CAMBRIDGE
UNIVERSITY PRESS

Biological Sciences

Characterization of coastal habitats and marine benthic communities of the sub-Antarctic Crozet archipelago using underwater imagery

Yann Lelièvre[1] , Line Le Gall[2] , Philippe Dubois[3] and Thomas Saucède[1]

[1]Biogéosciences, UMR 6282, Université Bourgogne Europe, CNRS, Dijon, France; [2]Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Paris, France and [3]Laboratoire de Biologie marine, Université Libre de Bruxelles, Brussels, Belgium

Abstract

Sub-Antarctic marine life exhibits unique ecological traits and pronounced endemicity levels. Despite their ecological uniqueness and high conservation value, studies on sub-Antarctic benthic communities are scarce. Using underwater video imagery, we assessed the nearshore diversity and structure of faunal and algal communities of the Crozet archipelago along 12 scuba and remotely operated vehicle transects performed at *Baie du Marin* and *Crique du Sphinx* (*Ile de la Possession*). The influence of habitat types on species distribution was evaluated in relation to the setting up of submarine cables. A total of 51 faunal (mainly represented by Echinodermata and Porifera) and 14 algal (mainly represented by Rhodophyta) taxa were identified. The high habitat heterogeneity found in shallow waters (from 0 to 20 m depth) enhances the species richness and diversity, whereas deeper (> 20 m depth) areas were dominated by large sandy stretches and a lower diversity. Rocky habitats had the highest richness and diversity values, promoting local diversity. Submarine cables act as a hard substrate for species, whose suspended sections influence the composition and structure of benthic communities. This study improves our limited knowledge of benthic habitats and diversity from Crozet and constitutes a baseline for further monitoring of marine communities for conservation strategies related to this part of the French Southern Territories National Nature Reserve.

Keywords: Benthic diversity; Crozet; nearshore ecosystems; Southern Ocean; submarine cables; underwater imagery

(Received 28 March 2024; revised 22 December 2024; accepted 23 December 2024)

Introduction

The Southern Ocean and sub-Antarctic islands are among the regions in the world that are the most exposed to the impacts of climate change (Turner *et al.* 2014, Auger *et al.* 2021). The multiple and synergistic effects of climate change (e.g. seawater temperature increase (Mélice & Servain 2003, Ansorge *et al.* 2009, 2014, Auger *et al.* 2021), ocean acidification (McNeil & Matear 2008), more extreme climatic events and intense seasonality (Turner *et al.* 2009, Turner *et al.* 2014, Blanchard-Wrigglesworth *et al.* 2021)) on Southern Ocean ecosystems are already perceptible (Morley *et al.* 2020). Alterations to the structure and functioning of marine ecosystems are particularly expected in response to these major environmental changes (Gutt *et al.* 2015, Morley *et al.* 2020, Lelièvre *et al.* 2023), leading to shifts in species distribution patterns and community compositions (Doney *et al.* 2012). Nearshore marine habitats of sub-Antarctic islands are particularly at risk because shallow-water species do not necessarily have the opportunity to migrate to more favourable areas. In addition, new conditions such as warmer waters, together with direct anthropogenic impacts and the

ever-increasing maritime traffic (i.e. fisheries, tourism and science), may favour the expansion of non-indigenous and invasive species (Smith 2002, Allan *et al.* 2013, Kargel *et al.* 2014, Garciá Molinos *et al.* 2015, Byrne *et al.* 2016), a major threat to polar ecosystems usually characterized by high endemism levels (McCarthy *et al.* 2019, Hughes *et al.* 2020).

The ecological uniqueness, endemicity, and prominent diversity of sub-Antarctic islands assign to these isolated territories a high conservation value (Chown *et al.* 2001) as they represent pristine marine ecosystems, still little impacted by direct anthropogenic disturbance (Lecomte *et al.* 2013), and they are priceless sentinels of climate change. For many of these islands, benthic ecosystems have been scarcely studied or remain undescribed. The few studies conducted on the benthic communities of sub-Antarctic islands highlighted high levels of species richness, diversity and biomass, such as in the Prince Edward Islands (Branch *et al.* 1993), the sub-Antarctic islands of New Zealand (Snares, Auckland, Campbell, Antipodes and Bounty Islands; Chown *et al.* 2001, Freeman *et al.* 2011, Clark *et al.* 2019), South Georgia Island and the South Sandwich Islands (Barnes *et al.* 2006, Hogg *et al.* 2011), the Kerguelen Islands (Arnaud 1974, Féral *et al.* 2019, 2021) and the Crozet archipelago (Lelièvre *et al.* 2023). These studies have highlighted the importance and the role of the substrate in shaping the composition and distribution of benthic communities (Branch *et al.* 1993, Barnes *et al.* 2006, Freeman *et al.* 2011). Species richness

and diversity can be closely related to habitat heterogeneity and complexity, which may be reflective of substrate type (Levin *et al.* 2010, Schlacher *et al.* 2010). Therefore, mapping substrate types and investigating the indicator species of these different habitats would be helpful for biodiversity management and conservation.

The increasing development and recent advances in imagery system equipment, such as remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs) or towed camera systems, have made imagery and digital video important components of benthic monitoring research programmes (Durden *et al.* 2016). In contrast to physical sampling, this repeatable and non-destructive approach provides researchers with a better understanding of benthic communities at a wide spatial scale. These techniques contribute to preserving the integrity of marine habitats and constitute suitable tools to study vulnerable and fragile communities such as sub-Antarctic benthic communities, characterized by a slow growth rate and long recovery time (Gutt & Starmans 2001, Teixidó *et al.* 2004, Smale & Barnes 2008). Underwater imagery has already proved effective for studying the structure and composition of benthic communities in a wide range of shallow marine ecosystems such as coral reefs (Moyer *et al.* 2003, Edgar & Stuart-Smith 2014), kelp forests (Włodarska-Kowalczuk *et al.* 2009), artificial reefs (Walker *et al.* 2007, Higgins *et al.* 2019) and natural rocky substrata (van Rein *et al.* 2011, Lelièvre *et al.* 2023). Along with the progress in these technologies, the development of new softwares for benthic image analysis (Kohler & Gill 2006, Teixidó *et al.* 2011, Trygonis & Sini 2012, Langenkämper *et al.* 2017) is constantly increasing, facilitating and encouraging the use of imagery in marine ecological studies. Imagery and digital video therefore provide new gateways and powerful approaches to study benthic communities in sub-Antarctic regions.

Studies on the marine ecosystems of the Crozet Islands remain limited (Sicinski & Gillet 2002, Lelièvre *et al.* 2023, Jossart *et al.* 2024). Benthic fauna data are rare and restricted to few campaigns undertaken on the plateau at the end of the nineteenth (*HMS Challenger*, 1872) and twentieth centuries (R/V *Marion Dufresne* MD08 1976, and MD30 1982) along with recent fishery bycatch analysis (Koubbi *et al.* 2016). At *Baie du Marin* (*Ile de la Possession*), Lelièvre *et al.* (2023) provided a first bentho-ecological baseline of the composition and structure of nearshore Crozet benthic communities associated with hard substrates. A total of 50 faunal and 14 algal taxa were identified using underwater imagery, with a distribution characterized by a high level of spatial heterogeneity. Through a trait-based approach, this study reported the high vulnerability of faunal benthic communities to current and future environmental changes (Lelièvre *et al.* 2023). A thorough knowledge of the biodiversity of these remote ecosystems is urgently needed to predict and subsequently monitor the influence of global change on these communities and to contribute to the protection and conservation of these habitats. Since December 2016, the maritime domain surrounding the Crozet archipelago has been classified as a nature reserve. Among the Crozet Islands, *Ile de la Possession* hosts a hydroacoustic monitoring station installed by the Preparatory Commission for the Comprehensive Nuclear-Test-Ban Treaty Organization (CTBTO) in December 2016. The French Southern and Antarctic Territories (TAAF) and CTBTO signed a contract for 'Nearshore Cable Inspection and Environmental Survey at IMS Hydroacoustic Station HA04 Crozet, France' in September 2021, and a first campaign took place on *Ile de la Possession* at Crozet in November 2021. The inspection of the HA04 station cable was completed by environmental surveys of nearshore habitats for conservation purposes and improving our knowledge of Crozet marine ecosystems. In this context, the aims of this study were 1) to provide an assessment and a comparison of the coastal benthic faunal and algal diversity associated with different habitat types between two sites of *Ile de la Possession*: *Baie du Marin* and *Crique du Sphinx*; 2) to investigate the relationships between habitat types, algal cover and faunal composition; and 3) to determine the indicator species associated with each of these habitats in order to establish a baseline for future monitoring of these sites.

Materials and methods

Study areas

The Crozet archipelago (45°48′S–46°26′S, 50°14′E–52°15′E) is composed of five main volcanic islands (from west to east: *Ile aux Cochons*, *Ile des Pingouins*, *Ilots des Apôtres*, *Ile de la Possession* and *Ile de l'Est*) located in the Southern Ocean, 2400 km north of the Antarctic continent and 2400 km south-east of the South African coast (Fig. 1a). *Ile de la Possession* (46°25′S, 51°45′E; Fig. 1a) is the largest island of the Crozet archipelago, with a total surface area of ~156 km^2; it culminates at 934 m above sea level (*Pic du Mascarin*). The western part of the island is dominated by rugged terrain, while the eastern part is characterized by plateaus and large valleys. The present study was focused on two sites located on the eastern coast of *Ile de la Possession*: *Baie du Marin* and *Crique du Sphinx* (Fig. 1b).

Baie du Marin (46°25′54″S, 51°52′11″E) is a marine inlet ~500 m long and 200 m wide in its shallowest part (down to 20 m); it opens to the ocean in a larger embayment of ~2 km wide at 40 m depth (Fig. 1c). The coast is mainly a rocky shore but for the sandy beach present at the end of the bay. The site is characterized by the presence of a large colony of over 10 000 king penguins *Aptenodytes patagonicus* (Miller, 1778) along with some elephant seals *Mirounga leonina* (Linnaeus, 1758) that occupy most of the beach inside the bay in spring. The bay has long been visited by vessels for the supply of Alfred Faure scientific base. Located next to *Baie du Marin*, at 2 km to the north, *Crique du Sphinx* (46°25′08″S, 51°52′44″E) is a small cove of ~250 m long and 150 m wide opening to the north-east (Fig. 1d). The site is mainly bordered by a rocky shore, with a small beach of pebbles and gravels at the end. *Crique du Sphinx* is a shelter for a handful of king penguins and elephant seals. It is never visited by ships and shows no anthropic activities.

Diving surveys and imagery acquisition

Imagery data acquisition was undertaken from the R/V *Marion Dufresne II* calling off *Ile de la Possession* from 4 to 9 November 2021. Operations were conducted by the TAAF in response to Contract No. 2021-0882 with the CTBTO for 'Nearshore Cable Inspection and Environmental Survey at IMS Hydroacoustic Station HA04 Crozet, France'. Video imagery transects were performed using a setting composed of three cameras, two GoPro HERO7 cameras (4K video and 20 megapixel photo resolution) with 80% field overlap and one underwater Paralenz Vaquita camera (4K resolution) mounted on a plexiglass board. Two lights and three 10 cm scaling lasers were also installed to estimate the filmed surface. To limit variations in video imaging acquisition, scuba divers scanned transects at a distance of ~50 cm from the sea bottom with a constant swimming speed.
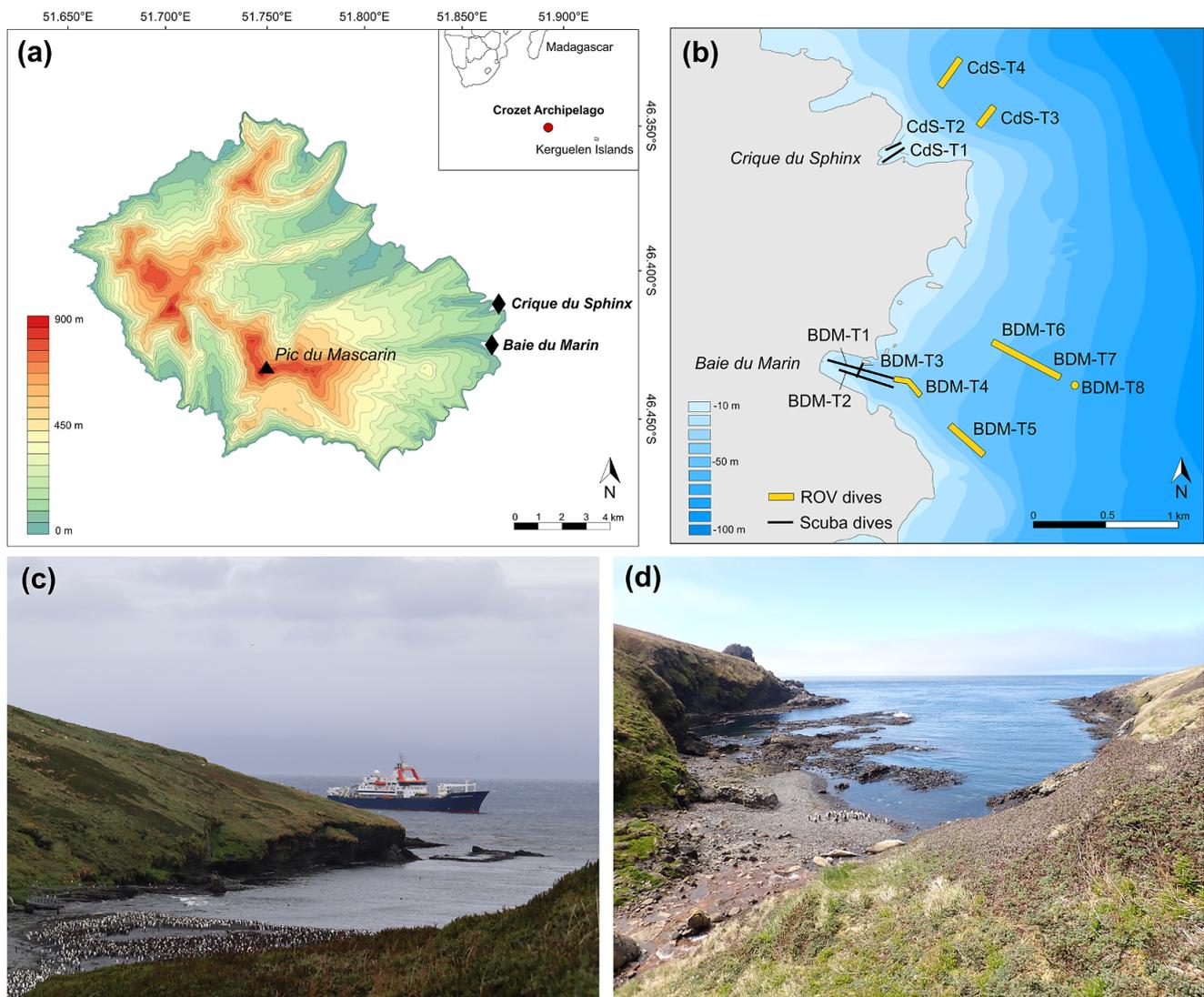
Figure 1 a. Topographic map of *Ile de la Possession* (Crozet archipelago, Southern Ocean) with the location of the two study sites: *Baie du Marin* and *Crique du Sphinx* (black diamonds). **b.** Imagery sampling design conducted at *Baie du Marin* and *Crique du Sphinx* with black transects corresponding to scuba dives and yellow transects to remotely operated vehicle (ROV) dives; Photographs of **c.** *Baie du Marin* (© P. Salvatico) and **d.** *Crique du Sphinx* (© T. Saucède).

