that significantly minimize impacts on sessile organisms. Image methods allow for direct observation, as well as a much greater study area in terms of extension and depth, compared to using destructive methods (Ninio et al., 2003; Matarrese et al., 2004; Rossi et al., 2008). As so, underwater video and photo technology has been used for studies on biomass (Mühlenhardt-Siegel et al., 1988; Pabis et al., 2011), animal behavior (Ekau and Gutt, 1991; La Mesa et al., 2019) demography and spatial distribution of benthic (Segelken-Voigt et al., 2016; Ambroso et al., 2017) and motile species (Ekau and Gutt, 1991; Lorance and Trenkel, 2006; Amsler et al., 2015; La Mesa et al., 2022). Moreover, some studies have provided the same results on the distribution and abundance of fish species by comparing catch sampling and image techniques, validating the usage of the later for fish community studies (Ekau and Gutt, 1991; Gutt et al., 1994; La Mesa et al., 2019). Yet, despite the possibilities offered by imaging techniques, few studies have focused on the macrobenthic species that accompany fish assemblages in different study areas (Gutt et al., 1994; Gutt and Ekau, 1996; La Mesa et al., 2019).

Hence, the present study aims to fill the said knowledge gap and respond to the hypothesis of a possible relationship between complex benthic communities and greater biodiversity of Antarctic fishes. In order to achieve this, three main objectives have been pursued through video analyses: (1) identification of demersal fish species, their density, spatial distribution and size-frequency distribution populations; (2) description of fish assemblages; and (3) a study of the relationship between benthic communities and the different fish species, including any behavioral patterns observed.

2. Material and methods

2.1. Study area

The study area was located in front of the Filchner-Ronne Ice Shelf (FRIS), in the southernmost part of the Weddell Sea (**Fig. 1**), which has, until now, been poorly studied due to heavy sea-ice conditions and consequently difficult access. Therefore, any new information about this region is of special relevance. This area is characterized by cold and dense water masses with a cyclonic clockwise flow (Deacon, 1979; Daae et al., 2020). Near the bottom, the Weddell Sea Bottom Water (WSBW) can be found, which is slightly warmer than the Weddell Sea Deep Water (WSDW). Above this, there is the Warm Deep Water (WDW), which occupies the layer of 200 – 1200 m depth and its temperature is between -1 and -2 °C (CTD data). In addition to this, the continental shelf includes two water masses that make up the Dense Shelf Water (DSW): The Ice Shelf Water (ISW) and the High-Salinity Shelf Water (HSSW). They originate from the sea ice production (Haid and Timmermann 2013) and, in turn, contribute to the formation of the Weddell Sea Deep and Bottom Waters (Gordon et al., 1993; Orsi et al., 1999). All of the conditions of the shelf water masses have remained practically stable since the 1980s (Janout et al., 2021). The entire area is mainly characterized by soft bottoms with different proportions of sand, gravel and boulders (Anderson et al., 1980; Haase, 1986).

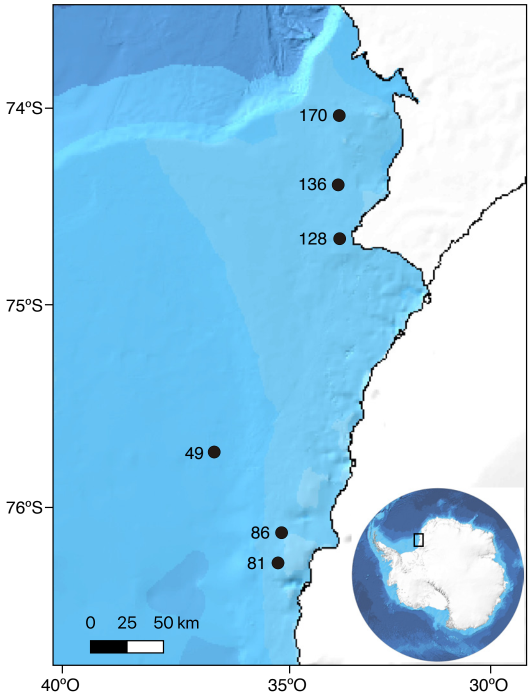

Figure 1. Study area. Location of the video transects in the study area in front of the Filchner Ronne Ice Shelf in the Weddell Sea.

2.2. Video recording

A total of six video transects were analyzed, covering a total area of 1,845.9 m^2 between 251 and 361 m depth, as part of the multidisciplinary scientific cruise PS82 (ANT XXIX/9) expedition on board the RV *Polarstern*, conducted from December 2013 to March 2014.

To study the composition and distribution of Antarctic fishes and their relationships with invertebrate benthic macrofauna, an inspection-class ROV (Ocean Modules V8Sii) was deployed at six stations in the area of the Filchner Trough (**Fig. 1**). The videos were acquired with a High Definition (HD) video camera (Kongsberg oe14–502) recording with a viewing angle of 29° x 45° (vertical x horizontal) and equipped with two lasers with a 4 cm separation that serves as a reference scale, used for the spatial density and fish size analyses. Furthermore, the ROV was equipped with ultra-short baseline (USBL) positioning data. All of the ROV video material pertaining to this study is available from the data publisher PANGAEA® at www.pangaea.de (Owsianowski et al., 2017).

2.3. Video analysis

Video transects were analyzed using Premiere Pro CC version 12.1.2 (Adobe Inc.) software and following the methodology described in Gori et al. (2011). Each track was edited before the analysis in order to remove pauses, loops or video sequences where the image quality was not suitable for the study, for example, when there was sediment resuspension. After editing, every benthic organism and fish observed along the transect was annotated, within a section of 0.3 m width around the central position of the laser beams. A reference time was assigned to each benthic organism and fish was when it was observed and their position along the transect was recorded with geographical coordinates. In addition, following the same analysis procedure, substrate type and depth was annotated along each transect. Substrate types were classified into three categories, namely: sand matrix with rocks, gravel matrix, and rock matrix. Seabed slope was also analyzed, and it was consistently found to be 0.

2.4. Data analysis

Once fish species and benthic organisms had been identified and georeferenced, it was decided to take an area of 50 m^2 as a sampling unit (0.3 m width and 166.5 m length) to analyze the data statically. Since the target fish of the study are demersal, but the benthic communities are mainly composed of sessile animals and could present a highly patchy distribution, the sampling unit chosen to study both of them is 50 m^2. Each sampling unit was characterized by a type of macrobenthic community and substrate. The slope of all the transects was zero, and the sea bottom was horizontal. This factor was therefore not considered to characterize the sampling units, and not used for statistical analysis either. Depth was also ruled out as an influencing factor in this study because an ADONIS test was carried out using the *vegan* package (Oksanen et al., 2013) from RStudio (RStudio Team, 2019), and no influence of depth was found on the studied fish assemblages. The study area corresponds to a unique water mass (WDW), and that could be the reason why depth did not appear to be an influent factor in this case. Regarding benthic classification, four benthic communities were defined by the most abundant engineer species: bryozoan community (B), when more than 85% of the macrobenthic organisms were bryozoans and no other macrobenthic phylum reached 10% coverage by itself; bryozoan and sponge community (BS), when bryozoan represented more than 60% and sponges more than 15% of the macrobenthos; sponge and bryozoan community (SB), which was dominated by sponges, with any inverse distribution (≥ 60% and ≥ 15%, respectively); and lastly, bryozoan, gorgonian and sponge community (BGS), where bryozoans represented more than 60%, gorgonians more than 20%, and sponges more than 10% (**Fig. 2**). Besides the types of benthic communities, two kinds of bottom substrate were defined: sand matrix with sparse rocks and gravel matrix. Each sampling unit usually presented a combination of both, but was defined by the most abundant (with a percentage of 80% or more).

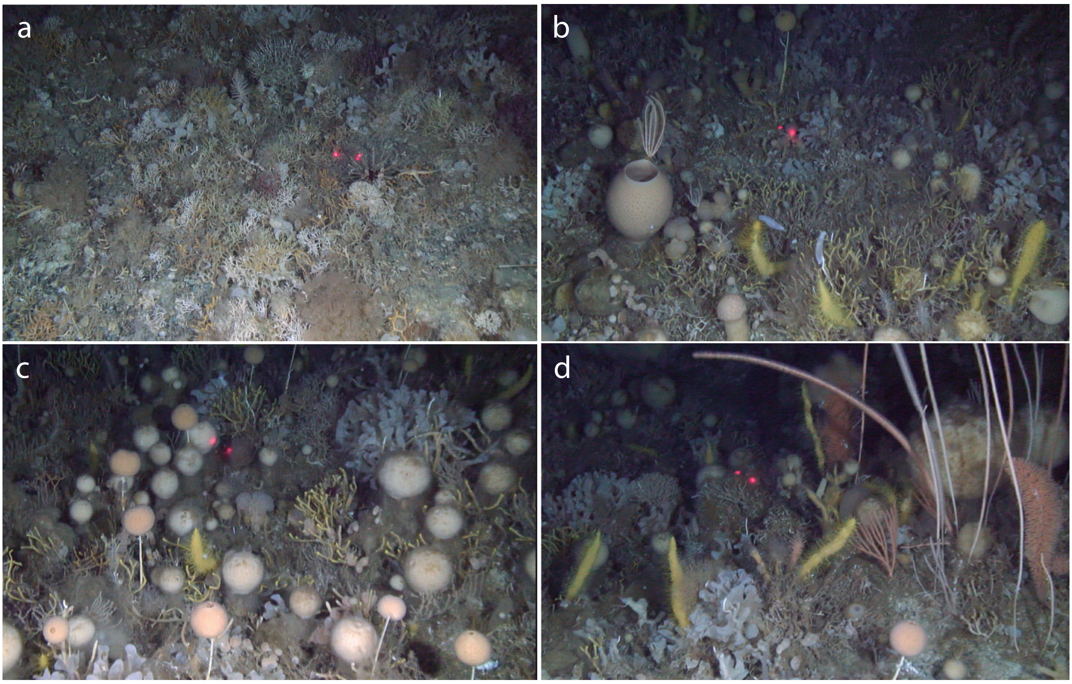

Figure 2. Benthic communities. **a**: Bryozoan community (B). **b**: Bryozoan and sponge community (BS). **c**: Sponge and Bryozoan community (SB). **d**: Bryozoan, gorgonian and sponge community (BGS).

2.5. Density and spatial distribution and size-frequency of fish populations

For statistical analysis, all of the transects were divided into sampling units of 50 m^2 (0.3 m width and 166.5 m length). A total of 37 sampling units were obtained from six transects, composed of four sampling units of transect 49, four more of transect 81, eight of transect 86, seven of transect 128, seven sampling units of transect 136, and seven more of transect 170, respectively. In order to study the distribution for the most representative species, a geographically-referenced map was generated using QGIS version 3.16 (QGIS.org, 2022), in which both fish density and the corresponding type of benthic community of the sampling unit were represented. In addition, the species composition was examined and their density (ind. 100 m^{-2}) were quantified.

The size frequency of fish populations was computed only for those species with more than 13 individuals documented. The ROV lasers were set at a known distance from each other (30 cm) and provided a scale for the measurement of fish individuals. When a fish appeared in the video transect, a photo was taken when the lasers were parallel to the individual, which was then analyzed for measurements by means of the software Macnification version 2.0.5 (Schols and Lorson, 2008) In order to compare species with different size population, size-frequency histograms were performed for each species by means of the *ggplot2* package (Wickham, 2016) from the R software platform (RStudio Team, 2019). In the High Antarctic, more than 90% of notothenioids do not reach 45 cm total length, and other fishes like artedidraconids are typically less than 15 cm. The variability of maximum fish sizes between observed fish species is the reason why the sizes of fishes are classified in small ranges of 3 cm.

2.6. Fish assemblage composition

Aiming to find some assemblage present in the study area, abundances of fish species were represented by means of a dendrogram and non-metric multi-dimensional scaling (nMDS). Before the analysis, the abundance data were transformed using the *square-root* method to normalize them, and then distances between pairs of sampling units were calculated using the Bray-Curtis dissimilarity index. To obtain the dendrogram, the hclust function of *vegan* package (Oksanen et al., 2013) was used from the RStudio platform (RStudio Team, 2019). In order to elaborate the nMDS, the *metaMDS* function was applied, again available via the *vegan* package (Oksanen et al., 2013). Three sampling units were discarded from the statistical analysis, having no fish because of the analysis requirements. Dendrograms and nMDS are only representations of how sampling units are grouped, as an exploratory method to graphically visualize if there might be some kind of relationship among the data. The ADONIS test was applied using the *vegan* package (Oksanen et al., 2013) to determine any statistical differences among fish assemblages with RStudio software (RStudio Team, 2019). To carry out these analyses, individuals classified at the genus or family level have not been considered, because they could be different species and, therefore, could have different substrate and benthic community preferences, which could introduce errors in the interpretation of the results.

2.7. Relationship with environmental features

The distribution of fish species, like all other animals, is determined by environmental features. In this sense, in the present study, the environmental factors determining fish distribution were explored by canonical correspondence analysis (CCA), which is a multivariate analysis. CCA allows the identification of probable relationships between fish species and environmental factors (Greenacre, 2013). The environmental features considered were depth, substrate, and benthic community. Sampling units without fish were excluded because of the statistical test requirements. For this reason, only a total of 34 sampling units were analyzed. Additionally, the individuals not classified at species level were deleted for this analysis, for the same reason as in the dendrogram analysis. Another statistical test to find out how fish species are related to environmental factors was Indicator Value Analysis (IndVal), which was described by Dufrêne and Legendre (1997). The analysis presents a table of indicator species that are quite abundant and significantly characteristic in a type of habitat and with a p-value of less than 0.05. In this study, this was tested with the different types of benthic communities and substrates previously defined, using the indval function of the labdsv package (Roberts and Roberts, 2016) of RStudio (RStudio Team, 2019). In addition, the richness and diversity of fish species were quantified by means of the Shannon Diversity Index, which was calculated for the different types of benthic communities and substrates. This is represented in two box plots carried out via the ggplot package (Wickham, 2016) of RStudio (RStudio Team, 2019).

3. Results

3.1. Density, spatial distribution and size-frequency of fish populations

A total of six stations of video transects of the seabed were conducted in the Weddell Sea from 251 m to 361 m water depth, covering an area of 1.845,9 m^2. Thanks to the high resolution of the camera, the majority of the fishes observed were identified at species level. The rest of them were identified within a family or genus category. In these cases, the high swimming speed or the incomplete vision of the body prevent identification with the highest level. Overall, 12 fish genera and 14 fish species were identified. A total of 414 specimens were recorded that could be identified to species level (87.2%), and the rest of the individuals have been identified to genus (11.3%) and family level (1.4%). Icefish of the genus *Chionodraco* were not identified to the species level, as we were not able to clearly distinguish between them. The major diversity and density of fish were found at stations 128, 136 and 170 (**Tables 1 and 2**). Fishes recorded belonged to four families, such as Artedidraconidae, Bathydraconidae, Channichthyidae and Nototheniidae. The family Nototheniidae was the most abundant, including in decreasing order of abundance *Trematomus scotti* (Boulenger, 1907) (30.7%), *T. lepidorhinus* (Pappenheim, 1911) (13.8%), and *T. eulepidotus* (Regan, 1914) (10.4%). The Channichtyidae was the second most abundant and speciose family, encompassing at least six different species, followed by the Bathydraconidae with four species, whereas the Artedidraconidae family was represented by a single specimen of *Pogonophryne scotti* (Regan, 1914). In terms of spatial distribution, only the six most abundant species were represented in maps (**Fig. 6**). *Chionodraco* spp. and *Chaenodraco wilsoni* (Regan, 1914) were observed only in northern stations, while T.*scotti*, *T. eulepidotus*, *T. lepidorhinus* and *Pagetopsis maculatus* (Barsukov and Permitin, 1958) were distributed both in the northern and southern stations. The size-frequency distributions are summarized in **Figure 3**. The size population of the fish species was described only when the number of observations of each species amounted to more than 13 individuals (**Fig. 4**). All nototheniids belonged to *Trematomus* genus and reached a maximum total length (TL) of 21 cm, with a modal size of 9 cm. This pattern of size distribution can also be observed with the specimens of *Pagetopsis*, whereas *Cryodraco antarcticus* (Dollo, 1900) and *Chionodraco* spp. showed the largest sizes reaching more than 30 cm TL. In *Chionodraco* spp. it should be highlighted the absence of individuals smaller than 18 cm TL.

Table 1. Geographical coordinates, depth and area analyzed and abundancy and density of fishes for each of the ROV dives analyzed in this study.

	South			North		
Track	49	81	86	128	136	170
Longitude (start)	76°31'92'' S	77°08'03'' S	76°95'64'' S	75°50'04'' S	75°33'32'' S	74°89'87'' S
Latitude (start)	3°30'96'' W	3°36'51'' W	3°29'87'' W	2°74'54'' W	2°71'40'' W	2°67'63'' W
Longitude (end)	76°32'15'' S	77°08'58'' S	76°96'53'' S	75°49'15'' S	75°33'35'' S	74°89'34'' S
Latitude (end)	3°30'98'' W	3°36'56'' W	3°29'52'' W	2°74'68'' W	2°71'77'' W	2°66'65'' W
Depth (m)	251	361	284	292	350	295
Square meters analised	203.38	208.09	400.24	346.51	334.51	353.04
Number of fishes	28	12	6	103	151	114
Density (ind. 100m^{-2})	13.77	5.77	1.50	29.72	45.13	32.29
Mean density (ind. 100m^{-2})	7.01 ± 6.22			35.71 ± 8.25		

3.2. Fish assemblage composition

To find out the fish assemblage composition, a dendrogram was performed representing the sample clustering based on a Bray-Curtis dissimilarity matrix (**Fig. 5**). Cluster analysis separated five assemblages (at 60% of dissimilarity), with the 8, 9 and 13 sampling units being considered as outliers. Most of the sample units classified as BGS benthic community (red colour in the cluster, **Fig. 5**) are grouped in the representation of the cluster, and all of them are characterized by sand as the most abundant substrate. The second group contains all the SB sampling units (grey colour, **Fig. 5**), and the majority of them correspond to the matrix of gravel substrate. The last group shows the majority of the BS sampling units (green colour, **Fig. 5**) and this grouping can be divided into two depending on the substrate. As a result, fish distribution appears to be related benthic communities and substrate.

Table 2. Fish species in the study area. Density, abundance and percentage of every species calculated over the total number of individuals recorded for each video transect.

Fish species	**Transect density (ind. 100 m^{-2})**						**Sum of transects**	
	49	**81**	**86**	**128**	**136**	**170**	**Nº ind.**	**% ind.**
Artedidraconidae								
Pogonophryne scotti	0	0.48	0	0	0	0	1	0.24
Bathydraconidae								
Cygnodraco mawsoni	0.49	0.48	0.25	0.29	0.6	1.13	10	2.42
Gerlachea australis	0	0	0	0	1.8	0.28	7	1.69
Gymnodraco acuticeps	0	0	0	0	0	0.57	2	0.48
Racovitzia glacialis	0	0	0	0	0.6	0.28	3	0.72
Channichthyidae								
Chaenodraco wilsoni	0	0	0	1.44	7.77	0	31	7.49
Chionodraco spp	0	0	0	0.29	2.69	9.91	45	10.87
Cryodraco antarcticus	0	0	0	0	2.99	1.13	14	3.38
Pagetopsis macropterus	0	0.48	0.25	2.89	1.2	0	16	3.86
Pagetopsis maculatus	0.59	0.96	0	4.62	6.28	1.13	44	10.63
Pagetopsis spp	0	0	0	0	0.6	0	2	0.48
Prionodraco evansii	0	0	0	0.29	0.6	0	3	0.72
Channichthyidae unidentify	0	0.48	0	0.29	0.9	0.28	6	1.45
Nototheniidae								
Trematomus eulepidotus	0.49	0.96	0.25	8.08	2.09	1.13	43	10.39
Trematomus lepidorhinus	11.8	1.44	0.75	2.75	0.3	4.25	57	13.77
Trematomus loennbergii	0	0	0	0	0.9	0	3	0.72
Trematomus scotti	0.49	0.48	0	8.4	15.84	12.18	127	30.68

The non-metric multi-dimensional scaling (nMDS) was another analysis to pursue some relation between benthic communities, substrate and fish distribution (**Fig. 6**). The ordination of the sampling units that correspond to the SB community are clearly grouped; the same occurs with the BGS community, and some grouping formed by the sampling units of the

BS community could also be seen. Consequently, there could be a correlation between fish biodiversity and density and these types of benthic communities. On the other hand, despite some sampling units of the B community also being grouped, others are not. Regarding the substrate, there is a spatial ordination of the different types of substrate that proves that there also seems to be a relationship between this environmental factor and the distribution and abundance of fish species. All this coincides with the result obtained from the dendrogram. In addition, the ADONIS test confirmed that benthic communities are different (p-value < 0.01) (**Table 3**). Comparing benthic communities in pairs, results show that all of them were different from each other, except for the B and BS communities (p-value = 0.238) (**Table 3**). The two categories of substrate, sand matrix with some rocks and gravel matrix, also appear to be different from each other (p-value < 0.001).

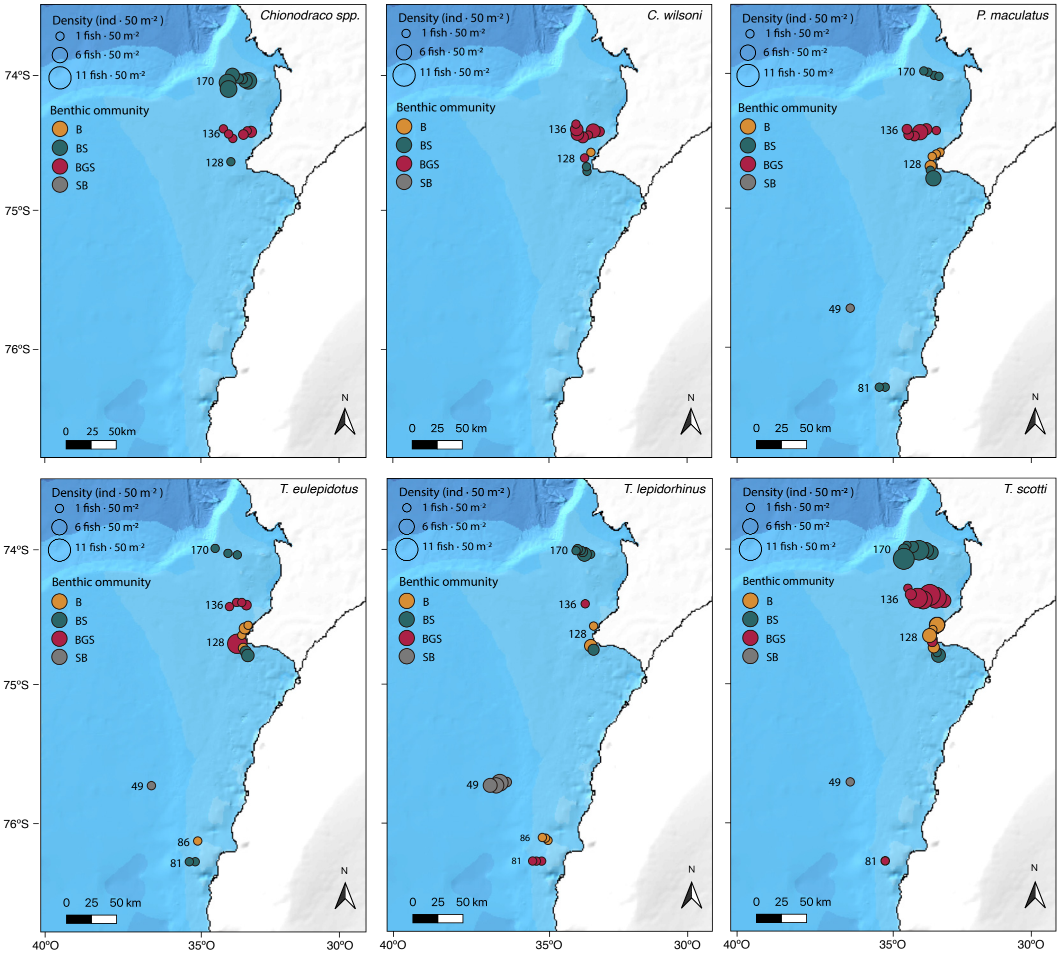

Figure 3. Geographical distribution in the study area of the most common fish species represented based on density and benthic community. Bryozoan community (B), bryozoan and sponge community (BS), sponge and bryozoan community (SB) and bryozoan, gorgonian and sponge community (BGS).

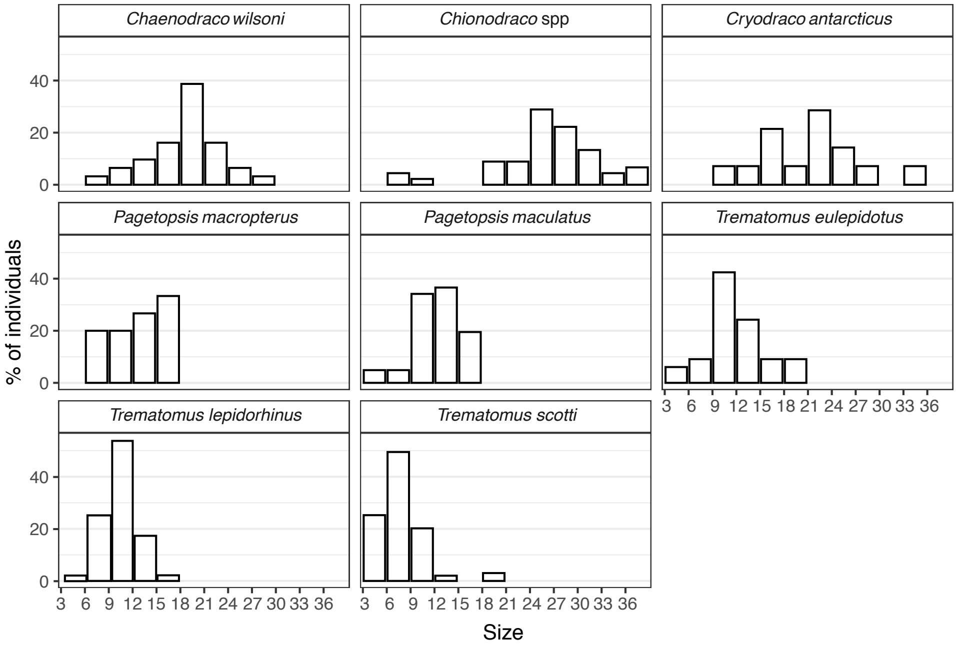

Figure 4. Size-frequency distribution for *Chaenodraco wilsoni*, *Chionodraco* spp. *Cryodaco antarcticus*, *Pagetopsis macropterus*, *Pagetopsis maculatus*, *Trematomus eulepidotus*, *Trematomus lepidorhinus*, *Trematomus scotti*.

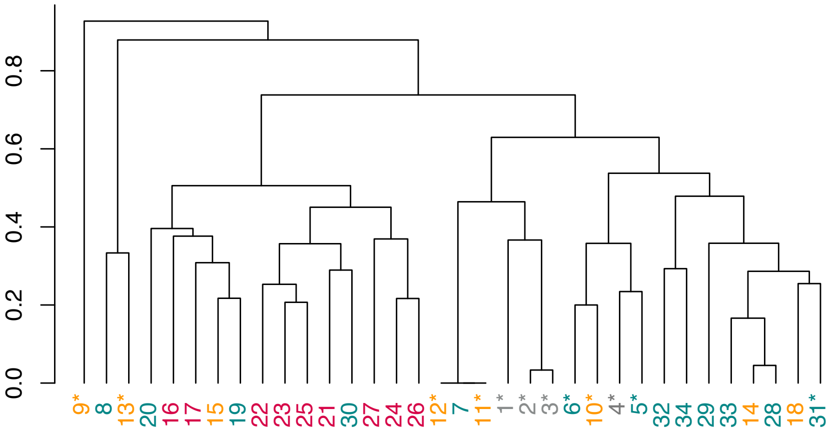

Figure 5. Dendrogram representing the sampling units clustering based on a Bray-Curtis dissimilarity. The colours of the sampling units indicate the type of benthic community. Orange: Bryozoan community. Green: Bryozoan and Sponge community. Red: Bryozoan, gorgonian and sponge community. Grey: Sponge and bryozoan community. The asterisk indicates sampling units with gravel bottom and the absence of it indicates sampling units defined as sand matrix with rocks.

