



## Potential macroalgal expansion and blue carbon gains with northern Antarctic Peninsula glacial retreat

Dolores Deregibus<sup>a,b,\*</sup>, Gabriela L. Campana<sup>a,c</sup>, Camila Neder<sup>d,e,g</sup>, David K.A. Barnes<sup>f</sup>, Katharina Zacher<sup>g</sup>, Juan Manuel Piscicelli<sup>h,b</sup>, Kerstin Jerosch<sup>g</sup>, María Liliana Quartino<sup>a,i</sup>

<sup>a</sup> Departamento de Biología Costera, Instituto Antártico Argentino, San Martín, Buenos Aires, Argentina

<sup>b</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

<sup>c</sup> Departamento de Ciencias Básicas, Universidad Nacional de Luján, Luján, Buenos Aires, Argentina

<sup>d</sup> Ecosistemas Marinos y Polares, Instituto de Diversidad y Ecología Animal (IDEA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Córdoba, Argentina

<sup>e</sup> Ecología Marina, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina

<sup>f</sup> British Antarctic Survey, NERC, Cambridge, UK

<sup>g</sup> Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

<sup>h</sup> Estación Hidrobiológica Puerto Quequén. Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires, Argentina

<sup>i</sup> Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires, Argentina

### ARTICLE INFO

#### Keywords:

Benthos  
Colonization  
Biomass  
Climate change  
Glacier retreat

### ABSTRACT

The West Antarctic Peninsula (WAP) is a hotspot of physical climate change, especially glacial retreat, particularly in its northern South Shetland Islands (SSI) region. Along coastlines, this process is opening up new ice-free areas, for colonization by a high biodiversity of flora and fauna. At Potter Cove, in the SSI (Isla 25 de Mayo/King George Island), Antarctica, colonization by macroalgae was studied in two newly ice-free areas, a low glacier influence area (LGI), and a high glacier influence area (HGI) differing in the presence of sediment run-off and light penetration, which are driven by levels of glacial influence. We installed artificial substrates (tiles) at 5 m depth to analyze benthic algal colonization and succession for four years (2010–2014). Photosynthetic active radiation (PAR, 400–700 nm), temperature, salinity, and turbidity were monitored at both sites in spring and summer. The turbidity and the light attenuation ( $K_d$ ) were significantly lower at LGI than at HGI. All tiles were colonized by benthic algae, differing in species identity and successional patterns between areas, and with a significantly higher richness at LGI than HGI in the last year of the experiment. We scaled up a quadrat survey on the natural substrate to estimate benthic algal colonization in newly deglaciated areas across Potter Cove. Warming in recent decades has exposed much new habitat, with macroalgae making up an important part of colonist communities 'chasing' such glacier retreat. Our estimation of algal colonization in newly ice-free areas shows an expansion of ~0.005–0.012 km<sup>2</sup> with a carbon standing stock of ~0.2–0.4 C tons, per year. Life moving into new space in such emerging fjords has the potential to be key for new carbon sinks and export. In sustained climate change scenarios, we expect that the processes of colonization and expansion of benthic assemblages will continue and generate significant transformations in Antarctic coastal ecosystems by increasing primary production, providing new structures, food and refuge to fauna, and capturing and storing more carbon.

### 1. Introduction

Regional warming will most likely continue to be one of the main factors of climate forcing in Antarctica during this century (Hendry et al., 2018; IPCC, 2021; Chown et al., 2022). The northern Western Antarctic Peninsula (WAP) is a hotspot of climate change, evidenced by

sea ice decreases and rapid glacial retreat (Meredith and King, 2005; Turner et al., 2009; Stammerjohn et al., 2012; Cook et al., 2016). Ice scour has increased in the shallows (<40 m) of this region as a result of fast ice losses, leading to higher benthic mortality (Barnes and Souster, 2011; Barnes et al., 2014).

The northern WAP is an ideal region to conduct 'in situ' experiments

\* Corresponding author. Departamento de Biología Costera, Instituto Antártico Argentino, San Martín, Buenos Aires, Argentina.

E-mail address: [ddu@mrecic.gov.ar](mailto:ddu@mrecic.gov.ar) (D. Deregibus).

<https://doi.org/10.1016/j.marenvres.2023.106056>

Received 17 February 2023; Received in revised form 19 April 2023; Accepted 11 June 2023

Available online 24 June 2023

0141-1136/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

to investigate how coastal ecosystems respond to rapid physical changes (Constable et al., 2014; Lagger et al., 2018). Responses include the exposure and biotic colonization of new substrate available (Grange and Smith, 2013; Constable et al., 2014; Lagger et al., 2017, 2018). These originate mainly through two processes: (1) glacier retreat which opens new ice-free areas (Quartino et al., 2013; Zwerschke et al., 2022), and (2) ice disturbance scraping substrate clear (Barnes et al., 2018), where a serial replacement of species, ‘succession’, occurs after the creation of new space expanding the existing substrate (Sousa and Connell, 1992). The creation of new space for colonization on the sea bed may be becoming more frequent around Antarctica (Barnes et al., 2018, 2020). However, the benthic marine colonization and succession processes in Antarctica remains little studied, especially concerning marine benthic algae (Barnes and Conlan, 2007; Campana et al., 2009) with only one recent, long-term study in the subtidal (Campana et al., 2018).

Potter Cove (Isla 25 de Mayo/King George Island), adjacent to Carlini Station at the northern WAP, is an example of a study site with a special focus on the impacts of climate-forced glacier retreat across the entire shallow water ecosystem (Quartino et al., 2020). Over the last few decades, the Fourcade glacier which surrounds this cove, has severely retreated exposing newly ice-free areas (Rückamp et al., 2011) that have been colonized by benthic organisms (Quartino et al., 2013; Lagger et al., 2017, 2018). In parallel, the phenomenon of glacier melting generates cascading effects in terms of freshwater input with sediment run-off and calving events, with significant impacts on the contiguous coastal ecosystem (Schloss et al., 2012; Torre et al., 2012; Sahade et al., 2015; Servetto et al., 2017; Jerosch et al., 2019; García et al., 2020). Macroalgae are mostly dependent on hard substrate and favorable light conditions to settle, grow, and develop (Zacher et al., 2009; Wiencke and Amsler, 2012). A recent study in these newly ice-free areas documented a negative relationship between the light penetration and the complexity of the algal assemblage present (Quartino et al., 2013). Light penetration was reduced by sediment input and the macroalgae complexity was decreased in terms of diversity and presence of large perennial species. Hence, the current study addresses the question of whether benthic algae not only recruit into but also persist in new and highly impacted areas of Antarctic fjord ecosystems.

Macroalgae are an integral part of nearshore marine communities, and ideal to study since they form a key part of the shallow benthic biodiversity hotspots of the WAP (Deregibus et al., 2017; Pellizzari et al., 2020) with fundamental roles as primary producers (Runcie and Riddle, 2012; Wiencke and Amsler, 2012; Gómez and Pirjo, 2020), providing refuge and food source for associated fauna (Amsler et al., 2005; Constable et al., 2014; Moreira et al., 2014; Marina et al., 2018; Barrera Oro et al., 2019). Although our understanding of carbon sequestration processes in seaweeds remains limited, macroalgae have been identified as globally important in carbon capture and export (Krause-Jensen and Duarte, 2016). Most of the carbon captured as a consequence of macroalgal colonization in newly ice-free areas around Antarctica, is exported in adult fronds (standing stock) and potentially sequestered as “Blue Carbon” (Quartino et al., 2020).

Species Distribution Models (SDMs) are applied to analyze the habitat suitability of benthic sessile species in areas of interest. However, the detection of habitats suitable for benthic colonization in newly ice-free areas requires glaciological knowledge (Lagler et al., 2017) and that of autecological life history of the considered species (Guisan and Thuiller, 2005). SDMs are further based on statistics and geoinformatics autocorrelation to relate environmental data with the presence/absence or abundance of a species or community. This relationship allows the detection of suitable habitats of species at non-sampled locations and/or habitat shifts under changing environmental conditions (Pearson and Dawson, 2003; Mateo et al., 2012; Neder, 2016). Recently, these models have been used to predict the probability of the occurrence of macroalgae in the coastal ecosystem of Potter Cove (Jerosch et al., 2019).