Five video transects were conducted: three at *Baie du Marin* and two at *Crique du Sphinx* (Table I). At *Baie du Marin*, a first video transect (BDM-T1) was performed along the track of the cable, a second transect (BDM-T2) was carried 10 m south of the cable and a third one (BDM-T3) was conducted across the bay, from the centre of the bay at 10 m depth to the north coast (Table I). At *Crique du Sphinx*, two video transects (CdS-T1 and CdS-T2) were performed along the cove (Table I). Imagery surveys deeper than 20 m were conducted using the ROV *SAAB Seaeye Cougar-XT Compact*. Six ROV transects were aligned with transect videos performed during scuba dives. Four ROV transects were realized at *Baie du Marin*: two over the cable (BDM-T4 and BDM-T5) and two to the north of the bay (BDM-T6 and BDM-T7). These were complemented by one deeper transect of a restricted area at 60 m depth (BDM-T8; Table I). Finally, two ROV dives were conducted in the south and north parts of *Crique du Sphinx* (CdS-T3 and CdS-T4, respectively; Table I). All video imagery data are available at the dat@UBFC repository (https://doi.org/10.25666/DATAUBFC-2024-03-15; Lelièvre *et al.* 2024a,b).

Benthic imagery processing

For each transect, still images were equally extracted from video imagery every 5 m along the transect. A total of 594 images were manually analysed using the open-source web platform BIIGLE 2.0 (Benthic Image Indexing and Graphical Labelling Environment; Langenkämper *et al.* 2017). BIIGLE 2.0 was developed with a special focus on benthic imagery and provides the advantage of a collaborative and interactive work with taxonomists who can contribute to the identification of organisms from images (Langenkämper *et al.* 2017). For each image, all faunal organisms were counted and expressed in terms of density (number of individuals m^{-2}), and algae cover was also measured (m^{-2}). In agreement with the taxonomists, organisms were identified to the lowest possible taxonomic level. Additionally, the substrate type was categorized into seven habitats, defined by the predominant features that create structural complexity in the environment (Airoldi & Beck 2007) and annotated for each image: 1) sand, 2) sand-cables, 3) sand-pebbles, 4) sand-pebbles-cables, 5) pebbles, 6) rock and 7) suspended cables (Fig. 2).

Table I. Summary of transect information for each dive carried out at *Baie du Marin* (BDM) and *Crique du Sphinx* (CdS).

Transect	Site	Imagery method	Latitude		Longitude		Depth	Transect
			Start	End	Start	End	(m)	length (m)
BDM-T1	BDM	GoPro set-up	–46.42618	–46.42731	51.86205	51.86817	2–20	483
BDM-T2	BDM	GoPro set-up	–46.42746	–46.42655	51.86808	51.86324	6–18	383
BDM-T3	BDM	GoPro set-up	–46.42688	–46.42636	51.86486	51.86529	1.5–10	67
BDM-T4	BDM	ROV	–46.42826	–46.42805	51.87023	51.87051	19.6–25.3	241
BDM-T5	BDM	ROV	–46.43027	–46.43175	51.87565	51.87315	31.7–41.0	305
BDM-T6	BDM	ROV	–46.42490	–46.42599	51.87692	51.87956	33.0–47.2	301
BDM-T7	BDM	ROV	–46.42595	–46.42691	51.87951	51.88248	46.6–56.7	455
BDM-T8	BDM	ROV	–46.42687	–46.42699	51.88319	51.88329	58.9–60.3	15
CdS-T1	CdS	GoPro set-up	–46.41293	–46.41400	51.86852	51.86663	4–16	165
CdS-T2	CdS	GoPro set-up	–46.41321	–46.41295	51.86715	51.86689	5–17	103
CdS-T3	CdS	ROV	–46.41048	–46.41140	51.87657	51.87538	40.6–45.4	186
CdS-T4	CdS	ROV	–46.40738	–46.40911	51.87368	51.87198	40.9–41.9	295

ROV = remotely operated vehicle.

Statistical analyses

To assess the sampling effort at *Baie du Marin* and *Crique du Sphinx*, individual-based rarefaction curves were computed for faunal communities and image-based rarefaction curves were computed for algal communities. Diversity metrics corresponding to Hill's number of order q were calculated for the faunal and algal communities of each transect performed at *Baie du Marin* and *Crique du Sphinx*: species richness ($q = 0$), Shannon diversity ($q = 1$), Simpson's inverse ($q = 2$; Jost 2006) and Pielou's evenness. These metrics were also calculated to compare the richness and diversity values between shallow (0–20 m depth) and deeper waters (20–60 m depth) at both sites.

To investigate the compositional benthic community variations between transects and sites, a principal component analysis (PCA) was performed on Hellinger-transformed faunal and algal cover densities at the transect scale. The Hellinger transformation was applied to minimize the high weight given to rare species (Legendre & Gallagher 2001). A redundancy analysis (RDA) was also performed on these Hellinger-transformed data to evaluate the relationships between substrate type, algal cover and faunal composition in shallow waters. Finally, indicator species analyses (Dufrêne & Legendre 1997, De Cáceres *et al.* 2010, Legendre & Legendre 2012) were performed to identify faunal and algal taxa significantly associated with substrate types. The indicator value index (IndVal) is only based on within-species abundance and occurrence comparisons and so would not be affected by the abundance values of other species (Legendre & Legendre 2012). Species with a high fidelity (the degree to which a species is found only in a given group of sites) and high specificity (the degree to which a species is present at all sites of a group) within a habitat or a combination of habitats would have a high indicator value. According to Dufrêne & Legendre (1997), a species is considered as characteristic of a substrate type or habitat if the species IndVal is > 25% for a significant *P*-value of < 0.05.

All statistical analyses were performed using the *R* environment (version 4.2.0; R Core Team 2022). Rarefaction curves and diversity metrics were conducted using the packages *iNEXT* (Hsieh *et al.* 2016) and *vegan* (Oksanen *et al.* 2020). PCA and RDA were realized

using the package *vegan* (Oksanen *et al.* 2020). Indicator species analysis was conducted using the package *indicspecies* (De Cáceres & Legendre 2011).

Results

Sampling effort and benthic communities diversity

The species lists for each transect conducted at *Baie du Marin* and *Crique du Sphinx* are presented in Table II (Table S1 for abundance and density data). A total of 51 faunal and 14 algal taxa were found at the two sites, corresponding to 43 faunal and 13 algal taxa at *Baie du Marin* and 35 faunal and 13 algal taxa at *Crique du Sphinx*, respectively. Among these taxa, 26 faunal and 11 algal taxa were shared between the two studied sites. Overall, rarefaction curves tend to reach a plateau (Fig. 3a,b), indicating that the total collection of analysed images gave a good representation of faunal and algal diversities at *Baie du Marin* and *Crique du Sphinx*.

At *Baie du Marin*, BDM-T1 fauna was dominated by the ophiuroid *Ophiosabine vivipara* (2.4 individuals m^{-2}; 26.6%), the polychaete Arenicolidae gen. indet. (1.4 individuals m^{-2}; 15.6%) and the ascidian *Aplidium variabile* (1.3 individuals m^{-2}; 14.8%). The algal component was dominated by *Desmarestia confervoides* (41.9%), followed by *Macrocystis pyrifera* (14.2%) and *Phycodrys quercifolia* (11.6%). Fauna of the BDM-T2 transect was dominated by the isopod *Spinoserolis latifrons* (3 individuals m^{-2}; 64%) and to a lesser extent by the gastropod *Nacella delesserti* (1.2 individuals m^{-2}; 26.3%); algae were also dominated by *D. confervoides* (35.7%), but also by *Palmaria* sp. (34%) and *Ulva* sp. (13.7%). BDM-T3 fauna was dominated by the holothurid *Echinopsolus splendidus* (124 individuals m^{-2}; 51.1%), by the actiniid Actiniaria fam. gen. sp.1 (34.4 individuals m^{-2}; 14.2%) and to a lesser extent by the polychaete *Parasabella* sp. (64.9 individuals m^{-2}; 26.7%). Algal flora was dominated by *Desmarestia chordalis* (55.2%), followed by *D. confervoides* (20.4%) and *Codium adhaerens* (12.9%). Fauna of the BDM-T4 transect was largely dominated by the isopod *S. latifrons* (38.3 individuals m^{-2}; 99.5%). BDM-T5 fauna was also dominated by the isopod *S. latifrons* (5.9 individuals m^{-2}; 81.9%) and to a lesser extent by the gastropod *Neobuccinum eatoni* (0.7 individuals m^{-2};

Table II. Faunal and algal taxa identified along the transects conducted at *Baie du Marin* and *Crique du Sphinx* using underwater imagery. Black circles indicate the presence of this taxon.

Taxa	Baie du Marin								Crique du Sphinx			
	BDM-T1	BDM-T2	BDM-T3	BDM-T4	BDM-T5	BDM-T6	BDM-T7	BDM-T8	CdS-T1	CdS-T2	CdS-T3	CdS-T4
Fauna												
Porifera												
Demospongiae												
Clathria sp. Schmidt, 1862	●	-	-	-	-	-	-	-	-	-	-	-
Crella sp. Gray, 1867	●	-	-	-	-	-	-	-	-	-	-	-
Demospongiae fam. gen. sp.1 Sollas, 1885	●	-	-	-	-	-	-	-	-	●	-	-
Demospongiae fam. gen. sp.2 Sollas, 1885	-	-	-	-	-	-	●	●	-	-	-	-
Halichondria sp. Fleming, 1828	●	-	-	-	-	-	-	-	-	-	-	-
Haliclona sp. Grant, 1841	●	-	-	-	-	-	-	-	-	-	-	-
Hymedesmia sp. Bowerbank, 1864	●	-	-	-	-	-	-	-	-	-	-	-
Hymeniacidon sp. Bowerbank, 1858	●	-	-	-	-	-	-	-	-	-	-	-
Mycale sp.1 Gray, 1867	●	-	-	-	-	-	-	-	●	●	-	-
Mycale sp.2 Gray, 1867	●	-	-	-	-	-	-	-	-	-	-	-
Mycale sp.3 Gray, 1867	●	●	●	-	-	-	-	-	-	-	-	-
Tetillidae gen. indet. Sollas, 1886	●	-	-	-	-	-	-	-	-	-	-	-
Cnidaria												
Hydrozoa												
Tubulariidae gen. indet. Goldfuss, 1818	●	-	-	-	-	-	-	-	-	-	-	-
Anthozoa												
Actiniaria fam. gen. sp.1 Hertwig, 1882	-	-	●	-	-	-	-	-	●	-	-	-
Actiniaria fam. gen. sp.2 Hertwig, 1882	●	-	-	-	-	-	-	-	●	-	-	-
Actiniaria fam. gen. sp.3 Hertwig, 1882	-	-	-	-	-	-	-	-	●	●	-	-
Actiniaria fam. gen. sp.4 Hertwig, 1882	-	-	-	-	-	-	-	-	●	●	-	-
Actiniaria fam. gen. sp.5 Hertwig, 1882	-	-	-	-	-	-	-	-	-	●	-	-
Actiniaria fam. gen. sp.6 Hertwig, 1882	-	-	-	-	-	-	-	-	●	●	-	-
Alcyoniidae gen. indet. Lamouroux, 1812	-	-	-	-	-	●	●	-	-	-	-	-
Alcyonium cf. *antarcticum* Wright & Studer, 1889	-	-	-	-	-	-	-	-	-	●	-	-

(Continued)

Table II. (Continued)

