

Article

Visual Imaging of Benthic Carbonate-Mixed Factories in the Ross Sea Region Marine Protected Area, Antarctica

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Abstract: Marine biogenic skeletal production is the prevalent source of Ca-carbonate in today's Antarctic seas. Most information, however, derives from the post-mortem legacy of calcifying organisms. Prior imagery and evaluation of Antarctic habitats hosting calcifying benthic organisms are poorly present in the literature, therefore, a Remotely Operated Vehicle survey was carried out in the Ross Sea region Marine Protected Area during the 2013–2014 austral summer. Two video surveys of the seafloor were conducted along transects between 30 and 120 m (Adelie Cove) and 230 and 260 m (Terra Nova Bay "Canyon"), respectively. We quantified the relative abundance of calcifiers vs. non-calcifiers in the macro- and mega-epibenthos. Furthermore, we considered the typology of the carbonate polymorphs represented by the skeletonized organisms. The combined evidence from the two sites reveals the widespread existence of carbonate-mixed factories in the area, with an overwhelming abundance of both low-Mg and (especially) high-Mg calcite calcifiers. Echinoids, serpulids, bryozoans, pectinid bivalves and octocorals prove to be the most abundant animal producers in terms of abundance. The shallower Adelie Cove site also showed evidence of seabed coverage by coralline algae. Our results will help in refining paleoenvironmental analyses since many of the megabenthic calcifiers occur in the Quaternary record of Antarctica. We set a baseline to monitor the future response of these polar biota in a rapidly changing ocean.

Keywords: Antarctica; Ross Sea region MPA; remotely operated vehicles; carbonate factories; benthos; carbonate polymorphs



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1. Introduction

The majority of studies concerning Antarctic marine carbonates rely upon outcrop, seafloor and core sediment sample evidence (e.g., [1–10]). On the contrary, little visual information on their source factories is available and this is particularly true regarding deep-sea habitats. Seafloor imagery (photos and videos) documenting benthic habitats within the reach of scuba diving abound (e.g., [11–19]), whilst considerably fewer studies imaged habitats from 50 m down to bathyal depths [20]. The geo-referenced transects by means of towed cameras are equally scant (e.g., [21–24]). The utilization of Remotely Operated Vehicles (ROV) and other robots to study Antarctic benthic habitats, although

still limited to date (e.g., [13,25,26]), represents one of the best options for investigating the deep seabed.

Polar marine biota are predominantly non-calcifying organisms; however, the mineralized parts of calcifying organisms endure a higher level of preservation post-mortem. This represents a taphonomic bias when attempting to reconstruct former benthic environments since paleoecological interpretations are by large necessarily based upon skeletal remains ([10,27,28]).

Calcified invertebrates and plants play an important role in carbon cycling and storage in Antarctic waters [29]. Bryozoans, mollusks, echinoderms, cnidarians together with barnacles, forams and serpulids are among the major contributors to the past and today Antarctic calcifier fauna [5]. In terms of CaCO_3 production rates, Antarctic echinoderms are abundant from the shelves to the deep-sea [30], and incorporate high-Mg calcite showing standing stocks 15 times higher than those measured in the Arctic [29]. Bryozoans represent another major calcifier component in Antarctic waters with a wide range of carbonate mineralogies, from completely aragonitic, mixed, and to entirely calcitic, and producing 800 up to 23,700 mg CaCO_3 /year under near-freezing conditions [31]. Further calcifiers that abundantly colonize the Antarctic seafloor are cnidarians, which can be composed of aragonite (scleractinians [32]) or calcite/aragonite (gorgonians and stylasterids [33,34]), and crustose coralline algae whose tissue skeletons contain high-Mg calcite [35].

With the aim to document the relative role of calcifiers in Antarctic benthic communities, we conducted two Remotely Operated Vehicle (ROV) surveys during the 2013–2014 austral summer in shelf areas of Terra Nova Bay area (Ross Sea, Antarctica) in proximity of the Italian research station “Mario Zucchelli”.

One dive explored the Adelie Cove from 30 m down to 120 m, while the second surveyed the shallower portion of an elongated depression in the Terra Nova Bay (TNB) in a depth range of 230–260 m, which is informally referred to as “TNB Canyon” [36]. From the deeper parts of this depression, which seems to act as a natural sink for the abundant organic matter produced during the summer phytoplanktonic bloom, new species of polychaetes were also recently described [37,38].

Here, we present the results of such ROV explorations with a focus on the calcifying component. The scope of this paper is to provide (i) the first ROV study on benthic ecosystems in this sector of the Ross Sea region Marine Protected Area, (ii) an assessment of the relative abundance of calcifiers in the macro- and mega-epibenthos and (iii) the typology of carbonate polymorphs secreted by the calcifiers identified along the transects.

2. Materials and Methods

2.1. Study Area

The Ross Sea region Marine Protected Area (RSRMPA) was established in December 2017 under Conservation Measure 91-05 (2016) [39]. After several years of laborious negotiations that have resulted in a significant reduction in area for protection, the MPA finally reached a consensus in 2016. By now, the RSRMPA encompasses a surface of ca. 1.55 million km^2 , which represents the world’s largest marine protected area established under an international agreement to date.

The Ross Sea is counted amongst the least human-impacted marine environments worldwide due largely to its remoteness, intense seasonality and extensive ice cover [24]. In the 19th and 20th centuries, commercial hunting of whales and seals was in force, resulting in the loss of thousands of individuals [40]. Between the 20th and 21st centuries, intensive fishing of toothfish resulted in over-exploitation and depletion of stocks [41,42] until 1996, when CCAMLR initiated a program to reduce the Antarctic toothfish biomass exploitation by fishing activities by 50% within 35 years [43].

Human activity in the area is strictly regulated after the establishment of the RSRMPA, encompassing a vast area (1.12 million km^2) under full protection (General Protection Zone, GPZ) where commercial fishing is prohibited, a special research zone (SRZ) where the krill and commercial toothfish research fishery is regulated and a zone where research for krill is regulated (krill research zone, KRZ, Figure 1) [44].

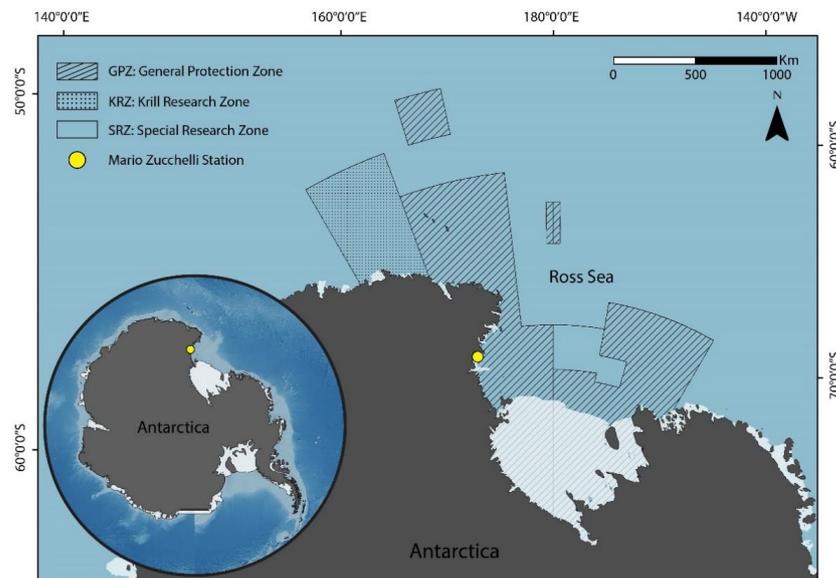


Figure 1. The Ross Sea region Marine Protected Area (RSRMPA). Map of the RSRMPA established in 2017. The Marine Protected Area is composed by (i) the General Protection Zone (GPZ), a fully protected area where no fishing is permitted; (ii) a Special Research Zone (SRZ), where the research fishing for krill and toothfish is limited; a (iii) Krill Research Zone (KRZ), with controlled research fishing for krill.