To deepen our understanding of the colonization and succession processes of benthic algae in newly ice-free areas of the WAP and to

especially identify their potential expansion into these areas, the following objectives were addressed:

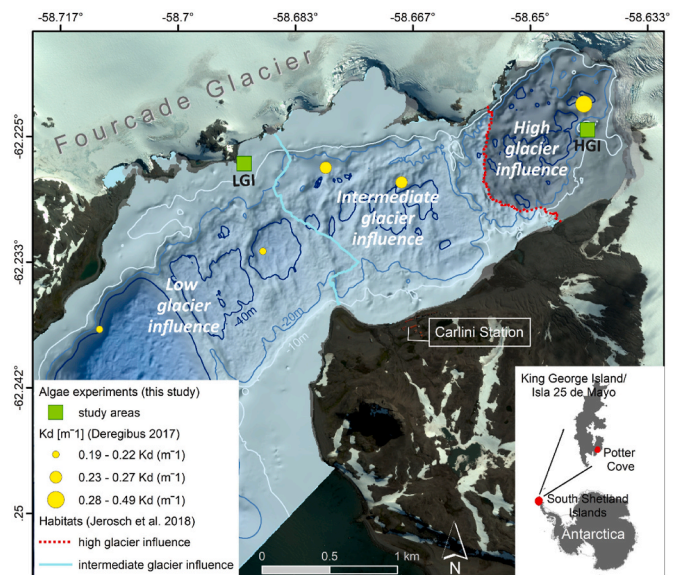
- (1) Determine macroalgae colonization patterns in two newly ice-free areas distinguished by different levels of glacier influence (gradient in turbidity, and thus light availability) based on a long-term colonization experiment in Potter Cove (WAP), and associated spatial-temporal environmental variations (turbidity, light, salinity and temperature).
- (2) Estimate potential benthic algal expansion and blue carbon gains in newly ice-free areas during recent decades.

## 2. Methods

### 2.1. Study site

The study was carried out in Potter Cove (58° 38' W; 62° 14' S), Isla 25 de Mayo/King George Island (KGI), South Shetland Islands, Antarctica (Fig. 1). All laboratory activities took place at Carlini Scientific Station/Dallman Laboratory. Potter Cove is a small fjord, ~5 km long and 1.8 km wide (Fig. 1). The north and east coasts of the inlet are bounded by the Fourcade glacier, and the south coast is bordered by gravel and sandy beach. Rocky hard substratum prevails at the north of the cove (Wöflf et al., 2014; Jerosch et al., 2019), suitable for the colonization of macroalgae. The seabed in the central area of the inner cove and the southern coast is characterized by soft substrate with little macroalgae (Klöser et al., 1996; Quartino et al., 2013; Sahade et al., 2015; Jerosch et al., 2019).

Potter Cove is characterized by (1) differing abiotic conditions (e.g.



**Fig. 1.** The study area, Potter Cove, on Isla 25 de Mayo/King George Island (KGI). The map presents high, intermediate, and low glacier influence habitats derived from Jerosch et al. (2018). The coefficient of light attenuation  $K_d$  in yellow dots is significantly higher in the inner cove than around the rest of the cove (Deregibus, 2017). Green squares mark the areas of algal experiments and environmental variables measurements, carried out in two newly ice-free areas: LGI (low glacier influence area, ice-free since 1990) located within the LGI habitat (low glacier influence habitat) and HGI (high glacier influence area, ice-free since 2000) located within the HGI habitat (high glacier influence habitat). The base map used is a compilation of the ESRI online base map version and a reprint of the WorldView-2 scene 103001001F612100, 07/03/2013 under a CC BY license, with permission from Maxar-EU Space Imaging-DigitalGlobe, original copyright 2013. Environmental variables listed in Table 1 were monitored in agreement with experiments and calculations performed throughout different periods.

optical properties) in the water column (yellow dots, Fig. 1 and Table 1) and (2) benthic assemblages of varying structure (Pasotti et al., 2015; Sahade et al., 2015). Low, intermediate, and high glacier-influenced habitats (LGI habitat, IGI habitat and HGI habitat, respectively, Fig. 1) were derived from Jerosch et al. (2018). We herein define “glacier influence” as decreased light penetration due to an increased sediment inflow, in response to glacier retreat. These habitats have different values of light attenuation ( $K_d$ ; Fig. 1), elevated in the HGI habitat (Quartino et al., 2013; Deregibus, 2017), which represents the most frequent and extreme glacier-influenced habitat in Potter Cove (Deregibus et al., 2016; Jerosch et al., 2018; Deregibus et al., 2020; Neder et al., 2020).

Two newly ice-free areas were selected for benthic algal colonization experiments located in the respective glacier influence habitat (Fig. 1):

- LGI (low glacier influence area, 62° 13' 37.865" S, 58° 41' 28.149" W, former Area 1 in Quartino et al. (2013)) free of ice since 1990
- HGI (high glacier influence area, 62° 13' 32.074" S, 58° 38' 32.453" W, former Isla D in Quartino et al. (2013)) uncovered since 2000. This newest ice-free island is of particular interest due to its close proximity to the glacier terminus.

The benthic algal assemblages in both areas have been monitored since they have been ice-free, more recently showing a higher macroalgal cover and more mature communities in LGI compared to HGI (Quartino et al., 2013; Deregibus, 2017).

## 2.2. Abiotic background: environmental variables

For a consistent spatio-temporal association within the experimental analyzed period, potentially important environmental variables for macroalgae growth were also measured.

Meteorological data was provided by the Servicio Meteorológico Nacional (SMN) station of the Argentinean Air Force located at Carlini Station. Average temperature and standard deviation were calculated for both austral seasons: spring (from September 21st to December 20th) and summer (from December 21st to March 20th) for the period 2005–2015.

Photosynthetic Active Radiation (PAR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), the turbidity of seawater converted to Nephelometric Turbidity Units (NTU), salinity measured in Practical Salinity Units, corresponding to grams of salt per

liter (PSU), and seawater temperature ( $^{\circ} \text{C}$ ) were all measured at both areas (LGI and HGI) during the springs seasons of 2010–2013 and summers of 2011–2014 (four consecutive years, Table 1). All measurements were performed at midday, once a week, when the weather conditions allowed navigation, from inflatable boats with outboard motors (Table 1).

Photosynthetic Active Radiation was measured at 0 m (just below the water surface) and 5 m depth using a datalogger LI-COR (LI 1400, LI-COR, Lincoln, USA) equipped with an underwater sensor LI-COR 192 PAR (LI-COR, Lincoln, USA). The coefficients of light attenuation ( $K_d$ ) were calculated at each area during the four summers, between the two different depths at 0 and 5 m depth according to Kirk (1994) (for details see Supplementary Text). The turbidity measurements reflected how much light is scattered by suspended particles in the water. The greater the scattering, the higher the turbidity (high NTU values indicate low water clarity, low NTU values indicate high water clarity). Turbidity, salinity and water temperature were measured with a Sea-Bird SBE 19 conductivity–temperature–depth (CTD) instrument.

## 2.3. Colonization and succession experiments

Our methodology followed Campana et al. (2018) performing *in situ* experiments in the two mentioned newly ice-free areas of Potter Cove. In each area, 23 artificial substrata (tiles) were fixed to solid rock with ~2 m distance across an area of ~100 m<sup>2</sup> at 5 m depth during April 2010 by SCUBA diving (Supplementary Fig. 1). Each tile consisted of 20 cm × 30 cm roughened high-density polyethylene.

Colonization and succession experiments were run for four years (April 2010–February 2014). Thus, the summer of 2010/2011 was the first year of colonization (Table 1). Every summer (end of January - beginning of February), five tiles (n = 5) were randomly collected by SCUBA diving in each area. Random selection of the tiles by number was made prior to the sampling. These tiles were placed in re-sealable bags with seawater and transported to the laboratory in dark conditions. Tiles were kept in filtered and temperature-controlled seawater (0  $^{\circ} \text{C}$ ) and an 18:6 h photoperiod while awaiting sample analysis.