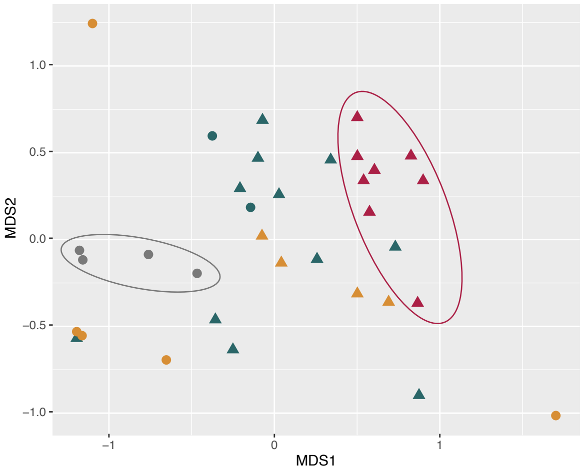

Figure 6. NMDS biplot of Bray-Curtis dissimilarity matrix of the different sampling units analyzed. Each sample unit was classified with a type of benthic community and substrate, as well as the abundances of the observed fish species were studied. Orange: Bryozoan community. Green: Bryozoan and Sponge community. Red: Bryozoan, gorgonian and sponge community. Grey: Sponge and bryozoan community. Triangle: Gravel substrate Circle: Sand matrix with rocks.

Table 3. Results of ADONIS test comparing the different benthic communities based on fish species abundances.

	B	BS	BGS	SB
B	-	0.238	0.001	0.011
BS		-	0.002	0.001
BGS			-	0.003
SB				-

3.3. Relationship with environmental features

Regarding geographical distribution and benthic communities' preferences of the studied fish species (**Fig. 3 and Table 4**), *P. scotti* and *Gymnodraco acuticeps* (Boulenger, 1902) were observed exclusively restricted to the BS community, whereas *Pagetopsis* spp. and *Trematomus loennbergii* (Regan, 1913) were recorded within the BGS community. *Gerlachea australis* (Dollo, 1900), *Racovitzia glacialis* (Dollo, 1900), *Chionodraco* spp., *C. antarcticus*, *Prionodraco evansii* (Regan, 1914) and some non-identified individuals belonging to the Channichthyidae family were associated to the BS and BGS communities. *Pagetopsis macropterus* (Boulenger, 1907) and *C. wilsoni* occurred within three benthic communities B, BS and BGS, whereas the remaining species were observed everywhere. The highest densities were found within the BS community, where *T. scotti* density was 8 ind. m^{-2}, and also in the BGS community, where the maximum density of *C. wilsoni* was 6.75 ind. m^{-2}, but the latter was the benthic community with the highest total density of fish species. All species were observed on sampling units with a matrix of sand with rocks, yet some species were also found on sampling units defined as having gravel bottoms, but with low densities, such as *P. maculatus* and *P. macropterus*.

Conversely, *T. lepidorhinus* is the only species that showed higher density on gravel bottoms, yet it occurred on both types of substrate.

As observed in the results obtained with the dendrogram and nMDS, it seems that fish assemblage has a relation with benthic communities and substrate. To delve further into this, a CCA was performed that shows the relations between fish species with the benthic community and substrate (**Fig. 7**). Sand substrate with rocks seems to have a strong relationship with the vast majority of identified species, except for *T. lepidorhinus*. Regarding the benthic communities, most fish species are positively related to BGS communities, such as *G. australis*, *T. loennbergii*, *C. wilsoni* and *C. antarcticus*. Differently, G. acuticeps and *P. scotti* prefer the BS community, and *Cygnograco mawsoni* (Waite, 1916) seems to be more associated with B community. The CCA analysis is complemented by a statistic analysis, the Indicator Value Analysis (IndVal), which shows, with a *p*-value of less than 0.05, that *T. lepidorrhinus* is characteristic of the SB community, *Chionodraco* spp. are common in the BS community, and the C. wilsoni, *C. antarcticus*, *T. scotti*, *G. australis* and *T. loennbergii* species are characteristic in the BGS community. Moreover, this same test shows, with a *p*-value of < 0.05, that *T. lepidorrhinus* is typical on gravel bottoms, while *T. scotti*, *T. eulepidotus*, *P. maculatus* and *C. wilsoni* are more characteristic on sandy ground.

Table 4. Density of fish species observed (ind. 100 m^{-2}) according to the type of benthic community and substrate.

Species	**Community**				**Substrate**	
	B	**BS**	**BGS**	**SB**	**Sand matrix with rocks**	**Gravel matrix**
Artedidraconidae						
Pogonophryne scotti	0	0.15	0	0	0.09	0
Bathydraconidae						
Cygnodraco mawsoni	0.44	0.77	0.5	0.5	0.61	0.55
Gerlachea australis	0	0.15	1.5	0	0.61	0
Gymnodraco acuticeps	0	0.31	0	0	0.17	0
Racovitzia glacialis	0	0.15	0.5	0	0.26	0
Channichthyidae						
Chaenodraco wilsoni	0.22	0.46	6.75	0	2.7	0
Chionodraco spp	0	5.54	2.25	0	3.3	1.28
Cryodraco antarcticus	0	0.62	2.5	0	1.13	0.18
Pagetopsis macropterus	1.78	0.46	1.25	0	1.3	0.18
Pagetopsis maculatus	1.78	2.15	5.25	0.5	3.65	0.36
Pagetopsis spp	0	0.00	0.5	0	0.17	0
Prionodraco evansii	0	0.15	0.5	0	0.26	0
Channichtydae indet.	0	0.46	0.75	0	0.52	0
Nototheniidae						
Trematomus eulepidotus	2.22	2.31	4.25	0.5	3.57	0.36
Trematomus lepidorhinus	2.22	3.38	0.25	12	2.26	5.64
Trematomus loennbergii	0	0.00	0.75	0	0.26	0
Trematomus scotti	4	8.00	14	0.5	10.52	1.09
TOTAL	12.66	25.08	41.5	14	31.38	9.64

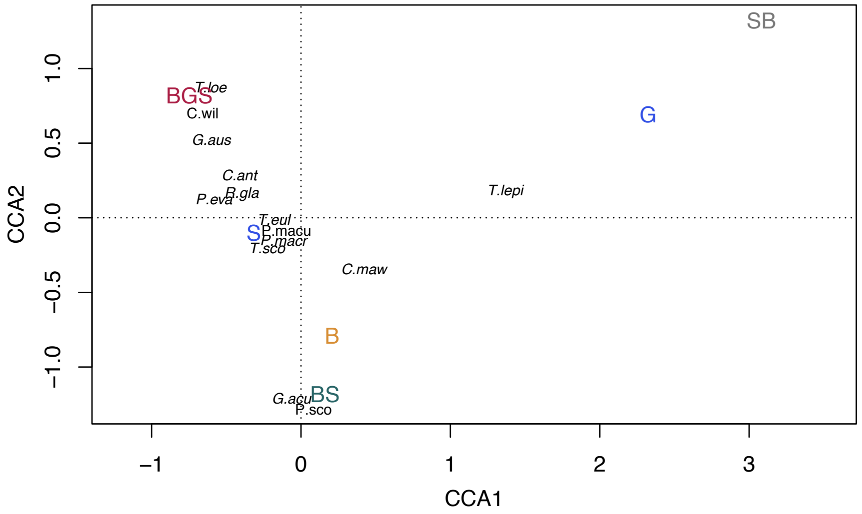

Figure 7. Canonical Correspondence Analysis (CCA) biplot of fish species constrained by benthic community and substrate. B: Bryozoan community, BS: Bryozoan and sponge community, BGS: Bryozoan, gorgonian and sponge community, SB: Sponge and bryozoan community, S: Sand matrix with rocks, G: Gravel matrix.

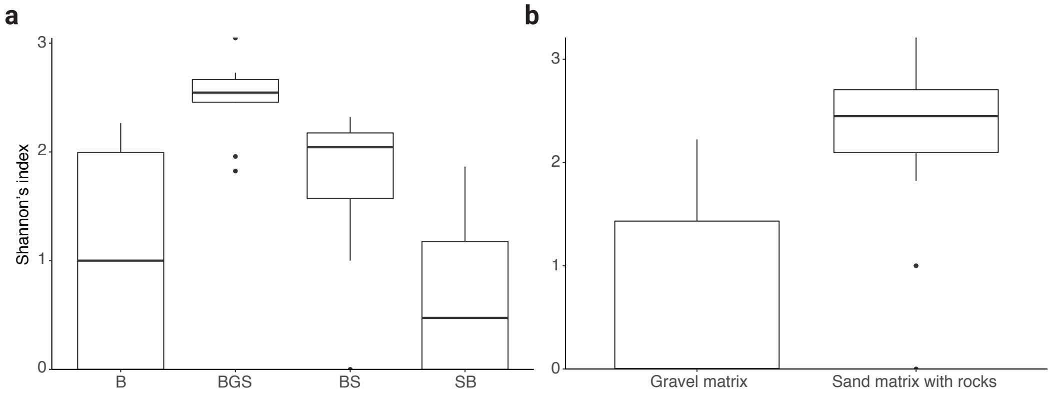

Figure 8. (a) Box plot of Shannon's index of the different benthic communities studied. **(b)** Box plot of Shannon's index of the different kind of substrate observed.

In agreement with our previous results, Shannon's index was highest in BGS community and lowest in SB community (**Fig. 8**). Regarding substrate, sand matrix with sparse rocks shows the highest Shannon values, so this type of substrate appears to favor fish biodiversity and abundance. In addition, it should be said that the most complex benthic communities studied (BGS) were observed only in sampling units with sand matrix with rocks, so a relationship might also be deduced. Conversely, in sampling units with a gravel matrix, simpler benthic communities have been observed. In fact, most of them were B communities. Indeed, the only three fishless sampling units that were excluded from the dendrogram and CCA analyses are predominantly characterized by a gravel substrate and B community. Therefore, the results seem to be consistent. The biodiversity indexes were calculated considering all the fishes identified at species and genus level. Following this, one genus could be represented by more than one species, so the biodiversity index calculated could be the same or less than real biodiversity index.

4. Discussion

The analysis of the images has allowed the identification of a total of four fish families: Artedidraconidae, Bathydraconidae, Channichthyidae and Nototheniidae of the perciform suborder Notothenioidei. These families are the most abundant in the High-Antarctic Zone, especially on the continental shelf of the Weddell Sea (Ekau, 1990). Nevertheless, other families occur in the High-Antarctic Zone, like Liparididae and Zoarcidae, which are less abundant but equally diverse as those mentioned, were not observed in this survey (Anderson, 1990). In this sense, some fishes may be so elusive to the presence of submersible devices, to the point of becoming undetectable (Katsanevakis et al., 2012). As a result of this circumstance, the number of observations in this study could be underestimated. Throughout the study area, the fish assemblage was mainly characterized by representatives of the family Nototheniidae, being Trematomus the most abundant genus, followed by the Channichthyidae family, whose most representative genera were *Pagetopsis* and *Chionodraco* (**Table 2**), in accordance with data from previous studies in the southeastern Weddell Sea and other regions of the High-Antarctic Zone (DeWitt, 1971; Ekau, 1990; La Mesa et al., 2019). This contrasts with the Antarctic Peninsula that belongs to Low-Antarctic Zone also called Seasonal Pack-Ice Zone, where the *Nototheniops* spp. and *Notothenia* spp. were predominant (Targett, 1981; Kock and Stransky, 2000).

Matching the size-frequency distributions of fishes with size (**Fig. 4**) at sexual maturity reported elsewhere, it was possible to infer the population structure of the species recorded. Among nototheniids, *T. eulepidotus* and *T. lepidorhinus* attain sexual maturity at 21 – 24 and 18 – 21 cm TL, respectively (DeWitt et al., 1990; Duhamel et al., 1993 La Mesa et al., 2008), so the population surveyed consisted exclusively of juveniles and subadults (**Fig. 4**). Conversely, the population of *T. scotti* was composed of both juveniles and adults, as they reach sexual maturity at 12 – 13 cm TL (Duhamel et al., 1993). In this sense, although belonging to the same genus, different species might present contrasting population demographics, highlighting the importance of accurate identification of the specimens. Among channichthyids, *P. macropterus* and *P. maculatus* attain sexual maturity at 18 – 19 cm TL, whereas for *C. wilsoni* it is at 23 – 25 cm TL (Duhamel et al., 1993; Kock et al., 2008), so their populations consisted solely of juveniles and, in the case of *C. wilsoni*, with the additional presence of just a few adults (**Fig. 4**). Similarly, all the specimens of *C. antarcticus* were juveniles, as they reach sexual maturity at a size larger than 35 cm (Kock and Jones, 2002), which were not observed in the present study (**Fig. 4**). Conversely, the populations of *Chionodraco* spp. included both juveniles and adults as *C. myersi* (DeWitt and Tyler, 1960) and *C. hamatus* (Lönnberg, 1905) attain sexual maturity at 25 – 30 cm and 35 cm TL, respectively) (Duhamel et al., 1993; La Mesa et al., 2003). In summary, *T. eulepidotus*, *T. lepidorhinus*, *T. scotti*, C. wilsoni, *P. maculatus* and *P. macropterus*, six of eight species whose size population has been analyzed, exhibited a population dominated by juvenile stages. These species have in common that they reflect some dependence on the water column, since much of their diet is made up of krill or other euphausiids (Targett, 1981; La Mesa et al., 2004). These results lead to hypothesize that adult individuals might show more active behavior for prey in the water column, while juveniles belonging to these species might prefer the most complex benthic communities formed by sponges, bryozoans and gorgonians, which provide a suitable place to hide from predators until they reach a larger size.

In this sense, observation in situ by means of video transects also allowed us to assess the relationships between fish and benthic communities, as well as to evaluate their habitat preferences and specific behaviors. As has been mentioned previously, benthic organisms such as sponges, gorgonians and bryozoans offer protection, food and a place for breeding and nursery for different notothenioid fishes (Ekau, 1990; Ekau and Gutt, 1991). In agreement with previous studies (Ekau and Gutt, 1991; Gutt and Ekau, 1996; La Mesa et al., 2019) *T. lepidorhinus* prefers benthic communities characterized by populations of sponges and bryozoans. In fact, during the course of this study *T. lepidorhinus* had often been observed resting on or hiding inside volcano sponges (more than 60% of observations for this species). Similarly, several species (*T. scotti*, *T. loennbergii*, *C. antarcticus*, *C. wilsoni* and *G. australis*) were common where bryozoans, gorgonians and sponges are abundant (**Table 4 and Fig. 7**). Some authors explain this preference by the three-dimensional structure that these engineer animals offer for protection against predators, being an advantage for the "sit-observe and hide" strategy of some fish species during their juvenile stage (Gutt and Ekau, 1996; La Mesa et al., 2019). Further, these kinds of complex benthic communities offer suitable habitats for sedentary species that use the same strategy but for hunting. They lie in wait hidden and hunt on the prowl (Ekau and Gutt, 1991). Conversely, was *C. mawsoni* the only fish species which showed a preferential relationship for bryozoan communities and more open areas without high-growing sponges (**Table 4 and Fig. 7**) (Ekau and Gutt, 1991). Regarding substrate preference observed, fish diversity rose in sandy areas with rocks where the most complex benthic communities were common and consequently, the variety of ecological niches were greater (**Fig. 8**). Conversely, fish biodiversity decreased in gravel areas hosting simpler benthic communities (**Fig. 8**). In this sense, the different kinds of substrates and benthic communities studied make that fish assemblage vary depending on them. Consistent with their benthic and sedentary behaviors, about 37% of all specimens recorded were resting on benthic invertebrates such as sponges and bryozoans or were using the tridimensional structures created by the macrobenthos to hide. The rest of the observed fishes were found swimming a few centimeters above the substrate. It should be also mentioned that *C. wilsoni* was observed seven times out of 31 sightings guarding eggs on nets composed of flat drop stones, with a behavior previously observed in the west Antarctic Peninsula (Ziegler et al., 2017) and the Weddell Sea (La Mesa et al., 2019; Kock et al., 2008). For this reason, in order to ward off potential predators such as starfish and other fish species, nesting and parental care are common in demersal species like *C. wilsoni* (Kock et al., 2006).

5. Conclusions

To conclude, the distribution and abundance of fish species depend on a large number of factors not considered in this research, but which are still important, such as temperature and food availability (Ekau and Gutt, 1991). Further, ice-scouring also represents a determining factor in the distribution of species at a small scale in High-Antarctic waters (Brenner et al., 2001). This study proves that seems to be a close relationship between the different species of fish observed and the different benthic communities defined by the predominant engineer organisms, and consequently, by their structural complexity. Fish species take advantage of the structures of benthic organisms to hide from predators, like *T. lepidorhinus*, or to hunt on the prowl as *C. antarcticus* does. Despite there not being a clear correlation with all of the fish species, biodiversity is indeed greater in sandy areas with rocks where complex benthic communities are more common.

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Data Availability Statement

PANGAEA® at www.pangaea.de

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Tú que has sangrado tantos meses de tu vida
Perdóname antes de empezar
Soy engreída y lo sabes bien

A ti que tienes siempre caldo en la nevera
Tú que podrías acabar con tantas guerras
Escúchame

Mamá, mamá, mamá
Paremos la ciudad
Sacando un pecho fuera al puro estilo Delacroix
Mamá, mamá, mamá
Por tantas ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma
Ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma, mamá
Todas las ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma
Ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma, mamá

Tú que amarraste bien tu cuerpo a mi cabeza
Con ganas de llorar, pero con fortaleza
Escúchame

Mamá, mamá, mamá
Paremos la ciudad
Sacando un pecho fuera al puro estilo Delacroix

Mamá, mamá, mamá
Por tantas ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma
Ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma, mamá
Vivan las ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma-ma
Ma-ma-ma-ma-ma-ma-ma-ma....

No sé por qué dan tanto miedo nuestras tetas
Sin ellas no habría humanidad ni habría belleza
Y lo sabes bien
Lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo
(Lo sabes bien) lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo-lo

Escúchame
Mamá, mamá, mamá

Ay Mamá, **Rigoberta Bandini**

CHAPTER 2

CHAPTER 2

Anthozoan communities of two Antarctic seamounts: a comparative study of Maud Rise and Astrid Ridge

Patricia Baena, Andreu Santín, Stefano Ambroso, Luis Martell, Joan J. Soto-Angel, Marina Biel-Cabanelas, Anne Kari Sveistrup, Covadonga Orejas, Anne Helene Solberg Tandberg

Abstract

Seamounts are underwater elevations that harbour relatively isolated ecosystems shaped by environmental forces such as flow intensification and complex hydrodynamics, favouring communities of benthic suspension feeders like anthozoans. In this study, we describe the taxonomical composition, density and spatial and bathymetric distribution of anthozoans by analysing video transects recorded on two seamounts east of the Weddell Sea (Southern Ocean), specifically Astrid Ridge and Maud Rise. Additionally, the relationship of these anthozoan assemblages with different study areas, substrate types, and the coexisting fauna were analysed. Our findings reveal marked differences between both seamounts. Maud Rise exhibits predominantly hard substrate, hosting a high density of anthozoans, particularly octocorals, co-occurring with other abundant benthic suspension feeders, mostly ascidians. In contrast, Astrid Ridge features soft substrate, with hexacorals and sea pens as the most abundant anthozoans coexisting with motile and detritivores species. Anthozoan distribution in both areas displays a patchy pattern, exhibiting greater small-scale diversity on Maud Rise and larger-scale diversity on Astrid Ridge. Further comparisons with prior studies in the Weddell Sea plain identify Actiniaria as the most taxonomically diverse group in both seamounts and plain, with Hexacorallia notably more abundant in the plain than in the seamounts. Therefore, despite their spatial proximity, the anthozoan communities we found on both seamounts differ from those observed on the surrounding plain. While the full complexity of anthozoan spatial dynamics in the area is still incompletely explored, our results show the significant influence of substrate and hydrodynamics in their structure, and highlight the importance of a good understanding of the distribution patterns for effective conservation management.

1. Introduction

Traditionally, seamounts have been defined as submarine mountains with summits rising more than 1000 m above the seafloor (Menard, 1964). However, modern research has adopted an ecological perspective recognizing their unique environmental conditions, and instead of the strict height limit of the first definition, hills and knolls are currently also considered seamounts (Epp and Smoot, 1989; Smith and Cann, 1990; Staudigel et al., 2010). As of today, there is no consensus on the total number of existing seamounts worldwide, as this number varies depending on bathymetric resolution and methodology, yet it is estimated that over 43,000 can be found on the ocean's floor (Kim and Wessel, 2011; Gevorgian et al., 2023). In this regard, the technological advancements along with the development of different visual methods have facilitated the study of these submarine features in the last few decades, enhancing our understanding of their ecology, diversity and hydrodynamics (e.g. Mosquera Giménez et al., 2019; Bo et al., 2021; Puerta et al., 2022; Baena et al., 2024).

Seamounts are usually surrounded by abyssal plains (Auster et al., 2005; Staudigel et al., 2010). Their steep topography and isolated geographical location create an obstacle to ocean circulation, resulting in complex hydrodynamic regimes that lead to enhanced currents associated with high food supply and exposed hard substrate (Lavelle and Mohn, 2010; Chivers et al., 2013; Vlasenko et al., 2018). Consequently, marine scientists often refer to seamounts as "biological oases", where marine life flourishes, exhibiting high levels of productivity and biomass (Genin et al., 1986; Rogers, 1994). These elevated features are usually regarded as biodiversity hotspots, a phenomenon that can be explained by two ecological hypotheses (Clark and Bowden, 2015). The first one, known as the "stepping stones" theory (Hamilton, 1956; Hubbs, 1959; Wilson and Kaufmann, 1987) posits that seamounts serve as a "stepping stones", facilitating transoceanic dispersal of species across the ocean basin. The second one is the "isolation" hypothesis (Hubbs, 1959), which suggest that seamounts are isolated habitats in which distinctive and sometimes endemic fauna evolve. The extent of species mobility and dispersal ability influences the validity of these hypotheses (Stocks and Hart, 2007), but despite all these assumptions, there are still numerous paradigms to resolve (Rowden et al., 2010). In fact, some studies show contrasting findings to the aforementioned hypotheses, suggesting that seamounts exhibit similar levels of biodiversity and endemicity compared to the neighbouring continental slope (Piepenburg and Müller, 2004; O'Hara, 2007; McClain et al., 2009; Howell et al., 2010; Narayanaswamy et al., 2013).

Seamounts often harbour diverse and abundant communities of benthic suspension feeders, with anthozoans (hexacorals, octocorals, and ceriantharians) being one of the major components (Stocks, 2004; Froese and Sampang, 2004; Rogers et al., 2007). These underwater formations not only exhibit favourable high hydrodynamic regimes for anthozoans, but also provide predominantly hard substrate within an environment surrounded by soft substrate (Rogers, 1994; Lundsten et al., 2009). In these environments, anthozoans such as sea pens, black corals and gorgonians act as ecosystem engineers (sensu Jones et al., 1994), since their three-dimensional structure enhance habitat heterogeneity (Gili and Coma, 1998; Rossi et al. 2017) and provides microhabitats that serve as a refuge against predators or as nursery grounds for a diverse array of associated species (Buhl-Mortensen and Mortensen, 2005; Clippele et al., 2015; Baena et al., 2023). When these ecosystem engineers are abundant, they give rise to what is known as "Antarctic Marine Animal Forests" (AMAF) (Gutt et al., 2017). Many anthozoan species are characterized by their long lifespan and slow growth (Sherwood and Edinger, 2009; Watling et al., 2011; Wagner et al., 2012; Martínez-Dios et al., 2016), a rate that is usually further attenuated due to low temperatures in Antarctic waters (Brey and Clarke, 1993). These biological traits make anthozoans highly vulnerable to any kind of impact, as the recovery of their populations is very slow (Bennecke et al., 2016). These characteristics combined with their ecological role have led to the classification of numerous taxa within Anthozoa as indicators of Vulnerable Marine Ecosystems (VMEs) by the Food and Agriculture Organization (FAO, 2009) and the Commission for the Conservation Antarctic Marine Living Resources (CCAMLR, 2009). Consequently, scientific research and conservation plans are a priority in order to protect these ecosystems from potential impacts such as intensive fisheries and climate change (Auster et al., 2011; Teschke et al., 2021). Following the United Nations General Assembly (UNGA) resolution 61/105 and CCAMLR Conservation Measure 22-07, seamounts should be managed as VMEs (Reid, 2011).

High-latitude seamounts in the Southern Ocean are notably understudied (Kvile et al., 2014) and only a small portion of the published studies delves into their ecological aspects (e.g. Clark et al., 2010; Figuerola et al., 2012; Clark and Bowden, 2015). While the Weddell Abyssal Plain is predominantly flat, there are notable elevated features such as Maud Rise and Astrid Ridge that emerge from the continental margin (Lowther et al., 2022). Astrid Ridge has never been faunistically studied and Maud Rise has only been biologically sampled once during the project UNDEEP (Brandt et al., 2007a), revealing distinct differences in macrobenthos when comparing it to the surrounding deeper plains of the Weddell Sea (Brandt et al., 2011). In this context, a Norwegian Antarctic cruise ROV (Remoted Operated Vehicle) to the King Haakon VII Sea was carried out in 2019 with the aim of expanding the knowledge about Astrid Ridge and Maud Rise across different scientific disciplines. Specifically, the present research focuses on the study of anthozoan communities inhabiting both study areas, testing the hypothesis of community-level differences between both seamounts, as well as variations between the slope and summit zones and substrates. Additionally, we expected to discover different anthozoan communities compared to those inhabiting the plain of the Weddell Sea.

To test this, the following objectives were established: (1) to study the density and spatial and bathymetric distribution of anthozoans, (2) to describe the anthozoan assemblages, (3) to analyse the relationship between these assemblages and the geomorphological features of the seamounts, type of substrate, and associated benthic fauna and, (4) to compare between anthozoan assemblages on seamounts and the adjacent plain.

2. Material and methods

2.1. Study area

The oceanographic cruise took place on board the research icebreaker Kronprins Haakon from 28th February to 10th April 2019, off the coast of Dronning Maud Land (DML), in the eastern end of Weddell Sea (**Fig. 1 and Table 1**). The aim of the cruise was to increase the scientific knowledge of the area to generate a base line for the conservation management of the King Haakon VII Sea. To achieve this, a comprehensive sampling and ground-truthing of the whole area was carried out, encompassing observations of whales and birds, as well as sampling of the planktonic communities, and sampling and video surveys of the benthic habitats. Additionally, conductivity, temperature, depth, nutrients, metals, and other physical and chemical data were collected.

This marine area is characterized by a continental shelf with a maximal depth of 600 meters and the Weddell Abyssal Plain (WAP) reaching depths of 4400 meters. Two seamounts, Maud Rise and Astrid Ridge, rise in the WAP, and are the focus of the present study. Maud Rise is an equidimensional volcanic plateau at 65° S and 3° E while Astrid Ridge constitutes a prominent seafloor elevation located between 9° E and 15° E but, extending in a north-south direction and closer to the coast in comparison to Maud Rise (Mizukoshi et al. 1986; Roeser et al., 1996). Both study areas are located on the WAP, therefore the main flow collides with them, altering its direction and thus creating a turbulent environment that favours the formation of eddies and local enhancement of productivity (Brandt et al., 2011; Lowther et al., 2022).

The extensive marine area of DML is primarily influenced by the Weddell Gyre, a large cyclonic clockwise circulation system linking the Antarctic Circumpolar Current (ACC) to the coastal circulation characterized by the Circumpolar Deep Water (CDW) (Vernet et al., 2019). The CDW originates in the tropics, is relatively warm, saline, nutrient rich, and presents low concentration of oxygen. When the CDW enters the Weddell Gyre, in its journey southwards, it is transformed into colder and fresher deep water known as Warm Deep Water (WDW) (Nicholls et al., 2009).

Table 1. Geographical coordinates, depth, area analyzed and density and total abundance of anthozoans.