Taxa	Baie du Marin								Crique du Sphinx			
	BDM-T1	BDM-T2	BDM-T3	BDM-T4	BDM-T5	BDM-T6	BDM-T7	BDM-T8	CdS-T1	CdS-T2	CdS-T3	CdS-T4
Mollusca												
Gastropoda												
Aeolidiidae gen. indet. Gray, 1827	-	-	-	-	-	-	●	●	-	-	-	-
Margarella violacea (P. P. King, 1832)	●	-	●	-	-	-	●	●	●	●	-	-
Nacella delesserti (R. A. Philippi, 1849)	●	●	●	-	●	-	-	-	●	●	-	-
Neobuccinum eatoni (E. A. Smith, 1875)	●	●	-	●	●	●	●	-	-	-	●	●
Bivalvia												
Gaimardia trapesina (Lamarck, 1819)	●	-	●	-	-	-	-	-	●	●	-	-
Annelida												
Polychaeta												
Arenicolidae gen. indet. Johnston, 1835	●	●	●	-	-	-	-	-	●	●	-	-
Lanice marionensis Branch, 1998	●	-	-	-	-	-	●	●	-	-	●	-
Parasabella sp. Bush, 1905	●	-	●	-	-	-	●	●	●	●	-	-
Thelepus spectabilis Ehlers, 1897	-	-	●	-	-	-	-	-	-	●	-	-
Arthropoda												
Malacostraca												
Halicarcinus planatus (Fabricius, 1775)	-	-	-	-	-	-	●	●	●	●	-	-
Spinoserolis latifrons (White, 1847)	●	●	-	●	●	●	●	-	-	-	●	●
Echinodermata												
Ophiuroidea												
Ophionotus hexactis (E. A. Smith, 1876)	-	-	●	-	-	-	-	●	-	-	-	-
Ophiosabine vivipara (Ljungman, 1871)	●	-	●	-	-	-	●	●	●	●	-	-
Ophiopyrgidae gen. indet. Perrier, 1893	-	-	●	-	-	-	-	-	-	-	-	-

(Continued)

Table II. (Continued)

Taxa	Baie du Marin								Crique du Sphinx			
	BDM-T1	BDM-T2	BDM-T3	BDM-T4	BDM-T5	BDM-T6	BDM-T7	BDM-T8	CdS-T1	CdS-T2	CdS-T3	CdS-T4
Asteroidea												
Anasterias antarctica (Lütken, 1857)	●	-	●	-	-	-	-	-	●	●	-	-
Diplasterias meridionalis (Perrier, 1875)	●	-	-	-	●	-	-	-	●	●	-	-
Glabraster antarctica (E. A. Smith, 1876)	-	-	-	-	-	-	-	●	●	-	-	●
Henricia sp. Gray, 1840	●	-	-	-	-	-	-	-	●	●	-	-
Leptychaster kerguelenensis E. A. Smith, 1876	●	●	●	-	-	-	-	-	●	●	-	-
Neosmilaster sp. Fisher, 1930	●	●	●	-	●	-	-	-	●	●	-	-
Pterasteridae gen. indet. Perrier, 1875	-	-	-	-	-	-	-	-	-	●	-	-
Smilasterias triremis (Sladen, 1889)	●	-	●	-	●	●	●	●	●	-	●	●
Holothuroidea												
Pentactella sp. Verrill, 1876	-	-	●	-	-	-	-	-	●	-	-	-
Echinopsolus splendidus (Gutt, 1990)	-	-	●	-	-	-	-	-	●	-	-	-
Chordata												
Ascidiacea												
Aplidium fuegiense (Cunningham, 1871)	-	-	-	-	-	-	-	-	-	●	-	-
Aplidium variabile (Herdman, 1886)	●	●	●	-	-	-	-	-	●	●	-	-
Morchellium cf. *giardi* Herdman, 1886	-	●	-	-	-	-	-	-	●	●	●	-
Sycozoa cf. *gaimardi* (Herdman, 1886)	●	-	-	-	-	-	-	-	-	●	-	-
Actinopterygii												
Gobionotothen marionensis (Günther, 1880)	-	-	-	-	-	-	-	-	-	-	●	●
Undertemined												
Undetermined sp.1	-	-	-	-	●	-	-	-	-	-	-	-

(Continued)

Table II. (Continued)

Taxa	Baie du Marin								Crique du Sphinx			
	BDM-T1	BDM-T2	BDM-T3	BDM-T4	BDM-T5	BDM-T6	BDM-T7	BDM-T8	CdS-T1	CdS-T2	CdS-T3	CdS-T4
Algae												
Ochrophyta												
Phaeophyceae												
Desmarestia chordalis J.D.Hooker & Harvey, 1845	●	●	●	-	-	-	-	-	●	●	-	-
Desmarestia confervoides M.E.Ramírez & A.F.Peters, 1993	●	●	●	-	-	-	-	-	●	●	-	-
Macrocystis pyrifera (Linnaeus) C.Agardh, 1820	●	●	●	-	-	-	-	-	●	●	-	-
Chlorophyta												
Ulvophyceae												
Codium adhaerens C.Agardh, 1822	-	-	●	-	-	-	-	-	●	●	-	-
Ulva sp. Linnaeus, 1753	●	●	●	-	-	-	-	-	-	●	-	-
Rhodophyta												
Florideophyceae												
Corallinales fam. gen. sp. P.C. Silva & H.W. Johansen, 1986	●	●	●	-	-	-	-	-	●	●	-	-
Delesseriaceae gen. indet. Bory, 1828	●	-	-	-	-	-	-	-	-	-	-	-
Heterosiphonia berkeleyi Montagne, 1842	●	-	●	-	-	-	-	-	●	-	-	-
Palmaria sp. Stackhouse, 1802	●	●	●	-	-	-	-	-	●	●	-	-
Phycodrys quercifolia (Bory) Skottsberg, 1922	●	●	●	-	-	-	-	-	●	●	-	-
Schizoseris sp. Kylin, 1924	●	●	●	-	-	-	-	-	●	●	-	-
Undertemined												
Undetermined sp.1	-	-	-	-	-	-	-	-	-	●	-	-
Undetermined sp.2	-	-	-	-	-	-	-	●	-	-	●	-
Undetermined sp.3	-	-	-	-	-	-	-	●	-	-	●	-
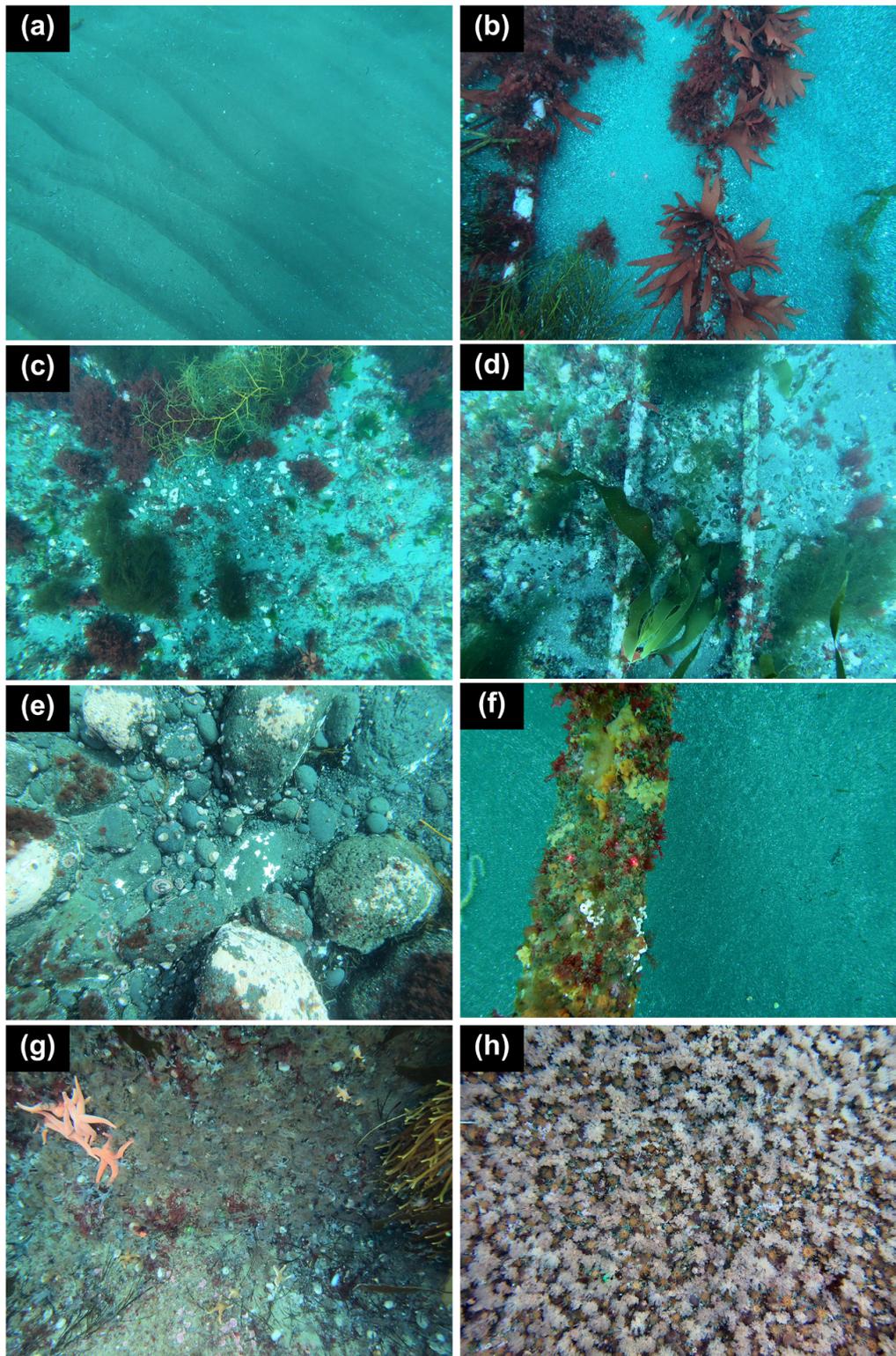
Figure 2. Classification of the different benthic habitats: **a.** sand, **b.** sand-cables, **c.** sand-pebbles, **d.** sand-pebbles-cables, **e.** pebbles, **f.** suspended cables and **g. & h.** rock habitats. Laser beams for image scaling are 10 cm spaced.

10.4%). Fauna of the BDM-T6 transect was largely dominated by the isopod *S. latifrons* (34.3 individuals m^{-2}; 95.6%). BDM-T7 fauna was dominated by the isopod *S. latifrons* (4 individuals m^{-2}; 42%) and the polychaete *Lanice marionensis* (3.9 individuals m^{-2}; 40.7%). No algal taxa were found along transects BDM-T4 to BDM-T7.

A high density of polychaete *L. marionensis* (1032.6 individuals m^{-2}; 85.9%) was found in BDM-T8, as well as the ophiuroid *O. vivipara* (44.2 individuals m^{-2}; 2.3%), whereas algae were only represented by two undetermined taxa: Undetermined sp.2 (5.7%) and Undetermined sp.3 (94.3%).
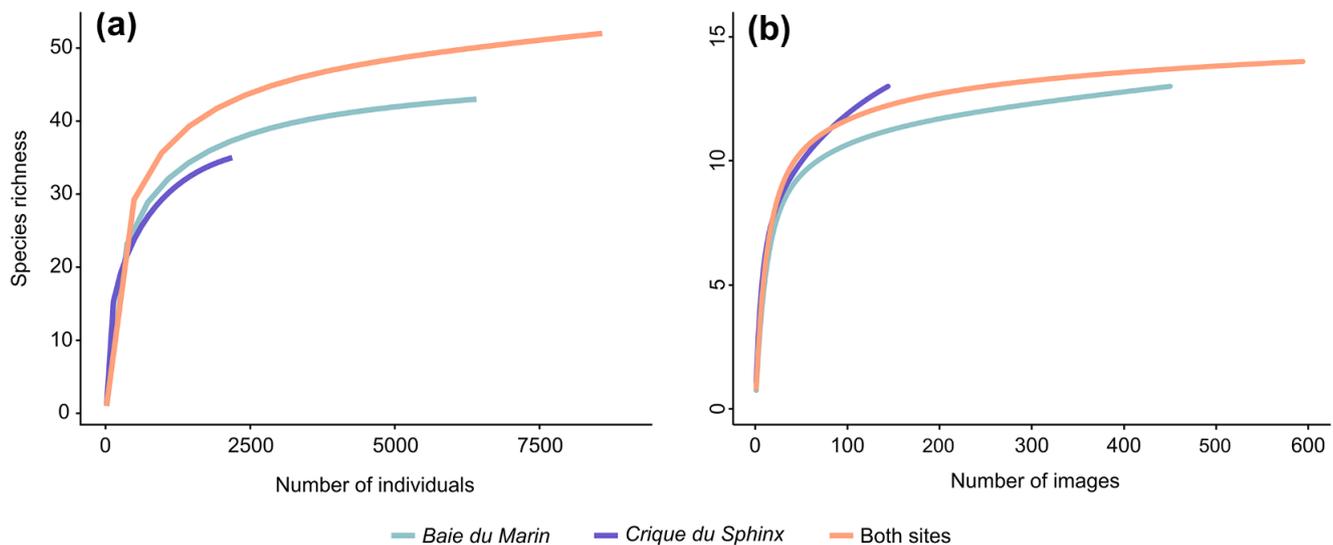
Figure 3. Rarefaction curves for **a.** faunal and **b.** algal communities at the *Baie du Marin* and *Crique du Sphinx* scale.