The percent cover of algae was assessed using the “point quadrat” method (Foster et al., 1991; Kim, 2001), on a central area of 256 cm<sup>2</sup> on each tile, in order to avoid edge effects. When overlaying occurred, the organism that was on the upper stratum was recorded, slightly moved, further the taxa in the lower stratum were also identified, leading in

**Table 1**

Methodological timeline. Ecological and environmental parameters measured throughout the different years in newly ice-free areas LGI (low glacier influence area) and HGI (high glacier influence area) of Potter Cove, with information regarding measuring location, period when it was sampled, and frequency of measurements. Glacier retreat calculations, benthic algal expansion, and carbon storage estimates were performed for all newly ice-free areas of Potter Cove.

Measured parameter & Analysis performed	Location	Years	Period	Frequency of sampling	Derived parameter
<b>Colonization experiment</b>	LGI and HGI	2010–2014	Summer	Yearly	Benthic algal % cover, richness, diversity, and biomass in artificial substrates (tiles).
<b>Quadrat Survey</b> performed to extrapolate into newly ice-free areas	LGI and HGI	2014	Summer	One year	Percent cover, biomass and organic carbon calculations
<b>Glacial retreat</b>	Fourcade glacier (surrounding Potter Cove)	2008–2018	One decade	Yearly	km <sup>2</sup> of newly ice-free exposed areas
<b>Estimation of benthic algal expansion. Quadrat Survey values (algal percent cover and dry mass) extrapolation into newly ice-free areas estimated through two different approaches</b>	Newly ice-free areas in Potter cove	–	2010–2014 1956–2018	Yearly	Benthic algal expansion, dry mass, and carbon storage in newly ice-free areas
<b>Air Temperature (<math>^{\circ} \text{C}</math>)</b>	Meteorological station, Potter Cove	2005–2015	Spring & Summer	Daily	Average temperature
<b>Photosynthetic Active Radiation (PAR, <math>\mu\text{mol photons m}^{-2} \text{s}^{-1}</math>)</b>	LGI and HGI	2010–2014	Spring & Summer	Weekly/bi-monthly (depending on weather)	Average $K_d$ ( $\text{m}^{-1}$ ) (0–5m)
<b>Turbidity (NTU), Practical Salinity Units (PSU), Water Temperature (<math>^{\circ} \text{C}</math>)</b>	LGI and HGI	2010–2014	Spring & Summer	Weekly/bi-monthly (depending on weather)	Average (0–10 m)

some occasions to more than 100% cover registered. Taxa were registered when their size, measured as maximum length, was at least 2 mm. The macroalgal identification was made to the lowest possible taxonomic level (using Wiencke and Clayton, 2002) but benthic diatoms were considered as one taxon. See Campana et al. (2018) for a detailed description of the cover assessment method.

The following attributes and ecological indices were determined for each tile (Magurran, 2004) to compare between years:

- Total cover % (benthic diatoms and macroalgal cover).
- Richness (S): total number of taxa.
- Shannon diversity index.
- Pielou's measure of species evenness
- Macroalgal size: by measuring five randomly selected individuals of each species utilizing a graduated caliper ( $\pm 0.5$  mm).
- Biomass: all the organisms in the central area of each tile (16 cm  $\times$  16 cm) were considered. Macroalgae were removed entirely with a scalpel, whilst diatom films were scraped using additionally a toothbrush, rinsed with filtered seawater, and filtered through pre-weighted glass-fiber filters (0.7  $\mu$ m). The material was dried for 48 h at 80 °C and biomass was expressed as dry mass (DM) per square meter.

#### 2.4. Quadrat survey. Algal percent cover, dry mass and organic carbon values used to extrapolate into newly ice-free areas

Additionally, a quadrat survey was performed during the summer of 2014 (the last colonization experiment year) at the same location of LGI and HGI areas to analyze the contiguous benthic algal assemblages where the colonization experiments were carried out. Five quadrats of 1 m<sup>2</sup> were selected haphazardly in each area at 5 m depth, photographed, and the benthic algal percent cover per taxon in each square meter calculated (Supplementary Text). Thus, the total cover (cm<sup>2</sup>) for each species in the quadrat was calculated.

Dry mass and mean organic carbon content were estimated by calculating the conversion factor (in g cm<sup>-2</sup>) for each macroalgal species present within its coverage area with known species-specific values of mean dry mass (g m<sup>-2</sup>) (Quartino and Boraso de Zaiuso, 2008) and carbon content (Gómez et al., 1997; Peters, 2005) obtained from the literature (for details see Supplementary Text). In order to predict percent cover, dry mass, and organic carbon of new macroalgae in the newly ice-free areas, two different approaches below explained were applied.

#### 2.5. Potential macroalgae colonization and expansion in newly ice-free areas

The marine area loss of the Fourcade glacier during the time of the experiment and since 1956 was calculated using the positional data of five glacier front lines recorded between 1956 and 2008 (for details see Supplementary Text).

The macroalgal percent cover, number and composition of taxa found in tile assemblages were similar to those on natural substrata (quadrat surveys) after four years (Supplementary Text). However, when the tile colonization experiments and the quadrat surveys were compared, the between-tile variability in percent cover and dry mass of benthic algae on tiles showed strong outliers with assumptions underlying Cochran's test. Consequently, the quadrat survey was used for scaling up percent cover, dry mass and carbon storage stock estimations.

From the calculated newly ice-free area, two different approaches were used to determine the regional area likely to be colonized by macroalgae (for details see Supplementary Text):

- (1) *High probability of hard substrate*: hard substrate as a single variable approach for benthic algal establishment and growth (Quartino et al., 2013). We assumed that the estimated area of the

newly available hard substrate between 0.5 and 20 m depth would be colonized by macroalgae, to a similar level in cover and biomass, as those found at 5 m depth in our quadrat surveys of the natural substrate in each LGI and HGI area. Such an assumption is supported by the fact that the percent cover of the benthic algal communities on the natural substrate, within the considered depth range, in both areas is similar or higher than the recorded in the quadrats at 5 m depth for each area (Deregibus, 2017).

- (2) *High habitat suitability*: macroalgal habitat definition based on a multivariate SDM approach identified suitable macroalgal habitats from published by Jerosch et al. (2019).

Finally, for both approaches, the mean percent cover, dry mass and macroalgal carbon standing stock registered in the survey quadrats respectively in LGI and HGI were multiplied up by the respective newly exposed substrate within each LGI and HGI habitat, for the experiment duration (2010–2014), and from the oldest known glacier position in 1956, until 2018, following the equation:

$$NIFA_{LGI} * MA_{LGI} + NIFA_{HGI} * MA_{HGI}$$

where NIFA is the newly ice-free area (m<sup>2</sup>) at a certain habitat (LGI or HGI) and MA the macroalgae attribute such as cover (as a proportion), total dry mass (g m<sup>-2</sup>) of the considered species present in the quadrats with its specific coverage, or the organic carbon content estimation from carbon factors conversion of such calculated dry mass (for more details see Supplementary Text).

Certain environmental variables, detailed in the following section, as Photosynthetic Active Radiation (PAR), are critical parameters when determining benthic algal colonization (Campana et al., 2018). We considered that the results found in the LGI habitat would be similar to those in the newly ice-free area of the IGI habitat as the LGI and IGI habitats had significantly lower  $K_d$  values (Fig. 1) (Quartino et al., 2013; Deregibus et al., 2016; Deregibus, 2017) and a higher macroalgal coverage (Quartino et al., 2013; Jerosch et al., 2019) than the HGI habitat. Hence, for spatial predictions in the potential carbon stock of this study, LGI and IGI habitats (renamed onwards as LGI habitat: low glacier influence habitat) extension were joint.