Terra Nova Bay is a coastal marine area of ca. 30 km² located between the Adélie Cove and Tethys Bay within the RSRMPA and is part of the no-take General Protection Zone (GPZ) of the RSRMPA (Figure 1). There, the Italian summer station “Mario Zucchelli” is located on a small rocky peninsula along the coast of northern Victoria Land between the tongues of the Campbell and Drygalski glaciers (74°42' S, 164°07' E, Figures 1 and 2).

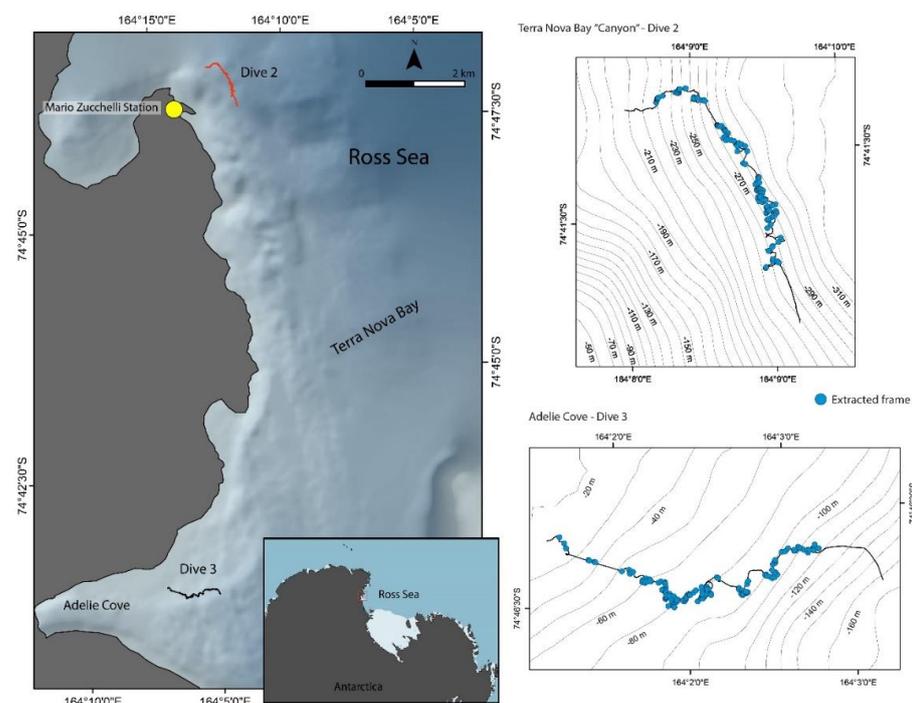


Figure 2. Location of visual benthic surveys. Map showing the location of ROV benthic surveys and of the extracted frames used for taxonomical identification at Terra Nova Bay “Canyon” and Adélie Cove.

Since 1986, the area has been the focus of a variety of biological studies on benthic, nektic and pelagic aspects of resident communities (Table 1). Systemic biological research in TNB resulted in the discovery of a variety of taxa new to science, including ampharetids, amphipods, Porifera and coralline algae (e.g., [37,38,45–49]). Checklists of species from TNB are systematically published and updated by the Italian national Antarctic Museum (MNA, Section of Genoa) [49–53]. The evidence of high diversity at both species and community levels fuelled the establishment of the Antarctic Specially Protected Area (ASPA) No. 161 of Terra Nova Bay (a coastal marine area encompassing 29.4 km² between Adélie Cove and Tethys Bay immediately to the south of the Italian Mario Zucchelli Station, MZS) and ASPA No. 173, which encompassed Cape Washington and Silverfish Bay in the northern Terra Nova Bay (a reproduction site for the for Antarctic silverfish *Pleuragramma antarctica* Boulenger, 1902).

Due to intrinsic difficulties, scant visual information is available about resident benthic communities in the RSRMPA, especially those that are out of reach by scuba diving. Only fragmentary information has been provided by cameras and, in later times, by ROV and other devices [15–19,50,54–59].

Rocky cliffs alternating with occasional beaches characterize the coastline of TNB. Offshore the Mario Zucchelli Station, the seafloor is mostly composed of granitic rocks, with patches of gravels, coarse sands and muddy sediments. A large incision (“TNB Canyon”) following the shoreline at ca. 0.4 km from the coast characterizes the seafloor geomorphology (Figure 2).

The benthic associations populating the coastal hard bottoms down to ~20 m are governed mainly by ice disturbance and melting. Here, macroalgae (mainly *Iridaea cordata* (Bory de Saint-Vincent, 1826) and *Phyllophora antarctica* (Gepp, A. and Gepp, E.S. 1905)), polychaetes, molluscs and peracarid crustaceans dominate the substrate [60–64]. Further south, the coastline is indented by an embayment known as Adélie Cove (Figure 2), which is the home of the Adélie penguin *Pygoscelis adeliae* (Hombron and Jacquinet, 1841) rookery hosting more than 7000 breeding pairs (Figure 2). Here, the seafloor is mostly constituted by coarse sands and muddy sediments [65,66].

Table 1. Scientific literature reporting information on the biological components investigated and sampling methods for Terra Nova Bay. NA was used when sampling method was not recovered. SCUBA is the acronym for Self-Contained Underwater Breathing Apparatus.

Area	Method	Research Target	Reference
Terra Nova Bay	Grab	Foraminifera	[4]
Terra Nova Bay	Grab/SCUBA	Nudibranchia	[67]
Terra Nova Bay	ROV	Shallow- and deep-water benthic communities	[68]
Terra Nova Bay	Fishing gears	Fish fauna	[69]
Terra Nova Bay	SCUBA	Phytobenthos	[60]
Terra Nova Bay	SCUBA	Phytobenthos	[61]
Terra Nova Bay	SCUBA	Phytobenthos	[70]
Terra Nova Bay	Grab/Dredge	Coastal benthic communities	[71]
Antarctica	NA	Demospongiae	[72]
Terra Nova Bay	Grab	Shallow- and deep-water mollusc communities	[73]
Terra Nova Bay	ROV	Benthic communities	[54]
Terra Nova Bay	SCUBA	Shallow-water benthic communities	[64]
Terra Nova Bay	Grab	Coastal soft bottoms communities	[74]
Terra Nova Bay	Trammel and gill nets, bottom longlines and traps	<i>Trematomus bernacchii</i> <i>T. centronotus</i> (Pisces, Nototheniidae)	[75]
Terra Nova Bay	Grab/Dredge	Benthic shallow-water communities	[76]
Terra Nova Bay	Ice-core	Sympagic algae	[77]
Terra Nova Bay	SCUBA	<i>Iridaea cordata</i> (Gigartinales), Rhodophyta)	[62]
Terra Nova Bay	Grab	<i>Adamussium colbecki</i>	[16]

Table 1. Cont.