	Astrid Ridge		Maud Rise		
	W Slope	E Slope	W Slope	Summit	E Slope
Initial latitude	-68.4612	-68.9186	-65.2214	-65.1999	-65.2358
Initial longitude	11.2784	11.9598	2.479	2.6466	2.7844
Final latitude	-68.4572	-68.9209	-65.2246	-65.1916	-65.2356
Final longitude	11.3796	11.7648	2.516	2.66	2.7513
Min. Depth (m)	1837.12	1114.3	1380.43	1194.76	1332.14
Max. Depth (m)	1988.94	1418.23	1760.66	1205.43	1797.2
Total area analysed (m^2)	1650	1800	700	600	550
Number of anthozoans	63	556	310	152	318
Density of anthozoans ($100m^2$)	1.79	29.77	38.81	29.98	45.71
Total of anthozoan OTUs	14	18	15	4	10

2.2. Video recording and analysis

Five video transects were recorded during the multidisciplinary Norwegian scientific cruise covering a total study area of 7,392 m^2 between 1114.3 and 1988.94 m depth (**Table 1**). The present research focuses on the study of the composition and spatial and bathymetric distribution of anthozoans by means of the ROV Ægir6000. The ROV was equipped with CampodLogger (version 3.0.39) developed at Institute of Marine Research (IMR) for recording navigational data, time and video transects, a transponder connected to the navigation vessel to record georeferenced videos, a suction system for sampling organisms, Niskin bottles for water sampling, an HD camera for filming and two separate laser pointers spaced 15 cm apart, serving as a constant reference scale throughout the operation as well as for subsequent video analyses.

Video transects were analysed using Premiere Pro CC version 12.1.12 (Adobe Inc.) software. Before the analysis, each video transect underwent editing to eliminate pauses or video sequences with inadequate image quality for the study, such as instances involving sediment resuspension during a sampling. After edition, every anthozoan observed along the transect was registered, within a section of 0.45 m width around the central position of the laser beams. Every record was assigned a reference time, depth and coordinates at the moment of sighting along the transects, and type of the substrate (hard or soft) was recorded. Each anthozoan specimen was identified to the lowest possible taxonomic level. Various factors, such as the distance of the organism from the ROV camera, the small size of some organisms and similar morphologies among species prevented identification to species level in many cases. In order to overcome this problem, we classified the specimens as Operational Taxonomic Units (OTUs), grouping visually identical organisms within the same OTU. Each

OTU was assigned a taxonomic category at the lowest possible level. Multiple cases of OTUs belonging to the same taxonomic group, which have not been successfully identified at a lower taxonomic level but exhibit morphological differences, have been categorised as OTUs within the same taxonomic group but also with a numerical identifier.

2.3. Data analyses

After georeferencing and identification of all anthozoans, different sample unit sizes (2, 5, 10, 20 and 50 m^2) were tested (nMDS and CCA; See sections 2.5 and 2.7) in order to determine the size of the sampling units necessary to adequately characterize the anthozoan communities, and to explore how sampling unit size may affect the identification of the anthozoan assemblages. Each sampling unit was characterized by the type of substrate and the co-occurring benthos. Substrate types were classified into two categories: soft matrix and hard matrix. The soft substrate matrix is characterized by the presence of rocks of about 15 cm or less, and the hard substrate matrix also presents some small surfaces of soft substrate. The co-occurring benthic fauna was defined by the most representative taxonomic groups (without considering anthozoans).

Since the inclusion of rare species in multivariate analyses might constrain or cause distortions in the final results (Marchant, 2002; Poos and Jackson, 2012), various analyses were conducted, considering: (1) all observed OTUs, (2) only those with more than two observations, and finally (3) focusing solely on those OTUs summing more than 10 observations. For this purpose, a non-metric multidimensional scaling (nMDS) analysis was performed for each possible combination, and the stress values were computed. After that, it was concluded that a 50 m2 area was the most suitable as a sampling unit for the present study (**Table 1 of Supplementary material**). The nMDS were performed by RStudio software (RStudio Team, 2020) by means of the function metaMDS, available via the vegan package (Oksanen et al., 2019). To obtain this specific size of sampling unit, 0.45 m width around the lasers beams and 111.11 m length were considered.

2.4. Density and spatial and bathymetrical distribution of anthozoans

For statistical analyses, all the transects were divided into sampling units of 50 m^2 (0.45 m width and 111.11 m length). A total of 106 sampling units were analysed for all (five) transects. Each transect included a different number of sampling units based on its total length. A total of thirty-three sampling units were included in transect 1, which was conducted at the western slope of Astrid Ridge, thirty-six units in transect 2 on the eastern slope of Astrid Ridge, fourteen in transect 3 on the western slope of Maud Rise, twelve in transect 4 at the top of Maud Rise and eleven in transect 5 on the eastern slope of Astrid Ridge. To study the composition and spatial and bathymetric distribution of the documented anthozoan OTUs, the density (OTUs/100 m^2) corresponding to the different study areas was quantified. All these data were included in a matrix, and a georeferenced map was generated using QGIS version 3.16 (QGIS.org, 2022), depicting the percentages of abundance of different taxonomic groups of observed anthozoans on the different study areas. The abundance of the anthozoan OTUs along the video transects recorded in the different study areas were displayed in histograms. The bathymetric distribution of anthozoans was also analysed by means of histograms representing the abundance of the different OTUs across depth, using the ggplot2 package (Wickham, 2016) from the R software platform (RStudio Team, 2020). For both spatial and vertical distribution histograms, only those OTUs with more than twenty observations were analysed.

2.5. Anthozoan assemblage composition

To identify potential anthozoan assemblages, a dendrogram and non-metric multi-dimensional scaling (nMDS) were constructed using the abundances of the OTUs found. Abundance data were *square-root* transformed, followed by the calculation of distances between pairs of sampling units using the Bray-Curtis dissimilarity index. The dendrogram was generated by the *hclust* function and nMDS by means of *metaMDS*, both available in the *vegan* package (Oksanen et al., 2019) from RStudio platform (RStudio Team, 2020). Both the dendrogram and nMDS graphical representations serve to explore possible groupings and, therefore, potential relationships among the data. Finally, the ADONIS test was applied using the vegan package (Oksanen et al., 2019) from Rstudio software (RStudio Team, 2020) to determine if there were any statistical differences among the anthozoan assemblages identified by the dendrogram and nMDS.

2.6. Relationships with environmental features

To explore the influence of the environmental factors in the distribution of the anthozoans, a Canonical Correspondence Analysis (CCA) was applied considering the anthozoan abundances (previously *square-root* transformed). Canonical correspondence analysis allows the detection of potential relationships between the anthozoan OTUs and the environmental factors (Ter Braak, 1994; Greenacre, 2013). The tested environmental factors included depth, substrate (soft matrix and hard matrix), seamount feature (Maud Rise and Astrid Ridge) and seamount slope and summit. To prevent possible misinterpretations of the results, rare OTUs (with less than 4 observations) were excluded from the CCA analysis (Marchant, 2002; Poos and Jackson, 2012). In addition, the diversity of anthozoan OTUs was estimated using the Shannon Diversity Index for different substrates, seamounts and slope/summit at different scales (for each sampling unit and for the entire area defined for each factor). An ADONIS test was applied to these data following the procedure already mentioned in section 2.5.

2.7. Spatial covariance in anthozoan distribution and co-occurrence with benthic fauna

Biological features, such as ecosystem engineers, also influence species distribution. To investigate this aspect, we conducted a spatial covariance analysis between pairs of anthozoan OTUs. Specifically, a Three Term Local Quadrat Covariance (3TLQC) using Passage 2.0 software (Rosenberg, 2008). For each transect from the different study areas, a representative 200 m long transect section was selected and previously transformed into a grid of continuous quadrats of 1 m^2. This spatial statistic assumes uniformity within the study area (Dale, 1999), therefore the selected scale was chosen to mitigate the influence of the variation of environmental factors, such as substrate changes, along the entire length of the transects. We quantified the density of the OTUs for every single quadrat. In the 3TLQC, the variance as a function of block size for species A (Var A), species B (Var B), and the combined number (Var A + B) (Cov = Var A + B - Var A - Var B) was examined (Dale, 1999). The null hypothesis of this analysis posits a random anthozoan distribution. To test the null hypothesis, a total of 999 randomizations were conducted for each pair of anthozoan OTUs. Subsequently, the values at the limit of 2.5% tails were considered to determine whether the distribution was dependent or independent. A significative positive result indicates a positive association, while significative negative values suggest a negative association, which means repulsion.

Finally, the benthic fauna that co-occurs with the anthozoans was also studied. Each sampling unit was characterized by the most representative taxonomic groups of benthos. Thus, we were able to analyse the degree of relationship between the anthozoans and the other benthic organisms present in the same locations.

3. Results

3.1. Density, spatial and bathymetric distribution of anthozoans

A total of 1400 anthozoan specimens were observed and these were identified to subclass (8.4%), suborder (21.6%), order (47.1%), genus (22.7%) and species level (0.2%). From these observations, 41 different Operational Taxonomic Units (OTUs) were defined (**Table 2**). Nearly half of which, specifically 17, belong to the order Actinaria. In terms of spatial distribution, the major density of anthozoans was observed in the eastern and western slopes of Maud Rise (**Table 2**). In both seamounts, all three subclasses of Anthozoa (i.e., Ceriantharia, Octocorallia and Hexacorallia) were observed (**Fig. 1 and Table 2**). The densities of octocorals and hexacorals were more similar in Astrid Ridge (7.28 and 7.80 OTUs/100 m^2, respectively) than in Maud Rise, where the difference was more pronounced, with octocorals being more abundant (36.43 and 4.54 OTUs/100 m^2, respectively). Ceriantharia also exhibited a higher density in Maud Rise than in Astrid Ridge (3.41 and 1.48 OTUs/100 m^2, respectively). In case of the two transects in the Maud Rise slope area, Stolonifera OTU1 clearly predominates, while at the summit of this seamount, a different type of octocoral, classified as Umbellula OTU dominated, with a density of 10.83 colonies/100 m^2 (**Fig. 1 and Table 2**). Comparing the slopes between the two study areas, differences were also observed. Even the two transects conducted in the eastern and western part of Astrid Ridge showed differences in the composition and density of anthozoans. On the western slope, Hexacorallia displayed the greatest density (4.08 OTUs/100 m^2) compared to Octocorallia and Ceriantharia (0.54 and 0.06 OTUs/100 m^2, respectively), with Actiniaria OTUs accounting for more than half of the Hexacorallia density. The eastern slope had higher densities than the western slope, with similar densities of Hexacorallia and Octocorallia (13.23 and 14.69 OTUs/100 m^2, respectively) and the highest densities represented by Pennatulacea OTUs and Scleractinia OTU (**Table 2**). The bathymetric distribution was described only when the number of observations of each OTU amounted to more than twenty (**Fig. 3**). Following these results, Ceriantharia OTU, Actiniaria OTU13, Anthomastus OTU1, Pennatulacea OTU1, Umbellula OTU and Scleractinia OTU exhibited a wide bathymetric distribution, since all six were found at around 1100 m and at depths exceeding 1700 m, with highest abundance values in the shallower zones (**Fig. 3**). Stolonifera OTU, Alcyonaria OTU1 and Actiniaria OTU2 appear to have an intermediate bathymetric distribution, being more abundant in the range from 1300 to 1600 m (**Fig. 3**). Actiniaria OTU9 was observed both in the shallowest and the deepest zones, yet it was absent at intermediate depths (**Fig. 3**).

3.2. Anthozoan assemblage composition

To identify the number of anthozoan assemblages, a dendrogram was constructed including all the sampling units based on a Bray-Curtis dissimilarity matrix (**Fig. 4**). The cluster analysis revealed three distinct main assemblages with a 90% dissimilarity level. Assemblage type 1 comprised sampling units classified as the eastern slope of Astrid Ridge (orange colour in **Fig. 4**). These units were characterized by the predominance of soft substrate, as indicated by the absence of an asterisk in the cluster (**Fig. 4**). Only one sampling unit from this area was associated with assemblage type 2, which consisted of all the sampling units located in Maud Rise (grey colour in **Fig. 4**). Within assemblage type 2, three different sub-assemblages are discernible based on seamount slope and summit (at a 75% dissimilarity). One of these sub-assemblages encompassed all sampling units from the summit Maud Rise (grey colour in **Fig. 4**) and some from the slope, most of which were classified as soft predominant substrate. The remaining sampling units, characterized mostly by hard substrate, were grouped from both the eastern (violet colour in **Fig. 4**)or western slopes of Maud Rise (red colour in

Fig. 4). The third sub-assemblage within the main assemblage type 2 comprised only three sampling units, each from different areas. Following the 90% dissimilarity threshold, assemblage type 3 included sampling units distributed along the western slope of Astrid Ridge (green colour in **Fig. 4**). These units were characterized by soft substrate. Additionally, only five sampling units from the western slope of Astrid Ridge, characterized by prevailing soft substrate, formed the last assemblage of the six mentioned at 90% dissimilarity.

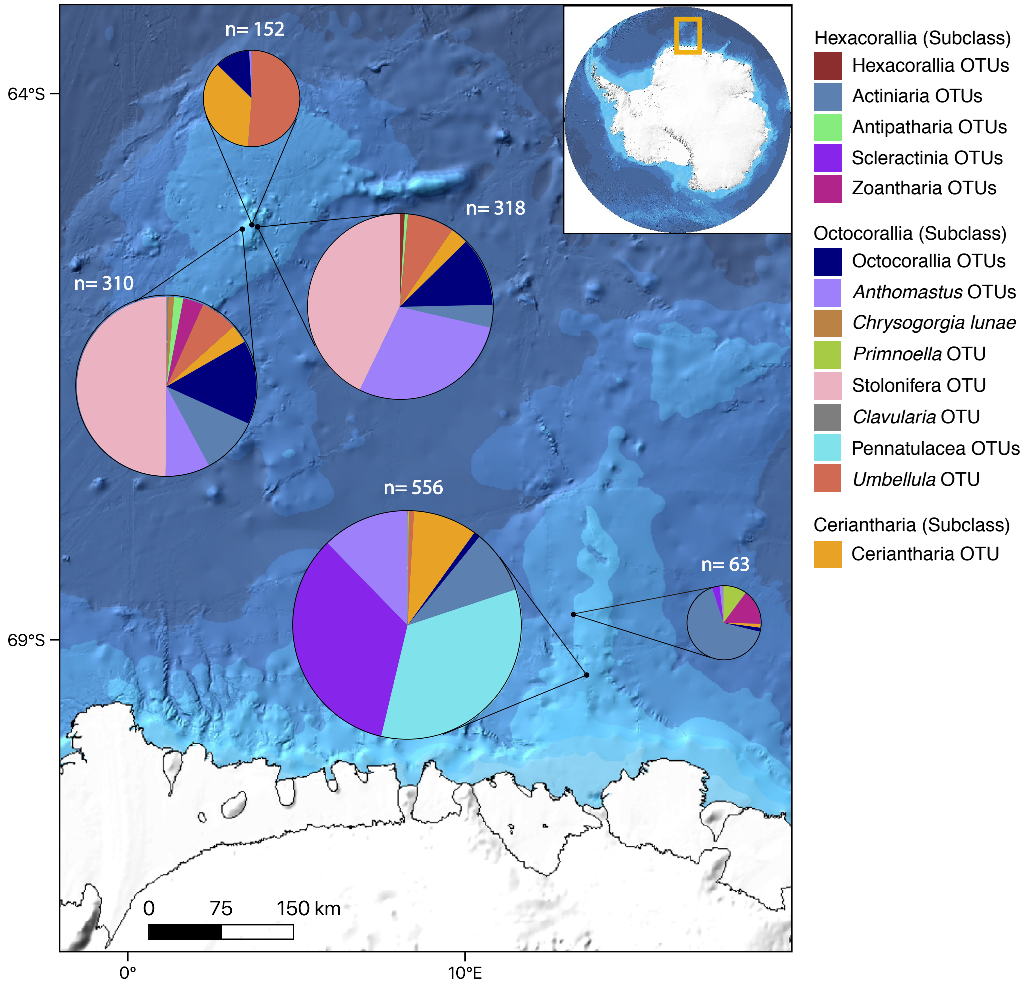


Figure 1. Composition and abundance of anthozoan taxa in Astrid Ridge and Maud Rise. The pie charts display the percentage of anthozoan taxa observed in each video transect and the size of them is proportional to the total abundance of anthozoans in each transect (n=number of anthozoans observed).

Table 2. Anthozoan taxa. Density (ind. 100 m-2) of different anthozoan OTUs according to study area and substrate, along with the abundance in the entire study area and the substrate to which each OTU was found.

Taxa	Astrid Ridge		Maud Rise			Hard substrate matrix	Soft substrate matrix	On hard/soft substrate	Sum of ind. (abundance)
	W Slope	E Slope	W Slope	Summit	E Slope				
Hexacorallia (Subclass)	**4.08**	**13.23**	**6.44**	**0**	**3.44**	**5.23**	**6.35**		**354**
Hexacorallia order indet.	0	0	0	0	0.54	0.26	0	H	3
Actiniaria (Order)									
Actiniaria OTU 1	0	0.11	0.43	0	0	0	0.12	H	5
Actiniaria OTU 2	0	0	2.86	0	2.36	2.70	0.05	H	33
Actiniaria OTU 3	0	0	0.71	0	0	0.44	0	H	5
Actiniaria OTU 4	0	0	0.14	0	0	0.09	0	H	1
Actiniaria OTU 5	0	0	0.29	0	0	0.17	0	H	2
Actiniaria OTU 6	0	0	0	0	0.18	0.09	0	H	1
Actiniaria OTU 7	0.24	0	0	0	0	0	0.10	H	4
Actiniaria OTU 8	0.18	0	0	0	0	0	0.07	H	3
Actiniaria OTU 9	1.09	0.06	0	0	0	0	0.48	S	20
Actiniaria OTU 10	0.18	0	0	0	0	0	0.07	H	3
Actiniaria OTU 11	0.30	0	0	0	0	0	0.12	S	5
Actiniaria OTU 12	0.18	0	0	0	0	0	0.07	S	3
Actiniaria OTU 13	1.12	1.67	0	0	0	0.09	0	S	32
Actiniaria OTU 14	0	0.39	0	0	0	0	0.17	H	7
Actiniaria OTU 15	0	0.06	0	0	0	0	0.02	H	1
Actiniaria OTU 16	0	0.22	0	0	0	0	0.10	S	4
Actiniaria OTU 17	0	0.28	0	0	0	0	0.12	S	5
Antipatharia (Order)									
Antipatharia OTU 1	0	0	0.29	0	0.18	0.26	0	H	3
Antipatharia OTU 2	0	0	0.43	0	0.18	0.35	0	H	4
Scleractinia (Order)									
Scleractinia OTU	0.12	10.44	0	0	0	0	4.59	S	190
Zoantharia (Order)									
Zoantharia OTU 1	0	0	1.29	0	0	0.78	0	H	9
Zoantharia OTU 2	0.67	0	0	0	0	0	0.27	H	11

Taxa	Astrid Ridge		Maud Rise			Hard substrate matrix	Soft substrate matrix	On hard/soft substrate	Sum of ind. (abundance)
	W Slope	E Slope	W Slope	Summit	E Slope				
Octocorallia (Sublass)	**0.54**	**14.69**	**34.72**	**15.16**	**54.08**	**49.05**	**8.78**		**931**
Octocorallia OTU1	0	0.06	6.43	4.17	7.81	9.04	0.24	H	114
Octocorallia OTU 2	0.06	0.17	0	0	0	0	0.10	H	4
Octocorallia OTU 3	0	0.06	0	0	0	0	0.02	H	1
Scleralcyonacea (Order)									
Coralliidae (Family)									
Anthomastus OTU 1	0.06	3.72	3.43	0.16	18.55	10.96	1.66	H	195
Anthomastus OTU 2	0	0.06	0	0	0	0	0.02	H	1
Chrysogorgiidae (Family)									
Chrysogorgia lunae (Baena et al., 2023)	0	0	0.43	0	0	0.26	0	H	3
Primnoidae (Family)									
Primnoella OTU	0.30	0.06	0	0	0	0	0.17	S	7
Stolonifera (Suborder)									
Stolonifera OTU	0	0	21.29	0	26.36	25.83	0.12	H	302
Clavulariidae (Family)									
Clavularia OTU	0	0	0.14	0	0	0.09	0	H	1
Pennatulacea (Order)									
Pennatulacea OTU 1	0.12	10.17	0	0	0	0	4.43	S	186
Pennatulacea OTU 2	0	0.17	0	0	0	0	0.07	S	3
Umbellidade (Family)									
Umbellula OTU	0	0.22	3	10.83	4.36	2.87	1.95	S	114
Ceriantharia (Subclass)									
Ceriantharia OTU	0.06	2.78	1.42	8.17	0.91	1.39	2.39	S	115
Total	3.70	30.67	45.57	23.33	61.45	55.65	18.31	-	1400

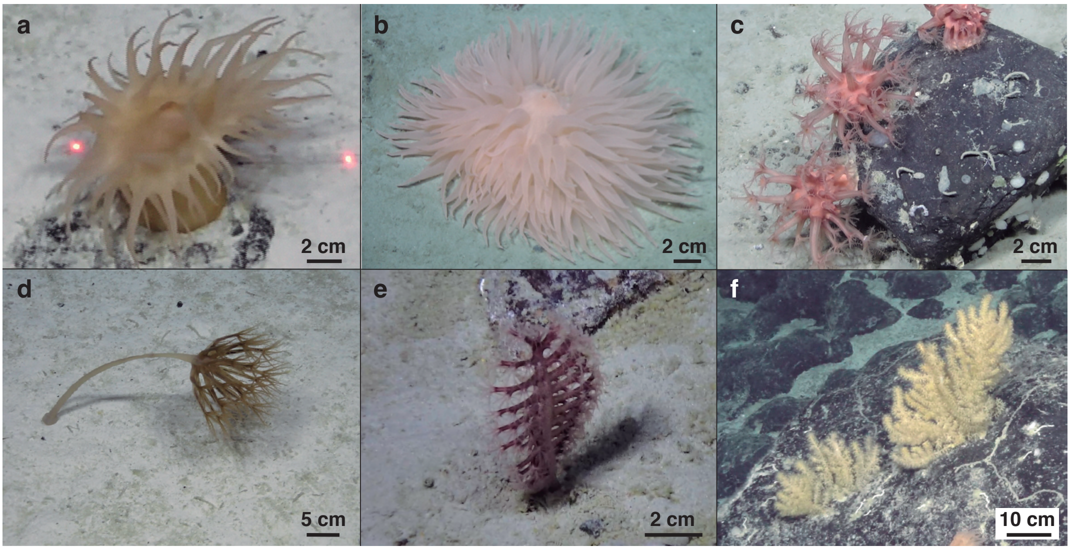


Figure 2. Photographs of some of the most abundantly observed Operational Taxonomic Units (OTUs). **a**: Actiniaria OTU 2 **b**: Actiniaria OTU 13 **c**: *Anthomastus* OTU 1 **d**: *Umbellula* OTU **e**: Pennatulacea OTU 1; **f**: Octocorallia OTU1. The size of the circles is proportional to the total abundance of anthozoans.

A non-metric multi-dimensional scaling (nMDS) was conducted to visually explore the relationships between anthozoans, seamount, slope/summit of the seamounts and substrate type (**Fig. 5**). The ordination of the sampling units revealed a clear distinction between the Maud Rise and the Astrid Ridge, and it also showcased differences based on substrate type. Besides, it could be observed that the sampling units with the most significant overlap corresponded to the Maud Rise western (red colour in **Fig. 4**) and eastern slopes (violet colour in **Fig. 4**). These results are aligned with those obtained through the dendrogram analysis. The ADONIS test confirmed the significant differences in anthozoan assemblages between the two seamounts, Maud Rise and Astrid Ridge, as well as between slope and summit of the seamounts and the two substrate types (soft and hard matrix). All these comparisons yielded a *p*-value = 0.001.

3.3. Relationship with environmental features

In the context of the distribution and substrate preferences of the examined anthozoans, we observed that Scleractinia, Pennatulacea, and *Primnoella* OTUs were exclusively present in Astrid Ridge and always found on soft substrate (**Figs. 1 and 6 and Table 2**). Among these, Scleractinia is one of the most abundant OTUs, reaching a density of 10.44 colonies/100 m^2 on the eastern slope (**Table 2**). The presence of Antipatharia and Stolonifera OTUs was limited to Maud Rise, specifically in the slopes, either on the eastern or western side. Antipatharia was exclusively distributed in areas where hard substrates were abundant. While Stolonifera dwelled in areas where either hard o soft substrate predominates, but it was always found attached to a hard substrate (**Figs. 1 and 7 and Table 2**). There was a single Stolonifera OTU, being the most abundant among all the anthozoan OTUs defined, with densities of 21.29 and 26.36 colonies/100 m^2 on the western and eastern slopes of the seamount (**Table 2**). Out of the total seventeen Actiniaria OTUs defined, eleven were unique to Astrid Ridge, while only six were seen in Maud Rise. Despite the lower number of OTUs found, the highest density of Actiniaria was observed in Maud Rise. Independently of the seamount considered, the greatest density of actinarians was observed in those sampling units characterized by soft substrate (**Table 2**).

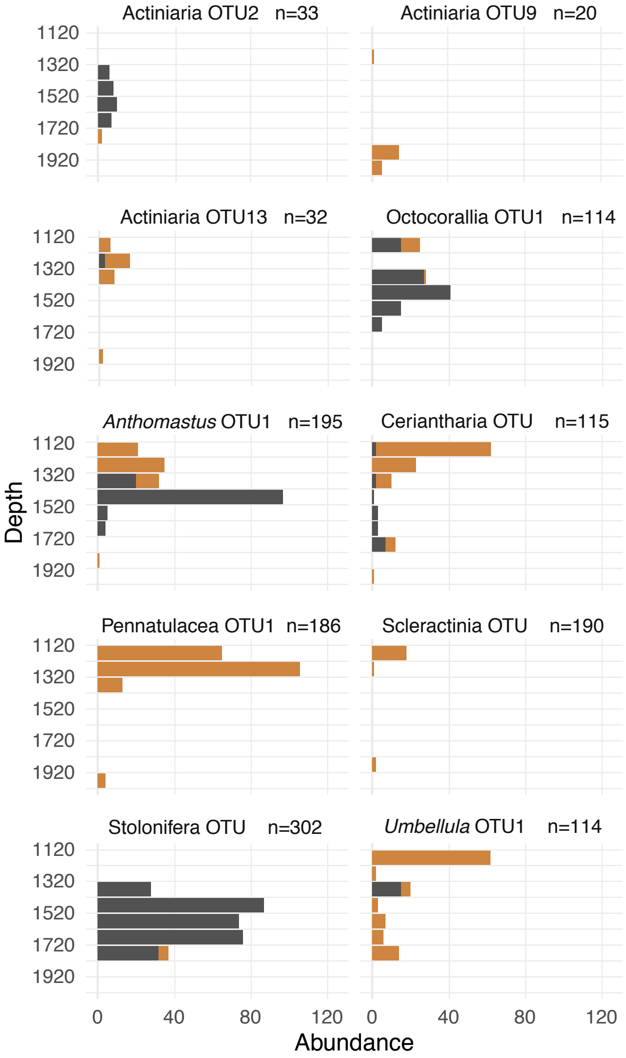
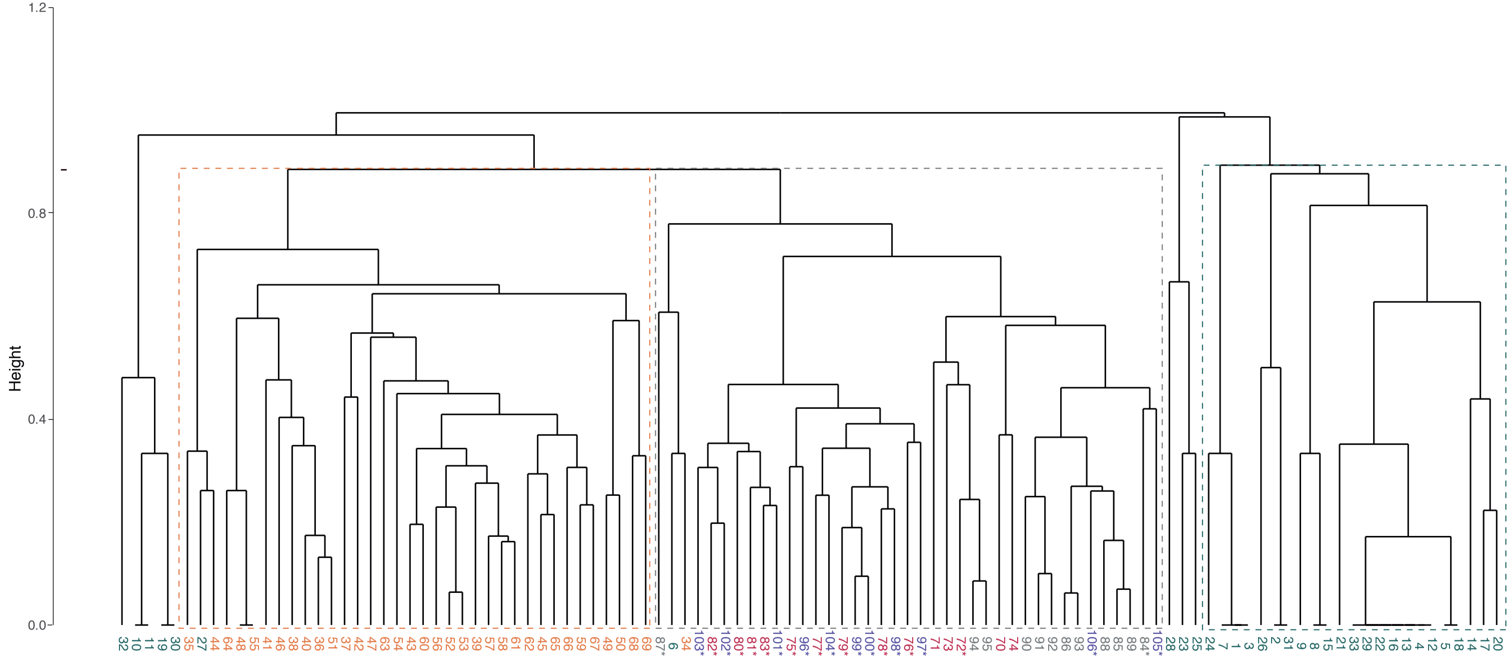


Figure 3. Bathymetric distribution of OTUs with more than 20 recorded observations in sampling units characterized by soft matrix substrate indicated with colour brown and grey for sampling units classified as hard matrix substrate.