#### 2.6. Data analysis

Potential biological differences explained by the interannual variability and environmental background between areas (LGI and HGI) were analyzed. For each year (2011, 2012, 2013 and 2014), the percent cover and ecological indices, macroalgal length and dry mass of the colonization experiment, as well the percent cover and dry mass of the quadrat survey, were compared between areas (LGI and HGI) using general linear models (GLM). Anomalously hot or cold springs and summers were defined as higher or lower than the standard deviation of the 2005–2015 season temperature average (Schloss et al., 2012). The environmental and seasonal effects of an area were tested on the light attenuation coefficient ( $K_d$ ), turbidity, salinity, and seawater temperature in spring and summer considering all the years together. The annual effect on the  $K_d$ , turbidity, salinity and seawater temperature was tested for each area. Homogeneity of variances was checked using Cochran's Test, and normality through the Shapiro-Wilks test. *Post hoc* multiple means comparisons were analyzed using the Di Rienzo, Guzmán & Casanoves (DGC) test. Kruskal-Wallis (K-W) analyses were performed when assumptions of normality and homogeneity of variance could not be met (Di Rienzo et al., 2008). All statistical analyses were performed using Infostat 2008 software (Di Rienzo et al., 2008).

### 3. Results

#### 3.1. Abiotic background for algal colonization

The average spring air temperature between 2005 and 2015 was  $-0.43\text{ }^{\circ}\text{C}$  (Fig. 2A). During the time of the experiment, the springs of 2010 and 2011 were above the standard deviation and thus, considered anomalously warm compared to the mean overall analyzed years, with average air temperatures of  $0.67\text{ }^{\circ}\text{C}$  and  $0.57\text{ }^{\circ}\text{C}$ , respectively (Fig. 2A). Further, the spring of 2012 was considered anomalously cold with an average air temperature of  $-1.7\text{ }^{\circ}\text{C}$  (Fig. 2A). The average summer air temperature between 2005 and 2015 was  $1.52\text{ }^{\circ}\text{C}$  (Fig. 2B). The summer of 2010 was anomalously cold, with an average air temperature of  $0.47\text{ }^{\circ}\text{C}$ . The trend in summer conditions does not always follow spring conditions; the warm spring in 2006 was followed by a warm summer but the warm spring in 2010 was followed by a very cold summer ( $0.47\text{ }^{\circ}\text{C}$ ; Fig. 2).

Generally, average PAR values at 5 m depth in each season were two to three times higher in LGI compared to HGI. During spring, in LGI the PAR values varied from  $38$  to  $256\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ , while in HGI from  $18\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$  (2011) to  $152\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$  (2012). In summer, PAR values were lower in LGI, irradiance values varied from  $11$  to  $274\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ , whilst in HGI it varied from  $5 \pm 3.55\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$  (2012),  $40 \pm 22.5\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$  (2014). These PAR values were reflected in the  $K_d$  results (Fig. 3 A-B). Spring  $K_d$  was significantly higher in HGI compared to LGI (K-W,  $H = 6.75$ ,  $p = 0.0094$ ), and also in summer,  $K_d$  was significantly higher in HGI compared to LGI (GLM, DGC test,  $F = 16.99$ ,  $p = 0.003$ ) (for details see Supplementary Text).

In general, turbidity, water temperature, and salinity also varied across the different seasons among areas (Fig. 3 C-H, for details see Supplementary Text).

#### 3.2. Colonization and succession

Tiles were colonized by benthic diatoms and macroalgae (Fig. 4A and Supplementary Fig. 2). Overall, seven taxa were identified across both areas: five macroalgal foliose species, coralline algae, and benthic diatoms. Six taxa were identified in LGI and five in HGI (Fig. 4 and Supplementary Table 1). These taxa were benthic diatoms, as well as the macroalgae; *Monostroma hariotii* Gain 1911, *Urospora penicilliformis* (Roth) Areschoug 1866, *Palmaria decipiens* (Reinsch) Ricker 1987, Coralline algae (*Lithothamnion- Hydrolithon*), *Adenocystis utricularis* (Bory) Skottsberg 1907, and *Desmarestia menziesii* J. Agardh 1848. The number of taxa present during each summer in each area varied between three and four in LGI, and between two and five in HGI. *Desmarestia menziesii* and coralline algae were only recorded in LGI, while *U. penicilliformis* was only present in HGI (Fig. 4). Diatom percent cover was higher in HGI than in LGI, and in LGI they were only visible in the first year (Fig. 4).

#### 3.2.1. Comparison of algal colonization and succession processes between areas

During the first year (2011) the percent cover (Fig. 4) and ecological indices (Supplementary Fig. 3) were similar between areas. During 2012 only richness was significantly higher in LGI than in HGI (K-W,  $H = 4.36$ ,  $p = 0.0476$ , S3 Fig). During 2013 the total percent cover (Fig. 4), diversity and the richness were significantly higher in HGI compared to LGI (GLM, DGC test,  $F = 8.49$  y  $p = 0.0226$ ,  $F = 10.77$  y  $p = 0.0135$ ,  $F = 12.44$ ,  $p = 0.0096$ , respectively, Supplementary Fig. 3). In the last year of the experiment, richness was significantly higher in LGI compared to HGI (GLM, DGC test,  $F = 14.39$ ,  $p = 0.0035$ , Supplementary Fig. 3, for details see Supplementary Text). In LGI, dry mass values ranged from  $\sim 5$  to  $10\text{ g DM m}^{-2}$  in the first three years and increased to  $4583 \pm 4540\text{ g DM m}^{-2}$  in 2014 (Fig. 4B) with the presence of one individual of *D. menziesii* in one of the tiles reaching a DM of  $470\text{ g}$  which grew almost  $2\text{ m}$  during the last year of the experiment (Supplementary Fig. 2 and Supplementary Fig. 4, see Supplementary Text).

#### 3.3. Quadrat survey: Algal percent cover, dry mass and organic carbon values used for macroalgal estimates in newly ice-free areas

Overall, seven taxa were identified across both areas in the quadrat survey: five macroalgal foliose species, coralline algae, and benthic diatoms. Six taxa were identified in LGI and seven in HGI (Supplementary Table 1). Percent cover was similar among areas (GLM,  $F = 3.18$ ,  $p = 0.11255$ ) with a  $73.4 \pm 10.86\%$  cover in LGI and  $52 \pm 5.1\%$  cover HGI (Supplementary Text). However, estimated dry mass was significantly higher in LGI ( $95.55 \pm 31.33\text{ g DM m}^{-2}$ ) compared to HGI ( $18.75 \pm 7.38\text{ g DM m}^{-2}$ ), (GLM,  $F = 5.69$ ,  $p = 0.0442$ ). The total organic carbon was  $29.55 \pm 18.81\text{ g m}^{-2}$  in LGI, compared to  $5.4 \pm 4.6\text{ g m}^{-2}$  in HGI (Supplementary Text).

#### 3.4. Newly ice-free areas in Potter Cove for potential macroalgal expansion

The updated Rückamp et al. (2011) map of the Fourcade glacier retreat map (1956–2008) with new front lines from 2010 to 2018 shows that the glacier retreated approximately  $1.5\text{ km}^2$  from 1956 to 2018 (Fig. 5 and Supplementary Table 2).

During the time of the experiment (2010–2014), the retraction of the Fourcade glacier generated  $0.079\text{ km}^2$  of newly ice-free area (Fig. 5 and Table 2). From this total, we assessed that  $85\%$  ( $0.067\text{ km}^2$ ) was hard substrate (Fig. 5 and Supplementary Table 3). Assuming similar macroalgal percent cover and total dry mass as in the quadrats survey respectively to LGI and HGI areas, this was potentially colonized with biota of a total dry mass of  $5.25 \pm 1.74\text{ tons DM}$  following the high probability of hard substrate approach or  $2.25 \pm 0.75\text{ tons DM}$  by the high habitat suitability method (Table 3 and Supplementary Text). A total estimation of algal colonization in the newly ice-free areas shows an expansion of  $\sim 0.005\text{--}0.012\text{ km}^2$  with a carbon standing stock of  $\sim 0.2\text{--}0.4\text{ C tons}$ , per year between 2010 and 2014 (Table 3, Supplementary Text).