Area	Method	Research Target	Reference
Terra Nova Bay	Grab	Shallow-water soft-bottom Polychaeta <i>Trematomus hansonii</i>	[78]
Terra Nova Bay	Hauls	<i>Trematomus loennbergii</i> (Pisces, Nototheniidae)	[79]
Terra Nova Bay	ROV	Benthic communities	[55]
Terra Nova Bay	Grab/Dredge	<i>Adamussium colbecki</i>	[80]
Terra Nova Bay	Planktonic net	<i>Pleuragramma antarcticum</i>	[81]
Terra Nova Bay	Grab/Dredge/SCUBA	Benthic Polychaeta	[82]
Terra Nova Bay	Grab/Dredge, SCUBA, ROV	Benthic littoral communities	[83]
Terra Nova Bay	Grab/Dredge	Shallow- and deep-water mollusc	[84]
Terra Nova Bay	SCUBA	Asteroidea	[85]
Terra Nova Bay	SCUBA/Grab/Dredge	Macrophytobenthos	[86]
Terra Nova Bay	Hauls	<i>Trematomus newnesi</i> (Pisces, Nototheniidae)	[87]
Terra Nova Bay	Trammel and gill nets	Coastal Fish Fauna	[88]
Terra Nova Bay	SCUBA/Dredge	<i>Adamussium colbecki</i> , <i>Sterechinus neumayeri</i> , <i>Odontaster validus</i>	[89]
Terra Nova Bay	Grab	Sea urchins, sea stars and brittle stars	[90]
Terra Nova Bay	Box corer	Benthic bacterial community	[65]
Ross Sea	Camera Tows	Benthic megafauna community	[91]
Terra Nova Bay	SCUBA	Epiphytic diatom communities	[66]
Terra Nova Bay	Mooring and cages	Seawater temperature	[92]
Terra Nova Bay	SCUBA/Grab/Dredge/ROV	Porifera	[50]
Terra Nova Bay	SCUBA/Grab/Dredge/ROV	Bryozoa	[59]
Terra Nova Bay	Grab	Macrobenthic invertebrates	[93]
Ross Sea	Towed-camera transect, multi-corer	Macro- and Mega-faunal Community	[24]

2.2. Benthic Visual Surveys

During the 2013–2014 austral summer, three ROV dives were performed in TNB in the frame of the XXIX Antarctic Italian expedition. The first one aborted due to bad meteorological conditions, while the following two were successful. The visual benthic surveys explored the seafloor offshore the Adélie Cove up to 120 m depth and TNB “Canyon” (a depressed segment of the seafloor) between 220 and 300 m depth (Table 2). The activities were performed onboard the “Malippo” and “Skua” motor vessels when the weather conditions were favorable.

Table 2. Benthic surveys metadata. The table reports the technical information on the ROV surveys performed at Terra Nova Bay.

ROV	Date	Site	Latitude	Longitude	Duration h.mm	Length	Depth Range
Dive 2	01 February 2014	Terra Nova Bay “Canyon”	74°41.319' S	164°08.549' E	03.15	2372 m	230–260 m
Dive 3	03 February 2014	Adélie Cove	74°46.399' S	164°01.405' E	02.52	1954 m	30–120 m

Video footage and still photographs were acquired using a ROV Pollux III (max working depth 500m) equipped with an underwater acoustic tracking system (USBL, Linkquest, TrackLink 1500 MA) which was connected to a Trimble dual-antenna system providing position and heading depth every 1 s. Three laser beams spaced 10 cm apart provided the scale bar on the videos. The ROV was equipped with a digital camera (Canon EOS 550, Canon EF-S 10–22mm f/3.5–4.5 USM lens with double Speedlite 270EX flash, Canon, Tokyo, Japan) and a high-definition video camera (SONY HDR-HD7, Tokyo, Japan).

2.3. Taxonomical Identification and Habitat Characterization

High-resolution images were collected with a digital camera during the surveys and analyzed for the taxonomic composition of biological communities. A total of 169 images were examined for Dive 2 and 148 for Dive 3. When necessary, the images were coupled with

low-definition video recording to improve taxonomic identification efficiency. Macrofauna and megafauna were identified to the lowest possible taxonomic rank by considering previous knowledge established in more than 35 years of research activities in the area and the large collection of museum vouchers curated by the Italian National Antarctic Museum (MNA, Section of Genoa; online database available at: <https://steu.shinyapps.io/MNA-generale/> (accessed on 27 July 2021)). Organisms unidentifiable at the genus or species level were categorized as morpho-species or morphological categories. The abundances of taxa along the exploration tracks were calculated and mapped by counting the number of taxa in each frame. Information about the different substrates and habitat explored was reported as a percentage of bottom covering. These percentages were converted to aerial extensions by considering that each image displayed 3 m (width) \times 2 m (height) of seabed on average, which corresponded to 6 m².

3. Results

3.1. Adélie Cove

Dive 3 explored ca. 2000 m of seafloor in length characterized by hard substrate between 30 m and 120 m depth. Along the entire transect, more than 7400 specimens belonging to 79 different taxa and 10 Phyla were classified (Table 3). Up to 100 m depth, the seafloor was characterized by a dense coverage from coralline algae of the order Hapalidiales (Figure 3A–C) with an extent of 351.6 m². Below 100 m, patches of hard substrate started to alternate with soft substrate. Among the most abundant taxa, we noticed that the regular echinoid *Sterechinus neumayeri* (Meissner, 1910) and the pectinid *Adamussium colbecki* (Smith, 1902) counted to 3046 and 521 specimens, respectively (Figure 3). Below 70 m depth, sponges and soft cnidarians were the dominant faunal components. Up to 30 different taxa of Porifera were identified along the ROV track. The morpho-species belonging to the genus *Haliclona* were common, counting over 290 specimens. *Isodictya erinacea* (Topsent, 1916) (134 ind.), *Dendrilla membranosa* (Pallas, 1766) (84 ind.) and *Isodictya kerguelensis* (Ridley and Dendy, 1886) (27 ind.) were also identified (Figure 3B,E,F). An individual of the Demospongia *Stylocordyla chupachups* (Uriz, Gili, Orejas and Pérez-Porro, 2011) was also recorded.

Table 3. Summary of the taxa identified. List of taxa identified in the ROV dives. The number of individuals counted and the skeleton mineralogy of calcifier organisms are also reported. AC refers to the “Adelie Cove” site; TNB refers to the “Terra Nova Bay” site.