Figure 4. Dendrogram representing the sampling units clustering based on a Bray–Curtis dissimilarity. The colours of the sampling units indicate the region of both seamounts studied. Green: Western Slope of Astrid Ridge. Orange: Eastern Slope of Astrid Ridge. Violet: Eastern Slope of Maud Rise. Red: Western Slope of Maud Rise. Grey: Summit of Maud Rise. The asterisk indicates sampling units with hard matrix substrate and the absence of it indicates sampling units defined as soft matrix substrate.



It is noteworthy that, yet soft substrate was prevalent, there were several small-sized volcanic rocks to which a high number of these actinarians were attached, specifically all the specimens of Actiniaria OTU 2, 7, 8, 10, 14 and 15 (**Table 2**). Despite that, there were others that seem to be adapted to live directly on soft substrate, such as Actiniaria OTU 12 and 13 (**Table 2**). While actinarians were observed in both seamounts, no observations were made in the summit of Maud Rise. Other anthozoan OTUs were documented in both, Astrid Ridge and Maud Rise, as well as in the slope and summit. This is the case for *Anthomastus* OTU1, Octocorallia OTU1, *Umbellula*, and Ceriantharia, all of them observed at the summit of Maud Rise. Furthermore, *Umbellula* and Ceriantharia OTUs displayed significantly higher densities on soft substrates of the summit, as compared to the densities encountered on the slopes (**Figs. 1 and 7 and Table 2**).

The results of the CCA analyses reveal that the studied environmental variables (seamount, slope/summit and substrate) explain 17.18% of the proportion of variance, with the first two axes accumulating 73.82% of the data's variance (**Fig. 8**). Based on these results, OTUs such as Antipatharia 1, Octocorallia 1, Actiniaria 2 and Zoantharia 1 seems to display a positive relationship with Maud Rise and hard substrate matrix, while OTUs like Actiniaria 13, Scleractinia and Pennatulacea 1 show correlations with Astrid Ridge and the soft substrate matrix. Concerning the effect of slope and summmit, we observed that *Umbellula* and Ceriantharia OTUs are closely linked to the summit, where they were also found in the highest densities observed. (**Figs. 1 and 7**). Conversely, the slope seems to be favourable for the occurrence of Anthomastus OTU1. Furthermore, the CCA analysis also explored the potential relationships between OTUs and depth, revealing that *Primnoella*, Zoantharia 2 and Actiniaria 7, 9 and 11 OTUs seem to be positively associated with greater depths.

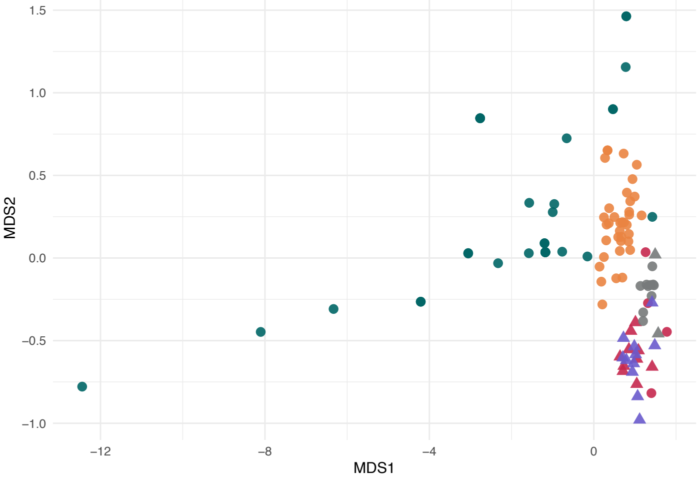


Figure 5. NMDS biplot of Bray–Curtis dissimilarity matrix of the different sampling units analyzed. Each sample unit was classified following the region of the studied seamounts. Green: Western Slope of Astrid Ridge. Orange: Eastern Slope of Astrid Ridge. Violet: Eastern Slope of Maud Rise. Red: Western Slope of Maud Rise. Grey: Summit of Maud Rise. Circle: Sampling units characterized by soft matrix substrate. Triangle: Sampling units characterized by hard matrix substrate.

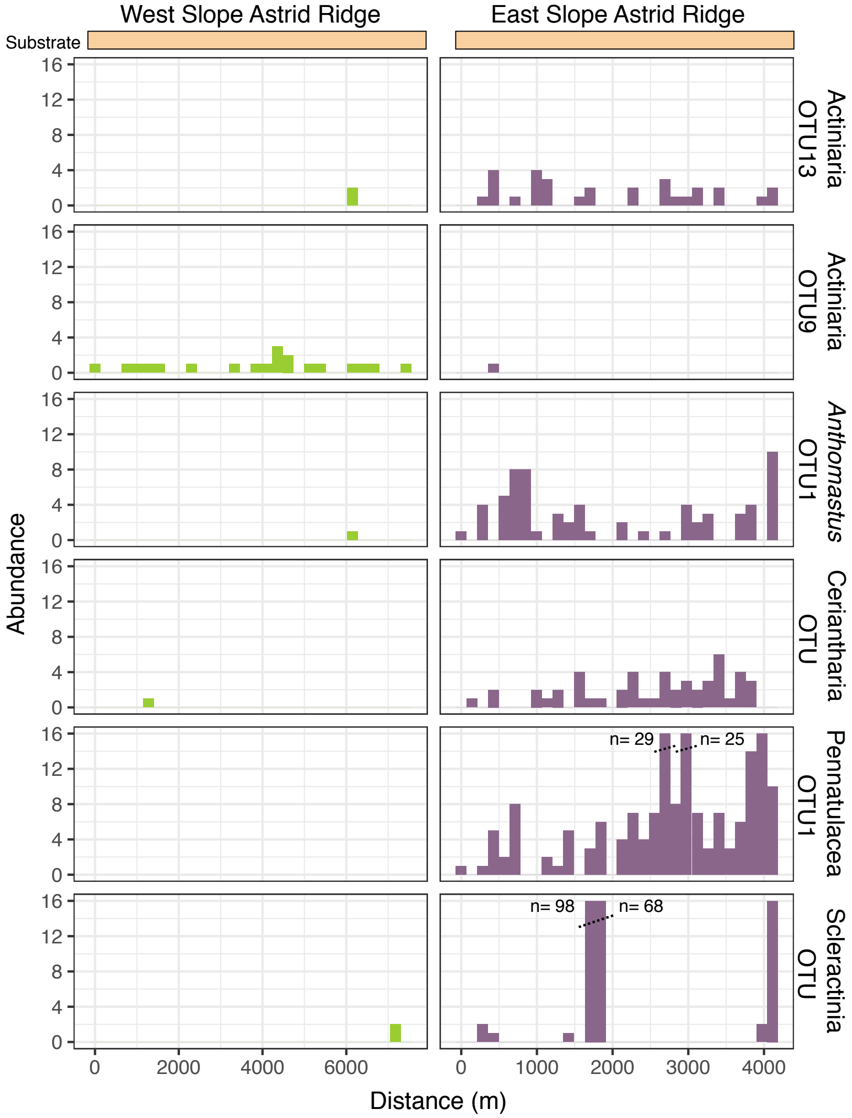


Figure 6. Anthozoan OTUs abundance along both slopes of Astrid Ridge with more than 20 observations. Bottom type and type of benthic community are indicated. The colour brown of the substrate indicates sand as the most abundant substrate. Violet: A benthic community with Malacostraca and Ophiuroidea as the most abundant benthos. Green: A benthic community with Holothuroidea and Ophiuroidea as the most abundant benthos. n = total abundance.

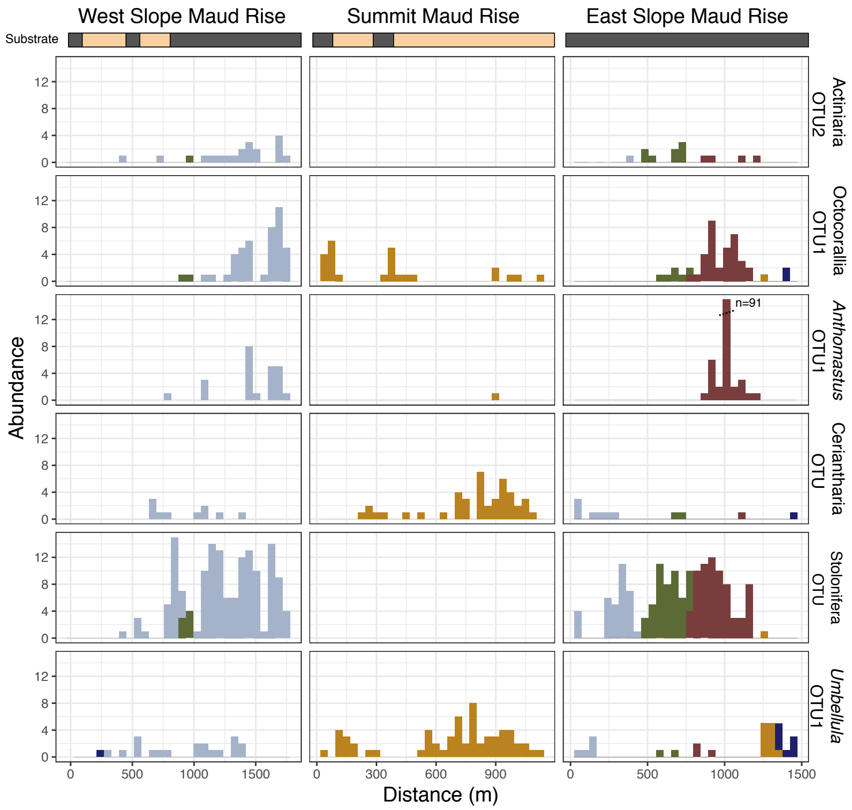


Figure 7. Anthozoan OTUs abundance along both slopes and summit of Maud Rise with more than 20 observation. Bottom type and type of benthic community are indicated. The colour brown of the substrate indicates soft as the most abundant substrate and grey, hard substrate matrix. Light blue: A benthic community with Ascidians, Teleostea and Ophiuroidea as the most abundant benthos. Green: A benthic community with Ascidias and Hexactinellida as the most abundant benthos. Dark blue: A benthic community with Teleostea, Ophiuroidea and Holothuroidea as the most abundant ones. Orange: Malacostraca and Teleostea and Ophiuroidea as the most abundant. Red: A benthic community with Hexactinellida and Ascidia as the most abundant co-occurring benthos. The arrangement of the classes reflects the order of abundances. n = total abundance.

The Shannon's index was calculated across various size scales: the entire area defined for each factor (**Table 3**) and for each 50 m^2 sampling unit, characterized for each factor too. The resulting values for the different sampling units were plotted in box plots according to the factors tested (**Fig. 9**) and they were also used in the ADONIS test (**Table 4**). The average diversity calculated for each sampling unit is significantly higher in Maud Rise compared to Astrid Ridge (*p*-value = 0.002) (**Fig. 9a and Table 4**). This result does not align with the total diversity of OTUs of these seamounts, as Astrid Ridge exhibits 24 different OTUs and a Shannon's index of 1.985 and Maud Rise presents 17 OTUs with a Shannon's index of 1.791 (**Tables 2 and 3**). A similar pattern emerges when analysing OTU diversity related to substrate type. In predominantly soft substrates, diversity is higher (24 OTUs, Shannon's index = 2.197)

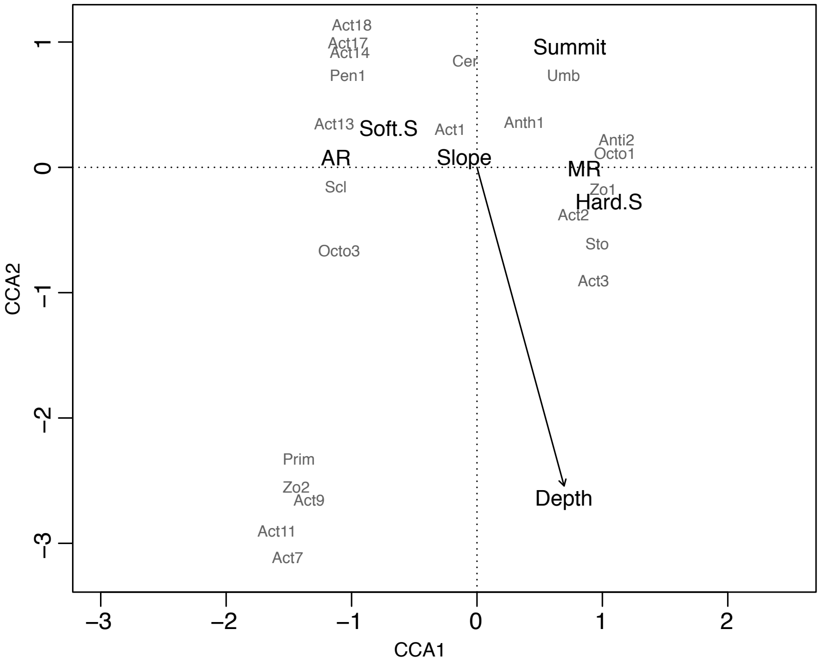


Figure 8. Canonical correspondence analysis (CCA) biplot of anthozoan OTUs with more than 4 observations constrained by both seamounts (AR: Astrid Ridge, MR: Maud Rise), summit and slope seamount and hard substrate matrix (Hard.S) and soft substrate matrix (Soft.S).

Table 3. Shannon Diversity Index calculated for the entire area defined for each pair of factors.

	Astrid Ridge	Maud Rise	Hard substrate matrix	Soft substrate matrix	Slope	Summit
Shannon's index	1.985	1.791	1.633	2.197	2.367	1.219

Table 4. Results of the ADONIS tests were based on Shannon Diversity Index calculated for each sampling unit (50m^2) which were characterized by different factors.

AR vs MR	Soft substrate vs Hard substrate	Slope vs Summit
0.002 **	0.002 **	0.238

than in hard substrates (16 OTUs, Shannon's index = 1.633) yet, the average diversity within each sampling unit is significantly lower in soft substrates (*p*-value = 0.002) (**Fig. 9b and Table 4**). The highest mean diversity is observed in seafloors dominated by hard substrates. When assessing OTU diversity according to the seamount slope or summit, there are no significant differences between them (**Table 4**) and it becomes evident that the eastern slopes of Maud Rise and Astrid Ridge exhibit very similar average Shannon diversity index per 50 m^2 (**Fig. 9c**). The western slope of Maud Rise stands out with the highest average diversity per sampling unit while the lowest average is in the western slope of Astrid Ridge (**Fig. 9c**).

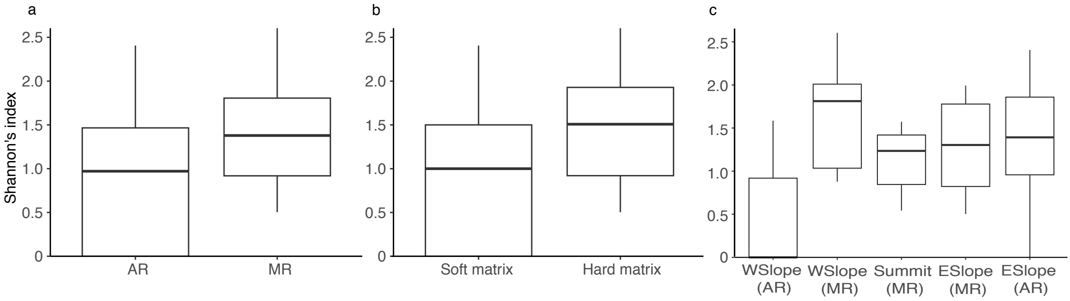


Figure 9. Box plot of Shannon's index of (**a**) the different seamounts (AR: Astrid Ridge, MR: Maud Rise), (**b**) substrates and (**c**) different slope and summit seamounts.

Table 5. Summary of the three-term local quadrat covariance (3TLQC). The scale (m) of any positive, negative or random associations between distributions of each pair of anthozoan OTUs.

Zone	OTUs associations	Scale < 9m	Scale 10–30m
Eastern slope of Astrid Ridge	Pennatulacea OTU1 – *Anthomastus* OTU1	Random	Random
Western slope of Maud Rise	Actiniaria OTU2 – Octocorallia OTU1	Random	Random
	Stolonifera OTU – Actiniaria OTU2	Random	Random
	Actiniaria OTU2 – *Umbellula* OTU	Random	Random
	Octocorallia OTU1– Stolonifera OTU	Random	Random
	Octocorallia OTU1 – *Umbellula* OTU	Random	Random
	Umbellula OTU – Stolonifera OTU	Random	Random
Eastern slope of Maud Rise	*Umbellula* OTU – Ceriantharia OTU	Random	Random
Summit of Maud Rise	Stolonifera OTU – *Anthomastus* OTU1	Random	Random
	Stolonifera OTU – Octocorallia OTU1	Random	Random
	Anthomastus OTU1 – Octocorallia OTU1	Random	Random

3.4. Spatial covariance in anthozoan distribution and co-occurrence with benthic fauna

To better understand the distribution of the observed anthozoans we also conducted an evaluation of potential associations between OTUs using the 3TLQV test (**Table 5**). The 3TLQV test revealed that all the OTUs analysed when the criteria were met displayed a random distribution at the various analysed scales. In other words, it seems that there was no clear positive or negative association among the evaluated OTUs. The 3TLQV test could not be applied on the western slope of Astrid Ridge, as any 200 meters of the total transect had insufficient observations of the OTUs found to conduct it.

To delve into the anthozoan distribution patterns, we analysed the benthic fauna co-occurring with the previously defined anthozoan assemblages (**Figs. 6 and 7**). In the Astrid Ridge, the class Malacostraca, specifically the order Decapoda, significantly dominated. On the western slope, malacostracans were abundant along with other detritivores such as Holothuroidea, while on the eastern slope, Ophiuroidea was the most prominent class alongside Malacostraca (**Fig. 6**). In contrast to Astrid Ridge, more heterogeneous benthic communities were found at Maud Rise, where mobile and detritivore organisms were not always dominant, coinciding with higher substrate variability. Both on the eastern and western slopes, the substrate was predominantly hard (**Fig. 7**). On the western slope, where Stolonifera OTU and Octocorallia OTU1 dominated, we encountered fauna primarily characterized by ascidians, followed by mobile organisms such as teleosts, ophiuroids, and holothurians. On the eastern slope, Stolonifera, *Anthomastus* OTU1, and Octocorallia OTU1 were also distributed abundantly, accompanied mostly by ascidians and hexactinellids but also motile organisms, like ophiuroids (**Fig. 7**). Finally, Malacostraca, Teleostei, and Ophiuroidea were the main components of the benthic fauna associated in the summit of Maud Rise. The summit was primarily characterized by soft substrate, with dominant OTUs of *Umbellula* and Ceriantharia (**Fig. 7)**. Hence, it seems that there were also different assemblages among the other accompanying benthic organisms depending on the seamount, slope or summit and the predominant substrate.

4. Discussion

4.1. Anthozoan comparison between seamounts and the surrounding plain in the Weddell Sea

There have been very few studies conducted in the marine area of Dronning Maud Land (eastern Weddell Sea). Only during the ANDEEP-III cruise (2005) benthic organisms were collected (Brandt et al., 2007a; Linse et al., 2007), and all photographic and video material available for this area since the late 1980s have been analysed (Gutt et al., 2013). Consequently, knowledge to date for these two seamounts is highly limited. In both studies, there is not extensive information on anthozoan fauna to allow any comparison with the present research. Nevertheless, general studies of benthic communities indicate differences between Weddell Sea plain and the seamounts rising above this plain (Brandt et al., 2011). In this regard, our study presents evidence that Actiniaria is the taxonomic group with the highest potential diversity, aligning with the previous observations carried out on Weddell Sea Plain at depths ranging from 1047–4931 m (Linse et al., 2007). However, in this study, actinarians did not exhibit the highest densities among all the anthozoan OTUs. The OTUs corresponding to the orders Scleractinia and Pennatulacea, along with the suborder Stolonifera, were the ones that showed the highest densities (**Table 2**). Our results contrasted with the findings from the plains, as the density of Octocorallia was much higher than Hexacorallia in the case of Maud Rise, whereas on Astrid Ridge, the densities of both groups were very similar. Despite of this, Hexacorallia boasted the highest count of identified OTUs at 22, whereas Octocorallia comprised 12 distinct OTUs.

Our results reflected disparities in anthozoan assemblages between the seamounts surveyed and the surrounding plain, where soft substrate dominated and hexacorals played a more prominent role than octocorals (Linse et al., 2007; Brandt et al., 2011; Lowther et al., 2022). Benthic suspension feeders, specially octocorals, were substantially more common on seamounts, and this could probably be attributed to the currents generated by the topology of these submarine features (Rogers, 1994; Lundsten et al., 2009; Bridges et al., 2021). Hydrodynamics could contribute to the relative isolation of anthozoans present in the seamounts, as their reproduction and settlement are greatly influenced by currents (Coelho and Lasker, 2016). This could lead to the generation of endemisms, further marking differences with the adjacent plain (Hubbs, 1959; Richer de Forges et al., 2000; Pante et al., 2015). In this regard, a study with greater taxonomic resolution in the Weddell Sea plain and surveyed seamounts would be crucial for a better understanding the biodiversity patterns. Additionally, the recent discovery of a new golden coral in Maud Rise, *Chrysogorgia lunae* Baena et al., 2024, highlights the possible presence of endemic species in this mountainous region, as it has only been observed in that seamount (Baena et al., 2024).

On the other hand, considering the composition and abundance of anthozoans from the transect recorded on the eastern slope of Astrid Ridge, we observed a greater similarity with the findings in Weddell Sea plain (Linse et al., 2007). This transect was recorded at almost 2000 m in depth, where the predominant substrate is soft. The environmental characteristics, such as substrate type and current regime, were more akin to those of the Weddell Sea plain (Michels et al., 2002; Jerosch et al., 2016). This similarity could be a plausible explanation for the greater resemblances among anthozoan compositions.

4.2. Ecological comparison between seamounts and anthozoan distribution

On both slopes of Maud Rise, a higher density of anthozoans was found compared to the other analysed zones, with hard substrate prevailing on these slopes (**Table 2**). The presence of an exposed bedrock seabed suggests that these areas are characterized by high bottom currents (Diesing et al., 2009). This hydrodynamics, coupled with the existence of hard substrate, promotes the presence of suspension feeders, as a significant proportion of them require a firm substrate for attachment (Rogers, 1994; Gili and Coma, 1998; Gutt, 2007; Rowden et al., 2010b; Lowther et al., 2022). Furthermore, not only differences were observed in the faunal composition between the two seamounts, but we also noted distinctions between the slopes and the summit of Maud Rise. Despite having a soft substrate similar to the slopes of Astrid Ridge, the summit of Maud Rise exhibited a distinct anthozoan assemblage, with Umbellula, Ceriantharia, and Octocorallia being the most abundant OTUs (**Figs. 4, 5 and 7 and Table 2**). In this context, benthic communities observed in various seamounts in the Ross Sea differed based on the slope/summit of the seamount and the substrate type, with Ceriantharia and *Umbellula* coexisting in large numbers on the summits with soft bottoms (Clark and Bowden, 2015). Additionally, it is noteworthy that the diversity of anthozoan OTUs was significantly low compared to other areas with soft substrate, and this might be attributed to substrate instability caused by the currents on the summit of Maud Rise (Josefson, 1981). Similarly, other studies have also shown distinct benthic assemblages depending on the seamount zone and substrate (e.g. Davies et al., 2015; Serrano et al., 2017; Bridges et al., 2021).

Beyond the differences in composition and density of anthozoans between the two seamounts, the mean diversity per sample unit was significantly higher in Maud Rise than in Astrid Ridge (**Fig. 9a and Table 5**), despite exhibiting lower Shannon diversity index at large scale (**Table 4**). This pattern also emerged when comparing the observed biodiversity on hard and soft substrates, where the total diversity of OTUs and Shannon diversity index were higher in soft bottoms (**Table 4**), although the mean diversity within sample units was lower (**Fig. 9b and Table 5**). A plausible explanation for this phenomenon lies in the patchy distribution of different OTUs. This kind of distribution was also observed in other studied seamounts in Ross Sea (Clark and Bowden, 2015) and in others non-Antarctic seamounts around the world (Rogers et al., 2007; Goode et al., 2021).

The patchy anthozoan distribution in this study might be attributed to the diverse characteristics of the substrate at a small scale. Additionally, other non-studied deterministic and stochastic forces might influence anthozoan assemblages (Dayton et al., 1974; Fukami, 2015). Colonization history could also play a determining role in this regard. Founder organisms are known to modify microscale conditions, as exemplified by engineering species. These habitat formers reduce current speed, facilitating food availability and the settlement of pelagic larvae which are typical of many invertebrate species such as anthozoans (Thorson, 1950; Gili and Coma, 1998; Coelho and Lasker, 2016). Patchiness distribution exhibits positive feedback for anthozoan communities, as the increasing colony density over time leads to a larger larval pool, consequently enhancing the probability of recruitment success and subsequent survival (Pineda, 2000). Besides, the aggregated distribution promotes reproductive success (Orejas et al., 2002; Sampayo et al., 2020). Additionally, reproduction cycle, dispersal abilities, predation and competitive interactions between species play a role in influencing distribution at small and large scales (Dayton et al., 1974; Connell and Slatyer, 1977; Fukami, 2015). At a small scale, the distribution of the studied OTUs appeared not to exhibit any discernible positive association with other OTUs, indicating that their distribution at a smaller scale was random. In this context, positive species interactions may be more common in unstable habitats, where the presence of certain species facilitates the settlement of others, while negative interactions are generally less common (Josefson, 1981; Schaffner, 1990). Furthermore, a higher taxonomic resolution of the anthozoans observed could have potentially revealed more nuanced positive associations.