At *Crique du Sphinx*, CdS-T1 fauna was dominated by the poly-chaete *Parasabella* sp. (44.2 individuals m^{-2}; 29.1%), followed by the gastropod *N. delesserti* (11.9 individuals m^{-2}; 40%) and the actiniid Actiniaria fam. gen. sp.3 (3.5 individuals m^{-2}; 11.8%). Algal flora was dominated by *C. adhaerens* (39.1%), *D. confervoides* (16.1%) and *Schizoseris* sp. (15.1%). Similarly, transect CdS-T2 fauna was dominated by the polychaete *Parasabella* sp. (11.2 individuals m^{-2}; 47.6%), by the actiniid Actiniaria fam. gen. sp.3 (3.2 individuals m^{-2}; 13.4%) and to a lesser extent by the gastropod *Margarella violacea* (1.5 individuals m^{-2}; 6.4%), whereas algae were dominated by *D. chordalis* (35.1%), followed by *C. adhaerens* (19.6%) and *D. confervoides* (17%). Fauna of the CdS-T3 transect was dominated by the polychaete *L. marionensis* (12.6 individuals m^{-2}; 49.2%) and the isopod *S. latifrons* (10.9 individuals m^{-2}; 42.4%). The algal component of CdS-T3 was dominated by Undetermined sp.2 (76.9%) and Undetermined sp.3 (23.1%). Finally, CdS-T4 fauna was largely dominated by the isopod *S. latifrons* (91.4 individuals m^{-2}; 42.4%). No algae were found in CdS-T4.

Taxonomic richness and diversity indices

The shallow waters of *Baie du Marin* and *Crique du Sphinx* showed higher faunal richness and diversity values compared to deeper areas (Table III). Diversity metrics showed that BDM-T1, filmed along submarine cables, displayed the highest faunal species richness (R_{rar} = 13) and diversity (N_{rar} = 8.245; 1/λ_{rar} = 6.225) values, followed by the two transects conducted at *Crique du Sphinx*, CdS-T2 (R_{rar} = 11; N_{rar} = 5.825; 1/λ_{rar} = 3.654) and CdS-T1 (R_{rar} = 10; N_{rar} = 4.973; 1/λ_{rar} = 3.631), respectively (Table III). Faunal species richness showed no major differences between the respective shallow waters and deeper waters of both sites. The Shannon and Simpson diversity indices for shallow-water faunal communities were highest at *Baie du Marin* (N_{rar} = 8.206; 1/λ_{rar} = 5.407) than at *Crique du Sphinx* (N_{rar} = 6.760; 1/λ_{rar} = 4.432). A similar pattern was observed for deeper waters, where the highest values were recorded at *Baie du Marin* (N_{rar} = 3.363; 1/λ_{rar} = 2.510) in contrast to *Crique du Sphinx* (N_{rar} = 2.598; 1/λ_{rar} = 1.970). Finally, both sites showed a similar faunal species richness, with R_{rar} = 32.802 for *Baie du Marin* and R_{rar} = 31 for *Crique du Sphinx*, respectively. However, diversity values were higher at *Baie*

du Marin (N_{rar} = 9.702; 1/λ_{rar} = 7.067) than at *Crique du Sphinx* (N_{rar} = 7.898; 1/λ_{rar} = 4.915; Table III).

For algal communities, the species richness was predominantly located in shallow waters (R_{rar} = 11 for both sites) compared to deeper waters (R_{rar} = 2 for both sites). No major algal species richness differences were found between transects where algae were found. The highest algal diversity was found at CdS-T2 (N_{rar} = 6.101; 1/λ_{rar} = 5.565), followed by BDM-T3 (N_{rar} = 5.844; 1/λ_{rar} = 5.176) and CdS-T1 (N_{rar} = 5.151; 1/λ_{rar} = 4.677). As reported for species richness, diversity indices were higher in shallow waters compared to deeper waters. Finally, algal diversity values were similar between *Baie du Marin* (N_{rar} = 8.504; 1/λ_{rar} = 7.409) and *Crique du Sphinx* (N_{rar} = 8.140; 1/λ_{rar} = 6.878; Table III).

Influence of habitat type on benthic communities

Diversity indices calculated on faunal communities showed that rocky habitats displayed the highest species richness (R_{rar} = 14) and the highest diversity values (N_{rar} = 7.201; 1/λ_{rar} = 5.193), followed by the suspended cables (N_{rar} = 5.394; 1/λ_{rar} = 3.378) and sand-pebbles-cables (N_{rar} = 3.753; 1/λ_{rar} = 3.137) habitats. In contrast, the lowest faunal diversity values were observed for the pebble habitat (N_{rar} = 1.245; 1/λ_{rar} = 1.092), followed by sand (N_{rar} = 2.039; 1/λ_{rar} = 1.493) and sand-cables (N_{rar} = 2.520; 1/λ_{rar} = 3) habitats. For algal communities, with the exception of sand habitats, rarefied species richness and diversity values were similar between the various habitats (Table IV).

Faunal and algal composition variations between transects

PCAs were performed to investigate benthic community variations between transects and sites (Fig. 4). For faunal communities (Fig. 4a), the PCA showed that no major faunal composition variations were found between *Baie du Marin* and *Crique du Sphinx*. However, the PCA highlighted significant differences between shallow-water and deeper-water faunal communities. Transects are distributed into four groupings: 1) transects conducted by scuba divers between 0 and 20 m depth, including BDM-T1, BDM-T3, CdS-T1 and CdS-T2 - these transects were characterized by high densities of the polychaete *Parasabella* sp.,

Table III. Species richness and diversity indices of faunal and algal communities for each transect conducted at *Baie du Marin* (BDM) and *Crique du Sphinx* (CdS). Diversity indices are taxonomic richness (R), rarefied taxonomic richness (R_{rar}), Shannon diversity (N), rarefied Shannon diversity (N_{rar}), Simpson diversity ($1/\lambda$), rarefied Simpson diversity ($1/\lambda_{rar}$) and Pielou's evenness (J'). The sampling effort is also provided with regards to the number of images analysed (n_{image}), transect total surface (TTS) and the mean image surface (IS).

Transect	Site	R	R_{rar}	N	N_{rar}	$1/\lambda$	$1/\lambda_{rar}$	J'	n_{image}	TTS (m²)	IS (m²) mean ± SD
Fauna											
BDM-T1	BDM	30	13[a]	10.084	8.245[a]	6.818	6.225[a]	0.679	97	125.42	1.3 ± 0.5
BDM-T2	BDM	9	5[a]	2.773	2.615[a]	2.080	2.047[a]	0.464	78	91.98	1.2 ± 0.6
BDM-T3	BDM	18	6[a]	3.769	3.448[a]	2.824	2.739[a]	0.459	14	12.50	0.9 ± 0.8
BDM-T4	BDM	2	1[a]	1.029	1.023[a]	1.009	1.009[a]	0.042	46	5.11	0.1 ± 0.1
BDM-T5	BDM	7	4[a]	1.943	1.865[a]	1.461	1.451[a]	0.341	61	53.74	0.9 ± 0.6
BDM-T6	BDM	4	2[a]	1.235	1.211[a]	1.093	1.092[a]	0.152	61	5.69	0.1 ± < 0.1
BDM-T7	BDM	11	7[a]	3.810	3.539[a]	2.870	2.791[a]	0.558	89	49.13	0.6 ± 0.5
BDM-T8	BDM	10	6[a]	1.965	1.829[a]	1.349	1.342[a]	0.293	4	0.43	0.1 ± < 0.1
BDM - Shallow	BDM	37	33[b]	8.251	8.206[b]	5.413	5.407[b]	0.584	189	229.90	1.2 ± 0.6
BDM - Deep	BDM	17	10[c]	3.570	3.363[c]	2.541	2.510[c]	0.449	261	114.10	0.4 ± 0.5
Baie du Marin	**BDM**	**43**	**37[d]**	**10.057**	**9.702[d]**	**7.080**	**7.067[d]**	**0.614**	**450**	**344.00**	**0.8 ± 0.7**
CdS-T1	CdS	24	10[a]	5.731	4.973[a]	3.798	3.631[a]	0.549	32	44.94	1.4 ± 0.7
CdS-T2	CdS	25	11[a]	6.719	5.825[a]	3.818	3.654[a]	0.592	20	30.32	1.5 ± 0.6
CdS-T3	CdS	6	6[a]	2.815	2.812[a]	2.363	2.362[a]	0.578	37	2.30	0.1 ± < 0.1
CdS-T4	CdS	5	5[a]	1.505	1.505[a]	1.195	1.195[a]	0.254	55	4.84	0.1 ± 0.1
CdS - Shallow	CdS	31	31[b]	6.760	6.760[b]	4.432	4.432[b]	0.557	52	75.26	1.5 ± 0.6
CdS - Deep	CdS	7	7[c]	2.598	2.598[c]	1.970	1.970[c]	0.491	92	7.14	0.1 ± 0.1
Crique du Sphinx	**CdS**	**35**	**35[d]**	**7.898**	**7.898[d]**	**4.915**	**4.915[d]**	**0.581**	**144**	**82.40**	**0.6 ± 0.8**
Total	**Both**	**51**	**-**	**12.093**	**-**	**8.326**	**-**	**0.634**	**594**	**426.40**	**0.7 ± 0.7**
Algae											
BDM-T1	BDM	10	5[e,i]	6.102	4.790[e,i]	4.300	4.362[e,i]	0.785	97	125.42	1.3 ± 0.5
BDM-T2	BDM	8	4[e,i]	4.612	3.862[e,i]	3.715	3.516[e,i]	0.735	78	91.98	1.2 ± 0.6
BDM-T3	BDM	10	7[e,i]	3.810	5.844[e,i]	2.736	5.176[e,i]	0.581	14	12.50	0.9 ± 0.8
BDM-T4	BDM	0	0	0	0	0	0	0	46	5.11	0.1 ± 0.1
BDM-T5	BDM	0	0	0	0	0	0	0	61	53.74	0.9 ± 0.6
BDM-T6	BDM	0	0	0	0	0	0	0	61	5.69	0.1 ± < 0.1
BDM-T7	BDM	0	0	0	0	0	0	0	89	49.13	0.6 ± 0.5
BDM-T8	BDM	2	2[e,i]	1.230	2[e,i]	1.111	2[e,i]	0.298	4	0.43	0.1 ± < 0.1
BDM - Shallow	BDM	11	10[f,i]	7.027	8.288[f,i]	5.109	7.305[f,i]	0.813	189	229.90	1.2 ± 0.6
BDM - Deep	BDM	2	1[g,i]	1.230	0.692[g,i]	1.111	0.425[g,i]	0.298	261	114.10	0.4 ± 0.5
Baie du Marin	**BDM**	**13**	**11[h,i]**	**7.062**	**8.504[h,i]**	**5.117**	**7.409[h,i]**	**0.762**	**450**	**344.00**	**0.8 ± 0.7**
CdS-T1	CdS	9	6[e,i]	5.437	5.151[e,i]	4.338	4.677[e,i]	0.771	32	44.94	1.4 ± 0.7
CdS-T2	CdS	10	7[e,i]	5.804	6.101[e,i]	4.706	5.565[e,i]	0.764	20	30.32	1.5 ± 0.6
CdS-T3	CdS	2	0[e,i]	1.682	0.472[e,i]	1.509	0.450[e,i]	0.750	37	2.30	0.1 ± < 0.1
CdS-T4	CdS	0	0	0	0	0	0	0	55	4.84	0.1 ± 0.1
CdS - Shallow	CdS	11	11[f,i]	6.337	7.412[f,i]	5.158	6.476[f,i]	0.770	52	75.26	1.5 ± 0.6

(Continued)

Table III. (Continued)

Transect	Site	R	R_{rar}	N	N_{rar}	$1/\lambda$	$1/\lambda_{rar}$	J'	n_{image}	TTS (m²)	IS (m²) mean ± SD
CdS - Deep	CdS	2	2[g,i]	1.682	1.649[g,i]	1.509	1.471[g,i]	0.750	92	7.14	0.1 ± 0.1
Crique du Sphinx	**CdS**	**13**	**13**[h,i]	**6.356**	**8.140**[h,i]	**5.162**	**6.878**[h,i]	**0.721**	**144**	**82.40**	**0.6 ± 0.8**
Total	**Both**	**14**	**-**	**8.274**	**-**	**6.579**	**-**	**0.801**	**594**	**426.40**	**0.7 ± 0.7**

[a] Rarefied to 58 individuals.
[b] Rarefied to 433 individuals.
[c] Rarefied to 58 individuals.
[d] Rarefied to 2172 individuals.
[e] Rarefied to 4 images.
[f] Rarefied to 52 images.
[g] Rarefied to 92 images.
[h] Rarefied to 144 images.
[i] Rarefied univariate measures for algae were estimated from presence-absence data.

Table IV. Species richness and diversity indices of faunal and algal communities for each habitat type, including taxonomic richness (R), rarefied taxonomic richness (R_{rar}), Shannon diversity (N), rarefied Shannon diversity (N_{rar}), Simpson diversity ($1/\lambda$) and rarefied Simpson diversity ($1/\lambda_{rar}$).