Phylum	Class	Order	Family	Genera	Species	AC (ind.)	TNB (ind.)	ind.	Mineral	
Rhodophyta	Florideophyceae	Hapalidiales			Hapalidiales spp.				Calcite	
	Calcarea				Calcarea sp. 1	35	0	35	Calcite	
Porifera	Demospongiae	Dendroceratida	Darwinellidae	<i>Dendrilla</i>	<i>Dendrilla membranosa</i> (Pallas, 1766)	84	0	84		
		Haplosclerida	Chalinidae	<i>Haliclona</i>	<i>Haliclona scotti</i> (Grant, 1841)		5	0	5	
					<i>Haliclona</i> sp. 1		269	1	270	
					<i>Haliclona</i> sp. 2		1	0	1	
					<i>Haliclona</i> sp. 3		10	23	33	
					<i>Haliclona</i> sp. 4		6	37	43	
					<i>Haliclona</i> sp. 5		4	0	4	
			Phloeodictyidae	<i>Calyx</i>	<i>Calyx arcuarius</i> (Topsent, 1913)		6	61	67	
		Poecilosclerida	Cladorhizidae	<i>Lycopodina</i>	<i>Lycopodina vacaleti</i> (van Soest and Baker, 2011)		0	2	2	
			Coelosphaeridae	<i>Inflatella</i>	<i>Inflatella belli</i> (Kirkpatrick, 1907)		0	3	3	
			Isodictyidae	<i>Isodictya</i>	<i>Isodictya erinacea</i> (Topsent, 1916)		160	62	222	
			Isodictyidae	<i>Isodictya</i>	<i>Isodictya kerguelenensis</i> (Ridley and Dendy, 1886)		37	0	37	
			Latrunculiidae	<i>Latrunculia</i>	<i>Latrunculia (Latrunculia) biformis</i> (Kirkpatrick, 1908)		6	5	11	
			Mycalidae	<i>Mycale</i>	<i>Mycale</i> sp. 1		1	5	6	
			Tedaniidae	<i>Tedania</i>	<i>Tedania (Tedaniopsis) oxeata</i> (Topsent, 1916)		0	15	15	
		Polymastiida	Polymastiidae	<i>Polymastia</i>	<i>Polymastia invaginata</i> (Kirkpatrick, 1907)		3	0	3	
		Suberitida	Stylocordylidae	<i>Stylocordyla</i>	<i>Stylocordyla chupachups</i> (Uriz, Gili, Orejas and Pérez-Porro, 2011)		1	1	2	
		Suberitida	Suberitidae	<i>Suberites</i>	<i>Suberites caminatus</i> (Ridley and Dendy, 1886)		10	8	18	
						Demospongiae sp. 1	5	9	14	
				Demospongiae sp. 2	0	61	61			
				Demospongiae sp. 3	134	0	134			
				Demospongiae sp. 4	6	5	11			
				Demospongiae sp. 5	0	1	1			
				Demospongiae sp. 6	0	1	1			
				Demospongiae sp. 7	0	1	1			
				Demospongiae sp. 8	1	2	3			
				Demospongiae sp. 9	0	5	5			
				Demospongiae sp. 10	0	1	1			
				Demospongiae sp. 11	3	0	3			

Table 3. Cont.

Phylum	Class	Order	Family	Genera	Species	AC (ind.)	TNB (ind.)	ind.	Mineral
					<i>Rossella fibulata</i> (Schulze and Kirkpatrick, 1910)	0	25	25	
					<i>Rossella nuda</i> (Topsent, 1901)	2	0	2	
					<i>Rossella racovitzae</i> (Topsent, 1901)	0	1	1	
	Hexactinellida	Lyssacinosida	Rossellidae	<i>Rossella</i>	<i>Rossella</i> sp. 1	0	28	28	
					<i>Rossella</i> sp. 2	0	5	5	
					<i>Rossella</i> sp. 3	0	1	1	
					<i>Rossella villosa</i> (Burton, 1929)	0	3	3	
					Porifera sp. 1	0	1	1	
					Porifera sp. 2	0	5	5	
					Porifera sp. 3	0	7	7	
					Porifera sp. 4	2	0	2	
					Porifera sp. 5	0	40	40	
					Porifera sp. 6	0	10	10	
					Porifera sp. 7	0	8	8	
					Porifera sp. 8	0	8	8	
					Porifera sp. 9	5	0	5	
					Porifera sp. 10	0	4	4	
					Porifera sp. 11	0	4	4	
					Porifera sp. 12	4	0	4	
					Porifera sp. 13	0	2	2	
					Porifera sp. 14	2	0	2	
					Porifera sp. 15	2	0	2	
					Porifera sp. 16	1	0	1	
					Porifera sp. 17	1	0	1	
					Porifera sp. 18	1	0	1	
					Porifera sp. 19	0	1	1	
					Porifera sp. 20	0	1	1	
		Actiniaria			Actiniaria sp. 1	2	0	2	
			Alcyoniidae	<i>Alcyonium</i>	<i>Alcyonium antarcticum</i> (Wright and Studer, 1889)	258	27	285	
					<i>Alcyonium</i> sp. 1	3	0	3	
			Isididae	<i>Primnoisis</i>	<i>Primnoisis (Delicatisis) delicatula</i> (Hickson, 1907)	2	858	860	Calcite
					<i>Isididae</i> sp. 1	1	9	10	Calcite
			Nephtheidae	<i>Gersemia</i>	<i>Gersemia antarctica</i> (Kükenthal, 1902)	0	17	17	
				<i>Arntzia</i>	<i>Arntzia gracilis</i> (Molander, 1929)	82	81	163	
				<i>Fannyella</i>	<i>Fannyella rossii</i> (Gray, 1872)	103	1	104	
					<i>Thouarella pendulina</i> (Roule, 1908)	73	206	279	
			Primnoidae	<i>Thouarella</i>	<i>Thouarella</i> sp. 1	0	2	2	
					<i>Thouarella</i> sp. 2	258	223	481	
					<i>Thouarella</i> spp.	1	0	1	

Table 3. Cont.