4.3. Co-occurring benthic fauna with anthozoan assemblages

The environmental characteristics mirrored changes in the benthic fauna co-occurring with the anthozoan assemblages described in both seamounts. The density of anthozoans and other benthic suspension feeders in the studied areas of Maud Rise was significantly higher than in the investigated zones of Astrid Ridge (**Table 1 and Fig. 7**). The present study confirms Maud Rise as an important Antarctic seamount characterized by the prevalence of hard substrates and, consequently, strong bottom currents, promoting the presence of sessile suspension feeders (Vogel, 1994; Orejas et al., 2000; Gutt, 2007; Lowther et al., 2022). In these zones, where Octocorallia and Stolonifera OTUs were abundant, the predominant co-occurring benthos was primarily composed of suspension feeders such as carnivorous ascidians and hexactinellids which are also known to be particularly prevalent in other Antarctic regions (Downey et al., 2012 and present study) (**Fig. 7**). As it is the case for octocorals and stolonifera corals, both Hexactinellida and carnivorous ascidians are known to benefit from high currents (Chu and Leys, 2010; Mecho et al., 2014), which would explain its coexistence in the area. In contrast, Astrid Ridge predominantly featured soft substrates, suggesting a lower hydrodynamic regime. This might contribute to the lower density of anthozoans observed, as many of them need hard substrate to attach to seabed (**Table 1**) (Vogel, 1994; Gutt, 2007; Almond et al., 2021), while motile and detritivorous organisms typically dominate in such environments (Galeron et al., 1992; Starmans et al., 1999; Lowther et al., 2022). This co-occurring fauna was composed by decapods, holothurians, and ophiuroids, among other taxa (**Fig. 6**). In addition, the anthozoan diversity was notably low at the summit of Maud Rise compared to the slopes, as predominantly soft substrate prevailed (**Table 1**). Umbellula stood out as the most abundant anthozoan OTU. Indeed, this genus is typically associated with soft substrates, facilitated by their long peduncle (Williams, 2011; Kushida et al., 2022). This exhibited a noteworthy resemblance to the Astrid Ridge area, where pennatulaceans were quite abundant too (**Fig. 1 and Table 2**). The co-occurring benthic fauna on the summit of Maud Rise was characterized by motile organisms such as Malacostraca and Ophiuroidea, mirroring the substrate conditions observed in Astrid Ridge. Besides, the presence of fishes was also pronounced on the summit. Both Malacostraca and Ophiuroidea were two widely distributed and abundant groups in the bathyal and abyssal depth of the Weddell Sea (Linse et al., 2007) as well as throughout the Southern Ocean (Brandt et al., 2007b). The fact that seamounts concentrate high fish aggregations has been acknowledged by fishermen for a long time and later confirmed by scientist (Hubbs, 1959; Pitcher et al., 2007). Although the reasons for the common occurrence of fishes on seamount summits remain unclear, several theories propose that the heightened primary productivity is transferred to higher trophic levels, while others posit that seamounts serve as preferred locations for a great number of migratory fishes (Hubbs, 1959; Morato et al., 2010; Rowden et al., 2010).

5. Conclusions

Despite the limited studies in Dronning Maud Land, this study confirms previously hypothesized differences in anthozoan faunal composition between the surrounding plains and the two studied seamounts. Actiniaria stood out as the most diverse anthozoan OTU in both seamounts and the surrounding plain, with Octocorallia being the most abundant taxa in the seamounts and Hexacorallia in the plain. In this regard, hydrodynamics and substrate composition emerge as crucial factors influencing anthozoan distribution. On hard substrate slopes of Maud Rise, a higher anthozoan density and high diversity is concentrated in small patches with the octocorals being the dominant taxonomic group. Conversely, Astrid Ridge shows higher diversity at a larger scale, with hexacorals and sea pens characterizing the soft seafloors.

Our results emphasize the influence of abiotic interactions on anthozoans although, further research is warranted to understand their distribution, especially on seamount ecosystems. Additionally, our findings underscore the importance of conservation strategies that consider patchiness distribution, common on deep-sea benthic communities, and multiscale variability as we observed different anthozoan assemblages between the surveyed seamounts and also the adjacent plain. This should bear significance in management decisions. The designation of Dronning Maud Land as a Marine Protected Area (MPA) would entail the preservation of diverse ecosystems within the same area, encompassing numerous anthozoans considered as indicators of VMEs.

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Supplementary material

Table 1. Applying nMDS, stress values were computed for various sizes of sampling units and OTUs, with consideration given to the number of observations associated with each. Analysis to determine the optimal size of sampling unit for subsequent statistical analysis.

	2m^2	5m^2	10m^2	20m^2	50m^2
All observations are considered	0.003173225	0.001516338	0.001216278	0.03295488	0.06494490
	0.002096786	0.001131528	0.001197766	0.03280398	0.06516715
	0.004047056	0.001065555	0.001330965	0.03280604	0.06528115
	0.003212273	0.001328210	0.001779284	0.03294306	0.06505340
	0.003064735	0.001073575	0.002062713	0.03282022	0.06506956
OTUs with more than 2 observations	0.003185035	0.001806507	0.002278838	0.03281798	0.06461414
	0.002806425	0.001326809	0.002701617	0.03281617	0.06450115
	0.003888555	0.001135078	0.002690339	0.03279900	0.06482730
	0.003108774	0.001938647	0.001260583	0.03277070	0.06493636
	0.003420508	0.001557847	0.002190366	0.03278247	0.06486173
OTUs with more than 10 observations	0.003468365	0.03935099	0.04798366	0.05877267	0.08822094
	0.001264879	0.03932416	0.04797884	0.05872541	0.08820940
	0.001335135	0.03930747	0.04794851	0.05877394	0.08821081
	0.001136856	0.03944957	0.04797056	0.05876192	0.08823455
	0.002341551	0.03929890	0.04798773	0.05875915	0.08821111

Vam coneixe'ns a l'estiu per Llançà
Birres i platja, quina tarda vam passar
Bufava tramuntana de risas entre onades
I la teva mirada se'm va quedar clavada

Després de mil històries al setembre ens hem plantat
I és que és una putada que es faci fosc tan aviat
I si tenim molt a perdre?
I si no ens tornem a veure?
No em diguis que això s'ha acabat

Que no s'acabi
Que no s'acabi
L'estiu
L'estiu
Que no s'acabi
Que no s'acabi
L'estiu
L'estiu

S'ha fet col·lega dels cambrers i no paguem res
I envoltat de francesos que van liant-la
Escapem de la gent agafats de la mà
I em diu: "anem-nos a banyar"

L'aigua és salada
I et vec tan dolça
I m'acosto a la teva galta
I ho dius tot amb la mirada

Que no s'acabi
Que no s'acabi
L'estiu
L'estiu

Sota la lluna prendiendo sativa
Sobre la panxa m'hi poso una petxina
I t'enyoro tant
Sé que s'està acabant

I allà
S'hi amagava alguna cosa
I allà
S'hi amagava una sorpresa
I no ho dèiem
Però sí que ho vèiem

Que no s'acabi
Que no s'acabi
L'estiu
L'estiu

Que no s'acabi, **Figa flawas**

CHAPTER 3

CHAPTER 3

A new deep-sea species of golden gorgonian (Octocorallia: Scleralcyonacea: Chrysogorgiidae) from Antarctic waters

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Abstract

The Southern Ocean harbours rich deep-sea ecosystems with local hotspots of benthic biodiversity. Still, many species, including deep-water octocorals, remain undescribed despite the fact that the exploration of the deep sea has improved thanks to recent technological advances. In this context, a new species of golden gorgonian has been collected at 1407–1581 m depth during a recent cruise to Dronning Maud Land in the Eastern Weddell Sea. Currently, after recent changes in *Chrysogorgia* taxonomy, *Chrysogorgia lunae* sp. nov. (Octocorallia: Scleralcyonacea) is the only known representative of the genus in Antarctic waters. It corresponds to the "Squamosae typicae" and is characterized by a bushy colony with branching sequence of 2/5L and bell-shaped polyps. A molecular comparison with published sequences of *Chrysogorgia* species is provided based on a concatenated sequence of two mitochondrial genes, mtMutS and COI, as well as the 28S nuclear ribosomal gene.

1. Introduction

The Southern Ocean harbours rich benthic assemblages with high levels of biodiversity and endemism (Clarke and Crame, 1992; Gage, 2004; Brandt et al., 2007). This is due to the high environmental stability, low disturbance and the relative isolation of the deep sea in Antarctic waters (Grebmeier and Barry, 1991). Benthic suspension feeders are among the major contributors to these high levels of biodiversity (Starmans et al., 1999; Orejas et al., 2000), and in particular octocorals play a key role in Antarctic deep ecosystems by providing niches for a high number of associated species (Roberts, 2006). Octocorals are sessile organisms that display three-dimensional structures that increase habitat complexity and provide refugia from predators and nursery grounds for the associated biodiversity (Jones et al., 1994; Bullimore et al., 2013; Baena et al., 2023). For these reasons, they are considered ecosystem engineers, despite the fact that they are non-reef forming species (Jones et al., 1994). Octocorals are also characterized by their long life span and slow growth (Arntz et al., 1992; Watling et al., 2011; Martínez-Dios et al., 2016). These biological traits make them highly vulnerable, as the recovery of their populations is very slow (Bennecke et al., 2016). As a result, octocoral meadows are one of the priority groups of organisms listed as Vulnerable Marine Ecosystems (VMEs) by the Food and Agriculture Organization (FAO, 2009), and they need to be protected from potential impacts of fishing in the high seas (Auster et al., 2011).

In order to achieve effective management for marine conservation, our current knowledge of taxonomy, biology and ecology of octocorals must be expanded. Thanks to technological advancements and progress in molecular techniques, both underwater exploration and identification of species have subsequently improved (Ramirez-Llodra et al., 2010). However, although octocorals have been collected extensively in many Antarctic expeditions, they have been treated only in a handful of studies (e.g. Bayer, 1993; Cairns, 2002; Núñez-Flores et al., 2020). A large number of specimens are therefore stored in museum collections, and still remain to be analyzed.

Most octocoral families occur in the deep sea, with highest species richness at depths greater than 200 m (Watling et al., 2011). Chrysogorgiidae Verrill, 1883 is one of these taxa. Its representatives are known worldwide, including species from Iceland to Antarctica (Madsen, 1944; Cairns, 2002). This family is an assemblage of different conspicuous species that structure the benthic communities on seamounts and slopes (Thoma et al., 2009; Xu et al., 2019), both on soft and hard bottoms (Grasshoff, 1995; Watling et al., 2011; Pérez et al., 2016). Not only is the distribution of chrysogorgiids wide, but the bathymetric range of the family is also extensive, ranging from 10 m to 4492 m depth and making it one of the three major deep-sea octocoral families (Watling et al., 2011; Pante et al., 2012; Cairns, 2018). Chrysogorgiidae includes genera with stenobathic distribution –like *Metallogorgia* Versluys, 1902 and *Iridogorgia* Verrill, 1883–, and others with eurybathic distribution like *Chrysogorgia* Duchassaing and Michelotti, 1864 (Watling et al., 2011; Pante et al., 2012).

Verrill (1883) described Chrysogorgiidae as “some of the most interesting and beautiful of all the known gorgonians” because of their golden and iridescent branches and their elegant branching pattern. Members of this family are commonly known as “golden corals”. Recently, the scope of family Chrysogorgiidae has been modified by reducing it to eight genera instead of 21 as previously considered (McFadden et al., 2022; 2023). The currently included genera are: *Chrysogorgia* Duchassaing and Michelotti, 1864; *Iridogorgia* Verrill, 1883; *Metallogorgia* Versluys, 1902; *Pseudochrysogorgia* Pante & France, 2010; *Radicipes* Stearns, 1883; *Ramuligorgia* Cairns, Cordeiro and Xu, 2021; Rhodaniridogorgia Watling, 2007 and *Parachrysogorgia* Xu et al., 2023. The type genus *Chrysogorgia* has the deepest observed distribution (4492 m depth) within the family (Watling et al., 2011; Pante et al., 2012). This genus is one of the most widespread and speciose among all octocoral genera (Cairns, 2001, 2007; Pante et al., 2012), including at least 68 valid nominal species to date (Xu et al., 2023). Many of these species have been described in the 21st century due to the increased effort in deep-sea exploration. The high phenotypic plasticity typical of this genus is often not reflected in significant genetic differences (Pante and Watling, 2012; Xu et al., 2021b). For this reason, taxonomic studies must be prudent and should have an integrative approach combining morphological and genetic analyses (e.g. Prada et al., 2008; López-González, 2022). In order to identify species of *Chrysogorgia*, a detailed examination of the branching pattern of the colonies, the polyp morphometrics, and the features of the sclerome is necessary, including observations by scanning electron microscopy (SEM) (Bayer and Stefani, 1988a; Cairns, 2001; Xu et al., 2021a). To facilitate species identification, taxonomists have traditionally categorized the species of *Chrysogorgia* into three different groups based on the nature of the sclerites observed in the polyp body wall and the tentacles (Wright and Studer, 1889; Versluys, 1902). Group A “Spiculosae” corresponds to species that have rod/spindle sclerites in the polyp body wall and tentacles; Group B “Squamosae aberrantes” is an intermediate group with scales in the body wall and rods/spindles in the tentacles; finally, Group C “Squamosae typicae” is characterized by species that have scales in both regions (Wright and Studer, 1889; Versluys, 1902; Cairns, 2001; Xu et al., 2020). A fourth group, “Spiculosae aberrantes”, was added by Cordeiro et al. (2015) for species with rods in the body wall and scales in the tentacles. Additionally, through the analysis of colony configuration, branching patterns, and sclerite morphology, Xu et al. (2023) classified the *Chrysogorgia* species into 12 distinct groups.

Cairns (2002) described the first-known species of *Chrysogorgia* within Antarctic waters, formally identified as *C. antarctica* Cairns, 2002. However, a recent molecular investigation conducted by Xu et al. (2023) led to a division of the previously established morphological framework of *Chrysogorgia*. This study culminated in the creation of a novel genus, *Parachrysogorgia* Xu, Zhan & Xu, 2023. Xu et al. (2023) further expanded this taxonomic shift by relocating thirteen species, including *C. antarctica*, from genus *Chrysogorgia* to their newly established genus.

In 2019, during a Norwegian Antarctic expedition on board RV Kronprins Haakon, the deep-sea Antarctic bottoms of Dronning Maud Land (concretely the two seamounts Maud Rise and Astrid Ridge) were explored by means of Remotely Operated Vehicles (ROVs). In one of the video-transects carried out in the study area, three specimens of an unidentified *Chrysogorgia* species were observed, and one of these specimens was collected to be analyzed in detail in the laboratory. The present paper gives a description of this golden gorgonian, providing information on colonial and sclerite morphology as well as molecular information on two mitochondrial markers (mtMutS and COI) and one ribosomal nuclear marker (28S). The results of these analyses confirm that this specimen belongs to a new species, the first one of the genus *Chrysogorgia* found in the Eastern of Weddell Sea and also the sole representative of the genus in Antarctic waters after the recent changes in chrysogorgiid taxonomy (Xu et al., 2023).

2. Materials and methods

2.1. Sample collection

The material for this study was collected during the multidisciplinary Norwegian Antarctic expedition off the coast of Dronning Maud Land in 2019 (**Figs. 1 and 2**). During this cruise, a total of five video transects were recorded in Astrid Ridge and Maud Rise by means of the ROV Aegir 6000. The transects covered a bathymetric range from 1121 to 1988 m depth. In one of these transects, specifically in Maud Rise, three colonies of an unidentified chrysogorgiid were detected, one of which was collected and subsequently fixed on board in 99% ethanol for morphological and molecular studies.

2.2. Morphological analyses

Bayer (1951) and Bayer et al., (1983) were followed for terminology and the description of the specimen. Sclerites from different colony parts (e.g. coenenchyme, polyp body, tentacles) were prepared by digestion of the tissues in a solution of sodium hypochlorite and then washed with deionized water repeatedly, let dry on slides, and finally mounted on SEM stubs using double-side carbon adhesive tape (see Bayer and Stefani, 1988b). Fragments of terminal branches with polyps were isolated and critical-point dried using an

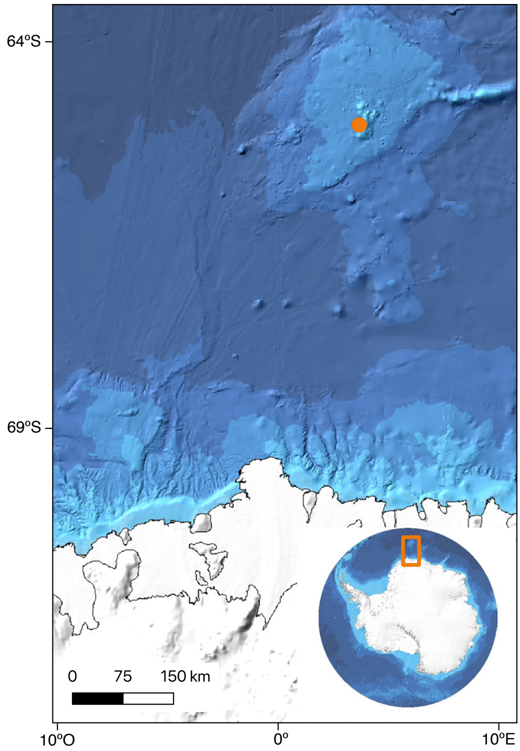

Figure 1. Location of the collection site and type locality of *Chrysogorgialunae* sp. nov. (Maud Rise, Eastern Weddell Sea).

adapted hexamethyldisilazane (HMDS) protocol, limiting the immersion of octocoral fragments in this chemical to 2–3 minutes (Nation, 1983; Braet et al., 1997; López-González, 2020; 2021). The SEM stubs were coated with gold-palladium under a Leica ACE600, and then observed under a scanning electron microscope (SEM) Zeiss EVO SEM at the General Research Services of Microscopy at the University of Seville. In addition, different parts of the polyps and branches were prepared using clove oil and these were subsequently observed maintaining their original arrangement under an optical microscope with an OPTIKA C-P20CC digital camera and the image software OPTIKA PROVIEW. Forty sclerites of each type and colony part were measured. The material studied (holotype) has been deposited in the Invertebrate Collections of the University Museum of Bergen (UMB, Norway), while some analyzed fragments were deposited in the collection of the research team Biodiversidad y Ecología Acuática in the University of Seville (BECA).

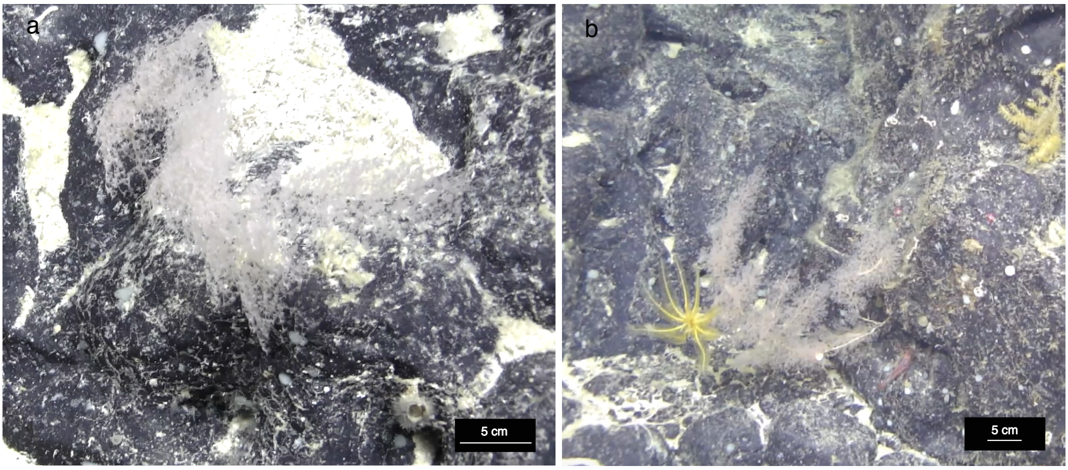

Figure 2. In situ photograph of *Chrysogorgia lunae* sp.nov. **a**: holotype colony **b**: colony of *Chrysogorgia lunae* sp.nov. observed also in Maud Rise.

2.3. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from the ethanol (EtOH)-preserved specimen using the QIAGEN DNeasy Blood and Tissue Kit, and the E.Z.N.A. DNA kit (OmegaBiotech) following the manufacturer's protocol (spin-column protocol). The mitochondrial regions mtMutS –a homologue of the bacterial DNA mismatch repair gene mutS (=msh1)– and cytochrome c oxidase subunit I (COI) were sequenced, as well as a fragment of the 28S nuclear ribosomal gene (28S rDNA). Following previous studies (e.g. McFadden et al., 2011; Quattrini et al., 2013; Muthye et al., 2022; Xu et al., 2023), these regions were selected for species delimitation in order to compare with other chrysogorgiids. mtMutS was amplified using primers ND42599F (5'-GCCATTATGGTTAACTATTAC-3') (France and Hoover, 2002) and Mut3458R (5'-TSGAGCAAAAGCCACTCC-3') (Sánchez et al., 2003). COI was amplified using primers COII8068F (5'-CCATAACAGGACTAGCAGCATC-3') (McFadden et al., 2004) and COIOCTR (5'-TCATAGCATAGACCATACC-3') (France and Hoover, 2002). 28S was amplified using the primers 28S-Far (5'-CACGAGACCGATAGCGAACAAGTA-3') and 28S-Rar (5'-TCATTTCGACCCTAAGACCTC-3') (McFadden and van Ofwegen, 2013). Each PCR reaction was performed using 0.15 µl of Takara Taq DNA Polymerase (Takara Bio), 1 µl of each primer (10 µM) in the corresponding marker set, 2.5 µl of 10x reaction buffer (Takara Bio), 2 µl of dNTP mixture (Takara Bio), and 2 µl of genomic DNA, and was brought to a final volume of 25 µL with ddH2O. PCR for mtMutS was carried out using the following cycle profile: initial denaturation at 94°C for 2min, 35 cycles of denaturation at 94°C for 30s, annealing at 55 °C for 30s, and extension at 72 °C for 30 s, and a final extension at 72 °C for 5 min. The COI and 28S PCR used the same cycle profile, but with 58°C as annealing temperature. All PCR products were purified using ExoSAP–IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific) following the manufacturer's instructions. Strong band-yielding PCR products of COI and mtMutS were sequenced in-house at the sequencing facility of the University of Bergen, while 28S was successfully amplified at the sequencing facility of the research team BECA in the University of Seville. All of the sequences are deposited in GenBank (**Table 1**).

2.4. Phylogenetic reconstruction

All chromatograms were visualized and sequence pairs matched and edited using Sequencer v4.0. The sequences obtained were BLASTED (using Blastn, implemented in Blast+ 2.14.1, released August 22, 2023) and the results compared with all publicly available sequences in genus *Chrysogorgia*. This preliminary molecular identification was consistent with the morphological description of the genus (see "3. Results" section). For our phylogenetic analysis, all the available mtMutS, COI and 28S sequences of *Chrysogorgia* species and three sequenced specimens of the genus *Radicipes* (as outgroup) were obtained from GenBank (**Table 1**). The specimens identified at the species level having both mitochondrial genes (mtMutS and

COI) were used for a mtMutS+COI concatenated matrix including nineteen different species of *Chrysogorgia*. Six more species with only mtMutS sequenced were also included in the analyses and in the calculation of genetic distances. A total of seventeen different species that have nuclear 28S sequences available were used for a phylogenetic analysis exclusive to this marker. Mitochondrial dataset was aligned using MUSCLE, as implemented in MEGA6 (Tamura et al., 2013), while 28S nuclear dataset was aligned online in Mafft v.7 (https://mafft.cbrc.jp/alignment/server/) (Katoh et al., 2019).

After alignment, pairwise genetic distances based on the Kimura 2-parameter (K2P) model of nucleotide substitution (Kimura, 1980) with pairwise deletion option were obtained for the mtMutS and 28S datasets in order to compare them with previous studies at species level within the genus *Chrysogorgia*, following the work of Pante and France (2010), Pante et al., (2012), López-González (2020), López-González and Drewery (2022), and Xu et al., (2023).

Table 1. Octocoral species involved in the molecular comparative analyses carried out in this study. (MBM: Marine Biological Museum of Chinese Academy of Sciences; ZMBN: Department of Natural History, University Museum of Bergen, Norway; USNM: Smithsonian National Museum of Natural History)

Species	Voucher Number	GenBank Accession Number			Reference
		mtMutS	COI	28S	
Chrysogorgia abludo Pante and Watling, 2012	isolate NAS102-3	GQ180138	GQ868324	-	Thoma et al., 2009; McFadden et al., 2011;
Chrysogorgia acanthella (Wright and Studer, 1889)	MBM286357	ON221827	ON207075	ON207665	Xu et al., 2023
Chrysogorgia acanthella	MBM286862	ON221828	ON207072	ON207666	Xu et al., 2023
Chrysogorgia arboriformis Xu, Zhan and Xu, 2023	MBM286465	ON221842	ON207094	ON207672	Xu et al., 2023
Chrysogorgia arboriformis	MBM286466	ON221843	ON207100	-	Xu et al., 2023
Chrysogorgia artospira Pante and Watling, 2012	isolate KEL619-1	GQ868346	GQ868315	-	McFadden et al., 2011
Chrysogorgia averta Pante and Watling, 2012	isolate LII-10-609	KC788265	KC788235	KC788258	Quattrini et al., 2013
Chrysogorgia carolinensis Xu, Zhan and Xu, 2020	MBM286495	MW418362	-	MW418375	Xu et al., 2021b
Chrysogorgia cylindrata Xu, Zhan and Xu, 2023	MBM286460	ON221818	ON207073	-	Xu et al., 2023
Chrysogorgia cylindrata	MBM286461	ON221824	ON207086	ON207667	Xu et al., 2023
Chrysogorgia cylindrata	MBM286464	ON221825	ON207082	ON207668	Xu et al., 2023
Chrysogorgia delicata Nutting, 1908	MBM286859	ON221829	ON207084	ON207671	Xu et al., 2023
Chrysogorgia dendritica Xu, Zhan and Xu, 2020	MBM286353	MT269888	-	-	Xu et al., 2020
Chrysogorgia fragilis Xu, Zhan and Xu, 2020	MBM286352	MN510470	-	-	Xu et al., 2020

Chysogorgia geniculata (Wright and Studer, 1889)	MBM286467	ON221845	ON207079	ON207673	Xu et al., 2023
Chrysogorgia geniculata	isolate HI-015	MT558738	MT726004	-	Baco et al. (unpublished)
Chrysogorgia geniculata	isolate HI-018	MT558739	MT726005	-	Baco et al. (unpublished)
Chrysogorgia geniculata	isolate HI-037	MT558740	MT726006	-	Baco et al. (unpublished)
Chrysogorgia gracilis Xu, Zhan and Xu, 2020	MBM286350	MN510472	-	ON207657	Xu et al., 2020
Chrysogorgia lunae sp. nov.	ZMBN138867	OR576812	OR575174	OR574989	Present study
Chrysogorgia monticola Cairns, 2007	USNM 1102452	JN227989	JN227955	-	Pante et al., 2012
Chrysogorgia pendula Versluys, 1902	MBM286870	ON221834	ON207074	ON207664	Xu et al., 2023
Chrysogorgia pendula	MBM286359	ON221814	ON207070	ON207661	Xu et al., 2023
Chrysogorgia pendula	MBM286865	ON221817	ON207080	-	Xu et al., 2023
Chrysogorgia pinnata Cairns, 2007	USNM1102450	JN227988	JN227956	-	Pante et al., 2012
Chrysogorgia pinniformis Xu, Zhan and Xu, 2021	MBM286504	MW085090	-	MW418372	Xu et al., 2021b
Chrysogorgia ramificans Xu, Li, Zhan & Xu, 2019	MBM286861	ON221826	ON207077	ON207675	Xu et al., 2023
Chrysogorgia rigida Versluys, 1902	MBM286356	ON221844	ON207095	ON207674	Xu et al., 2023
Chrysogorgia tenuis Xu, Zhan and Xu, 2023	MBM286858	ON221831	ON207093	ON207670	Xu et al., 2023
Chrysogorgia tricaulis Pante and Watling, 2012	n.d.	OL616221	OL616221	-	Muthye et al., 2022
Chrysogorgia varians Xu, Zhan and Xu, 2021	MBM286502	MW085091	-	MW418381	Xu et al., 2021b
Chrysogorgia varians	MBM286440	MW418369	-	MW418383	Xu et al., 2021b
Radicipes gracilis (Verrill, 1884)	USNM 100900	JN227987	HM590861	-	Pante et al. 2012
Radicipes stonei Cordeiro, Cairns and Pérez,	USNM:IZ:1418007	MG986912	MG986961	MG980134	Cairns and Wirshing, 2018
Radicipes sp.	RB-19-195	-	-	OM799018	Saso et al. (unpublished)

The Maximum Likelihood approach (ML) was carried out in MEGA6 using the NNI (Nearest Neighbor Interchange) heuristic method with 1000 bootstrap replications and using the nucleotide substitution model (T92+G) (nucleotide model search implemented in MEGA6). In addition, Bayesian Inference (BI) analyses were carried out with MrBayes v3.2.6 (Huelsenbeck and Ronquist, 2001) using the substitution model GTR+G (lsetnst=6 Rates=gamma), 10^7 generations, and discarding 25% of the initial trees. The stationary of the chains and convergence of two runs were monitored for each parameter by Tracer (v.1.7.1), determining whether the effective sample size (ESS) of all parameters was larger than 200, as recommended (Rambaut et al., 2018).