	Species richness		Shannon diversity		Simpson diversity	
Habitat type	R	R_{rar}	N	N_{rar}	$1/\lambda$	$1/\lambda_{rar}$
Fauna						
Sand	14	6[a]	2.117	2.039[a]	1.499	1.493[a]
Sand-cables	2	1[a]	1.890	2.520[a]	1.800	3.000[a]
Sand-pebbles	14	10[a]	3.601	3.457[a]	2.489	2.468[a]
Sand-pebbles-cables	7	7[a]	3.753	3.753[a]	3.137	3.137[a]
Pebbles	5	4[a]	1.262	1.245[a]	1.093	1.092[a]
Rock	40	14[a]	7.950	7.201[a]	5.366	5.193[a]
Suspended cables	14	12[a]	5.526	5.394[a]	3.402	3.378[a]
Algae						
Sand	8	0[b,c]	4.476	0.230[b,c]	3.898	0.229[b,c]
Sand-cables	7	7[b,c]	4.950	6.340[b,c]	4.029	5.973[b,c]
Sand-pebbles	8	7[b,c]	5.206	6.046[b,c]	4.032	5.590[b,c]
Sand-pebbles-cables	8	7[b,c]	3.175	6.751[b,c]	2.201	6.412[b,c]
Pebbles	5	4[b,c]	4.192	3.860[b,c]	3.875	3.527[b,c]
Rock	14	7[b,c]	5.575	6.380[b,c]	4.185	5.629[b,c]
Suspended cables	5	5[b,c]	3.611	4.559[b,c]	3.119	4.235[b,c]

[a] Rarefied to 128 individuals.
[b] Rarefied to 5 images.
[c] Rarefied univariate measures for algae were estimated from presence-absence data.

the ophiuroid *O. vivipara* and the gastropod *N. delesserti*; 2) ROV transects conducted in the 20–60 m depth area, including BDM-T4, BDM-T5, BDM-T6, CdS-T4 and BDM-T2 - these transects were characterized by the presence of the isopod *S. latifrons*; 3) transect BDM-T8 at 60 m depth and characterized by a high density of the polychaete *L. marionensis*; and 4) transects BDM-T7 and CdS-T3, with an intermediate faunal composition between BDM-T8 and the transects of group 2 (Fig. 4a). For algal communities (Fig. 4b), the PCA showed a clear distinction between shallow waters and deeper waters. No algal composition variations were found between the BDM-T1 and BDM-T2 transects. These two transects were characterized by a dominance of *Ulva* sp., *Palmaria* sp. and *D. confervoides*. However, the BDM-T3 transect showed an algal composition that was similar to CdS-T1 and CdS-T2

transects, with a dominance of *C. adhaerens*, *D. chordalis* and several species of Corallinales (Fig. 4b).

Relationships between faunal communities, algal cover and habitat types

The RDA showed a high discrimination level between the different habitat types and the distribution of faunal and algal diversity (Fig. 5). The RDA highlighted three main benthic habitats: 1) sandy bottoms, 2) mixtures between soft and hard sediments (cables and pebbles) and 3) hard bottoms (rocky habitats and submarine cable suspended sections). Although no algae appeared to be associated with sandy habitats, the isopod *S. latifrons* and the polychaete Arenicolidae gen. indet. showed a close
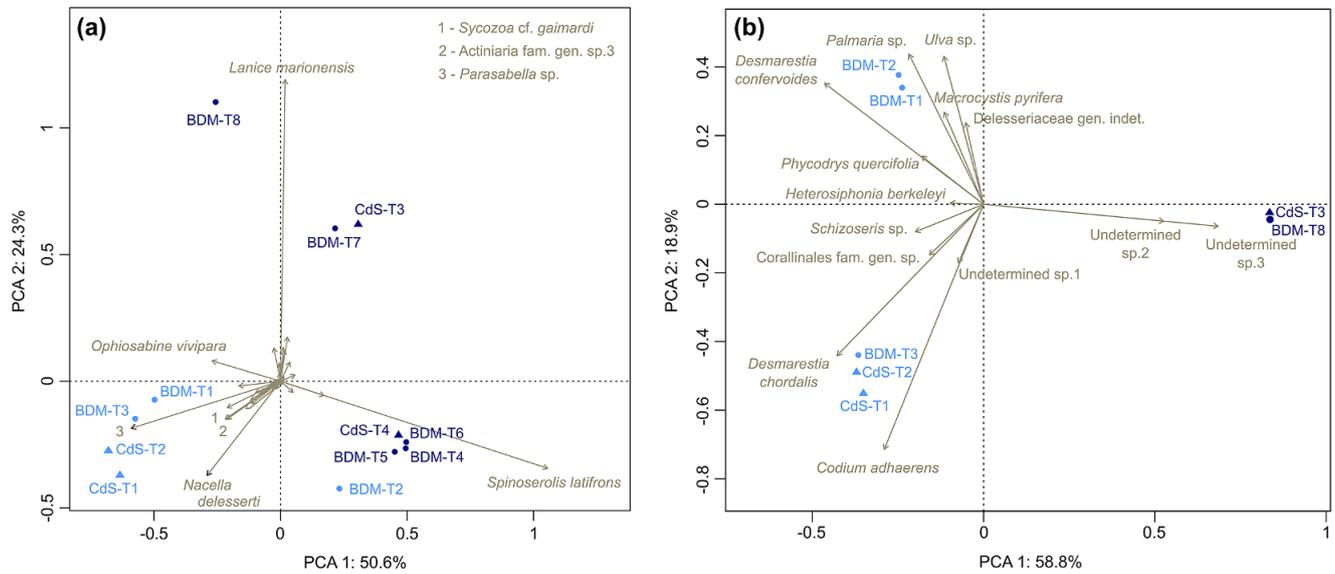
Figure 4. Principal component analysis (PCA) on the Hellinger-transformed **a.** faunal and **b.** algal cover densities of the 12 imagery transects conducted at *Ile de la Possession*. The first two PCA axes captured 74.9% and 77.7% of the total variance of Hellinger-transformed faunal and algal composition, respectively. Circles and triangles correspond to transects conducted at *Baie du Marin* and *Crique du Sphinx*, respectively; light blue corresponds to shallow-water scuba diving surveys and dark blue to deeper remotely operated vehicle transects. Only species names that best fit the first two canonical axes are shown on the plot. BDM-T4 to BDM-T7 and CdS-T4 transects were not represented in **b.** due to the absence of algae.
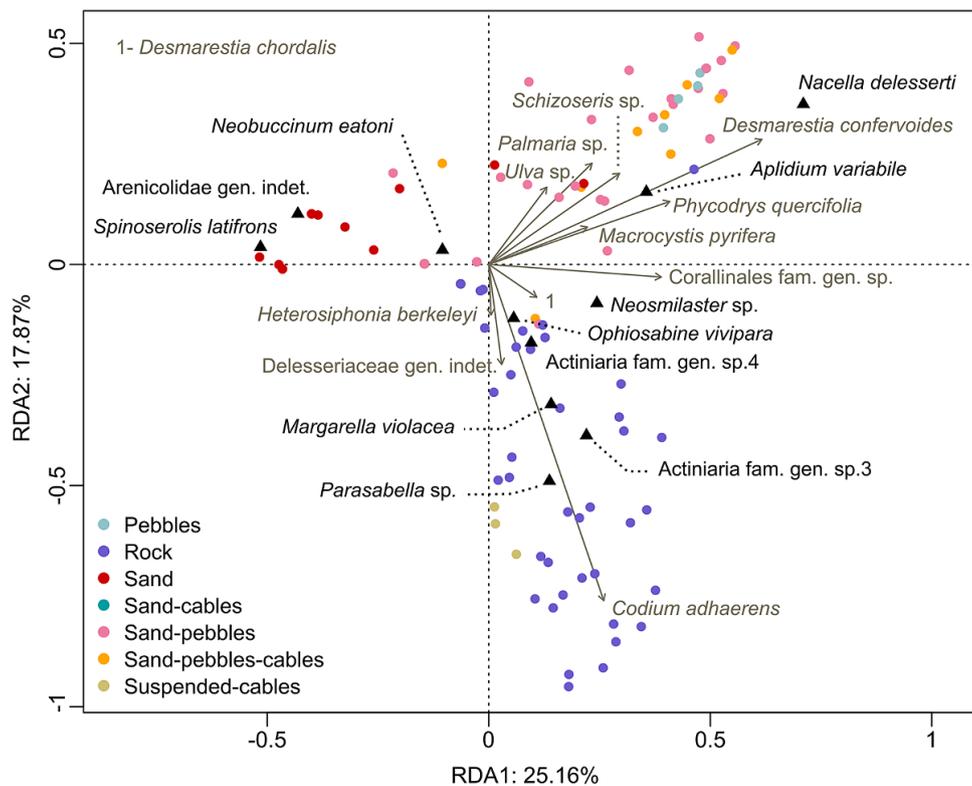
Figure 5. Redundancy analysis (RDA) between the Hellinger-transformed faunal densities and algae surface cover across the habitat types identified within underwater transects conducted at the shallow waters of *Baie du Marin* and *Crique du Sphinx*. The first two canonical axes represented account together for 43.03% of the total variance.

relationship with such environments. In environments characterized by a mixture between sand, pebbles and/or submarine cables, the algal diversity and surface cover are more important, with a high affinity degree of the gastropod *N. delesserti* and ascidian *A. variabile*. In contrast, rocky habitats showed a specific faunal and algal composition, dominated by the algae *C. adhaerens* and the polychaete *Parasabella* sp., the actiniids Actiniaria fam. gen. sp.3 and Actiniaria fam. gen. sp.4, as well as the gastropod *M. violacea* (Fig. 5). Interestingly, suspended cables and rocky habitats were closely associated.

Indicator species

Among the 51 benthic faunal and 14 algal taxa identified at the two studied sites of *Ile de la Possession*, 24 faunal and 9 algal taxa were found to be indicator species of substrate types (Table V). The isopod serolid *S. latifrons* was the only significant indicator species of sandy habitats. Pebbles environments were characterized by three indicator faunal taxa, including the gastropod *N. delesserti*, the holothurid *Pentactella* sp. and the sea star *Anasterias antarctica*; and two indicator algal taxa, the crustose coralline Corallinales fam. gen. sp. and the Rhodophyta *Schizoseris* sp. No indicator faunal taxa were found to be specifically associated with the sand-pebbles habitats. However, the Chlorophyta *Ulva* sp. and Rhodophyta *Palmaria* sp. were recognized as indicator algal taxa. Seven faunal taxa, including the actiniids Actiniaria fam. gen. sp.3 and Actiniaria fam. gen. sp.4, the gastropod *M. violacea*, the sea stars *Neosmilaster* sp. and *Smilasterias triremis*, the brittle star *O. vivipara* and the Chlorophyta *C. adhaerens* algal taxa were identified as indicator species of rocky substrates. For the suspended cables habitat, a high diversity of Demospongiae were identified as indicator taxa, including *Crella* sp., *Haliclona* sp., *Mycale* sp.1, *Mycale* sp.2, *Hymedesmia* sp., Demospongiae fam. gen. sp.1, Tetillidae gen. indet., *Halichondria* sp. and *Hymeniacidon* sp. In addition, the tubulariid Tubulariidae gen. indet., the polychaete *Parasabella* sp. and the ascidian *Sycozoa* cf. *gaimardi* were also identified as indicator faunal taxa, and the Rhodophyta Delesseriaceae gen. indet. and *Heterosiphonia berkeleyi* were identified as indicator algal taxa. Whereas the alga *M. pyrifera* was identified as an indicator taxon of sand-cables substrate, no faunal taxa were specially associated at this habitat type. Finally, the sand-pebbles-cables habitat was characterized by two faunal indicator taxa: the sponge *Mycale* sp.3 and the ascidian *A. variabile*, as well as one algal taxa: *D. confervoides*.

Discussion

Crozet coastal habitats and benthic communities

Whereas Lelièvre *et al.* (2023) were focused on subtidal communities associated with the hard substrates of *Baie du Marin*, this study provides important ecological information on the structure of faunal and algal communities associated with a wide range of habitats at two sites located on the eastern coast of *Ile de la Possession*: *Baie du Marin* and *Crique du Sphinx*. As reported by Lelièvre *et al.* (2023) at *Baie du Marin* and in numerous sub-Antarctic and Antarctic environments (Downey *et al.* 2012, Le Bourg *et al.* 2022), Crozet faunal communities were dominated by a high diversity of Porifera (12 Demospongiae) and Echinodermata (3 Ophiuroidea, 8 Asteroidea and 2 Holothuroidea). Interestingly, some characteristic subtidal sub-Antarctic groups such as barnacles and mussels (Arnaud 1974, Freeman *et al.* 2011) appear to be absent in Crozet studied areas. The algal diversity found in Crozet coastal waters was similar to the marine vegetation identified at the Kerguelen Islands, with a dominance of Rhodophyta taxa (Féral *et al.* 2021). Whereas Kerguelen coastal waters are characterized by vast and dense *M. pyrifera* kelp forests (Féral *et al.* 2021), the distribution of *M. pyrifera* in the investigated sites of Crozet is sporadic and in small patches. However, drawing comparisons between the benthic richness and diversity of Crozet and other sub-Antarctic islands remains difficult given the highly different collecting methods and depth ranges used and the large disparity in the sampling effort carried out off the different islands.

Table V. List of the significant indicator faunal and algal taxa through the different habitat types identified at *Baie du Marin* and *Crique du Sphinx*, with their associated indicator value index (IndVal) percentages and *P*-values.