Phylum	Class	Order	Family	Genera	Species	AC (ind.)	TNB (ind.)	ind.	Mineral
					Alcyonacea sp. 1	145	421	566	
					Alcyonacea sp. 2	0	38	38	
					Alcyonacea sp. 3	8	246	254	
	Hydrozoa				Hydrozoa sp. 1	0	1	1	
					Hydrozoa sp. 2	18	13	31	
	Bivalvia	Pectinida	Pectinidae	<i>Adamussium</i>	<i>Adamussium colbecki</i> (Smith, 1902)	521	0	521	Calcite
		Nudibranchia	Tritoniidae	Tritoniella	<i>Tritoniella belli</i> (Eliot, 1907)	0	1	1	
			Dorodidae	Doris	<i>Doris</i> sp.	4	0	4	
Mollusca	Gastropoda				Gastropoda sp. 1	1	0	1	
					Gastropoda sp. 2	1	0	1	
	Neogastropoda		Buccinidae	Neobuccinum	<i>Neobuccinum eatoni</i> (Smith, E.A. 1875)	2	0	2	Aragonite
					Mollusca sp. 1	0	1	1	Calcite
					Mollusca sp. 2	0	5	5	Calcite
		Sabellida	Sabellidae	<i>Perkinsiana</i>	<i>Perkinsiana magalhaensis</i> (Kinberg, 1867)	44	67	111	
					<i>Perkinsiana</i> sp. 1	22	27	49	
Annelida	Polychaeta			<i>Serpula</i>	<i>Serpula narconensis</i> (Baird, 1864)	603	823	1426	Calcite
					<i>Serpulidae</i> sp. 1	1	0	1	
		Terebellida	Flabelligeridae	<i>Flabelligerida</i>	<i>Flabelligerida mundata</i> (Gravier, 1906)	1	4	5	
	Malacostraca	Decapoda	Crangonidae	<i>Notocrangon</i>	<i>Notocrangon antarcticus</i> (Pfeffer, 1887)	0	50	50	Calcite
Arthropoda			Hippolytidae	<i>Chorismus</i>	<i>Chorismus antarcticus</i> (Pfeffer, 1887)	1	174	175	Calcite
	Pycnogonida				Pycnogonida sp. 1	16	0	16	
	Gymnolaemata	Cheilostomatida	Bugulidae	<i>Klugella</i>	<i>Klugella buski</i> (Hastings, 1943)	1	50	51	
			Phidoloporidae	<i>Reteporella</i>	<i>Reteporella</i> sp. 1	21	92	113	
			Fron diporidae	<i>Fasciculipora</i>	<i>Fasciculipora ramosa</i> (d'Orbigny, 1842)	4	0	4	
Bryozoa	Stenolaemata	Cyclostomatida	Horneridae	<i>Hornera</i>	<i>Hornera</i> sp. 1	2	30	32	
					<i>Hornera</i> sp. 2	2	5	7	
					Bryozoa sp. 1	37	57	94	
					Bryozoa sp. 2	7	6	13	
		Forcipulatida	Asteriidae	<i>Marthasterias</i>	<i>Marthasterias</i> sp. 1	10	0	10	Calcite
		Valvatida	Odontasteridae	<i>Odontaster</i>	<i>Odontaster validus</i> (Koehler, 1906)	24	0	24	Calcite
Echinodermata	Asteroidea				Asteroidea sp. 1	25	20	45	
					Asteroidea sp. 2	0	1	1	
					Asteroidea sp. 3	0	1	1	
					Asteroidea sp. 4	0	1	1	

Table 3. Cont.

Phylum	Class	Order	Family	Genera	Species	AC (ind.)	TNB (ind.)	ind.	Mineral
	Crinoidea	Comatulida	Antedonidae	<i>Anthometrina</i>	<i>Anthometrina adriani</i> (Bell, 1908)	1	38	39	Calcite
			Notocrinidae	<i>Promachocrinus</i>	<i>Promachocrinus kerguelensis</i> (Carpenter, 1879)	0	2	2	
				<i>Notocrinus</i>	<i>Notocrinus virilis</i> (Mortensen, 1917)	2	8	10	Calcite
Echinoidea	Camarodonta	Echinidae	<i>Sterechinus</i>	<i>Sterechinus neumayeri</i> (Meissner, 1900)	3046	57	3103	Calcite	
Holothuroidea						1022	208	1230	
	Ophiuroidea	Euryalida	Gorgonocephalidae	<i>Astrotoma</i>	<i>Astrotoma agassizii</i> (Lyman, 1875)	0	1	1	
		Ophiurida	Ophiuridae	<i>Ophiacantha</i>	<i>Ophiacantha vivipara</i> (Ljungman, 1871)	0	1	1	Calcite
				<i>Ophiura</i>	<i>Ophiura</i> sp. 1	151	291	442	Calcite
					<i>Ophiura</i> sp. 2	60	69	129	Calcite
Hemichordata	Graptolithoidea	Cephalodiscoidea	Cephalodiscidae	<i>Cephalodiscus</i>	<i>Cephalodiscus densus</i> (Andersson, 1907)	1	7	8	
Chordata	Ascidiacea	Stolidobranchia	Styelidae	<i>Cnemidocarpa</i>	<i>Cnemidocarpa</i> sp. 1	7	3	10	
					<i>Cnemidocarpa verrucosa</i> (Lesson, 1830)	2	0	2	
					Tunicata sp. 1	3	0	3	
	Tunicata				Tunicata sp. 2	1	0	1	
					Tunicata sp. 3	3	4	7	



Figure 3. Benthic assemblages at Adélie Cove. (A) Hard substrate with pebble and boulders encrusted by coralline algae (*Hapalidiales* spp.) at 76 m with the echinoid *Sterechinus neumayeri* (s) and the serpulid *Serpula narconensis* (sn); (B) Assemblage dominated by the sponges *Isodyctia erinacea* (ie), *Isodyctia kerguelensis* (ik) and specimens belonging to the genus *Haliclona* (hc) colonizing hard substrate covered by coralline algae at 82 m, with the subordinate presence of *Serpula narconensis* (sn), cnidarians such as *Fannyella rossii* (Gray, 1872) (f), specimens of the genus *Thouarella* (t) and *Unbranched gorgonians* (ug) and individuals of *Holothuroidea* spp. (h). (C) The portion of seafloor at 99 m dominated by cnidarians of genus *Thouarella* (t) and *Alcyonium antarcticum* (aa), with polychaetes *Serpula narconensis* (sn) and *Perkinsiana magalhaensis* (p), echinoderms such as *Ophiacantha vivipara* (Ljungman, 1871) (ov), *Ophiuroidea* sp. (o) and *Holothuroidea* sp. (h) and *Chelicerata pycnogonida* sp. (py); note the presence of the sponge *Latrunculia biformis* (l) (D) assemblage dominated by cnidarians at 100 m including *Fannyella rossii* (f), *Alcyonium antarcticum* (aa) and specimens of genus *Thouarella* (t) and subordinately by sponges represented by *Rossella nuda* (rn), *Haliclona* sp. (h) and individuals of class *Calcarea* (c), with the presence of the serpulid *Serpula narconensis* (sn), bryozoans belonging to genus *Reteporella* (r), *Ophiuroidea* such as *Ophiacantha vivipara* (ov) and *Ophiuroidea* sp. (o) and *Holothuroidea* sp. (h); (E) aggregations of the echinoid *Sterechinus neumayeri* (s) and the pectinid *Adamussium colbecki* (a) at 82 m with sponges *Dendrilla membranosa* (d) and *Haliclona* sp. (hc); (F) seafloor dominated by sponges at 112 m comprising *D. membranosa* (d) and specimens of genus *Haliclona* (hc) and class *Calcarea* (c), with sporadic presence of cnidarians of genus *Thouarella* (t) and echinoderms belonging to *Ophiuroidea* (o) and class *Holothuroidea* (h); observe the lack of coralline algae (*Hapalidiales* spp.) cover. Yellow letters refer to calcifier fauna.