3. Results

Subclass Octocorallia Haeckel, 1866

Order Scleralcyonacea McFadden, van Ofwegen & Quattrini, 2022

Family Chrysogorgiidae Verrill, 1883

Chrysogorgia Duchassaing and Michelotti, 1864

Chrysogorgia lunae sp. nov.

3.1. Type material

ZMBN138867, Holotype, deposited in the Invertebrate Collections of the University Museum of Bergen (UMB, Norway). Antarctica, Eastern Weddell Sea, Maud Rise seamount, “Dronning Maud Land” cruise, RV Kronprins Haakon, Aegir 6000 ROV, dive 05, 65°13’25.68” S, 2°30’17.64” E, 1581m depth, 28 March 2019, whole colony, ca. 25.9 cm height. Some fragments with polyps of the holotype deposited in the morphological and molecular collection of BECA under the code OCHRYS-31 (G-4101). This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN (International Code of Zoological Nomenclature). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for the present publication is: urn:lsid:zoobank.org:pub:60DE6F13-2509-4776-89F4-40B6587F9458

3.2. Diagnosis

Chrysogorgia in Versluys’ (1902) group C “Squamosae typicae” group with a bushy colony, large branches pinnately branched and subdivided dichotomously, the branching sequence is 2/5L. The polyps are bell-shaped with a narrow base. The scales have different shapes and are distributed throughout the colony, including the coenenchyme and the polyp. Each pinnule has a single curved and rib-like scale. All coenenchyme and polyp body scales have minute warts on their surface. The coenenchymal sclerites usually have a central projection.

3.3. Description of the holotype

The colony corresponds to Versluys' (1902) group C "Squamosae typicae". It is 25.9 cm in height, 20.1 cm in width, bushy, branching in different planes, and shows a golden metallic luster (**Figs. 2 and 3a**). Despite the complete holdfast is lacking, the colony was apparently broken during collection very close the basal-most part. As the main stem widens considerably towards the end, a discoidal shape can be expected, as it occurs in other hard-bottoms species in the genus (e.g. Xu et al., 2023). The main stem is short and circular, 3.3 mm in diameter, and is bent in a zigzag manner because it undergoes angular bending at the origin of each branch. Large branches subdivided dichotomously, irregularly and upright-directed, with its branchlets arising from the stem in a spiral, and forming a bushy colony. The lateral branchlets are subdivided dichotomously with its twigs nearly on one plane with the first branch internode at 17 mm above the supposed holdfast. The interbranch distance is 3 – 6 mm depending on how thick (or old) the main branch is. For basal branches ca. 3 mm in diameter, the interbranch distance is longer, usually, 5 – 6 mm; in thinner/younger stems (ca. 1 – 2 mm), the interbranch distance is 3 – 4 mm. The branches arise from the stem at a right angle and give rise to lateral twigs that stand at angles of 40 – 45° and end up in a dichotomous fashion. The branching sequence is 2/5L giving a spiral appearance to the axis. The orthostiche interval is 13 – 18 mm (**Fig. 3d**). No nematozooids (cnidal papillae) have been observed. The polyps are absent along the stem but present and well-spaced on twig internodes, arranged usually one and sometimes two in the twig internodes and two on the terminal twigs (**Fig. 3b**). Those polyps that are continuous on twig internodes are located at a distance of 2 – 7 mm. They are bell-shaped with a narrow base and 1.8 – 3.5 mm height (n= 40) (**Figs. 3c and 4a**). Thicker branches have larger polyps. The tentacular crown is shown mostly expanded, with tentacles (1.0 – 1.4 mm long) with 18 – 20 pinnules and two rows of 9 – 10 each side of the rachis. Pinnules are slightly capitate due to the cnidae accumulation (**Figs. 4b, 4c and 4d**).

The coenenchymal sclerites are longitudinally arranged in abundance and in the sense of the growth of the branch (**Fig. 4f**), oval to irregularly rounded scales (**Fig. 5a**), up to 0.39 mm in length, and 0.09 mm in width, with prominent tubercles and minute warts on the surface, usually narrowing in the center, some scales have serrated minute edges. Also, many of them present a central projection which occurs only on one side of the sclerite. The sclerites of the polyp base are warty scales with different forms and some of them with serrated edges, longitudinally arranged and usually with a constricted middle section (**Fig. 5b**), up to 0.37 mm length and 0.22 mm width. The sclerites of the distal part of the polyp are asymmetric scales, some of them with minute serrated, lobed and irregular edges (**Fig. 5c**), up to 0.46 mm length and 0.24 mm width. The scales of the tentacular rachis occur on the aboral side, are transversally placed and they overlap slightly instead of being well separated (**Fig. 4e**). They present different shapes such as arched butterfly scales up to 0.32 mm in length and 0.24 mm in width, and asymmetric planar scales up to 0.42 mm in length and 0.03 mm in width (**Figs. 6a and 6b**), some of them with serrated edges like the scales present in other body parts. There is one long toothed rib-like scale on each pinnule longitudinally arranged with less prominent warts and a serrated arched side and another planar end with a few rounded lobes, up to 0.61 mm in length (**Fig. 6c**).

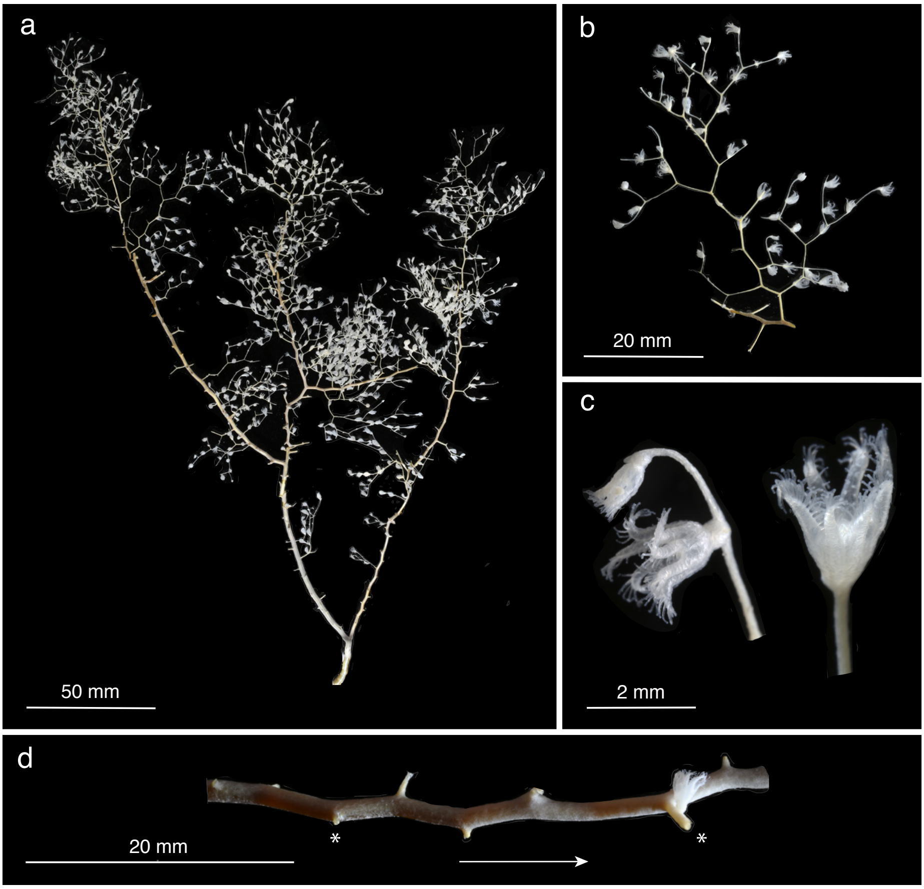

Figure 3. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). a: colony. The colony was broken during collection, depicted in this photo is the reconstructed arrangement of branches. b: details of polyp arrangement on branches; c: details of bell-shaped polyps and d: details of the pattern of ramification (2/5L).

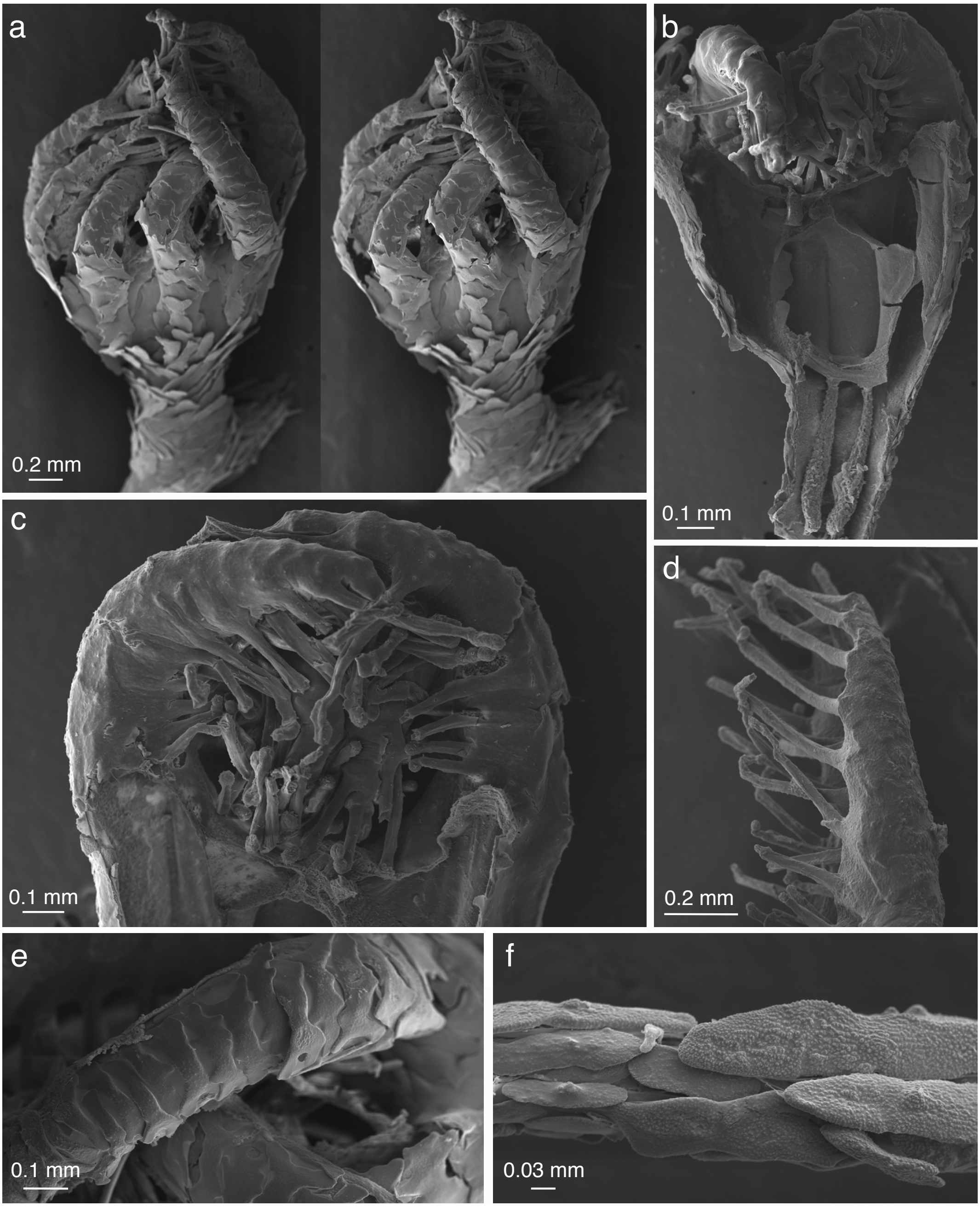

Figure 4. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs. **a**: lateral vision of a polyp, stereopair; **b**: longitudinal section of a polyp showing contracted tentacles, pharynx and two mesenteria; **c**: details of contracted tentacles and pinnules; **d**: details of pinnules; **e**: sclerite arrangement in tentacles; **f**: sclerite arrangement in coenenchyme.

Figure 5. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs. **a**: coenenchymal scales; **b**: basal part of the polyp; **c**: distal part of the polyp.

Figure 6. *Chrysogorgia lunae* sp. nov. Holotype (ZMBN138867). SEM photographs of tentacular scales; **a**: planar scales with asymmetric shapes; **b**: butterfly scales with arched forms; **c**: pinnular scales with arched forms.

3.4. Geographic and bathymetric distribution

The holotype is the only collected colony (**Figs. 2 and 3a**); however, two more colonies were observed also at Maud Rise seamount during the same video transect (**Figs. 1 and 2b**). Both observed colonies apparently belong to the same species described here base on macroscopic characters. These colonies were observed at 1407 and 1491 m depth, thus the known bathymetric range for *Chrysogorgia lunae* sp. nov. is 1407–1581 m. The three colonies were observed attached to hard substrates.

3.5. Etymology

The specific epithet *lunae* is chosen in honor of the natural satellite of the Earth. The species name aims to draw an analogy between moon and deep-sea exploration, revealing landscapes akin to those from science fiction, yet entirely real. While space ignites a greater popular curiosity than the deep sea, hidden beneath the waves are still unraveling secrets, such as new species, inviting us to explore. Perhaps, a Google search for information on the satellite might unexpectedly lead to the ocean depths, where another *luna*, moon in Spanish, takes the form of a gorgonian.

3.6. Phylogenetic analyses

The aligned datasets comprised a total of 741 nucleotide positions for mtMutS, 785 for COI, and 772 for 28S. The ML tree for mtMutS+COI clustered the sequences of the newly described species *C. lunae sp. nov*. alongside other sequences identified as *C. geniculata* and *C. arboriformis* within a clade supported by a bootstrap (bst) value of 63% (**Fig. 7**). Conversely, the BI tree for mtMutS+COI associated the novel species with three out of a total of four specimens designated as *C. geniculata* supported by a posterior probability of 0.55 (**Fig. 8**). This congruence is in line with the findings from both ML and BI trees for 28S wherein *C. lunae* sp. nov. was grouped together with *C. arboriformis* in a clade sister to one specimen identified as *C. geniculata* (MBM286467) (bootstrap = 82%, posterior probability =0.99; **Figs. 9 and 10**). Otherwise, in both trees based on mtMutS+COI and the two derived from 28S, it is evident that *C. lunae* sp. nov. clusters with *C. geniculata*, *C. arboriformis* and *C. rigida*, exhibiting strong supported values ranging from 89% to 100% (**Figs. 7–10**).

The average KP2 distance between *C. lunae* sp. nov. and any other species of *Chrysogorgia* is 0.89% for mtMutS and 8.44% for 28S. The interspecific distances for mtMutS range from 0 to 1.82% (**Table 2**) and for 28S range from 0.13 to 16.41% (**Table 3**). The mtMutS sequences of *Chrysogorgia lunae* sp. nov. are identical to those from *C. arboriformis* and three specimens identified as *C. geniculata*. Conversely, a distance of 0.15% was identified between all these sequences and a fourth specimen of *C. geniculata* (specimen MBM286467). Based on 28S, *C. lunae* sp. nov., *C. arboriformis*, and *C. geniculata* display distinct sequences (**Fig. 8**) with corresponding distances of 1.27% and 3.07% between the pairs *C. lunae* sp. nov.–*C. arboriformis* and *C. lunae* sp. nov.–*C. geniculata*, respectively. Following the calculated genetic distances for mtMutS and 28S and four phylogenetic trees obtained, the new described species is consistently related to *C. geniculata* and *C. arboriformis*.

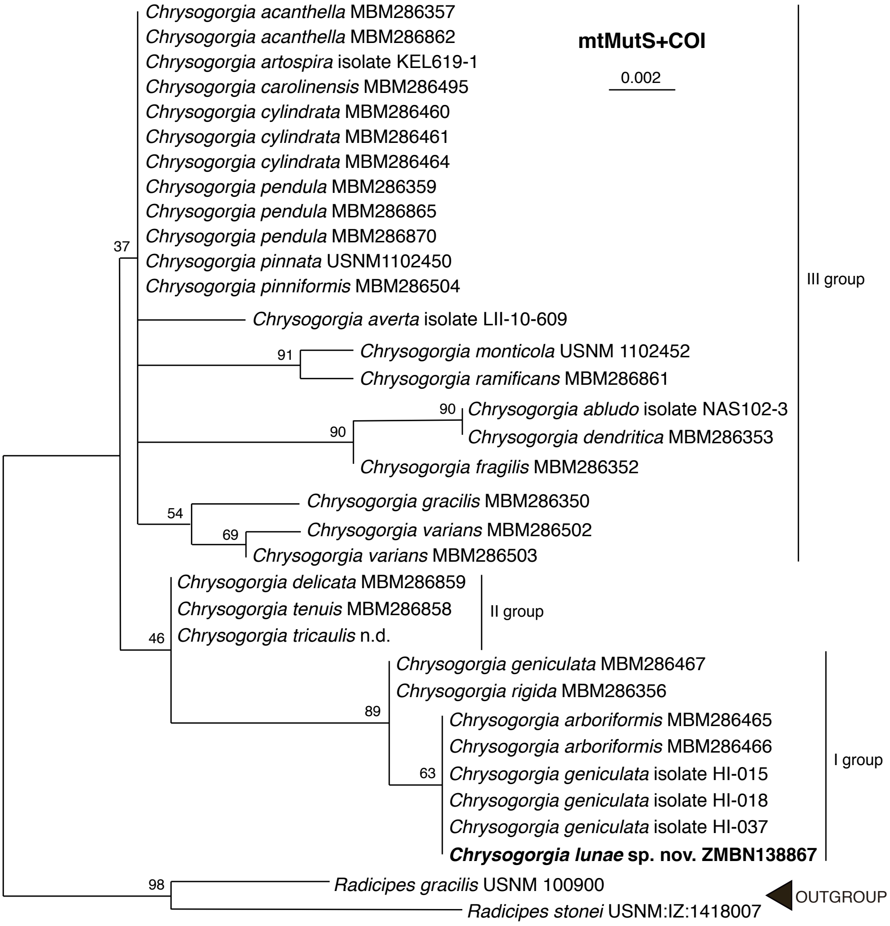

Figure 7. Maximum likelihood (ML) tree of the MutS+COI dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The present hypothesis is based on the concatenated dataset comprising two markers: mtMutS+COI, along with only mtMutS sequences for *C. carolinensis, C. dendritica, C. fragilis, C. gracilis, C. pinniformis* and *C. varians*. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as bootstrap (%)/posterior probability.

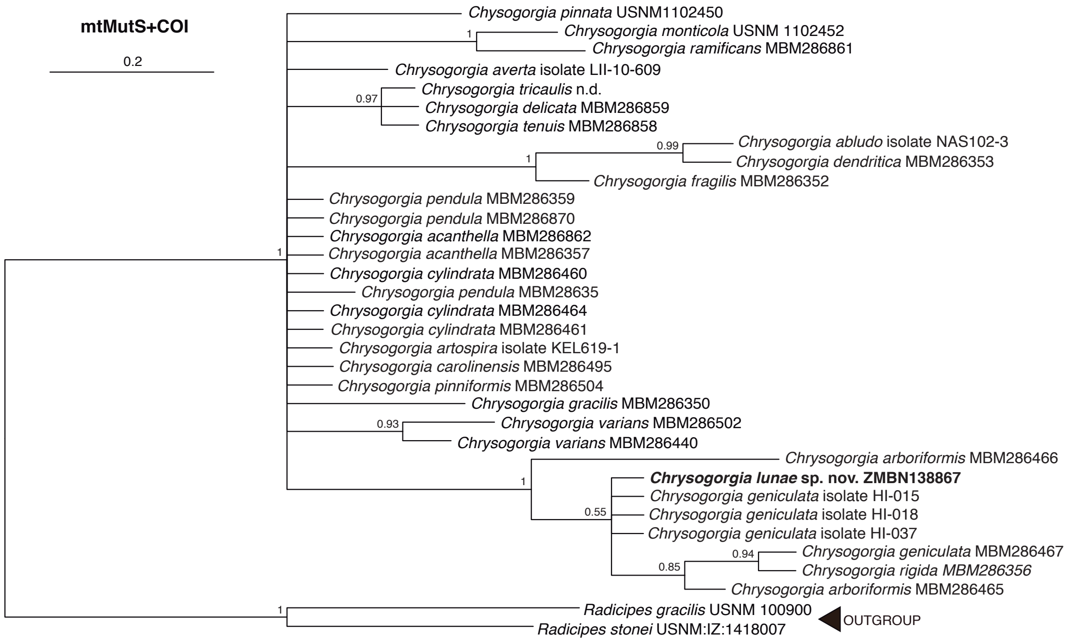

Figure 8. Bayesian Inference (BI) tree of the MutS+COI dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The present hypothesis is based on the concatenated dataset comprising two markers: mtMutS+COI, along with only mtMutS sequences for *C. carolinensis*, *C. dendritica*, *C. fragilis*, *C. gracilis*, *C. pinniformis* and *C. varians*. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as posterior probability.

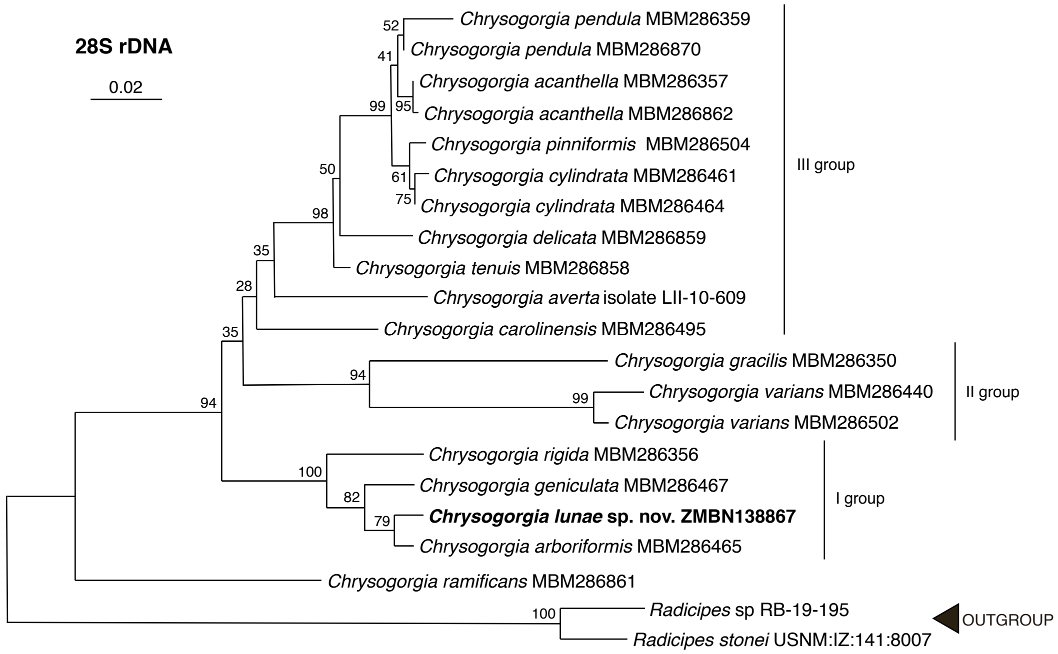

Figure 9. Maximum likelihood (ML) tree for 28S showing phylogenetic relationships among *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as bootstrap (%).

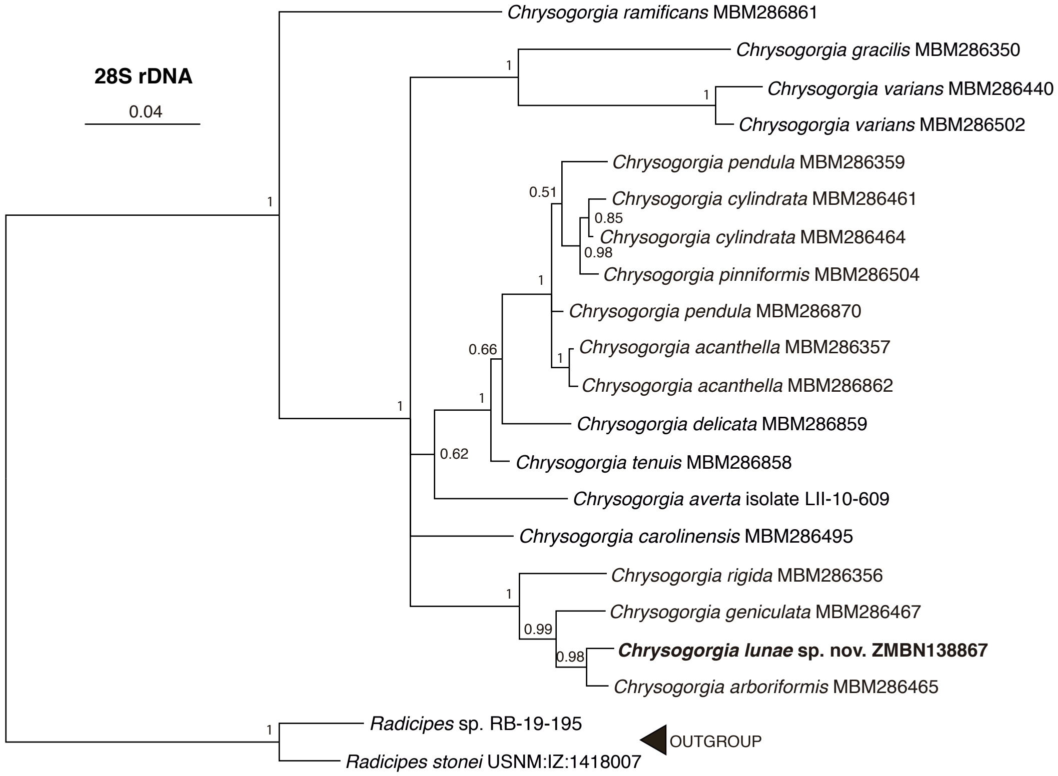

Figure 10. Bayesian Inference (BI) tree of the 28S dataset showing phylogenetic relationships between *Chrysogorgia lunae* sp. nov. and other congeners with the corresponding voucher numbers. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. Supporting values of nodes as posterior probability.

Table 2. Interspecific distances at mtMutS between *Chrysogorgia lunae* sp. nov. and select groups of *Chrysogorgia* species as delineated by the Maximum likelihood (ML) tree based on mtMutS+COI (Fig.7).

Comparisions within	Min	Average	Max
C. lunae sp. nov. - I group	0	0.04	0.15
C. lunae sp. nov. - II group	0.74	0.77	0.83
C. lunae sp. nov. - III group	0.89	1.11	1.79

Table 3. Interspecific distances at 28S between *Chrysogorgia lunae* sp. nov. and select groups of *Chrysogorgia* species as delineated by the Maximum likelihood (ML) tree based on 28S (Fig. 8).