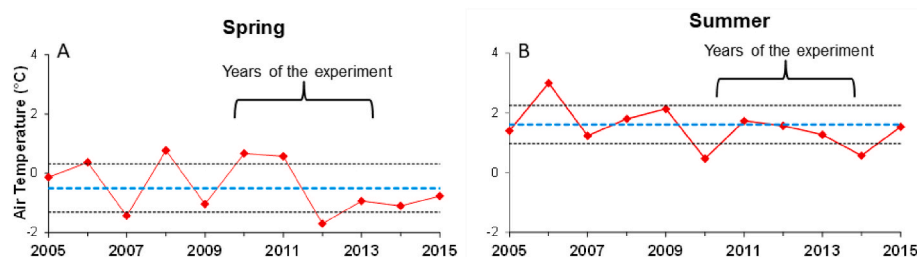
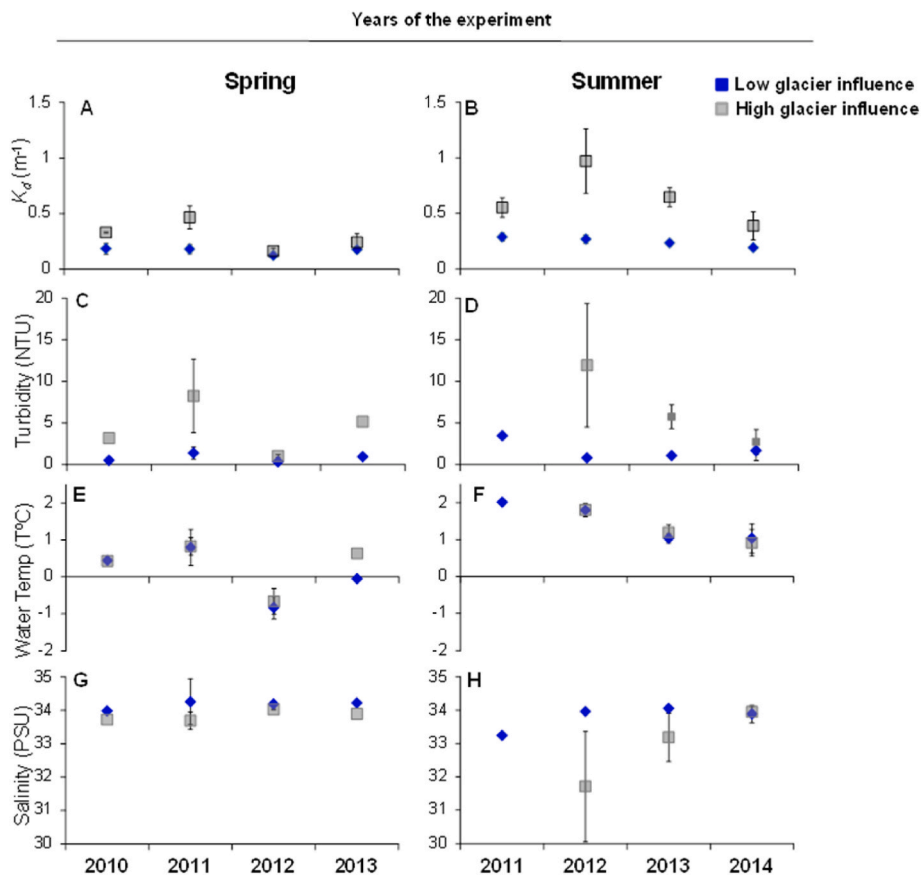
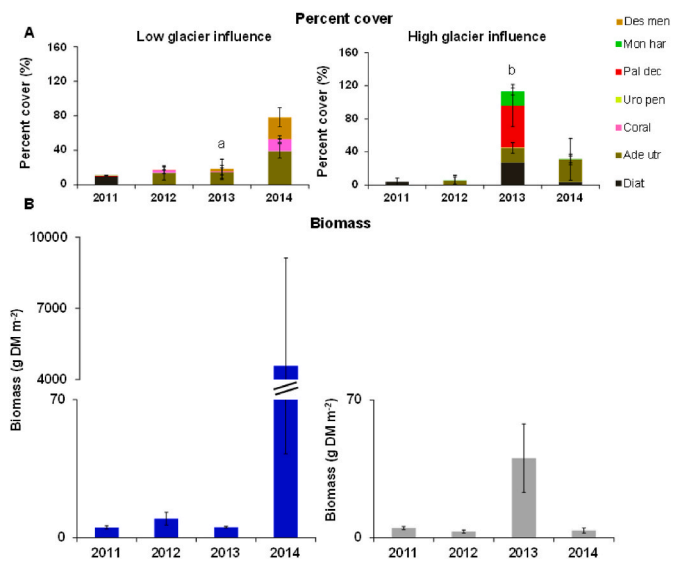


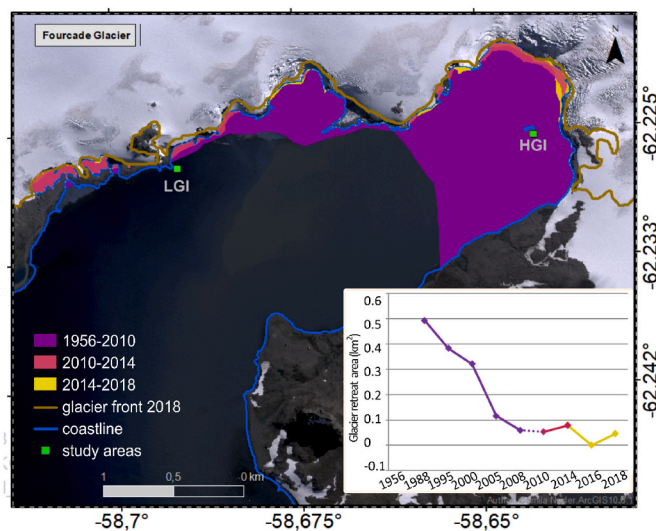
Fig. 2. Air Temperature. Average air temperature in spring (A) and summer (B) showing means (light blue dotted) and standard deviations (black dotted) for the period 2005–2015 (data from the Servicio Meteorológico Nacional at the Carlini weather station).



**Fig. 3.** Light attenuation coefficient, salinity, water temperature, and turbidity measurements in two newly ice-free areas. Average values of light attenuation coefficient ( $K_d$ , from 0 to 5 m) (A and B), turbidity (NTU) (C and D), water temperature ( $^{\circ}$ C) (E and F), and salinity (PSU) (G and H) in spring and summer among the experiment studied years (2011–2014) in the low glacier influence area (LGI) and the high glacier influence area (HGI). Bar: mean  $\pm$  SE.



**Fig. 4.** Colonization experiment in two newly ice-free areas. (A) Algal percent cover on tiles in a low glacier influence area (LGI) and a high glacier influence area (HGI) in Potter Cove. Lowercase letters indicate significant differences ( $p < 0.05$ ) in total cover between years in HGI. Bar: mean  $\pm$  SE. *Monostroma hariotii*: Mon har, *Desmarestia menziesii*: Des men, *Urospora penicilliformis*: Uro pen, *Adenocystis utricularis*: Ade utr, *Palmaria decipiens*: Pal dec, Coralline algae: coral, benthic diatoms: diat. (B) Algal biomass values expressed in g of dry mass (DM)  $m^{-2}$  were present in the tiles of LGI and HGI in the summers of 2011, 2012, 2013, and 2014 (mean  $\pm$  SE).



**Fig. 5.** Fourcade glacier loss in Potter Cove at King George Island, West Antarctic Peninsula. Glacier lines are shown at three different retreat stages between 1956 and 2018 (represented in colored areas purple, pink, and yellow). The inset graph represents ice loss over the years in  $km^2$ . Green squares mark correspond to the study sample sites carried out in two newly ice-free areas: LGI (low glacier influence area, ice-free since 1990) located in the LGI habitat (low glacier influence habitat), and HGI (high glacier influence area, ice-free since 2000) located in the HGI habitat (high glacier influence habitat). Base map resource ESRI and reprinted from DigitalGlobe (2014).

**Table 2**

Different stages of the Fourcade glacier retreat from the earliest recorded glacier position in 1956–2010. And additional losses rates from 1956 to 2010, 2010–2014 and 2014–2018. Only ice-free areas were considered. See the in-graph in Fig. 5 for the area of glacier retreat across the years 1956–2018.