Cnidarians were mostly represented by octocorals of the genus *Thouarella* (332 ind.), together with the soft coral *Alcyonium antacticum* (Wright and Studer, 1889) (258 ind., Figure 3, Table 3). Bryozoans were sporadic along the track with 74 individuals censused.

Beside *S. neumayeri*, echinoderms were abundant in the surveyed area. Holothurians were largely represented (Figure 3C,D,F) and amounted to more than 1000 individuals; however, they cannot be confidently determined from images as their taxonomy largely depends on microscopic features, i.e., the shape of the calcareous ossicles. Ophiuroids and asteroids were also very frequent with more than 270 specimens identified.

The serpulid polychaete *Serpula narconensis* (Baird, 1864) was recurrently observed to colonize both hard substrates and fouling other megafauna, amounting to 603 specimens (Figure 3).

Sources of biogenic carbonates were different at Adélie Cove site. Firstly, the seafloor was characterized by the coralline algae of the order Hapalidiales belonging to a new genus and new species (I. Moro, pers. comm. 2021) in course of description. Secondly, a noticeable portion of the benthic community included calcifiers, with 13 taxa and more than 4450 individuals counted, which corresponded to ca. 60% of the identified organisms. The major contributors were *S. neumayeri*, *S. narconensis* and *A. colbecki*, amounting to 4170 individuals. Other echinoderms such as ophiuroids, asteroids and crinoids also concurred to the calcifiers component, with 6 different taxa and 248 individuals. A smaller contribution was provided by sponge specimens of the class Calcarea (35 ind.) and by octocorals belonging to the family Isidiidae (3 ind.).

3.2. Terra Nova Bay “Canyon”

Dive 2 explored over 2300 m of seabed between 230 m and 260 m depth, transiting an area of hard substrate covered by a thin layer of soft sediment and sporadic segments of mobile substrate with patches of organic matter in degradation (Figure 4).

In total, 10 Phyla, 86 different taxa and more than 4700 specimens were identified and mapped (Table 3). The sessile megafauna was dominated by cnidarians and sponges that densely colonized the hard substrates. The octocorals of family Isidiidae (bamboo coral), such as *Primnoisis (Delicatosis) delicatula* (Hickson, 1907), dominate the assemblages in the investigated area, with over 850 individuals counted and mapped (Table 3). A total of 11 morpho-species of alcyonaceans were identified, corresponding to more than 1200 individuals. Among these, the most frequent taxa in the whole investigated area included the genus *Thouarella* (420 ind.), *Arntzia gracilis* (Molander, 1929) (81 ind.) and *Alcyonium antarcticum* (27 ind., Figure 4).

The phylum Porifera comprised 39 different taxa with 473 organisms detected. *Isodictya erinacea* and *Calyx arcuarius* (Topsent, 1913) were abundant, with 62 and 61 individuals recognized, respectively. Specimens belonging to the hexactinellid genus *Rossella* were also frequent (53 ind.). One individual of *Stylocordyla chupachups* was also identified.

Erect bryozoans occurred consistently along the transect, with the genera *Reteporella* (Busk, 1884) and *Hornera* (Lamouroux, 1821) and the species *Klugella buski* (Hastings, 1943) as main representatives (92, 35 and 50 individuals, respectively).

The echinoderms were less common when compared to the Adélie Cove site, with Ophiuroidea representing the most abundant taxa (360 ind.). Holothurians colonizing the substrate and epibionts on cnidarians were also frequently observed (Figure 4). The echinoid *S. neumayeri* was occasionally present, counting 57 individuals (Figure 4). Crinoids were also a consistent presence.

The polychaete *S. narconensis* and specimens of the genus *Perkinsiana* (Knight-Jones, 1983) were recurrent, amounting to 823 and 94 individuals, respectively (Figure 4, Table 3).

The site presented high densities of the Antarctic shrimps of the species *Chorismus antarcticus* (Pfeffer, 1887) (174 ind., Figure 5B).