Comparisions within	Min	Average	Max
C. lunae sp. nov. - I group	1.27	3.03	4.74
C. lunae sp. nov. - II group	8.21	10.80	12.68
C. lunae sp. nov. - III group	7.33	8.52	9.23

4. Discussion

4.1. Geographical and bathymetric distribution of Chrysogorgia

The family Chrysogorgiidae is poorly represented in Antarctic waters when compared to other scleralcyonacean families such as Primnoidae, which is often dominant in Southern Ocean seabeds (Cairns and Bayer, 2009). Only two chrysogorgiid species have previously been reported in the Antarctic region, *Parachrysogorgia antarctica* (Cairns, 2002) and *Radicipes* sp. (Cairns, 2002; Watling et al., 2011; Pante et al., 2012). The majority of *Chrysogorgia* species are found in the northern Pacific Ocean and most of them in tropical latitudes (Watling, 2011; Pante and Watling, 2012; Cairns, 2018). Within the southern hemisphere, only two *Chrysogorgia* species, *C. lunae* sp. nov. and C. flexilis (Wright and Studer, 1889) have been documented beyond 45º S latitude. Specifically, the distribution of *C. flexilis* encompasses the waters surrounding Wellington Island, in the fjord region of Southern Chile; while, *C. lunae* sp. nov. stands as the singular representative of its genus in Antarctic waters. Regarding bathymetric distribution, the genus *Chrysogorgia* is eurybathic, but the majority of the species occur at depths greater than 600 m while the shallowest species (< 500 m depth) have been found only at tropical and subtropical latitudes (-5°S – 34°N) (Cairns, 2001; Pante et al., 2012). In this sense, *C. lunae* sp. nov. conforms to the pattern observed so far as it was found at 1407–1581 m depth. Furthermore, like many other *Chrysogorgia* species, *C. lunae* sp. nov. has been observed on a seamount (Cairns, 2007; Pante and Watling, 2012; Xu et al., 2021b). Seamounts are relatively isolated topographic rises with environmental conditions that enhance high levels of biodiversity and endemism (Hubbs 1959; Genin et al., 1986; Richer de Forges et al., 2000; Clark and Bowden, 2015). Following the case study of endemism of *Chrysogorgia* on seamounts by Pante et al. (2015a), there is a possibility that *C. lunae* sp. nov. may be endemic to Maud Rise or to a group of nearby seamounts. However, the current information about latitudinal and bathymetric distribution of the genus is scarce, as the majority of species have been observed only once (Pante et al., 2012). Consequently, any geographical and bathymetric comparison within the genus must be taken with caution since it represents merely a snapshot in our knowledge of chrysogorgiid distribution.

4.2. Morphological comparisons within Chrysogorgia

To date, twenty-one valid *Chrysogorgia* species are included in Versluys' (1902) "Squamosae typicae" group C, including *C. lunae* sp. nov. (Cairns 2001, 2002; Pante and Watling 2012; Xu et al., 2021b; Xu et al., 2023; this study). Only five of these species have been recorded in the southern hemisphere: *C. acanthella*, *C. axillaris* (Wright and Studer, 1889), *C. pendula*, *C. sibogae* Versluys, 1902 and *C. lunae* sp. nov. (**Table 4**). Of these species, besides *C. lunae* sp. nov., only *C. pendula* and *C. acanthella* have a branching sequence 2/5L. However, *C. pendula* is characterized by a typically bottle-brush colony and descending-oriented secondary branches (Versluys, 1902) while *C. lunae* sp. nov. has a bushy colony shape and ascending-oriented secondary branches. *Chrysogorgia acanthella* resembles *C. lunae* sp. nov. in its bushy colony shape with upright-directed secondary branches; however, this species differs from *C. lunae* sp. nov. in having a stem with polyps and, in the pinnules, slender and little curved sclerites extend from the tentacles into pinnules. Conversely, in *C. lunae* sp. nov. the scales in pinnules are independent of the tentacles and are long, toothed, rib-like. On the other hand, the polyps of *C. acanthella* are pitcher-shaped while those of *C. lunae* sp. nov. are bell-shaped (Wright and Studer, 1889; Versluys, 1902; this study).

Other four "Squamosae typicae" *Chrysogorgia* species have been described with branching sequence 2/5L: *C. campanula* Madsen, 1944, C. artospira Pante and Watling, 2012, *C. cylindrata*, and *C. cavea* Kinoshita, 1913, all of them occurring in the northern hemisphere (Wright and Studer, 1889; Versluys, 1902; Pante and Watling, 2012) (see **Table 4**). *Chrysogorgia campanula* is known from Icelandic waters and it resembles *C. lunae* sp. nov. in the presence of sclerites in the pinnules, but *C. campanula* has more than one sclerite in each pinnule while *C. lunae* sp. nov. has only one sclerite per pinnule (Madsen, 1944). *Chrysogorgia artospira* resembles *C. lunae* sp. nov. as neither of these species have polyps on the stem; however, C. artospira forms a bottlebrush colony in the adult stage, presents pitcher-shaped polyps, and its sclerome is characterized by smooth scales, while *C. lunae* sp. nov. has a bushy colony, bell-shaped polyps, and its sclerites are warty scales (Pante and Watling, 2012; this study). Similar to *C. lunae* sp. nov., *C. cylindrata* displays 1 or 2 terminal polyps at the tips of terminal twigs, and there are sclerites arranged in the pinnules but no scales with toothed rib-like shape. It also differs from the newly described species due to the presence of polyps on the stem and bottlebrush-shaped colonies in adults. Finally, *C. cavea* resembles *C. lunae* sp. nov. on account of a long rib-like scale within each pinnule. However, in contrast to the new species, *C. cavea* has bottlebrush colonies in adult stage and smooth scales in stem, while *C. lunae* sp. nov. present warty texture throughout all its parts and also has prominent tubercles in the stem scales (Kükenthal, 1924; Xu et al., 2023).

4.3. Molecular analysis

Chrysogorgia lunae sp. nov. shares the complete analyzed fragments of mtMutS with three specimens identified as *C. geniculata* and two specimens identified as *C. arboriformis* (**Table 1 of Supplementary material**). The mitochondrial genomes of anthozoans evolve slowly and exhibit high conservative barcodes among congeneric species (Shearer et al., 2002; Hellberg, 2006; McFadden et al., 2017), which may explain the absence of variation between *C. lunae* sp. nov. and *C. geniculata* and *C. arboriformis*. In this sense, in a previous study case, only 70% of different octocoral morphospecies were identified by mitochondrial genes (McFadden et al., 2011). Conversely, considering the 28S gene sequences, there are clear differences between *C. lunae* sp. nov., *C. arboriformis*, and *C. geniculata* (**Figs. 9 and 10 and Table 2 of Supplementary material**). The potential variability of the 28S segment will only be understood when several colonies per species are sequenced, a situation that is still far from being achieved. In the meantime, our findings suggest that 28S could potentially serve as a successful marker to discriminate *Chrysogorgia* congeners, even when mitochondrial markers do not show differences that can support other observed morphological differences. All three species included in this clade belong to "Squamosae typicae" and possess long toothed rib-like scales in pinnules (**Table 5**).

In octocorals, further investigation is warranted for divergent sequences assigned to a specific species, a task influenced by whether these sequences belong to mitochondrial or nuclear segments (Hellberg, 2006). Mitonuclear incongruities in particular, offer a compelling avenue to explore diverse evolutionary processes including interspecific hybridization, explosive radiation, incomplete lineage sorting, or the presence of multicopy nuclear DNA segments (Vollmer and Palumbi, 2004; Forsman et al., 2010; Bilewitch et al., 2010; McFadden et al., 2010). These factors may also contribute to the challenge of distinguishing closely related species (e.g., Soler-Hurtado et al., 2017). Our mtMutS+COI analysis revealed two divergent sequences for C. varians. In this specific example, nine mtMutS sequences are archived in GenBank, with eight of them being identical and just one differing by a single base. Considering the suggestion that multilocus barcodes (mtMutS+COI) can discriminate approximately 70% of octocoral morphospecies (McFadden et al., 2011), even minor discrepancies, such as those observed in mtMutS, underline the need for additional research to uncover potential species complexes (McFadden et al., 2017) or genuine mtMutS variations, as indicated in certain gorgonians (Moore et al., 2016), pending further sequencing endeavors. RADseq analyzes on a selected number of *Chrysogorgia* species (Pante et al., 2015b) are broadly consistent with mtMutS hypotheses (~70% of species recovered in well-supported clades). However, they also identify potential cryptic speciation under identical sequences of mtMutS, as well as suggesting potential variability of mtMutS. Unfortunately, detailed morphological studies and molecular information of species in this genus are rarely presented together or encompass a limited number of species (Pante and Watling, 2012; Pante et al., 2015b; Xu et al., 2023). Therefore, it is challenging to more accurately assess the information provided by currently available mitochondrial and nuclear markers (e.g., mtMutS, COI, 28S) or other promising molecular techniques (e.g., RADseq, UCE). Moreover, discrepancies in the nuclear 28S gene, as evident in our phylogenetic tree for *C. acanthella*, *C. pendula*, and *C. cylindrata* (**Fig. 10**), align with findings by Xu et al. (2021b, 2023). The full utility of the 28S segment remains incompletely elucidated, despite its proven higher interspecific variability, as our results demonstrate. This characteristic has reinforced the discriminatory capacity of the proposed barcode mtMutS+COI+28S (McFadden and van Ofwegen, 2012; McFadden et al., 2014). Furthermore, a more comprehensive understanding of the multicopy nuclear 28S gene in octocorals is needed, akin to what is known for other previously employed markers (Gilbert et al., 2007; Concepcion et al., 2008).

Table 4. Morphological comparison of all “Squamosae typicae” *Chrysogorgia* species distributed in the southern hemisphere and four more from the northern hemisphere with 2/5L as branching sequence as well as *Chrysogorgia lunae* sp. nov. “-” means missing data.

Species / Characters	***C. lunae* sp. nov.**	***C. pendula***	***C. acanthella***	***C. axillaris***	***C. sibogae***	***C. cavea***	***C. campanula***	***C. artospira***	***C. cylindrata***
Colony shape	Bushy	Bottlebrush	Bushy bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush	Bottlebrush
Branching sequence	2/5L	2/5L	3/7L, 2/5L	1/3L	1/3L	1/3L, 2/5L	2/5L	2/5L	2/5L
Orthostiche interval	13 – 18 mm	6 – 28 mm	26 – 50 mm	8 – 9 mm	-	-	-	11 – 30 mm	5 – 30 mm
Polyps shape	Bell-shaped	Cylindrical (terminal polyps) or oval body (non-terminal polyps)	Pitcher shaped	Pitcher shaped	-	-	Trumped-shaped	Pitcher-shaped	Cylindrical (terminal polyps) or oval body (non-terminal polyps)
Polyps on the stem	Absent	Present	Present	Absent	Present	Absent	Present	Absent	Present
Polyps on terminal twigs	Often 2	Up to 4	Up to 5	1	-	-	1	1 or 2	1 or 2
Sclerites in coenenchyme	Warty scales with prominent tubercles and minute warts and narrowing in the center	Scales smooth, elongate with a medial contraction and lobed with irregular shape	Scales elongate and smooth with medial contraction, with irregular shape	Scales small, oval and irregular shape	Scales smooth, rounded or oval, some of them with irregular lobed edges	Scales smooth, elongate with serrated edges and a narrow median	Scales usually 8-shaped with a median contraction, small spines and finely denticulate edges with irregular shape	Absent	Scales smooth and slender, some of them with lobed and irregular edges
Sclerites in polyp body	Warty and asymmetric scales and a constricted middle	Scales elongate and nearly smooth with a medial contraction with irregular shape	Scales smooth and elongate with a medial contraction	Scales large with irregular and toothed edges, and little wrinkles	Scales thin with finely toothed edges	Scales slightly elongate with minute warts and serrated edges, and with a medial contraction	Scales 8-shaped with a median contraction, some of them with irregular edges	Scales smooth with rounded ends and a medial contraction	Scales smooth and elongate with a medial contraction and irregular edges and shape
Sclerites in tentacles	Arched butterfly scales and asymmetric planar scales with serrated edges	Scales nearly smooth, elongate, with irregular shape and lobed edges	Scales nearly smooth and usually irregular shape	Scales irregular with one or two large scales projecting above the base of tentacle	Scales thick, elongate with sparse fine warts, irregular shape	Scales elongate with irregular lobed edges and scales curved with deep lobed edges	Scales usually x-shaped	Scales smooth, flat or with idiosyncratic shapes	Scales elongate to slender, nearly smooth with irregular shape and lobed edges

Sclerites in pinnules	Toothed rib-like scales	Scales slender and slightly curved, nearly smooth or with sparse fine warts	Slender and little curved scales extend from the tentacles into pinnulae	Absent	The sclerites of the tentacles extend into the pinnules	Toothed rib-like scales	Scales long with one end forked and the other end gutter-shape	Some sclerites partially extend into the pinnules, which are otherwise sclerite-free	Scales slender and nearly smooth with minute warts
Location (depth)	Antarctica, Eastern Weddell Sea (1407–1581m)	Banda Sea, W Indian and NW Pacific, Caroline Ridge (1595m)	S Pacific, Kermadec Islands (1097m)	NW Pacific, Kermadec Islands (1097m) Philippines (150 and 186m)	Banda Sea, W Indian (204m)	NW Pacific, Japan (640–752m)	Iceland waters, Denmark Strait (2448m)	N Atlantic, New England (2253 and 1965m) and Corner Seamounts (1846 and 1650m)	NW Pacific, Caroline Ridge (1877–870m)
Reference	Present study	Versluys, 1902; Xu et al., 2023	Wright and Studer, 1889; Versluys, 1902; Xu et al., 2023	Wright and Studer, 1889	Versluys, 1902	Kinoshita, 1913; Kükenthal, 1919; Xu et al., 2023	Madsen, 1944; Xu et al., 2023	Pante and Watling, 2012	Xu et al., 2023

Table 5. Morphological comparison between *Chrysogorgia lunae* sp. nov. and the genetically closely related species. All these species are included in "Squamosae typicae" Verluys' (1902) group and present toothed rib-like scales in pinnules.

Species / Characters	***C. lunae* sp. nov.**	***C. geniculata***	***C. arboriformis***	***C. rigida***
Colony shape	Bushy	Bottlebrush	Tree-shaped	Bottlebrush
Branching sequence	2/5L	1/3L	1/3L	1/3L
Orthostiche interval	13 – 18 mm	10 – 11.5 mm	8 – 23 mm	12 – 13 mm
Polyps shape	Bell-shaped	Pitcher-shaped	Expanded oval body	Conical
Polyps on the stem	Absent	Present	Rare	Absent
Polyps on terminal twigs	Often 2	1 or 2	Up to 7	Up to 3
Sclerites in coenenchyme	Warty scales with prominent tubercles and minute warts and narrowing in the center	Elongate and nearly smooth or with many minute warts and one or more distinct large warts	Scales slender, nearly smooth or with one or more large warts and many little warts	Scales with minute warts, many of them with a large wart on center
Sclerites in polyp body	Warty and asymmetric scales and a constricted middle	Elongate scales with irregular blunted or notched edges and with minute warts or nearly smooth	Nearly smooth scales with a medial contraction, usually with one or two broad and straight ends or irregular shape	Irregular scales with a strong medial contraction and nearly smooth
Sclerites in tentacles	Arched butterfly scales and asymmetric planar scales with serrated edges	Curved and warty scales with different shapes	Curved scales with branched, forked or irregular shapes and with many fine coarse warts	Scales curved with irregular shape and many obvious warts
Location (depth)	Antarctica, Eastern Weddell Sea (1407–1581m)	NW Pacific, Philippines (150 and 186m) and South Japan waters (630m)	NW Pacific, Caroline Ridge, (1482–1573)	NW Pacific, Caroline Ridge (522m) and Philippines waters (691m)
Reference	Present study	Wright and Studer, 1889; Xu et al., 2023	Xu et al., 2023	Versluys, 1902; Kükenthal, 1919; Xu et al., 2023

5. Conclusions

The assignment of *C. lunae* sp. nov. to the genus *Chrysogorgia* was supported by both morphological and phylogenetic results. The known species richness of this genus has been increased especially in recent decades (e.g. Cordeiro et al., 2015; Xu et al., 2023). However, more than half of *Chrysogorgia* species occur in the deep sea and often inhabiting locations such as seamounts, and that also hinders their study (Watling et al., 2011; Pante et al., 2012). This frequently leads to situations where species such as *C. lunae* sp. nov. are described based on a limited number of specimens. Furthermore, environmental plasticity is characteristic of octocorals, whereby certain characters like colony shape may vary depending on the growth stage, occasionally obscuring species boundaries (Untiedt et al., 2021; Xu et al., 2023). In the case of *Chrysogorgia*, some morphological features remain highly consistent thus enabling differentiation among species, as demonstrated also in our study. This appears to be the case with the growth direction of the colony (clockwise or counterclockwise), as well as the morphology of the sclerites in different parts of the colony (Versluys, 1902; Cordeiro et al., 2015; Untiedt et al., 2021; Xu et al., 2023; present study). All the aforementioned factors emphasize the strong need for further studies in *Chrysogorgia* and other deep-water octocorals.

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Supplementary material

Table 1. Interspecific and intraspecific distances for mtMutS of *Chrysogorgia* species (in %)

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*Chrysogorgia lunae* sp. nov. ZMN138867																
2	*Chrysogorgia geniculata* isolate HI-015	0.0000															
3	*Chrysogorgia geniculata* isolate HI-018	0.0000	0.0000														
4	*Chrysogorgia geniculata* isolate HI-037	0.0000	0.0000	0.0000													
5	*Chrysogorgia arboriformis* MBM286465	0.0000	0.0000	0.0000	0.0000												
6	*Chrysogorgia arboriformis* MBM286466	0.0000	0.0000	0.0000	0.0000	0.0000											
7	*Chrysogorgia rigida* MBM286356	0.1479	0.1479	0.1479	0.1479	0.1479	0.1479										
8	*Chrysogorgia geniculata* MBM286467	0.1490	0.1490	0.1490	0.1490	0.1490	0.1490	0.0000									
9	*Chrysogorgia delicata* MBM286859	0.7425	0.7425	0.7425	0.7425	0.7425	0.7425	0.5936	0.5981								
10	*Chrysogorgia tenuis* MBM286858	0.7425	0.7425	0.7425	0.7425	0.7425	0.7425	0.5936	0.5981	0.0000							
11	*Chrysogorgia tricaulis* n.d.	0.8282	0.8282	0.8282	0.8282	0.7425	0.7425	0.5936	0.5981	0.0000	0.0000						
12	*Chrysogorgia pendula* MBM286359	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453					
13	*Chrysogorgia acanthella MBM286862*	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453	0.0000				
14	*Chrysogorgia acanthella* MBM286357	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453	0.0000	0.0000			
15	*Chrysogorgia pendula* MBM286865	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453	0.0000	0.0000	0.0000		
16	*Chrysogorgia cylindrata* MBM286464	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453	0.0000	0.0000	0.0000	0.0000	
17	*Chrysogorgia cylindrata* MBM286461	0.8922	0.8922	0.8922	0.8922	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.1453	0.0000	0.0000	0.0000	0.0000	0.0000
18	*Chrysogorgia pendula* MBM286870	0.8949	0.8949	0.8949	0.8949	0.8949	0.8949	0.7453	0.7487	0.1458	0.1458	0.1458	0.0000	0.0000	0.0000	0.0000	0.0000
19	*Chrysogorgia varians* MBM286503	0.8971	0.8971	0.8971	0.8971	0.9011	0.9011	1.0518	1.0597	0.4407	0.4407	0.4388	0.2934	0.2934	0.2934	0.2934	0.2934
20	*Chrysogorgia cylindrata* MBM286460	0.8989	0.8989	0.8989	0.8989	0.8989	0.8989	0.7487	0.7487	0.1464	0.1464	0.1464	0.0000	0.0000	0.0000	0.0000	0.0000
21	*Chrysogorgia pinniformis* MBM286504	0.9002	0.9002	0.9002	0.9002	0.9002	0.9002	0.7498	0.7555	0.1466	0.1466	0.1466	0.0000	0.0000	0.0000	0.0000	0.0000
22	*Chrysogorgia carolinensis* MBM286445	0.9043	0.9043	0.9043	0.9043	0.9043	0.9043	0.7532	0.7532	0.1486	0.1486	0.1486	0.0000	0.0000	0.0000	0.0000	0.0000
23	*Chrysogorgia pinnata* USNM1102450	0.9668	0.9668	0.9668	0.9668	0.8922	0.8922	0.7431	0.7487	0.1453	0.1453	0.2704	0.0000	0.0000	0.0000	0.0000	0.0000
24	*Chrysogorgia artospira* isolate KEL619-1	0.9688	0.9688	0.9688	0.9688	0.8935	0.8935	0.7442	0.7498	0.1464	0.1464	0.1361	0.0000	0.0000	0.0000	0.0000	0.0000
25	*Chrysogorgia varians* MBM286502	1.0923	1.0923	1.0923	1.0923	1.0923	1.0923	1.2488	1.2488	0.6099	0.6099	0.6099	0.4568	0.4568	0.4568	0.4568	0.4568
26	*Chrysogorgia gracilis* MBM286350	1.1182	1.1182	1.1182	1.1182	1.1182	1.1182	0.9577	0.9577	0.6341	0.6341	0.6341	0.4749	0.4749	0.4749	0.4749	0.4749
27	*Chrysogorgia averta* isolate LII-10-609	1.2462	1.2462	1.2462	1.2462	1.1920	1.1920	1.0424	1.0502	0.4368	0.4368	0.4061	0.2909	0.2909	0.2909	0.2909	0.2909
28	*Chrysogorgia monticola* MBM286870	1.3864	1.3864	1.3864	1.3864	1.4941	1.4941	1.3440	1.3541	0.7301	0.7301	0.8154	0.5833	0.5833	0.5833	0.5833	0.5833
29	*Chrysogorgia ramificans* MBM286861	1.5068	1.5068	1.5068	1.5068	1.5068	1.5068	1.3557	1.3557	0.7364	0.7364	0.7364	0.5882	0.5882	0.5882	0.5882	0.5882
30	*Chrysogorgia fragilis* MBM286352	1.6060	1.6060	1.6060	1.6060	1.6060	1.6060	1.4449	1.4449	0.7949	0.7949	0.7949	0.6349	0.6349	0.6349	0.6349	0.6349
31	*Chrysorgorgia abluda* NAS102-3	1.6909	1.6909	1.6909	1.6909	1.8246	1.8246	1.6721	1.6849	1.0402	1.0402	1.1050	0.8902	0.8902	0.8902	0.8902	0.8902
32	*Chrysogorgia dendritica* MBM286353	1.7919	1.7919	1.7919	1.7919	1.8000	1.8000	1.6495	1.6620	1.0264	1.0264	1.0219	0.8785	0.8785	0.8785	0.8785	0.8785
33	*Radicipes stonei* USNM:IZ:1418007	1.9661	1.9661	1.9661	1.9661	2.1210	2.1210	1.9685	1.9835	1.8062	1.8062	1.8171	1.6533	1.6533	1.6533	1.6533	1.6533
34	*Radicipes gracilis* USNM 100900	2.0936	2.0936	2.0936	2.0936	1.9507	1.9507	1.8000	1.8136	1.6203	1.6203	1.9235	1.4709	1.4709	1.4709	1.4709	1.4709

	Species	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
18	*Chrysogorgia pendula* MBM286870	0.0000																
19	*Chrysogorgia varians* MBM286503	0.2934	0.2943															
20	*Chrysogorgia cylindrata* MBM286460	0.0000	0.0000	0.2956														
21	*Chrysogorgia pinniformis* MBM286504	0.0000	0.0000	0.2934	0.0000													
22	*Chrysogorgia carolinensis* MBM286445	0.0000	0.0000	0.3000	0.0000	0.0000												
23	*Chrysogorgia pinnata* USNM1102450	0.0000	0.0000	0.2921	0.0000	0.0000	0.0000											
24	*Chrysogorgia artospira* isolate KEL619-1	0.0000	0.0000	0.2943	0.0000	0.0000	0.0000	0.1360										
25	*Chrysogorgia varians* MBM286502	0.4568	0.4568	0.1534	0.4568	0.4610	0.4610	0.4568	0.4603									
26	*Chrysogorgia gracilis* MBM286350	0.4749	0.4749	0.4747	0.4749	0.4749	0.4771	0.4749	0.4756	0.6337								
27	*Chrysogorgia averta* isolate LII-10-609	0.2909	0.2917	0.5854	0.2930	0.2934	0.2973	0.4060	0.2722	0.7629	0.7932							
28	*Chrysogorgia monticola* MBM286870	0.5833	0.5850	0.8804	0.5875	0.5884	0.5963	0.6781	0.6832	1.0711	1.1137	0.9517						
29	*Chrysogorgia ramificans* MBM286861	0.5882	0.5882	0.8917	0.5882	0.5935	0.5970	0.5882	0.5926	0.7635	1.1149	0.8838	0.2930					
30	*Chrysogorgia fragilis* MBM286352	0.6349	0.6349	0.9541	0.6349	0.6349	0.6380	0.6349	0.6359	1.1149	1.1149	0.9541	1.2762	1.2780				
31	*Chrysorgorgia abluda* NAS102-3	0.8902	0.8929	0.8851	0.8969	0.8902	0.9105	0.9644	0.9723	1.0872	1.1202	1.2433	1.3834	1.5039	0.3180			
32	*Chrysogorgia dendritica* MBM286353	0.8785	0.8811	0.8812	0.8850	0.8863	0.8982	0.8747	0.8811	1.0722	1.1149	1.1681	1.4644	1.4838	0.3165	0.0000		
33	*Radicipes stonei* USNM:IZ:1418007	1.6533	1.6583	1.9667	1.6658	1.6683	1.5214	1.6738	1.6821	2.0504	1.9482	1.9578	2.1005	2.2850	2.1159	2.2744	2.4116	
34	*Radicipes gracilis* USNM 100900	1.4709	1.4752	1.7760	1.4818	1.4839	1.1996	1.7816	1.6555	1.8499	1.7609	2.0613	2.2017	2.0869	1.9266	2.5182	2.3640	1.3934

Table 2. Interspecific and intraspecific distances for 28S of *Chrysogorgia* species (in %).

	Species	1	2	3	4	5	6	7	8	9	10
1	*Chrysogorgia lunae sp. nov.* ZMN138867										
2	*Chrysogorgia arboriformis* MBM286465	1.2701									
3	*Chrysogorgia geniculata* MBM286467	3.0721	2.5488								
4	*Chrysogorgia rigida* MBM286356	4.7378	4.4428	4.1368							
5	*Chrysogorgia tenuis* MBM286858	7.3283	6.7126	7.4857	7.1505						
6	*Chrysogorgia pendula* MBM286870	8.1697	7.4876	8.1088	7.6265	2.1383					
7	*Chrysogorgia carolinensis* MBM286445	8.2060	7.5814	7.9294	8.4124	4.8610	6.3616				
8	*Chrysogorgia pendula* MBM286359	8.3470	7.8766	8.8376	8.5070	3.1230	1.2694	6.7537			
9	*Chrysogorgia cylindrata* MBM286464	8.6856	7.8875	8.6675	8.1617	2.4054	0.8476	6.4519	1.6902		
10	*Chrysogorgia acanthella* MBM286357	8.7153	7.7048	8.3824	7.8883	1.9682	0.7028	5.9693	1.6813	0.8417	
11	*Chrysogorgia delicata* MBM286859	8.7232	8.0849	9.1760	8.9926	2.3825	3.3163	6.8247	4.1700	3.5708	3.2925
12	*Chrysogorgia cylindrata* MBM286461	8.8634	8.1799	9.1483	8.6370	2.7798	1.2748	6.8751	2.1130	0.4180	1.2588
13	*Chrysogorgia acanthella* MBM286862	8.9005	7.9111	8.5442	7.8883	2.1232	0.8445	6.1593	1.8287	0.9827	0.1391
14	*Chrysogorgia pinniformis* MBM286504	9.2338	8.5948	9.4758	8.7771	2.6116	1.0204	6.7922	1.5907	0.5765	1.0068
15	*Chrysogorgia averta isolate* LII-10-609	9.2765	9.3462	9.5377	9.0179	5.8322	6.8092	6.8111	7.2590	7.2408	7.0921
16	*Chrysogorgia gracilis* MBM286350	10.4279	11.7792	9.7065	10.1986	10.4075	8.4291	9.9554	9.4792	8.3641	8.9605
17	*Chrysogorgia varians* MBM286502	11.8828	12.5632	12.9244	13.3539	10.3048	11.0067	10.5050	10.8305	10.6404	11.1833
18	*Chrysogorgia varians* MBM286440	12.6783	13.3430	13.7070	14.1220	11.2163	11.5530	11.6093	11.3757	11.1833	11.7307
19	*Chrysogorgia ramificans* MBM286861	13.4963	12.0541	12.1912	11.8756	11.7052	11.5697	11.8475	11.8228	11.6247	11.3458
20	*Radicipes stonei* USNM:IZ:1418007	16.8843	15.1563	16.0085	16.4472	13.9082	14.5424	15.1297	14.7429	14.3183	14.7429
21	*Radicipes sp.* RB-19-195	19.8079	18.8727	19.4258	20.7043	18.9604	19.1348	18.9939	19.3131	19.0165	19.5457

	Species	11	12	13	14	15	16	17	18	19	20
12	*Chrysogorgia cylindrata MBM286461*	4.0117									
13	*Chrysogorgia acanthella MBM286862*	3.4392	1.4079								
14	*Chrysogorgia pinniformis MBM286504*	3.9957	1.0064	1.1586							
15	*Chrysogorgia averta isolate LII-10-609*	6.6386	7.7529	7.2642	7.7529						
16	Chrysogorgia gracilis MBM286350	9.6333	10.0504	8.3712	9.4491	12.1051					
17	*Chrysogorgia varians MBM286502*	10.8039	11.1833	11.3678	11.1833	11.6595	10.0985				
18	*Chrysogorgia varians MBM286440*	11.5310	11.7307	11.9169	11.7307	12.8209	10.4546	1.7127			
19	*Chrysogorgia ramificans MBM286861*	12.4857	12.1283	11.5165	12.2272	11.5447	14.6490	15.4314	16.4110		
20	*Radicipes stonei USNM:IZ:1418007*	15.1224	14.9440	14.9566	14.7308	16.6241	17.1451	16.7756	17.8879	14.9040	
21	*Radicipes sp. RB-19-195*	20.3731	19.6373	19.7603	19.6373	20.1548	20.8286	20.4520	21.3011	18.6618	3.2331

GENERAL DISCUSSION

General discussion

Marine ecosystems, including those in the Southern Ocean, are facing increasing pressure from anthropogenic threats (Massom and Stammerjohn, 2010; Doney et al., 2012; Clark et al., 2016; Gutt et al., 2021). The loss of biodiversity impacts the functioning of these ecosystems, leading to direct consequences for the ecosystem services they provide (Danovaro et al., 2008). For the effective conservation of these environments, a robust knowledge base is essential. Understanding biodiversity is critical for identifying suitable marine areas to designate as Marine Protected Areas (MPAs), as well as for assessing ecosystem resilience to potential impacts. This includes determining the types of species present, their vulnerability status, and their ecological roles (Jenkins and Van Houtan, 2016; Zhao et al., 2020). Furthermore, it is important to investigate any differences in taxonomic composition among nearby ecosystems and determine their level of connectivity for successful management (Clark et al., 2012). Therefore, the study of species reproduction and larval biology, coupled with the analysis of hydrodynamics and other physical characteristics such as substrate, becomes crucial (Clark et al., 2012; Dubois et al., 2016). Connectivity plays a pivotal role in the resilience of ecosystems, as it can facilitate the recolonization of areas impacted by disturbances (Brooks et al., 2006; Danovaro et al., 2020). Furthermore, a deeper understanding of species distribution allows us to anticipate potential responses to scenarios such as climate change (Kaiser and Barnes, 2008; Tittensor et al., 2009; Kaiser et al., 2013). An example of this would be predicting the movement of certain species to deeper zones of a seamount due to rising temperatures (Rowden et al., 2010).