	1956–2010	2010–2014	2014–2018
Glacier retreat (km <sup>2</sup> )	1.426	0.079	0.046
Loss rate (km <sup>2</sup> y <sup>-1</sup> )	0.034	0.020	0.023

**Table 3**

Estimated new colonized area, biomass and carbon standing stock by benthic algae for the different periods within newly ice-free areas by two approaches methods. Extrapolation of *in situ* quadrat surveys in areas with a *high probability of hard substrate* (>80%, approach 1) and *high habitat suitability* (>50.9%, approach 2) for two periods (total ± SE).

	High probability of hard substrate approach		High habitat suitability approach	
	2010–2014	1956–2018	2010–2014	1956–2018
Area covered by algae (km <sup>2</sup> )	0.046 ± 0.006	0.45 ± 0.06	0.02 ± 0.003	0.25 ± 0.034
Biomass standing stock (tons DM)	5.25 ± 1.74	43.52 ± 14.64	2.25 ± 0.75	27.61 ± 9.17
Carbon standing stock (C tons)	1.61 ± 1.01	13.34 ± 8.83	0.69 ± 0.45	8.5 ± 5.52

Between 1956 and 2018 glacier retreat exposed ~1.5 km<sup>2</sup> (Table 2 and Fig. 5), of which 0.695 km<sup>2</sup> were estimated to be hard substrate (Fig. 6 and Supplementary Table 3). Thus, the predicted total colonizable area in Potter Cove was ~0.45 ± 0.06 km<sup>2</sup>, yielding a dry mass of 43.52 ± 14.64 tons DM and 13.84 ± 8.83 tons DM of organic carbon accumulated in algal biomass during that time by benthic algae (Table 3). In contrast the second approach by the *multivariate-habitat suitability*, estimated that the potential carbon gains were significantly lower (see Supplementary Text).

#### 4. Discussion

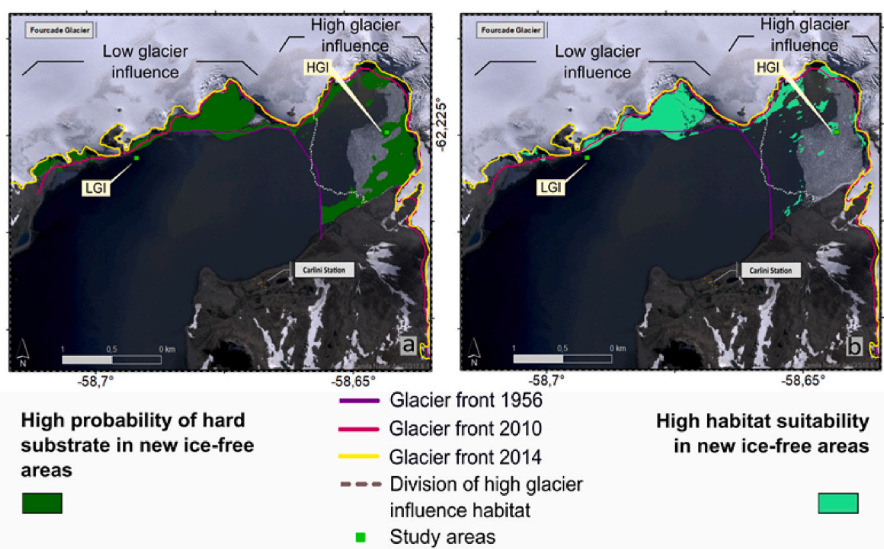
A wide variety of biological responses are expected to ice and snow loss from the polar regions on land and sea, including growth of some coastal carbon sinks of which macroalgae are likely to play an important but hitherto little explored component. In the current work we distinguished marked differences in macroalgae colonization patterns in two

new ice-free areas of an Antarctic fjord with different levels of glacier influence. Glacier retreat is clearly generating new space for benthic colonization in some Antarctic shallow areas, but there are some important constraints imposed by as light attenuation and sedimentation (Hoffmann et al., 2019; Braeckman et al., 2021). Our results show that colonization and succession can follow different paths even in environments that are in close proximity. We found that newly ice-free areas can be colonized by benthic algae in relatively short periods. After four years, algae occupied ~80% of the tile substrate in LGI and ~30% in HGI. Also, at the end of the experiment LGI had higher richness than HGI, with different species identities and successional patterns between both areas. We attribute this primarily to two factors: light penetration and sedimentation, directly affecting benthic algal settlement success, and/or growth (Campana et al., 2018). In LGI, the community resembled more mature stages of succession than in HGI, with the presence of *Desmarestia menziesii*, a perennial species more characteristic of late-successional stages at this water depth (Wiencke and Clayton, 2002; Campana et al., 2020).

Macroalgae are highly productive marine macrophytes that are likely to be globally important in carbon sinks and negative feedback on climate change (Krause-Jensen et al., 2018). Quantitative estimation of macroalgal gains associated with ice loss around coastal Antarctica is important to understand the role of macroalgae in relation to blue carbon. Hence, the second aim of our study was to estimate the spatial macroalgal expansion in Potter Cove. We calculated the new area available for macroalgal benthic colonization at our study fjord, which is one of the best studied and therefore with the most contextual information around Antarctica (eg see Sahade et al., 2015). The Fourcade glacier retreat between 2010 and 2014 opened 0.034–0.067 km<sup>2</sup> in the studied area of Potter Cove, increased therefore the habitat for macroalgal colonization and the presence of primary producers over time. This means that over the last few decades benthic algae could have been expanding annually on average ~0.0085–0.016 km<sup>2</sup> at Potter Cove.

##### 4.1. Climate forcing

Sediment load -and resulting turbidity-is emerging as a key factor determining benthic community structure close to glacial outflows, such as in Potter Cove (Braeckman et al., 2021). This seems especially the case in newly ice-free areas (Quartino et al., 2013; Sahade et al., 2015) and glacier-influenced sites (Campana et al., 2018). Predominantly, areas become ice-free in summer with increasing sediment load (Neder et al., 2020; Ruiz Barlett et al., 2021). In the current work, substantial



**Fig. 6.** Two approaches to estimating the area suitable for benthic algae colonization in newly ice-free areas. (A) Area of a *high probability of hard substrate* since 1956 glacier line front (Rückamp et al., 2011). (B) Area of *high habitat suitability* for benthic algae (based on the model by Jerosch et al. (2019)) since 1956. Green squares correspond to the study sample sites carried out in two newly ice-free areas: LGI (low glacier influence area, ice-free since 1990) located in the LGI habitat (low glacier influence habitat) and HGI (high glacier influence area, ice-free since 2000) located in the HGI habitat (high glacier influence habitat). Pointed line: limit of the HGI habitat (Jerosch et al., 2018). Base map resource ESRI and reprinted from DigitalGlobe (2014).

interannual differences were found in environmental variables between the two study areas even when they are located only 2 km apart. Variations in salinity and water temperature changes between areas, seasons and years were observed, with similar interannual values and patterns to other studies performed in the area (Schloss et al., 2012; Campana et al., 2018; Ruiz Barlett et al., 2021). Underwater irradiance was always higher in the low glacier than in the high glacier influence area. LGI presented similar intra- and interannual values of PAR and turbidity, indicating a lower influence of the Fourcade glacier melting process. In contrast, environmental factors of HGI's water column varied considerably within the study years, indicating that discharges mainly occur closeby. Glacial discharge levels can be strongly dependent on local air temperature and accumulate in surface layers generating elevated turbidity (Meredith et al., 2018; Neder et al., 2020).

Changes in the extension of the north WAP glaciers seem to be mainly air temperature-driven, in contrast to those further south, which were mainly sea temperature influenced (Cook et al., 2016). Specifically in HGI of Potter Cove, turbidity was extremely high following high air temperatures in spring 2011 resulting in significant light attenuation, while Spring 2012 experienced high PAR penetration due to low glacier run-off. Previous investigations indicate that the highest turbidity occurs during summer, whilst high water transparency is typical in winter (Schloss et al., 2012).