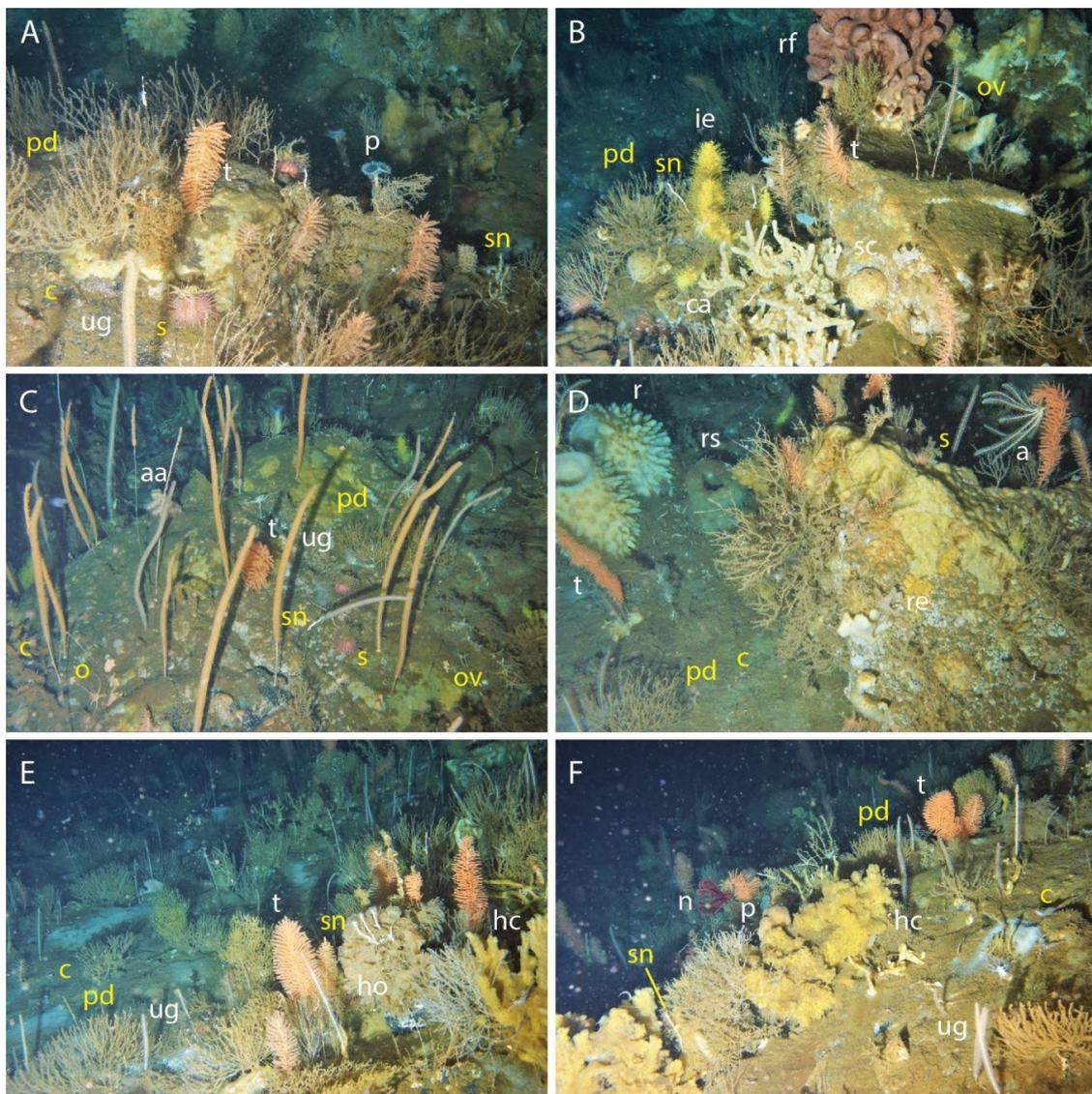


Figure 4. Benthic assemblage at Terra Nova Bay “Canyon”. (A) Seafloor at 245 m characterized by hard substrates with a prevalence of the calcifier cnidarian *Primnoisis (Delicatisis) delicatula* (pd), specimens of genus *Thouarella* (t) and unbranched gorgonian (ug); other macrobenthic organisms included the polychaetes *Serpula narconensis* (sn) and *Perkinsiana magalhaensis* (p), the echinoid *Sterechinus neumayeri* (s) and the crustacean *Chorismus antarcticus* (c); (B) assemblage at 265 m comprising the sponges *Calyx arcuarius* (ca), *Isodyctia erinacea* (ie) and *Suberites caminatus* (sc); the cnidarians *Primnoisis (Delicatisis) delicatula* (pd); and specimens of genus *Thouarella* (t), *Serpula narconensis* (sn) and *Ophiacantha vivipara* (ov); (C) hard substrate at 248 m with high densities of unbranched gorgonians (ug), *Primnoisis (Delicatisis) delicatula* (pd), *Alcyonium antarcticus* (aa) and *Thouarella* sp. (t); other noticeable components are *Serpula narconensis* (sn), *Sterechinus neumayeri* (s), ophiuroids such as *Ophiacantha vivipara* (ov) and *Ophiura* sp. (o) and the *Chorismus antarcticus* (c), these latter all concurring to the calcifier fauna; (D) assemblage at 267 m composed by the sponges *Rossella* sp. (r) and *Rossella nuda* (rn), cnidarians represented by the calcifier *Primnoisis (Delicatisis) delicatula* (pd) and specimens of the genus *Thouarella* (t), together with bryozoans as *Reteporella* sp. (re); *Sterechinus neumayeri* (s) and *Chorismus antarcticus* (c) represent the vagile fauna; (E) bottom at 272 m colonized by *Primnoisis (Delicatisis) delicatula* (pd), *Thouarella* sp. (t), unbranched gorgonians (ug) and sponges *Haliclona* sp. (hc); among the calcifiers, individuals of *Serpula narconensis* (sn) fouling the bryozoan *Hornera* sp. (ho) and the crustacean *Chorismus antarcticus* (c) were observed; note whitish patches of decaying organic matter; (F) hard bottom at 281 m colonized by sponges *Haliclona* sp. (hc), *Primnoisis (Delicatisis) delicatula* (pd), *Thouarella* sp. (t) and unbranched gorgonians (ug); note the serpulids *Perkinsiana magalhaensis* (p) and *Serpula narconensis* (sn), the crinoid *Notocrinus virilis* (Mortensen, 1917) (n) and *Chorismus antarcticus* (c). Yellow letters refer to calcifier fauna.

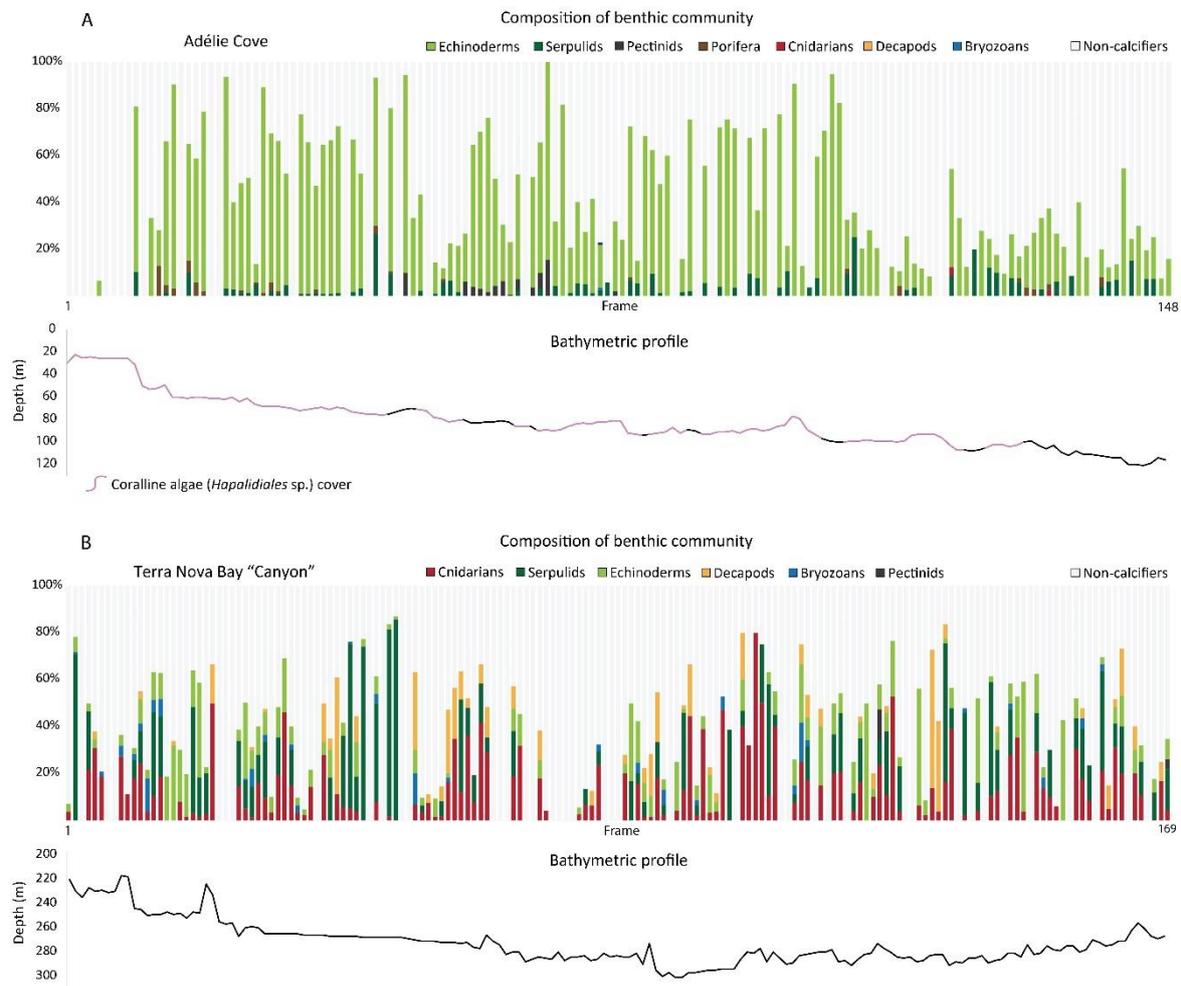


Figure 5. Composition of biological assemblages and depth profile of the visual surveys. Percentage composition of benthic community (bars) and depth (lines) of frames extracted from video recordings performed in the Adélie Cove (A) and the Terra Nova Bay Canyon (B). Colors refer to the different calcifiers groups. “Decapods” class represents an abundance of *Chorismus antarcticus* and *Notocrangon antarcticus*. Black lines refer to bathymetric profile of frames. In A, colored depth profile segments represent portions of seafloor characterized by coralline algae (*Hapalidiales* spp.) covering.