The aim of this thesis is to deepen the understanding of biodiversity across various perspectives within distinct Antarctic ecosystems, with the ultimate goal of providing useful insights for the effective management of ecosystem conservation. To achieve this, **Chapter 1** examined the relation of different benthic communities on the biodiversity of demersal fish. **Chapter 2** investigated the variation in anthozoan biodiversity focusing on the influence of seamounts and different environmental factors, and also elucidating how anthozoan assemblages differ from those in the surrounding plain. Lastly, **Chapter 3** described a new species of a golden gorgonian found in one of the seamounts studied in the second chapter.

In **Chapter 1**, the marine area in front of the Filchner-Ronne Ice Shelf, in the southernmost part of the Weddell Sea, was examined within a bathymetric range of 251–361 meters. Through video analysis, the density, spatial distribution, and size of observed demersal fish were described. Additionally, the study aimed to investigate the role of engineer animals in forming different types of benthic communities, defined based on the percentage coverage of the most abundant engineer animals, such as gorgonians, sponges, and bryozoans. Engineer species enhance the three-dimensional complexity of ecosystems by providing refuge and nursery grounds, thereby promoting biodiversity in associated fauna (*sensu* Jones et al., 1994). In this chapter, the goal was to better understand the potential relationship or influence of different benthic communities on the presence and, consequently, the distribution of the demersal fish species recorded. According to the obtained results, the majority of the observed fish species were positively related with structurally more complex benthic communities, particularly those where bryozoans, gorgonians, and sponges dominated. These communities, in turn, were associated with sand matrix bottoms with rocks. Fish biodiversity was higher in both the more complex benthic communities and areas with sandy matrix with rocks. However, not all species followed this trend. An example is *Cygnodraco mawsoni*, a species that prefered open areas where communities were dominated by bryozoans. Additionally, differences were observed based on the growth stage of the fish. In simpler terms, juveniles of some species, like *Trematomus lepidorhinus* and *T. scotti*, sought refuge among engineer animals to protect themselves from predators, and it was the adults that had a more water-column-dependent lifestyle. These findings enabled us to conclude that the interactions between ecosystem engineers and the associated fauna within the benthic communities they form are highly intricate. While fish biodiversity was indeed positively associated with structurally more complex benthic communities, preferences could vary among certain species, as well as in their growth stages.

Throughout **Chapter 2**, the biodiversity variation of a large benthic taxonomic group, the anthozoans, was studied in relation to the study area and substrate type. This investigation was conducted on two Antarctic seamounts in the eastern part of the Weddell Sea. Similar to the methodology employed in the first chapter, the same direct observation approach using Remoted Operated Vehicle (ROV) was applied, followed by the analysis of video transects. The findings of this study revealed that, despite being two aparently similar environments, the biodiversity and taxonomic composition of anthozoans differed on the two seamounts under investigation. In Maud Rise, the overall density of anthozoans was higher than in Astrid Ridge, with Octocorallia exhibiting a density eight times greater than Hexacorallia (36.43 and 4.54 OTUs/100 m^2, respectively). In the case of Astrid Ridge, the density of both taxonomic groups was very similar (7.28 and 7.80 OTUs/100 m^2, respectively). The slopes of Maud Rise were characterized by predominantly hard substrate, where Stolonifera was one of the OTUs with the highest density. In contrast, Astrid Ridge features soft substrates with small rocks, where Pennatulacea, Scleractinia, and Actiniaria were prominent OTUs. Similar to previous studies (e.g. Davies et al., 2015; Bridges et al., 2021), substrate was identified as a determining factor for observed differences. It was noteworthy that most observed OTUs were attached to hard substrate, even in those areas where substrate was predominantly soft. While some OTUs are adapted to attach to soft substrate, such as *Umbellula*, due to this adaptation, it was found in abundance at the summit of Maud Rise, where the substrate was predominantly soft. On the summit and slopes of Astrid Ridge, the co-occurring animals with observed anthozoans were mostly mobile and detritivores, such as decapods and ophiuroids. In contrast, on the slopes of Maud Rise, the presence of bedrock favoured the occurrence of other benthic suspension feeders, such as carnivorous ascidians and hexactinellids. Apart from the significant differences between the two seamounts and between substrate types and mountain zones (slope vs summit), there also appeared to be differences when comparing the Weddell Sea plain with the seamounts in terms of anthozoan taxonomic composition. Octocorals were much more prevalent in the surveyed seamounts, whereas hexacorals dominated in the plain (Linse et al., 2007). Overall, suspension feeders thrive in the seamounts, while detritivores flourish in the plain (Starmans et al., 1999; Linse et al., 2007; Bridges et al., 2021; Lowther et al., 2022). Furthermore, it has been observed that anthozoan biodiversity was concentrated at small scales, indicating a patchy distribution. A strategy that seems to favor the reproduction and recruitment of anthozoans should be considered in strategic conservation efforts (Pineda, 2000; Orejas et al., 2002; Sampayo et al., 2020; Miatta et al., 2021). Therefore, the results of this chapter highlighted that relatively close seamounts with apparently similar environments could harbour distinct communities, as well as, the anthozoan assemblages of these seamounts differed from those found in the adjacent plain.

In addition to characterising the anthozoan community in **Chapter 2**, during one of the video transects conducted on a slope of the Maud Rise seamount, a colony of *Chrysogorgia* was sampled. This turned out to be a new species of golden coral, and its description constitutes **Chapter 3**, thereby expanding the knowledge of the biodiversity present in that seamount. Representatives of the Chrysogorgiidae family are distributed across all the world's oceans and within a broad bathymetric range ranging from 10 to 4492 m deep (Watling et al., 2011; Cairns, 2018). However, this family is notably sparse in Antarctic waters. In this regard, following the latest taxonomic revision of the *Chrysogorgia* genus (Xu et al., 2023), *C. lunae* sp. nov. stands as the sole representative of this genus in the Southern Ocean (Baena et al., 2024). To describe this new species, an integrative approach was employed, examining its morphology at both the colonial and sclerite levels. The growth direction of the colony (clockwise or counterclockwise) and the morphology of the sclerites were some of the morphological features that helped to identify with consistency the new *Chrysogorgia* species. Additionally, two mitochondrial genes (mtMutS and COI) and one nuclear gene (28S) were sequenced. According to the phylogenetic studies of *C. lunae* sp. nov., 28S has proven to be a valuable gene for differentiation among closely related congeners. This was attributed to the absence of mitochondrial differences compared to other species, whereas distinctions were evident with 28S. However, the comprehensive utility of 28S still necessitates further investigation and more extensive sampling, as many of the studied octocorals lack sequencing data for this gene. This chapter further underscores the existing understanding that certain marine areas, such as Maud Rise, necessitate intensified assessment efforts. Nevertheless, with the advancements in ROV technology, equipped with sampling tools, comprehensive evaluation of these areas is already feasible. Enhanced biodiversity knowledge contributes to a deeper appreciation of the significance of ecosystem conservation.

The findings from the three chapters of this thesis consistently indicate that the presence of hard substrate promotes biodiversity in different ways. Many engineering species, including several anthozoans studied, such as the newly described golden coral species, necessitate hard substrate for attachment. In turn, the presence of such engineering species fosters associated biodiversity, as demonstrated in **Chapter 1**. But not all fish species were favoured by complex benthic communities, and this also varied depending on the growth stage. Furthermore, a significant proportion of the organisms observed on this type of substrate were indicative of Vulnerable Marine Ecosystems (VMEs), such as gorgonians, sponges, and bryozoans. All these factors contribute to the high value of hard substrate ecosystems, thereby making their conservation a priority mandated by both the Food and Agriculture Organization (FAO, 2009) and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, 2009). In a similar vein, the findings from **Chapter 2** were noteworthy, where various anthozoan assemblages were observed on the two seamounts, with the majority of recorded anthozoan OTUs being considered indicators of VMEs. Furthermore, in line with the directives of the United Nations General Assembly (UNGA) resolution 61/105 and CCAMLR Conservation Measure 22-07, it is recommended that seamounts be managed as VMEs (Reid, 2011). On another note, significant differences were observed in the anthozoans inhabiting the Weddell Sea plain. This renders the Dronning Maud Land marine area particularly intriguing for designation as a potential MPA, given its diverse ecosystems hosting a wide array of animal species. Moreover, some of these species could be endemic due to the relative isolation of the mountains, thereby further enhancing their ecological value (Hubbs, 1959; Richer de Forges et al., 2000; Pante et al., 2015). In this regard, the potential endemism of the newly described species *C.lunae* in **Chapter 3** remains speculative as the information regarding its distribution, as well as other species found on Astrid Ridge and Maud Rise, remains scarce (Brandt et al., 2007b; Lowther et al., 2022; Baena et al., 2024). Lastly, this thesis validates the use of ROV as a method for studying the behavior and distribution of sessile and motile species. Conversely, in **Chapter 3**, the *in-situ* observation of the *Chrysogorgia* colony proves insufficient for a comprehensive description of the new species, necessitating sample collection for subsequent laboratory analyses to obtain more detailed information. Hence, understanding the limitations of each method and aligning them with the study’s objectives is crucial in determining the most appropriate methodology.

Challenges

The material and data utilised in this thesis are derived from diverse Antarctic oceanographic cruises. One of these expeditions was the multidisciplinary scientific cruise PS82 (ANT XXIX/9) aboard the RV Polarstern, conducted between December 2013 and March 2014 in front of the Filchner-Ronne Ice Shelf, which is directly pertinent to **Chapter 1** of this thesis. The second cruise occurred off the coast of Dronning Maud Land, in the eastern sector of the Weddell Sea, aboard the icebreaker Kronprins Haakon, spanning from 28th February to 10th April 2019. This latter expedition is associated with **Chapters 2** and **3**. Both campaigns transpired prior to the inception of this thesis.

In both expeditions, video transects were conducted using ROV. The direct observation of specimens in their natural habitat represents a significant advancement in studying the ecology and behaviour of species, some aspects that were not feasible with conventional sampling methods (e.g. Ambroso et al., 2017; Corbera et al., 2019; Baena et al., 2023). In **Chapter 1**, the analysis of videos from the first cruise facilitated the identification of demersal fish species, along with insights into their distribution, behaviour, and their relationship with benthic communities and substrate types. However, it is important to note that this study methodology had certain limitations related to species identification and, consequently, the estimation of biodiversity. In our study, the presence of the ROV may have deterred the presence of some fish, potentially influencing abundance, density, and biodiversity index values. Furthermore, on certain occasions, the species-level identification of fish proved challenging due to various factors such as the swimming speed of individuals, concealment behind engineering organisms like sponges, or simply, suboptimal observation perspectives for more accurate identification. Despite this difficulty, a total of 414 fish specimens were recorded and could be identified to species level (87.2%). The remaining individuals were identified at genus level (11.3%) and family level (1.4%).

During the development of **Chapter 2**, we encountered a challenge similar to that discussed earlier, specifically related to taxonomic resolution in the identification of anthozoans. Not only did this task demand extensive and diverse taxonomic knowledge due to the great biodiversity of anthozoans. Additionally, the potential phenotypic variability within the same species, coupled with marked morphological similarities between different species, complicated the identification process (Prada et al., 2008; Grinyó et al., 2018). Given the impracticality of sampling all observed organisms during the scientific expedition, a pragmatic approach was taken to address this issue. In the absence of the ability to identify all anthozoans at the species level and aiming to mitigate the consequences of this difficulty, the term 'Operational Taxonomic Unit' (OTU) was introduced in the progression of the second chapter. Moreover, visually distinct OTUs were classified with the name of the minimal identifiable taxonomic group, accompanied by an identifying number. Despite these efforts, the inherent difficulties in identification may lead to an underestimation of the actual biodiversity in the study area.

During the 2019 expedition to Dronning Maud Land, the heightened density of ice posed challenges in accessing specific areas outlined in the previously planned itinerary. Specifically, the ice reached depths of 1500–2000 m in the southernmost regions of Astrid Ridge, necessitating adjustments to the sampling and ROV stations by relocating them further north along the ridge. Regrettably, it was not feasible to study the shallow zone of the ridge. These circumstances precluded the collection of data from the summit of Astrid Ridge. Consequently, in the comparative study between the Maud Rise and Astrid Ridge seamounts, a comparison of anthozoan assemblages present on both summits could not be undertaken. Nevertheless, undeterred by these limitations, the second chapter of this thesis delves into an exploration of the relationship between the different anthozoan assemblages and different factors that could affect their distribution. In this regard, the study focused on examining differences between both seamounts (Astrid Ridge vs Maud Rise), slope vs summit, and substrate types (hard matrix substrate vs soft matrix substrate). This analysis led to the conclusion that significant differences existed among the various observed anthozoan assemblages when considering any of these three factors.

In the context of **Chapter 3**, despite the recent revision of the Chrysogorgiidae family (Xu et al., 2023), the existing information on the latitudinal and bathymetric distribution of many species is very limited. Numerous species have only been documented only once (Pante et al., 2012). Specifically, for the species addressed in this chapter, *C. lunae* sp. nov., only the holotype colony has been sampled. However, based on the macromorphological characteristics of the colony of this species, it seems to have been observed on two additional occasions within the same video transect recorded on western slope of the Maud Rise seamount. Even considering these other two colonies as the same species, information about their distribution is very limited. Additionally, the other gorgonian species observed both on Maud Rise and Astrid Ridge were morphologically quite distinct compared to the new one. Therefore, caution is warranted in interpreting such data, not only for *C. lunae* sp. nov. but also for other species within the Chrysogorgiidae family.

On the other hand, the absence of more specimens of the same species can also obscure small genetic divergences in the sequences of a single species. This was evidenced in the case of *C. varians*, for which we had 9 sequences for mtMutS gen; 8 of them were identical, while one presented a mutated base. Considering that anthozoan mitochondrial genes evolve very slowly and exhibit a high conservation of barcodes among congeneric species (Shearer et al., 2002; Hellberg, 2006; McFadden et al., 2017), it was deemed necessary to establish more reliable foundations in describing the new species of *Chrysogorgia*. For this reason and given the limitation to a single sample, we decided to sequence two mitochondrial genes, mt-MutS and COI, along with the nuclear gene 28S. When comparing only the gene sequence of mtMutS from *C. lunae* sp. nov., we observed that it was exactly the same as three specimens identified as *C. geniculata* and two specimens identified as *C. arboriformis*, aligning with the aforementioned theory. However, sequencing the other two genes revealed sufficient genetic differences that, when complemented with morphological differences at both the colonial and sclerite levels, allowed for the identification of the species as new. Therefore, an integrative approach that considers the genetics and morphology of the species promotes a more solid foundation in describing any species.

Future perspectives

Better understanding of the ecological role of ecosystem engineers

Both gorgonians, bryozoans, and sponges are considered ecosystem engineers, and their presence in the ecosystem usually promotes the occurrence of other species by increasing the structural complexity of the ecosystem (*sensu* Jones et al., 1994). However, a thorough understanding of the ecological function and relationship with each associated species needs to be expanded. As seen in **Chapter 1**, the relationship and utilization by each fish species concerning observed benthic communities can vary depending on the species and whether the specimen is juvenile or adult. Moreover, not all species prefer the same level of structural complexity in the ecosystem. Thus, further exploration into these kinds of intricate interactions is not just a scientific pursuit but a crucial step towards fostering the resilience and sustainability of the oceans.

Scientific knowledge for MPA declaration

One of the objectives of the Convention on Biological Diversity (CBD) is to achieve the protection of 30% of the global marine and coastal environment. While the Southern Ocean is not included in these agreements, the CCAMLR has also incorporated this objective into its strategic plan. Once this objective is defined in Antarctica, the first step involves conducting a benthic bioregionalization analysis using all available information. This process is crucial for spatial planning, facilitating the establishment and subsequent management of MPAs. Currently, some areas are already designated as MPAs, such as the South Orkney Islands Southern Shelf MPA and the Ross Sea Regional MPA. Meanwhile, other regions are in the process of being designated as MPAs, as seen in the case of the marine area in Dronning Maud Land. To achieve this, extensive efforts have been made to compile all available information, and a multidisciplinary cruise to this area was developed in 2019. This expedition has contributed to expanding our knowledge about physical, geochemical, and biological aspects, as exemplified in **Chapters 2** and **3**. The results from this scientific cruise, combined with prior knowledge, provide a baseline for the future designation of this area as MPA and the corresponding conservation management. In this context, the Norwegian Polar Institute and other researchers involved in scientific activities of this cruise are currently working towards the prompt declaration of the aforementioned MPA.

Further exploration about seamounts paradigms for conservation management

In recent years, the biodiversity exploration of seamounts has revealed new perspectives. These underwater features can harbour relict fauna, which might have been isolated during past temperature changes or anoxia episodes in interglacial periods (Hubbs, 1959; Galil and Zibrowius, 1998; Samadi, 2007). Thus, during climatological changes, seamounts could have served as havens for fauna. Similar to terrestrial ecosystems, where a 'cool refuge' has proven crucial for certain species (Wright et al., 2009), it is plausible that the deeper and cooler waters along seamount slopes might act as close sanctuaries, shielding benthic fauna from the consequences of ongoing ocean warming (Rowden et al., 2010) or ocean acidification (Tittensor et al., 2010).

Furthermore, seamounts can play a key role as a source of larvae that may settle in the surroundings of these marine elevations, thereby enhancing the density and biodiversity of other populations in the deep sea (McClain et al., 2009; Rowden et al., 2010). In this context, it would be highly beneficial to intensify studies on population connectivity to ascertain the true extent of isolation theory of underwater mountains, owing to the active hydrodynamics that typically characterise them, and to understand the potential influence they may have on nearby populations. While there are publications addressing these aspects (e.g. Hubbs, 1959; O'Hara, 2007; Howell et al., 2010), current studies remain insufficient, compounded by the substantial variability in environmental characteristics among seamounts. Expanding this knowledge would be instrumental in devising and implementing conservation management plans. This necessitates heightened sampling efforts coupled with genetic studies, enabling the development of predictive models capable of calculating the connectivity of less-explored mountainous regions.

Protecting biodiversity through new methods and collaborative knowledge

Taxonomy, although gradually losing adherents (De Broyer et al., 2011) remains a discipline of paramount significance acknowledged by the scientific community. This decline in interest has implications for our limited understanding of biodiversity and, consequently, hampers effective conservation management. In simple terms, if we lack knowledge of what exists, our ability to protect it is compromised. Therefore, a key challenge for the future is to intensify efforts in enhancing and developing new methods for species identification to make this task easier and perhaps increase interest. In this regard, some online identification guides and interactive keys have emerged in recent years (David et al., 2005; Coleman et al., 2010) and, there is also a pressing need for broader dissemination of these innovative tools. Ideally, all these new types of tools should be made freely accessible to encourage widespread usage.

Furthermore, it is noteworthy that our understanding of biodiversity could be significantly enhanced by examining thoroughly the specimens currently stored in museums and other research centers. Many samples collected during past oceanographic campaigns end up “forgotten” in storage facilities due to financial constraints or a shortage of personnel with the required expertise. An example of this is the newly described golden gorgonian species in this thesis, *C. lunae* sp. nov. (**Chapter 3**). The holotype was collected during a Norwegian expedition to Antarctica in 2019, and its description resulted from collaboration among the Bergen Museum, the University of Seville, and the Institute of Marine Sciences. Scientists at the museum holding the holotype possessed genetic expertise, while the University of Seville complemented the study by investigating the species’ morphology. In this regard, **Chapter 1** was also an example of collaboration, as researchers from the Instituto di Scienze Polari and the Stazione Zoologica Anton Dohrn, with their expertise in fish taxonomy, assisted in the identification of the Antarctic specimens. Therefore, both chapters emphasizes the importance of collaborative initiatives that not only promotes knowledge about biodiversity but also foster mutual learning among researchers.

CONCLUSIONS

Conclusions

1. The use of ROV is suitable for studying the distribution and behavior of both mobile and sedentary species. Although, its use should be complemented with sampling in some cases, such as in the description of a new species.

2. 414 specimens of Antarctic demersal fishes belonging to the families Nototheniidae, Channichtyidae, Bathydraconidae, and Artedidraconidae with a total of 14 different species identified in the marine area in front of the Filchner-Ronne Ice Shelf.

3. There seems to be a relationship between the distribution of the Antarctic fish species and the different benthic communities.

4. The population of *Trematomus eulepidotus*, *T. lepidorhinus, T. scotti, Pagetopsis maculatus, P. macropterus, Chaenodraco wilsoni,* and *Cryodraco antarcticus* was represented by juveniles. The specimens in early stages of these species prefered the most complex benthic communities, which in turn were associated with areas where the substrate was characterized by sand with rocks.

5. As seen through video analysis, 37% of fish records were related to behavior associated with the use of three-dimensional structures of engineer ecosystems, either because individuals rested on these structuring organisms or because they hided behind them.

6. Similarly, not all species prefered three-dimensionally more complex benthic communities. This was the case of *Cygnodraco mawsoni*, which prefered more open areas.

7. Currently, and following the recent taxonomic review, *Chrysogorgia lunae* sp. nov. is the sole representative of its genus in the Southern Ocean.

8. Growth direction of the colony and the morphology of sclerites are the morphological characteristics that appear to be robust for differentiating species within the genus *Chrysogorgia*.

9. Species genetically closest to the newly described species are *C. geniculata*, *C. arboriformis*, and *C. rigida*. All belong to the “Squamosae typicae” group and share the characteristic of presenting toothed rib-like scales in pinnules.

10. *Chrysogorgia lunae* sp. nov shares complete mtMutS with three specimens of *C. geniculata*. While the 28S marker does indicate differences between the two species. Therefore, this marker may prove to be a successful tool for differentiating congeneric

species within this genus.

11. The slow evolution of mtMutS and the high environmental plasticity characteristic of octocorals can pose challenges for species differentiation.

12. The study of complementary markers to mtMutS, as well as, an integrative approach considering colonial and sclerite morphology and distribution, is key to the proper description of a new species.

13. Despite comparing two seamounts, differences were found in the anthozoan assemblages present in both. Additionally, differences were observed between the slopes and the summits. These disparities were partly caused by differences in substrate type and hydrodynamics.

14. Maud Rise was characterized by a varied substrate, mainly hard on the slopes and soft at the summit. It was on the slopes where we saw greater diversity of anthozoans, with octocorals being the dominant group alongside other non-anthozoan suspension feeders. Meanwhile, at the summit, diversity was much lower and predominantly represented by Ceriantharia OTUs and *Umbellula* OTUs.

15. Astrid Ridge was characterized by predominantly soft substrate with occasional small rocks. Here, the presence of hexacorals and octocorals was more evenly matched, accompanied by a predominantly detritivorous fauna.

16. The density of anthozoans was higher at Maud Rise, especially on the slopes where hard substrate was abundant. Therefore, the results showed a positive relationship between substrate type and the presence of anthozoans, although not all were favoured.

17. Furthermore, it was observed that the anthozoan composition of the mountains differed from those inhabiting the Weddell Sea plain, with hexacorals being the most abundant group within the anthozoans.

18. The significant differences observed between both mountains and the adjacent plain make this area an interesting place to protect due to the wide variety of communities found.

19. A more detailed taxonomic study of the species present in Maud Rise and Astrid Ridge would allow us to make a more accurate calculation of the number of endemic species. This would help determine the degree of isolation of these mountains from the nearest ecosystems as well as their resilience and vulnerability to potential impacts.

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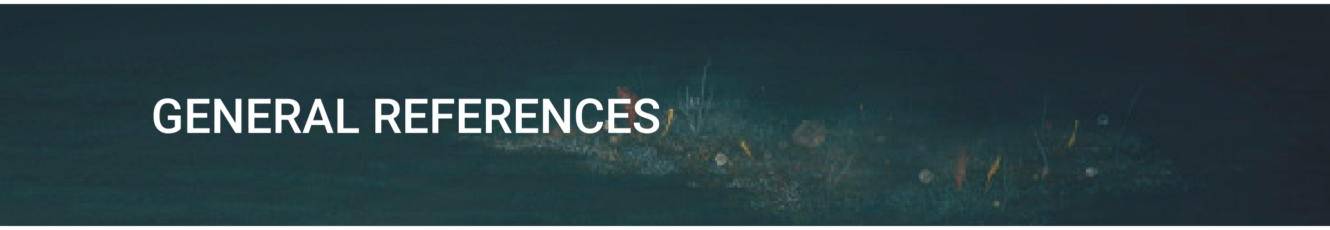

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- ¿De verdad no quieres saberlo? - dijo Natvel

- ¿Qué?

- ¿No quieres saber quién eres?

- Sé perfectamente quién soy.

- Lo dudo.

Y Bruna, mortificada, tuvo que reconocer para su coleto que, en efecto, estaba lejos de tener las cosas claras. Pero jamás lo admitiría.

-Natvel, gracias por tu colaboración, nuevamente has sido muy amable y muy útil, pero prefiero que no me cuentes eso que dices que ves en mí.

- Tu dibujo esencial. Tu forma. Lo que eres.

-Pues eso. Me da igual. No quiero saberlo.

- Si te diera de verdad igual, no te importaría que te lo dijera. Hay una parte en ti que cree. Por eso te da miedo.

No fastidies, pensó Bruna irritada. No fastidies.

- Me tengo que ir, Muchas gracias de nuevo.

Sonrió, apenas una pequeña mueca dura, y salió de la tienda a toda prisa. A su espalda todavía escuchó las palabras del esencialista...

- ¡Esa línea que te atraviesa el cuerpo! No sólo te parte, también es una cuerda que te ata...

Lágrimas en la lluvia, **Rosa Montero**