#### 4.2. How does glacial influence shape benthic algal colonization process in newly ice-free areas?

Following the study, we can infer that benthic algae are not only recruiting into but also persisting in new and highly impacted areas of Antarctic fjord ecosystems. The most remarkable result in LGI was the presence, rapid growth, and biomass of *D. menziesii* during the third year. After four years, the presence of a 2 m long individual of this perennial seaweed with biomass of ~500 g DM in an artificial substrate within an area of 600 cm<sup>2</sup> represented a substantially higher value than in other tiles and years. This further demonstrates the extremely patchy nature of benthic colonization and shows the value of high replication. This species can be considered a late-successional taxon and dominates mature communities in many other environments (Littler and Littler, 1980), provides habitat and refuge to numerous organisms (Huang et al., 2007), and contributes to ~80% of the total biomass of macroalgae in Potter Cove (Quartino and Boraso de Zaixso, 2008).

In LGI, the constancy in richness was probably due to gradual replacement of taxa over time, as found in many benthic marine assemblages elsewhere (Noël et al., 2009). Diatom films were only observed in the first summer, which is a typical pattern of succession in this type of environment (Noël et al., 2009; Campana et al., 2020). In LGI, algal assemblages proceeded towards higher three-dimensional complexity and cover, including a foliose perennial species and diatom replacement by macroalgae (Campana et al., 2018). LGI was less impacted by Fourcade glacier melting and this may have promoted the development of stable 'underwater forests', which were relatively constant in terms of biomass and density over time (Quartino et al., 2005; Wiencke and Amsler, 2012). At HGI, the most significant finding from this succession process was the observed marked increase in percent cover of macroalgae between the second and the third year despite being an area exposed to high sedimentation and disturbance. *Palmaria decipiens* and *M. hariatii*, pioneers with a high capacity to withstand stress (Quartino et al., 2013) were key space occupiers of HGI. Benthic diatom blooms and higher levels of diatom cover can be associated with glacial melting, although the underlying mechanisms have not yet been elucidated (Ahn et al., 2016).

Spring is a decisive period influencing the phenology (e.g. growth and reproduction) of polar macroalgae (Wiencke and Amsler 2012). Anomalously warm conditions during the first two springs in HGI might have impacted the colonization and succession in this area. The very low PAR values ( $36 \pm 18.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) during spring 2011 were unlikely

to be sufficient for photosynthetic requirements and may have led to negative carbon balance for macroalgal species growing there (Wiencke and Amsler 2012; Deregibus et al., 2016; Deregibus 2017). However in HGI, elevated light penetration ( $110 \pm 42.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) during the spring of 2012 could have supported the growth of macroalgae detected during the third summer of the experiment. The rapid growth in summer 2013 of *M. hariatii* and *P. decipiens* was most likely driven by higher light availability together with the high tolerance to high luminosity conditions, as both species are also very frequent in the intertidal (Wiencke and Clayton, 2002). High values of irradiance are unusual for HGI in both spring and summer due to glacial melting (Schloss et al., 2012). Without that cold spring (and hence more light availability), the high occupation of the artificial substrate by macroalgae may not have happened (Deregibus, 2017).

Other environmental variables affected by rapid glacier melting could be influencing the macroalgal colonization patterns. For example, ice scouring events are noticeably altering the nature of the benthic communities (Barnes and Souster 2011). Potter Cove is also directly influenced by calving ice from Fourcade Glacier, and by icebergs entering from outside the cove (personal observation; Pasotti and others 2014; also see bathymetric data in Wöfl et al., 2014). The frequency and intensity of ice scouring in these areas varies interannually, and the impact of ice disturbance at HGI is higher than LGI as it is closer to the glacier, where mainly landslides of ice blocks impact directly on the sea floor (Quartino et al., 2013; Deregibus et al., 2017). In this sense, the differences in the patterns of colonization and succession, and in the macroalgal assemblages between LGI and HGI may also be due to the differential influence of the ice scouring events in each area. In addition, salinity and water temperature variations have been documented in this heavily impacted areas, although studies reported up to now suggest that such changes do not stress the photosynthetic performance of macroalgae significantly (Karsten et al., 1991a, 1991b; Eggert and Wiencke 2000; Wiencke and Amsler 2012, Matula et al., 2022).

The macroalgal richness registered in this study was low in comparison to the 42 species registered in areas with non/less glacial influence in the outer Potter Cove in 1994 (Klöser et al., 1996). Also, other studies performed in Admiralty Bay reported 42 species (Oliveira et al., 2009), and even more than double of richness taxa of macroalgae was registered in King George Island/Isla 25 de Mayo (Sanchez et al., 2016; Pellizzari et al., 2017; Oliveira et al., 2020; Pellizzari et al., 2020). However, our results are consistent with a previous study carried out at the same site, where the number of algal species encountered on the artificial substrates was discussed in the context of Potter Cove macroalgal assemblages (Campana et al., 2018). Other studies in the natural substrate of newly ice-free areas in Potter Cove also showed similarly low values in macroalgal richness and in the identity of the assemblages (Quartino et al., 2013; Deregibus, 2017). The latter could be attributed to several causes as the level of stress and disturbance-due to the reduction of the light penetration and ice disturbance, depth and site-specific available substrate (Quartino et al., 2013).

In this context, we think that the different glacial influences shaping the benthic algal colonization process in newly ice-free areas could be driven by (1) the conditions of stress and disturbance generated by glacier retreat, and (2) marked interannual variations of environmental conditions. Other polar studies also report that high frequencies of disturbance prevent benthic communities from reaching stages close to climax (Barnes and Conlan, 2007; Beuchel and Gulliksen, 2008). In terms of succession, our results in newly ice-free areas in Potter Cove resemble and confirm succession patterns described by Campana et al. (2018).

#### 4.3. Benthic algal expansion and carbon standing stock in newly ice-free areas

Fourcade glacier has retreated ~1.5 km<sup>2</sup> since 1956, changing the physiognomy of one of the most comprehensively studied fjords in



Antarctica, Potter Cove. In the last decade (2008–2018) Fourcade glacier has retreated  $\sim 0.18 \text{ km}^2$  (Supplementary Table 2). This area is small compared with some as e.g. Marian Cove and Borgen Bay but comparable with others such as Sheldon Glacier (Barnes et al., 2020; Zwierschke et al., 2022).

The different estimation values gained by using two different approaches to quantify potential macroalgae colonization and carbon gains in the newly ice-free show the importance of using more than one approach. The *hard substrate probability* approach predicts 2.3 times more colonized substrate, with 2.6 times more biomass by benthic algae during that period (2010–2014) than the *multivariate-habitat suitability* approach. Meanwhile, the second approach revealed  $\sim 40\%$  and  $\sim 55\%$  less area during 2010–2014 and 1956–2018, respectively, compared to the first approach (Table 3 and Supplementary Table 3). Both techniques have strengths and weaknesses. The *multivariate habitat suitability* approach (from Species Distribution Model) predicts the probability of macroalgae presence spatially, based on several correlating environmental variables (Jerosch et al., 2019). Some environmental variables included in the model were not measured *in situ* in this study (and vice versa). Since the model represents a slightly divergent study design, we included the *hard substrate probability* approach, which has previously proved to be a critical variable for regional macroalgal settlement (Wiencke and Amsler, 2012).

Further estimate can improve on the applied methods when the prediction of macroalgal spatial colonization, total biomass or carbon are calculated as a sum of the resulting estimation of the newly ice-free area suitable for each single species colonization (extracted from species-specific distribution model) multiplied up by its target attribute (biomass or carbon standing stock), following the equation:

$$= \sum_{i=1}^n NIFA_{LGI(i)} * MA_{LGI(i)} + NIFA_{HGI(i)} * MA_{HGI(i)}$$

where (*i*) is the species present in the quadrant survey, *n* is the amount of total species involved in the calculation, *NIFA* is the newly ice-free area (in  $\text{m}^2$ ) dependent on the SDM species-specific cutoff function at a low (LGI) or high (HGI) glacier influence habitat, and  $MA_{(i)}$  the species-specific macroalgae attribute to consider at a certain habitat.