Habitat type	Fauna		Algae	
	IndVal (%)	P	IndVal (%)	P
Sand				
Spinoserolis latifrons	75.6	< 0.001	-	-
Pebbles				
Nacella delesserti	87.2	< 0.001	-	-
Pentactella sp.	65.9	< 0.001	-	-
Anasterias antarctica	43.8	0.018	-	-
Corallinales fam. gen. sp.	-	-	79.5	< 0.001
Schizoseris sp.	-	-	71.5	< 0.001
Sand-pebbles				
Ulva sp.	-	-	63.5	0.002
Palmaria sp.	-	-	58.7	0.007
Rock				
Margarella violacea	62.0	< 0.001	-	-
Actiniaria fam. gen. sp.3	62.0	< 0.001	-	-
Neosmilaster sp.	59.0	0.003	-	-
Actiniaria fam. gen. sp.4	57.2	0.003	-	-
Ophiosabine vivipara	55.5	0.005	-	-
Smilasterias triremis	43.2	0.026	-	-
Codium adhaerens	-	-	72.1	< 0.001
Suspended-cables				
Tubulariidae gen. indet.	63.2	< 0.001	-	-
Crella sp.	63.2	< 0.001	-	-
Haliclona sp.	63.2	< 0.001	-	-
Mycale sp.2	63.2	< 0.001	-	-
Mycale sp.1	62.4	< 0.001	-	-
Hymedesmia sp.	57.9	< 0.001	-	-
Parasabella sp.	49.0	0.013	-	-
Demospongiae fam. gen. sp.1	44.7	0.009	-	-
Tetillidae gen. indet.	44.7	0.009	-	-
Halichondria sp.	44.7	0.009	-	-
Hymeniacidon sp.	44.7	0.009	-	-
Sycozoa cf. *gaimardi*	40.8	0.016	-	-
Delesseriaceae gen. indet.	-	-	88.1	< 0.001
Heterosiphonia berkeleyi	-	-	39.8	0.039
Sand-cables				
Macrocystis pyrifera	-	-	53.4	0.008
Sand-pebbles-cables				
Mycale sp.3	59.3	0.001	-	-
Aplidium variabile	44.8	0.047	-	-
Desmarestia confervoides	-	-	53.7	0.017

The coastal environments of *Baie du Marin* and *Crique du Sphinx* may be divided into two areas: 1) shallow waters (spanning from the coastline to 20 m depth) and 2) deeper waters (from 20 to 60 m depth). In both sites, shallow waters are inhabited by various invertebrate taxa and marine vegetation. The highest species richness and diversity values observed in shallow waters may be attributed to the high degree of habitat heterogeneity at the site scale. The habitat mosaic, formed by the alternation and combination of different habitats (e.g. sandy, pebbles and rocky substrates), enhances the coexistence of a wide range of benthic taxa by providing varied abiotic (e.g. environmental conditions) and biotic (e.g. resource availability, species interactions) conditions, thereby shaping the composition and diversity of benthic communities (Huston 1994, Guégan *et al.* 1998, Hewitt *et al.* 2005, Thrush *et al.* 2006, Stein *et al.* 2014). In the shallow waters of the Prince Edward Islands, substrate heterogeneity is also linked to spatial variation in benthic communities, thereby supporting a rich benthic diversity (Branch *et al.* 1993). Among the French sub-Antarctic territories, the Kerguelen archipelago is composed of numerous islands and islets favouring complex and diverse nearshore environments and promoting high diversity levels (Arnaud 1974, Féral *et al.* 2019, 2021). In addition, habitat-forming species such as marine vegetation also contribute to increasing habitat heterogeneity and complexity. Algal physical characteristics may alter local environmental conditions (e.g. hydrodynamic conditions, wave energy, deposition of sedimentary material, oxygen concentration) and generate a wide range of ecological niches that increase species richness and diversity (Gambi *et al.* 1994, Delille *et al.* 2009, Amsler *et al.* 2014). With the exception of the BDM-T1 transect conducted along the cable, the shallow benthos at *Crique du Sphinx* was characterized by higher richness and diversity values than that of *Baie du Marin.* This difference may be explained by the predominance of rocky habitats at *Crique du Sphinx*, whereas the shallow bottom at *Baie du Marin* was characterized by large sandy stretches. In contrast to the shallow waters, deeper areas at *Baie du Marin* and *Crique du Sphinx* were dominated by vast sandy stretches, leading to a homogeneous habitat and low diversity. From 20 m depth, algae were nearly absent.

Apart from the BDM-T2 transect, no major faunal and algal composition differences were found between the two studied sites. The dominance of sandy stretches along the BDM-T2 transect and consequently the presence of a high abundance of the isopod *S. latifrons* explain the faunal similarity between the BDM-T2 and ROV transects. The BDM-T8 transect, conducted at 60 m depth, showed specific benthic faunal communities that could be explained by the presence of a long rocky area off *Baie du Marin*, colonized by a very dense colony of the polychaete *L. marionensis*. Finally, two ROV transects, BDM-T7 and CdS-T3, showed high diversity values compared to the other ROV transects, with an intermediate species composition between BDM-T8 and other ROV transects. This results from the presence of rocky patches in a seascape dominated by sandy sediments along these transects. The abundance and diversity is generally higher in structurally complex habitats compared to homogeneous environments (Hewitt *et al.* 2008, Törnroos *et al.* 2013, Henseler *et al.* 2019). The presence of hard substrates on the sandy sediment bottom increases habitat structural complexity and thereby enhances the development (diversity, abundance and biomass) of epibenthic communities by offering an additional space to colonize and to shelter from predation and unfavourable abiotic conditions, as well as offering food sources (Downes *et al.* 1998, Grzelak & Kuklinski 2010, Levin *et al.* 2010, Lelièvre *et al.* 2023). Our results emphasize the important role of habitat heterogeneity as well as substrate type in the composition and structure of Crozet benthic communities.

Habitat types and benthic diversity

Baie du Marin and *Crique du Sphinx* sandy bottoms showed poorly diversified epifaunal communities and were largely dominated by the sand-dwelling isopod *S. latifrons* (up to 99.6% of species densities) and, to a lesser extent, by the gastropod *Neobuccinum eatoni*. The isopod *S. latifrons* was identified as a good indicator taxa of sandy bottoms and is widely distributed in Antarctic and sub-Antarctic waters (Castelló 2004, Xavier *et al.* 2020). The presence of pebbles on the soft sediments provides a hard substrate for the settlement of a wide variety of seaweeds, promoting the abundance of the grazer gastropod *N. delesserti* that mainly feeds algal spores and sporelings (Blankley & Branch 1985). The genus *Nacella* is distributed across the Southern Ocean, including temperate and sub-Antarctic areas of South America and the Falkland/Malvinas Islands, Antarctica and the sub-Antarctic islands, such as Marion, Kerguelen, Heard, Macquarie and Campbell islands (González-Wevar *et al.* 2019). However, the species *N. delesserti* is restricted to Marion and Crozet islands (Cantera & Arnaud 1985, González-Wevar *et al.* 2019). This limpet is the most abundant gastropod on the shores of Marion Island and is the main component of intertidal and shallow-water benthic communities (Blankley & Branch 1985). In contrast to sandy and pebble habitats, *Baie du Marin* and *Crique du Sphinx* bedrocks are covered with more diverse and dense communities. In accordance with Lelièvre *et al.* (2023), shallow rocky habitats were characterized by a wide diversity of invertebrate species, including the presence of dense colonies of the sessile suspension-feeding polychaete *Parasabella* sp. and the ophiuroid *O. vivipara*. The ophiuroid *O. vivipara* also occurs in numerous sub-Antarctic islands, including the Falkland/Malvinas Islands, South Georgia Island, Marion Island, the Prince Edwards Islands and the Kerguelen Islands (O'Hara & Thuy 2022). Deeper down (i.e. beyond 20 m), the polychaete *Parasabella* sp. was scarce on hard substrata and was replaced by dense colonies of the sessile deposit- and suspension-feeding tube-dwelling polychaete *L. marionensis*. High densities of the polychaete *L. marionensis* were also found at *Baie du Marin* on the rock located at the centre of the bay, at 19 m depth (Lelièvre *et al.* 2023). Similarly, a high abundance of the tube-dwelling polychaete *L. marionensis* was reported in the Prince Edward Islands and Marion Island (Sicinski & Gillet 2002, von der Meden *et al.* 2017), but the species was not reported from the Kerguelen Islands (Sicinski & Gillet 2002). The high abundance of the polychaete *L. marionensis* may be favoured on the one hand by the high flow rates off *Baie du Marin*, bringing a lot of suspended food, and on the other hand by its high trophic plasticity, as shown for the polychaete *Lanice conchilega*, which, in addition to suspension feeding, is able to actively switch to deposit feeding when suspended food is limited (Rabaut *et al.* 2007, Allan 2011).

Influence of submarine cables on benthic communities

At *Baie du Marin*, transect BDM-T1 performed along cables displayed the highest species richness and diversity values in contrast to transect BDM-T2 performed parallel to BDM-T1 and characterized by the lowest diversity values. The submarine cable suspended section was marked by high diversity values. Image analysis of the cables showed an important diversity of sponge taxa that were not observed along other transects, suggesting a

potential influence of the cables on species diversity. Artificial structures such as submarine cables may have a reef effect on benthic communities depending on the surrounding environment and native species assemblages (Langhamer 2012, Taormina *et al.* 2018). Many studies showed that artificial structures do not host exactly the same species diversity and composition as natural hard substrata (Connell & Glasby 1999, Connell 2001, Kogan *et al.* 2006). Sherwood *et al.* (2016) investigated the effects of the *Basslink High Voltage Direct Current* (HVDC) cable and its associated metallic return cable across Bass Strait in south-east Australia and reported that: 1) the ecological impacts of the cable on benthic communities have been transient and minor for soft sediments where the cable is buried; and 2) on hard substrata, the armoured cable provides a colonizable surface similar to the rocky substrata and is quickly utilized by reef species as new habitat with a species composition comparable to the surrounding reef (Sherwood *et al.* 2016). These findings were consistent with other studies on the effects of submarine cables on benthic communities, which found no significant differences in communities between powered cables and natural hard bottoms (Andrulewicz *et al.* 2003, Dunham *et al.* 2015, Kuhnz *et al.* 2020). In contrast, sections of unburied cables on soft substrata may have stronger effects on the composition and structure of benthic communities and host new species assemblages. Kogan *et al.* (2006) reported more abundant actinarians (sea anemones) on unburied sections of the *Acoustic Thermometry of Ocean Climate* (ATOC)/Pioneer Seamount cable (Half Moon Bay, CA, USA) than in the surrounding habitats, probably due to the greater habitat complexity provided by the cable compared to soft bottom sediments (Kogan *et al.* 2006). At *Baie du Marin*, sections of unburied cables on sandy bottoms were characterized by crustose Corallinales fam. gen. sp. and other algae taxa that use it as a substrate for attachment.

The introduction of a new type of substrate at *Baie du Marin* increased habitat diversity and enhanced species recruitment, potentially including non-native species (Dumont *et al.* 2011, Macreadie *et al.* 2011, Adams *et al.* 2014). Several studies reported artificial habitats acting as stepping stones or even corridors for some exotic and/or invasive marine species to survive, settle and spread (Glasby *et al.* 2007, Hulme 2009, Airoldi *et al.* 2015). In well-established subtidal assemblages, the numbers of non-native species settled on new artificial substrata were 1.5–2.5 times higher than on natural substrata (Glasby *et al.* 2007). At Crozet, greater knowledge of the potential impacts of the HA04 station cables on the benthic communities of *Baie du Marin* is needed to provide practical information and guidance for biodiversity conservation and management. Such knowledge will only be obtained through continuous environmental monitoring of community dynamics, which is one of the objectives of the current agreement between the TAAF and the CTBTO for the conservation of nearshore benthic environments of Crozet.

Monitoring strategies for enhanced benthic community conservation

Through a trait-based approach, Lelièvre *et al.* (2023) have reported the high degree of vulnerability of Crozet marine communities to current and future environmental changes (e.g. global warming, biological invasions). Identifying sensitive or endangered species in the Crozet benthic communities is challenging due to the limited knowledge and only sporadic accessibility of these ecosystems. Monitoring indicator taxa associated with each habitat type during upcoming campaigns will be instrumental to evaluating the overall health and evolutionary trends of these ecosystems. By tracking changes in abundance and distribution, these indicator taxa serve as barometers in the detection of potential disturbances over time, providing valuable insights into ecosystem health (Carignan & Villard 2002).

In addition to indicator taxa, the conservation of habitat-forming species is a priority, as they are key organisms for the preservation of local biodiversity and its resilience to changing environments. Habitat-forming species are of high ecological importance and warrant special management measures (Braeckman *et al.* 2014). Their three-dimensional structure impacts the local biotic and abiotic conditions through a wide range of ecological mechanisms (e.g. water motion dampening, sediment deposition, refuge from predation, secondary substrate for sessile/vagile species or larval settlement, food source partitioning), therefore increasing the number of potential ecological niches and promoting species richness and local diversity (Jones *et al.* 1994). In this regard, previous studies have identified the polychaete *Lanice* as an important habitat-structuring and engineer genus (Rabaut *et al.* 2007, Van Hoey *et al.* 2008). These tube-building polychaetes introduce complexity and heterogeneity in habitats and exert a strong influence on ecosystem properties, including bottom sediment stabilization and bottom flow alteration (Rabaut *et al.* 2007, Van Hoey *et al.* 2008). In addition, the habitat provisioning and structural complexity provided by these tubeworms enhance the development of faunal communities, promoting species richness, abundance and diversity (Van Hoey *et al.* 2008). Such a positive effect on the diversity and abundance of benthic ecosystems was already reported for the tube-building polychaete *L. conchilega* in the North Sea (Rabaut *et al.* 2007, Van Hoey *et al.* 2008). The preservation of biogenic habitats such as those provided by the tube-building polychaete *L. marionensis*, which is found in high density at Crozet, will also protect the range of species and communities that are associated with those habitats.