4. Discussion

4.1. Adélie Cove

The shallow situation observed in Adélie Cove reveals the occurrence of four main calcifiers in the order of relative abundance: *Hapalidiales* coralline algae, which predominates in the shallower part of the transect (30–100 m, Figure 5) (which belong to a new genus and a new species, currently under study); *S. neumayeri*, *A. colbecki* and *S. narconensis*. Algal thalli calcify by large in the polymorph high-Mg calcite. *S. neumayeri* is characterized by a high-Mg exoskeleton (mean 9.58 mol% MgCO_3 [30]). *S. narconensis* is equally made up of high-Mg calcite [36]. The shell of *Adamussium colbecki* possesses low-Mg calcite [92], with minor presences of myostrocal aragonite [94,95].

Subordinate to such main skeletal carbonate producers, other mega-epibenthic components representing a minor contribution of post-mortem carbonates were observed in the ROV frames. For instance, high-Mg calcitic ossicles and spicules derive from other echinoderm groups such as asteroids, ophiuroids, crinoids and holothuroids (e.g., [30]); bryozoans produce particles of mixed mineralogy, but with a net prevalence of calcite at polar latitudes [6,95]; the calcareous sponges shed spicules (actines) composed of Mg-calcite [96].

Only one aragonite producer was identified by the ROV survey, i.e., two individuals of the gastropod *Neobuccinum eatoni*. This species was repeatedly documented in the Terra Nova Bay area between 15–100 m of depth, as documented by MNA vouchers (Schiaparelli, S. pers. comm.).

4.2. Terra Nova Bay “Canyon”

The carbonate-producing organisms were ca. 50% (>2300 ind., Figure 5) of the overall benthic community, with the bamboo coral *P. delicatula* and *S. narconensis* as main contributors (858 and 828 ind., respectively). Octocorals such as the *Primnois* contribute to the carbonate sediment by shedding calcified internodes post-mortem, which is made up of high-Mg calcite [97] together with the serpulids, as mentioned above.

The erect calcitic bryozoans *Reterporella* spp., *Hornera* spp. and (although only lightly calcified) *K. buski* contribute significantly (ca. 10%) to the TBN carbonate-mixed factory.

Although minor producers in absolute terms, other octocorals, ophiuroids (high-Mg calcite) and decapods (low-Mg calcite: [98]), which are represented by the shrimps *Notocrangon antarcticus* and *Chorismus antarcticus*, were also a noticeable component among calcifiers, amounting to 50 and 174 individuals (Figure 5, Table 3). A minor high-Mg calcite contribution was accounted by the sporadic presence of *S. neumayeri* (57 ind.) and of the crinoid *Anthometrina adriani* (Bell, 1908) (38 ind.).

4.3. Ross Sea Carbonate Factories: Traits, Legacy and Future

The ROV surveys disclosed the supremacy of calcitic megabenthos over other calcifiers inside the carbonate-mixed factories of shallow to relatively deep settings in the Ross Sea. The taphonomic resilience of calcite polymorphs finds confirmation in the paleontological legacy of Quaternary Antarctica. By referring only to megabenthic organisms, shallow-water deposits are often enriched by *A. colbecki* shells [7], while more distal and deeper situations document their richness in bryozoans, isidids, serpulids and echinoids [1,5,10,27,99].

The mega-epibenthos carbonate-mixed factories only accounts for part of the total carbonate biogenic production in the study context. Therefore, these results are conservative and somewhat biased in terms of carbonate polymorphs. It does not account for any additional skeletal input derived by infauna, which could be relevant especially at shallow depths (such as the aragonitic bivalves *Aequiyoldia eightsii* (Jay, 1839) and *Laternula elliptica* (King, P.P. 1832)), relative to the holopelagic input (mainly aragonitic pteropods), the occasional aragonitic and vateritic otolith shed by fishes (e.g., [100]), but mostly the important contribution provided by macrobenthos (such as molluscs, which are predominantly aragonitic) and microbenthos (mainly calcitic foraminifers and subordinate ostracods and serpulids). Furthermore, our case studies deal with intermediate water situations in the range of 30–260 m, but do not account for other important factories in the Ross Sea, i.e., the very shallow ones [101] which are significantly represented in the fossil record [1,7] as well as the offshore banks [5,20]; all of these are meritable for exploration in the future.

The current structure of marine communities inhabiting the Ross Sea region Marine Protected Area as described here could well change some traits in the near future under the pressure of global climatic perturbations. Indeed, Antarctic organisms are exposed to increasing pressure from multiple stresses, including seawater warming (e.g., [102,103]) and freshening [104], changes in sea ice dynamics and productivity (e.g., [105,106]) and ocean acidification (e.g., [107]). In particular, ocean acidification and the decrease in seawater pH and carbonate ion concentration due to the absorption of large amounts of CO₂ by the oceans are expected to be the most critical changes facing Antarctic waters (e.g., [108–111]). Antarctic calcifying organisms, which are already living close to aragonite and calcite undersaturation, may not be able to cope with the projected changes, resulting in potential cascading consequences that might ultimately affect food webs and higher trophic levels. However, the responses of Antarctic marine calcifiers to ocean acidification may vary among taxa depending on their ability to actively control seawater chemistry at the site of calcification, with some species being more vulnerable than others. Additional

studies on the physiology of marine calcifiers living at high-latitudes in the Southern Ocean are required to understand their long-term ability to adapt to ocean acidification and other climate-related changes.

5. Conclusions

Our study recognized the relative abundance and typology of macro- and megapibenthic calcifiers from two sectors of the Ross Sea of contrasting bathymetric setting. As expected from carbonate factories located at high latitudes, calcitic taxa (mainly high-Mg calcite) present an almost total dominance.

With the exception of the shallow depths of Adélie Cove where coralline algae strongly prevailed, calcifiers equalize and are, on occasion, quantitatively comparable to other non-calcifying megabenthic taxa. Many such calcifiers are among the more common taxa encountered in the Quaternary record of Antarctica. As shown by ROV imagery, the original living carbonate factories are far more diverse than resulting fossil assemblages. This suggests an obvious taphonomic loss of important ecological information with respect to the structure and diversity of the original communities.

The ROV transects represent an important in situ photographic documentation of the current situation of carbonate-mixed factories in the Ross Sea. They provide, therefore, a geo-referenced and replicable baseline that is useful for monitoring future effects of progressive ocean acidification and global warming, both in terms of the hypothesized decline of calcifying vs. non-calcifying mega and macrobenthos, and of a selective taxon-based resilience.

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