The value of image analysis as a conservation approach

Imaging techniques allowed us to assess an important benthic surface across two sites located on the eastern coast of *Ile de la Possession*, thereby providing an overview of coastal marine ecosystems in this region. However, despite many advantages, image analysis can only provide a partial and first estimate of the total benthic diversity and limit the taxonomic description of novel species, which rely on the deposition of type material according to the codes of nomenclature. Species identification is limited by image resolution and to organisms that can be seen on images, with small-sized taxa and endobenthic organisms remaining undetected. Additionally, diversity assessment of ill-known benthic communities from rarely explored regions requires a first biological sampling before further investigations and species identification can be performed from images (Solan *et al.* 2003, Thistle 2003, Hanafi-Portier *et al.* 2021). Both approaches (biological and image sampling) are complementary to each other and are essential to improve our knowledge of the structure, composition and distribution of benthic communities. Whereas these results constitute a biodiversity baseline and are valuable to monitoring the potential impacts of climate change and anthropic stressors on Crozet benthic communities, additional imagery data and complementary biological sampling are therefore needed to complement this diversity assessment and to implement further monitoring protocols to be conducted in the French Southern Territories National Nature Reserve.

Conclusion

The present study investigated the composition, abundance and diversity of benthic communities along 12 imagery transects performed at two sites - *Baie du Marin* and *Crique du Sphinx* - located on the eastern part of *Ile de la Possession*, and it evaluated the role of the habitat on species distribution. Our results showed the benefits of imaging techniques for monitoring vulnerable and sensitive sub-Antarctic benthic communities such as those in Crozet (Lelièvre *et al.* 2023). The imagery analysis results also contributed to improving our still-limited knowledge of the nearshore marine ecosystems of this sub-Antarctic archipelago and highlighted the significant influence of habitat heterogeneity and substrate complexity on species richness and diversity. Our study reveals that substrate diversity plays a crucial role in shaping the richness and composition of benthic communities in Crozet's coastal habitats. We found that transects with diverse habitats - especially those where hard substrates are predominant - support the highest levels of species richness and diversity compared to those dominated by homogeneous substrates such as sandy stretches. These findings contribute to the refinement of the baseline knowledge of benthic biodiversity in Crozet, and the identification of indicator species provides essential tools for ongoing monitoring efforts, facilitating the assessment of ecosystem health and the detection of potential environmental disturbances. Particular attention must be paid to monitoring the sessile epibenthic community associated with submarine cables laid at the bottom of *Baie du Marin* (IMS-HA04 station) considering its original composition and structure. Monitoring the development and evolution of biological communities settled on submarine cables is therefore a need for conservation strategy regarding native and endemic species.

References

Adams, T.P., Miller, R.G., Aleynik, D. & Burrows, M.T. 2014. Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *Journal of Applied Ecology*, **51**, 10.1111/1365-2664.12207.

Airoldi, L. & Beck, M.W. 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanography and Marine Biology*, **45**, 345–405.

Airoldi, L., Turon, X., Perkol-Finkel, S. & Rius, M. 2015. Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, **21**, 10.1111/ddi.12301.

Allan, E.L. 2011. *Trophodynamics of the benthic and hyperbenthic communities inhabiting the sub-antarctic Prince Edward Islands: stable isotope and fatty acid signatures.* PhD thesis. Rhodes University, 154 pp.

Allan, E.L, Froneman, P.W, Durgadoo, J.V., McQuaid, C.D., Ansorge, I.J. & Richoux, N.B. 2013. Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. *Ecology and Evolution*, **3**, 10.1002/ece3.678.

Amsler, C.D., McClintock, J.B. & Baker, B.J. 2014. Chemical mediation of mutualistic interactions between macroalgae and mesograzers structure unique coastal communities along the western Antarctic Peninsula. *Journal of Phycology*, **50**, 10.1111/jpy.12137.

Andrulewicz, E., Napierska, D. & Otremba, Z. 2003. The environmental effects of the installation and functioning of the submarine SwePol Link HVDC transmission line: a case study of the Polish Marine Area of the Baltic Sea. *Journal of Sea Research*, **49**, 10.1016/S1385-1101(03)00020-0.

Ansorge, I.J., Durgadoo, J. V. & Pakhomov, E.A. 2009. Dynamics of physical and biological systems of the Prince Edward Islands in a changing climate. *Papers and Proceedings of the Royal Society of Tasmania*, **143**, 10.26749/rstpp.143.1.15.

Ansorge, I.J., Durgadoo, J.V. & Treasure, A.M. 2014. Sentinels to climate change. The need for monitoring at South Africa's Subantarctic laboratory. *South African Journal of Science*, **110**, 10.1590/sajs.2014/a0044.

Arnaud, P.M. 1974. Contribution à la bionomie marine benthique des régions Antarctiques et subantarctiques. *Téthys*, **6**, 467–653

Auger, M., Morrow, R., Kestenare, E., Sallée, J.B. & Cowley, R. 2021. Southern Ocean in-situ temperature trends over 25 years emerge from interannual variability. *Nature Communications*, **12**, 10.1038/s41467-020-20781-1.

Barnes, D.K.A., Linse, K., Waller, C., Morely, S., Enderlein, P., Fraser, K.P.P. & Brown, M. 2006. Shallow benthic fauna communities of South Georgia Island. *Polar Biology*, **29**, 10.1007/s00300-005-0042-0.

Blanchard-Wrigglesworth, E., Roach, L.A., Donohoe, A. & Ding, Q. 2021. Impact of winds and Southern Ocean SSTs on Antarctic sea ice trends and variability. *Journal of Climate*, **34**, 10.1175/JCLI-D-20-0386.1.

Blankley, W.O. & Branch, G.M. 1985. Ecology of the limpet *Nacella delesserti* (Philippi) at Marion Island in the sub-Antarctic southern ocean. *Journal of Experimental Marine Biology and Ecology*, **92**, 10.1016/0022-0981(85)90099-1.

Braeckman, U., Rabaut, M., Vanaverbeke, J., Degraer, S. & Vincx, M. 2014. Protecting the commons: the use of subtidal ecosystem engineers in marine management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 10.1002/aqc.2448.

Branch, G.M., Attwood, C.G., Gianakouras, D. & Branch, M.L. 1993. Patterns in the benthic communities on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology*, **13**, 10.1007/BF00236580.

Byrne, M., Gall, M., Wolfe, K. & Agüera, A. 2016. From pole to pole: the potential for the Arctic seastar *Asterias amurensis* to invade a warming Southern Ocean. *Global Change Biology*, **22**, 10.1111/gcb.13304.

Cantera, J.R. & Arnaud, P.M. 1985. Les gastéropodes prosobranches des Iles Kerguelen et Crozet (Sud de l'Océan Indien) comparison écologique et particularités biologiques. *CNFRA (Comité National Français des Recherches Antarctiques)*, **56**, 1–169.

Carignan, V. & Villard, M.-A. 2002. Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment*, **78**, 10.1023/A:1016136723584.

Castelló, J. 2004. Isopods (Crustacea, Isopoda) from the Spanish 'Bentart-94/95' expeditions to the South Shetland Islands (sub-Antarctic). *Polar Biology*, **28**, 10.1007/s00300-004-0646-9.

Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M. & Gaston, K.J. 2001. World Heritage status and conservation of Southern Ocean Islands. *Conservation Biology*, **15**, 10.1046/j.1523-1739.2001.015003550.x.

Clark, G.F., Pastorino, S., Marzinelli, E.M., Turney, C.S.M., Fogwill, C.J. & Johnston, E.L. 2019. Nearshore marine communities at three New Zealand sub-Antarctic islands. *Polar Biology*, **42**, 10.1007/s00300-019-02591-4.

Connell, S.D. 2001. Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Marine Environmental Research*, **52**, 10.1016/S0141-1136(00)00266-X.

Connell, S.D. & Glasby, T.M. 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Marine Environmental Research*, **47**, 10.1016/S0141-1136(98)00126-3.

De Cáceres, M. & Legendre, P. 2011. *Indicspecies*: functions to assess the strength and significance of relationship of species site group associations. *R* package Version 1.7.12. Retrieved from https://cran.r-project.org/web/packages/indicspecies/indicspecies.pdf

De Cáceres, M., Legendre, P. & Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos*, **119**, 10.1111/j.1600-0706.2010.18334.x.

Delille, B., Borges, A.V. & Delille, D. 2009. Influence of giant kelp beds (*Macrocystis pyrifera*) on diel cycles of pCO_2 and DIC in the Sub-Antarctic coastal area. *Estuarine, Coastal and Shelf Science*, **81**, 10.1016/j.ecss.2008.10.004.

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A., *et al.* 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, **4**, 10.1146/annurev-marine-041911-111611.

Downes, B.J., Lake, P.S., Schreiber, E.S.G. & Glaister, A. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs*, **68**, 10.1890/0012-9615(1998)068[0237:HSAROL]2.0.CO;2.

Downey, R.V., Griffiths, H.J., Linse, K. & Janussen, D. 2012. Diversity and distribution patterns in high southern latitude sponges. *PLoS ONE*, **7**, 10.1371/journal.pone.0041672.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Dumont, C.P., Harris, L.G. & Gaymer, C.F. 2011. Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan *Bugula neritina*. *Marine Ecology Progress Series*, **427**, 95–103, 10.3354/meps09040.

Dunham, A., Pegg, J.R., Carolsfeld, W., Davies, S., Murfitt, I. & Boutillier, J. 2015. Effects of submarine power transmission cables on a glass sponge reef and associated megafaunal community. *Marine Environmental Research*, **107**, 10.1016/j.marenvres.2015.04.003.

Durden, J.M., Schoening, T., Althaus, F., Friedman, A., Garcia, R., Glover, A.G., *et al.* 2016. Perspectives in visual imaging for marine biology and ecology: from acquisition to understanding. *Oceanography Marine Biology Annual Review*, **54**, 10.1201/9781315368597.

Edgar, G.J. & Stuart-Smith, R.D. 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, **1**, 10.1038/sdata.2014.7.

Féral, J.-P., Verlaque, M., Rosenfeld, S., Poulin, E., Chenuil, A. & Saucède, T. 2021. The marine vegetation of the Kerguelen Islands: history of scientific campaigns, inventory of the flora and first analysis of its biogeographical affinities. *Cryptogamie, Algologie*, **42**, 10.5252/cryptogamie-algologie2021v42a12.

Féral, J.P., Poulin, E., González-Wevar, C.A., Améziane, N., Guillaumot, C., Develay, E. & Saucède, T. 2019. Long-term monitoring of coastal benthic habitats in the Kerguelen Islands: a legacy of decades of marine biology research. *Symposium on Kerguelen Plateau Marine Ecosystem and Fisheries*, 10.5281/zenodo.3249143.

Freeman, D., Cooper, S., Funnell, G. & Neale, D. 2011. Nearshore benthic community structure at the Bounty and Antipodes Islands, Subantarctic New Zealand. *Polar Biology*, **34**, 10.1007/s00300-011-1006-1.

Gambi, M.C., Lorenti, M., Russo, G.F. & Scipione, M.B. 1994. Benthic associations of the shallow hard bottoms off Terra Nova Bay, Ross Sea: zonation, biomass and population structure. *Antarctic Science*, **6**, 10.1017/S0954102094000696.

Garcíá Molinos, J., Halpern, B.S., Schoeman, D.S., Brown, C.J., Kiessling, W., Moore, P.J., *et al.* 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, **6**, 10.1038/nclimate2769.

Glasby, T.M., Connell, S.D., Holloway, M.G. & Hewitt, C.L. 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Marine Biology*, **151**, 10.1007/s00227-006-0552-5.

González-Wevar, C.A., Hüne, M., Rosenfeld, S., Nakano, T., Saucède, T., Spencer, H. & Poulin, E. 2019. Systematic revision of *Nacella* (Patellogastropoda: Nacellidae) based on a complete phylogeny of the genus, with the description of a new species from the southern tip of South America. *Zoological Journal of the Linnean Society*, **186**, 10.1093/zoolinnean/zly067.

Grzelak, K. & Kuklinski, P. 2010. Benthic assemblages associated with rocks in a brackish environment of the southern Baltic Sea. *Journal of the Marine Biological Association of the United Kingdom*, **90**, 10.1017/S0025315409991378.

Guégan, J.F., Lek, S. & Oberdorff, T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, **391**, 10.1038/34899.

Gutt, J. & Starmans, A. 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biology*, **24**, 10.1007/s003000100263.

Gutt, J., Bertler, N., Bracegirdle, T.J., Buschmann, A., Comiso, J., Hosie, G., *et al.* 2015. The Southern Ocean ecosystem under multiple climate change stresses - an integrated circumpolar assessment. *Global Ecology and Biogeography*, **21**, 10.1111/gcb.12794.

Hanafi-Portier, M., Samadi, S., Corbari, L., Chan, T.Y., Chen, W.J., Chen, J.N., *et al.* 2021. When imagery and physical sampling work together: toward an integrative methodology of deep-sea image-based megafauna identification. *Frontiers in Marine Science*, **8**, 10.3389/fmars.2021.749078.

Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M. & Bonsdorff, E. 2019. Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach. *Estuarine, Coastal and Shelf Science*, **226**, 10.1016/j.ecss.2019.106272.

Hewitt, J.E., Thrush, S.F. & Dayton, P.D. 2008. Habitat variation, species diversity and ecological functioning in a marine system. *Journal of Experimental Marine Biology and Ecology*, **366**, 10.1016/j.jembe.2008.07.016.

Hewitt, J.E., Thrush, S.F., Halliday, J. & Duffy, C. 2005. The importance of small-scale habitat structure for maintaining beta diversity. *Ecology*, **86**, 10.1890/04-1099.

Higgins, E., Scheibling, R.E., Desilets, K.M. & Metaxas, A. 2019. Benthic community succession on artificial and natural coral reefs in the northern Gulf of Aqaba, Red Sea. *PLoS ONE*, **14**, 10.1371/journal.pone.0212842.

Hogg, O.T., Barnes, D.K.A. & Griffiths, H.J. 2011. Highly diverse, poorly studied and uniquely threatened by climate change: an assessment of marine biodiversity on South Georgia's continental shelf. *PLoS ONE*, **6**, 10.1371/journal.pone.0019795.

Hsieh, T.C., Ma, K.H. & Chao, A. 2016. *iNEXT*: an *R* package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, **7**, 1451–1456.

Hughes, K.A., Pescott, O.L., Peyton, J., Adriaens, T., Cottier-Cook, E.J., Key, G., *et al.* 2020. Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. *Global Change Biology*, **26**, 10.1111/gcb.14938.

Hulme, P.E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, **46**, 10.1111/j.1365-2664.2008.01600.x.

Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press, 702 pp.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. *In* Samson, F.B. & Knopf, F.L., *eds*, *Ecosystem management*. New York: Springer, 130–147.

Jossart, Q., Lelièvre, Y., Kelch, A., Figuerola, B., Moreau, C. V., Di Franco, D., *et al.* 2024. A first glimpse into the biogeographic affinities of the shallow benthic communities from the sub-Antarctic Crozet archipelago. *Frontiers in Ecology and Evolution*, **12**, 10.3389/fevo.2024.1455329.

Jost, L. 2006. Entropy and diversity. *Oikos*, **113**, 10.1111/j.2006.0030-1299.14714.x.

Kargel, J.S., Bush, A.B.G., Cogley, J.G., Leonard, G.J., Raup, B.H., Smiraglia, C., *et al.* 2014. A world of changing glaciers: summary and climatic context. *In* Kargel, J.S., Leonard, G.J., Bishop, M.P., Kääb, A. & Raup, B.H., *eds.*, *Global land ice measurements from space*. New York: Springer, 781–840.

Kogan, I., Paull, C.K., Kuhnz, L.A., Burton, E.J., Von Thun, S., Gary Greene, H. & Barry, J.P. 2006. ATOC/Pioneer Seamount cable after 8 years on the seafloor: observations, environmental impact. *Continental Shelf Research*, **26**, 10.1016/j.csr.2006.01.010.

Kohler, K.E. & Gill, S.M. 2006. Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, **32**, 10.1016/j.cageo.2005.11.009.

Koubbi, P., Hulley, P.A., Raymond, B., Penot, F., Gasparini, S., Labat, J.P., *et al.* 2016. Estimating the biodiversity of the subantarctic Indian part for ecoregionalisation: part I. Pelagic realm of CCAMLR Areas 58.5.1. and 58.6. CCAMLR. WS-MPA-11. 11, 1–39. Retrived from https://meetings.ccamlr.org/en/ws-mpa-11/10

Kuhnz, L.A., Buck, K., Lovera, C., Litvin, S., Whaling, P.J. & Barry, J.P. 2020. Potential impacts of the Monterey Accelerated Research System (MARS) cable on the seabed and benthic faunal assemblages. Retrieved from https://sanctuarysimon.org/regional_docs/monitoring_projects/100391_MBARI_MARS_2020_report.pdf

Langenkämper, D., Zurowietz, M., Schoening, T. & Nattkemper, T.W. 2017. BIIGLE 2.0 - browsing and annotating large marine image collections. *Frontiers in Marine Science*, **4**, 10.3389/fmars.2017.00083.

Langhamer, O. 2012. Artificial reef effect in relation to offshore renewable energy conversion: state of the art. *The Scientific World Journal*, **2012**, 10.1100/2012/386713.

Le Bourg, B., Saucède, T., Charpentier, A., Lepoint, G. & Michel, L.N. 2022. What is the menu today in a subantarctic kelp food web from the Kerguelen Islands? Phytodetritus, phytoplankton and phytobenthos; not living kelp. *Marine Biology*, **169**, 10.1007/s00227-022-04105-z.

Lecomte, F., Beall, E., Chat, J., Davaine, P. & Gaudin, P. 2013. The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biology*, **36**, 10.1007/s00300-012-1281-5.

Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 10.1007/s004420100716.

Legendre, P. & Legendre, L. 2012. *Numerical ecology*, 3rd edition . Amsterdam: Elsevier B.V., **1006** pp.

Lelièvre, Y., Specq, L., Lamy, T., Boyé, A., Downey, R.V. & Saucède, T. 2023. Taxonomic and functional diversity of subtidal benthic communities associated with hard substrates at Crozet archipelago (sub-Antarctic, Southern Ocean). *Frontiers in Marine Science*, **10**, 10.3389/fmars.2023.1291038.

Lelièvre, Y., Motreuil, S., Specq, L., Marschal, C., Dubois, P., Wauters, L., *et al.* 2024a. MEDUSA: Marine benthic Ecological Data from Underwater imagery Surveys of sub-Antarctic Crozet environments. *Scientific Data*, **11**, 10.1038/s41597-024-03460-4.

Lelièvre, Y., Motreuil, S., Specq, L., Marschal, C., Dubois, P., Wauters, L., *et al.* 2024b. MEDUSA: Marine benthic Ecological Data from Underwater imagery Surveys of sub-Antarctic Crozet environments. *dataUBFC*. Retrieved from https://search-data.ubfc.fr/FR-13002091000019-2024-03-15_MEDUSA-Marine-benthic-Ecological-Data-from.html

Levin, L.A., Sibuet, M., Gooday, A.J., Smith, C.R. & Vanreusel, A. 2010. The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction. *Marine Ecology*, **31**, 10.1111/j.1439-0485.2009.00358.x.

Macreadie, P.I., Fowler, A.M. & Booth, D.J. 2011. Rigs-to-reefs: will the deep sea benefit from artificial habitat? *Frontiers in Ecology and the Environment*, **9**, 10.1890/100112.

McCarthy, A.H., Peck, L.S., Hughes, K.A. & Aldridge, D.C. 2019. Antarctica: the final frontier for marine biological invasions. *Global Change Biology*, **25**, 10.1111/gcb.14600.

McNeil, B.I. & Matear, R.J. 2008. Southern Ocean acidification: a tipping point at 450-ppm atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 10.1073/pnas.0806318105.

Mélice, J.L. & Servain, J. 2003. The tropical Atlantic meridional SST gradient index and its relationships with the SOI, NAO and Southern Ocean. *Climate Dynamics*, **20**, 10.1007/s00382-002-0289-x.

Morley, S.A., Abele, D., Barnes, D.K.A., Cárdenas, C.A., Cotté, C., Gutt, J., *et al.* 2020. Global drivers on Southern Ocean ecosystems: changing physical environments and anthropogenic pressures in an Earth system. *Frontiers in Marine Science*, **7**, 10.3389/fmars.2020.547188.

Moyer, R.P., Riegl, B., Banks, K. & Dodge, R.E. 2003. Spatial patterns and ecology of benthic communities on a high-latitude South Florida (Broward County, *USA) reef system*. *Coral Reefs*, **22**, 10.1007/s00338-003-0334-1.

O'Hara, T.D. & Thuy, B. 2022. Biogeography and taxonomy of Ophiuroidea (Echinodermata) from the Îles Saint-Paul and Amsterdam in the southern Indian Ocean. *Zootaxa*, **5124**, 10.11646/zootaxa.5124.1.1.

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., *et al.* 2020. *vegan*: Community Ecology Package. *R package* Version 2.5-7. Retrieved from https://cran.r-project.org/web/packages/vegan/vegan.pdf

Rabaut, M., Guilini, K., Van Hoey, G., Vincx, M. & Degraer, S. 2007. A bio-engineered soft-bottom environment: the impact of *Lanice conchilega* on the benthic species-specific densities and community structure. *Estuarine, Coastal and Shelf Science*, **75**, 10.1016/j.ecss.2007.05.041.

Schlacher, T.A., Williams, A., Althaus, F. & Schlacher-Hoenlinger, M.A. 2010. High-resolution seabed imagery as a tool for biodiversity conservation planning on continental margins. *Marine Ecology*, **31**, 10.1111/j.1439-0485.2009.00286.x.

Sherwood, J., Chidgey, S., Crockett, P., Gwyther, D., Ho, P., Stewart, S., *et al.* 2016. Installation and operational effects of a HVDC submarine cable in a continental shelf setting: Bass Strait, Australia. *Journal of Ocean Engineering and Science*, **1**, 10.1016/j.joes.2016.10.001.

Sicinski, J. & Gillet, P. 2002. Biogeographical affinities of polychaetes from Îles Crozet. *Antarctic Science*, **14**, 10.1017/S0954102002000172.

Smale, D.A. & Barnes, D.K.A. 2008. Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century, based primarily on evidence from the West Antarctic Peninsula region. *Ecography*, **31**, 2 10.1111/j.0906-7590.2008.05456.x.

Smith, V.R. 2002. Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change*, **52**, 10.1023/A:1013718617277.

Solan, M., Germano, J.D., Rhoads, D.C., Smith, C., Michaud, E., Parry, D., *et al.* 2003. Towards a greater understanding of pattern, scale and process in marine benthic systems: a picture is worth a thousand worms. *Journal of Experimental Marine Biology and Ecology*, 285–286, 10.1016/S0022-0981(02)00535-X.

Stein, A., Gerstner, K. & Kreft, H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 10.1111/ele.12277.

Taormina, B., Bald, J., Want, A., Thouzeau, G., Lejart, M., Desroy, N. & Carlier, A. 2018. A review of potential impacts of submarine power cables on the marine environment: knowledge gaps, recommendations and future directions. *Renewable and Sustainable Energy Reviews*, **96**, 10.1016/j.rser.2018.07.026.

Teixidó, N., Garrabou, J., Gutt, J. & Arntz, W.E. 2004. Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms. *Marine Ecology Progress Series*, **278**, 10.3354/meps278001.

Teixidó, N., Albajes-Eizagirre, A., Bolbo, D., Le Hir, E., Demestre, M., Garrabou, J., *et al.* 2011. Hierarchical segmentation-based software for

cover classification analyses of seabed images (Seascape). *Marine Ecology Progress Series*, **431**, 10.3354/meps09127.

THISTLE, D. 2003. The deep-sea floor: an overview. *Ecosystems of the World*, **28**, 5–38.

THRUSH, S.F., GRAY, J.S., HEWITT, J.E. & UGLAND, K.I. 2006. Predicting the effects of habitat homogenization on marine biodiversity. *Ecological Applications*, **16**, 10.1890/1051-0761(2006)016[1636:PTEOHH]2.0.CO;2.

TÖRNROOS, A., NORDSTRÖM, M.C. & BONSDORFF, E. 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PLoS ONE*, **8**, 10.1371/journal.pone.0078910.

TRYGONIS, V. & SINI, M. 2012. *PhotoQuad*: a dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine Biology and Ecology*, 424–425, 10.1016/j.jembe.2012.04.018.

TURNER, J., BARRAND, N.E., BRACEGIRDLE, T.J., CONVEY, P., HODGSON, D.A., JARVIS, M., *et al.* 2014. Antarctic climate change and the environment: an update. *Polar Record*, **50**, 237–259.

TURNER, J., COMISO, J.C., MARSHALL, G.J., LACHLAN-COPE, T.A., BRACEGIRDLE, T., MAKSYM, T., *et al.* 2009. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. *Geophysical Research Letters*, **36**, 10.1029/2009GL037524.

VAN HOEY, G., GUILINI, K., RABAUT, M., VINCX, M. & DEGRAER, S. 2008. Ecological implications of the presence of the tube-building polychaete *Lanice conchilega* on soft-bottom benthic ecosystems. *Marine Biology*, **154**, 10.1007/s00227-008-0992-1.

VAN REIN, H., SCHOEMAN, D.S., BROWN, C.J., QUINN, R. & BREEN, J. 2011. Development of benthic monitoring methods using photoquadrats and scuba on heterogeneous hard-substrata: a boulder-slope community case study. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **21**, 10.1002/aqc.1224.

VON DER MEDEN, C.E.O., ATKINSON, L.J., BRANCH, G.M., ASDAR, S., ANSORGE, I.J. & VAN DEN BERG, M. 2017. Long-term change in epibenthic assemblages at the Prince Edward Islands: a comparison between 1988 and 2013. *Polar Biology*, **40**, 10.1007/s00300-017-2132-1.

WALKER, S.J., SCHLACHER, T.A. & SCHLACHER-HOENLINGER, M.A. 2007. Spatial heterogeneity of epibenthos on artificial reefs: fouling communities in the early stages of colonization on an East Australian shipwreck. *Marine Ecology*, **28**, 10.1111/j.1439-0485.2007.00193.x.

WŁODARSKA-KOWALCZUK, M., KUKLIŃSKI, P., RONOWICZ, M., LEGEŻYŃSKA, J. & GROMISZ, S. 2009. Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (Hornsund, Svalbard). *Polar Biology*, **32**, 10.1007/s00300-009-0590-9.

XAVIER, J.C., CHEREL, Y., BOXSHALL, G., BRANDT, A., COFFER, T., FORMAN, J., *et al.* 2020. *Crustacean guide for predator studies in the Southern Ocean.* Cambridge: Scientific Committee on Antarctic Research, 253 pp.