Crustose coralline algae were major space occupiers in the low glacier influenced habitat, and benthic diatoms were similarly important in the high glacier influenced habitat. Assuming equal biomass of these taxa as the artificial substrates, the newly ice-free areas during the 1956–2018 period could have been colonized with a dry mass of  $0.64 \pm 0.29$  tons of coralline algae, and a dry mass of  $1.1 \pm 0.63$  tons of benthic diatoms with. Given that coralline algae have high preservation potential (Heijden and Kamenos, 2015), and contribute substantial carbon, including them in total carbon calculations in future studies should improve estimate accuracy.

Scaling up from an *in situ* experiment to a larger local area, and from local to regional scales is a challenging and difficult task in fjords with many intrinsic errors (Barnes et al., 2020; Zwierschke et al., 2022). In our analysis it is important to consider, that the data used to estimate the benthic algal expansion is from 10 years before present, and as climate change continues to impact in this region (IPCC, 2021), patterns could be different again now – all of which shows the importance of getting baseline data out for robust time comparisons. However, to date Fourcade glacier is almost land terminated. In terms of biomass, the quadrats survey results in LGI indicate for example biomass values of  $110\text{--}205 \text{ g DM m}^{-2}$  for *D. menziesii* and  $15\text{--}20 \text{ g DM m}^{-2}$  for red macroalgal species. Previous studies quantifying biomass in Potter Cove in non glacier influenced habitats almost three decades ago recorded biomass values of  $379 \pm 45 \text{ g DM m}^{-2}$  for *D. menziesii* and  $24 \pm 4 \text{ g DM m}^{-2}$  for red macroalgal species (Quartino et al., 2005). The average biomass values from our quadrat surveys in LGI were similar to surrounding mature macroalgal assemblages in Antarctica (Quartino et al., 2005, 2020), showing how quickly substantial biomass can be established.

Our estimations indicate that over the last few decades benthic algae

have been expanding annually on average  $\sim 0.005\text{--}0.012 \text{ km}^2$  at Potter Cove with dry mass standing stock averaging  $\sim 0.6\text{--}1.3$  tons per year, as Fourcade glacier retreated. This has enhanced the presence of primary producers over time. During 1994–1995 in Potter Cove, the macroalgal biomass standing stock was estimated to be 792 DM tons with a production of 1400 DM tons per year (Quartino and Boraso de Zaisso, 2008). Thus, our findings suggest that in the last two decades the macroalgal standing stock and production, and organic carbon incorporated into the system might have increased  $\sim 10\%$  in this cove.

Several ecosystem consequences could occur due to primary production changes in marine systems. Climate change-induced glacial melt is likely to affect primary production of phytoplankton (Schloss et al., 2002) and macroalgae (Deregibus et al., 2016), and result in a lower benthic primary production (Braeckman et al., 2021). On the contrary, other studies indicate recent phytoplankton blooms (Schloss et al., 2014), and a high contribution of benthic diatoms have been observed in close proximity to the retreating glacier (Ahn et al., 2016; Pers. Obs.). In addition, a higher macroalgal productivity can be expected, as these organisms are rapidly colonizing newly ice-free areas (Quartino et al., 2013), and earlier sea-ice break-out is likely to induce an increase in the light availability, causing ecosystems to shift from predominantly heterotrophic to autotrophic states (Clark et al., 2013). With the increased macroalgal and microalgal production no restriction of food sources may affect herbivores that depend on them (Amsler et al., 2019). Macroalgae mainly contribute to food webs through the detrital pathway (Wiencke and Clayton, 2002), and are creating habitats in newly ice-free areas for a diverse mobile and sessile fauna and substrate for epiphytes that will also contribute as food sources (Amsler et al., 2014). Further studies must be carried out in order to unravel the potential consequences for the structure and function of the ecosystem, including the effects on food webs and blue carbon changes.

This study provides results indicating the ongoing environmental changes that continue to stress the coastal ecosystems in the WAP. Conservation of the Antarctic sea bed is needed due to its unique and high biodiversity, and because it provides strong blue carbon ecosystem services that could potentially have a role in mitigating wider  $\text{CO}_2$  emissions (Chown et al., 2022; Morley et al., 2022). The latter highlights the relevance of protecting the ecosystems of the WAP, reinforcing the importance of spatial management in this region and the adoption of the proposed Domain 1 Marine Protected Area (D1MPA) (CCAMLR-41/34) under scenarios of environmental changes and increased human presence.

#### 4.4. Blue carbon and future implications

Coastal zones provide valuable ecosystem services (Barbier et al., 2001), such as the ‘Blue Carbon’ captured and stored as biomass, and eventually sequestered into sediments, which is considered important as a climate regulating service (Laffoley and Grimsditch, 2009; Chung et al., 2011; Krause-Jensen and Duarte, 2016; Krause-Jensen et al., 2018; Queirós et al., 2019; Zwierschke et al., 2021). Although macroalgae are abundant and productive in the northern WAP and hold considerable biomass (Klöser et al., 1996; Ha et al., 2019; Wulff et al., 2009), there is still a lack of knowledge of its importance within blue carbon assessments in Antarctica. Macroalgae could be colonizing more newly ice-free areas in fjords experiencing glacier retreat at higher latitudes in the WAP now and in the future. In addition, decreases in the duration and extension of fast ice in polar regions have driven macroalgal expansion (Bartsch et al., 2016; Clark et al., 2013, 2017; Deregibus et al., 2020), potentially increasing their contribution to carbon sinks by adding new valuable carbon storage in the Antarctic coastal areas (Quartino et al., 2020).

Responding to our study question, we show that benthic algae are not only recruiting but persisting in new and highly impacted areas of Antarctic fjords ecosystems. In Potter Cove, our current estimates indicate that macroalgal blue carbon gains generated in newly ice-free areas

have increased ~0.2–0.4 tons C per year. There are hundreds of fjords emerging from glacier retreat and these values are similar to estimated WAP fjordic fauna biomass per unit area (Barnes et al., 2020). A global analysis of macroalgae by Krause-Jensen and Duarte (2016) found that ~11% of the macroalgal production (of which on average 30% is organic carbon (Peters, 2005)) is sequestered in deep water (as DOC and POC). Considering the high macroalgal production of a 75% more than its standing stock in Potter Cove (Quartino and Boraso de Zaixso, 2008), the macroalgal contribution to stored carbon in newly ice-free areas could be considered as the new carbon standing stock plus the exported carbon (in this case we consider only sequestered carbon). Thus, the increase in macroalgal carbon after glacier retreat in Potter Cove we estimated to be ~0.2–0.4 C tons per year.

Macroalgae and fauna differ in their accumulation of blue carbon standing stock in shallow newly ice-free areas. According to this study, new macroalgal carbon standing stock (13.8 tons per year/km<sup>2</sup>) following glacier retreat seems to be almost an order of magnitude smaller to zoobenthos (100.34 tons per year/km<sup>2</sup>) in fjords along the Antarctic Peninsula (Barnes et al., 2020), but are comparable when allowing for macroalgal export losses (Krause-Jensen and Duarte, 2016). Macroalgae are highly productive; and colonize, grow and expand faster than benthic fauna in these areas, while small zoobenthic carbon storage per unit area occurs over a much larger area -than macroalgae occur. The fact we still have a limited understanding of carbon sequestration processes for seaweeds and associated species (e.g. how much is likely to get sequestered, where, etc) as well as exportation (possible albedo changes due to ice melting), guides us to continue on research in order to achieve deepen responses of Blue Carbon effects and climate change mitigation (Gogarty et al., 2019; Dolliver and O'Connor, 2022).

Benthic blue carbon around Antarctica could potentially have a role in mitigating wider CO<sub>2</sub> emissions because it is increasing with climate change (Barnes, 2015; Barnes et al., 2018, 2020; Alurralde et al., 2019; Zwerschke et al., 2022). Losses of marine ice have recently led to gains in West Antarctic benthic biota biomass and stored carbon on open continental shelves (Barnes, 2015) and in fjords emerging from glacier retreat (Zwerschke et al., 2022). Pineda-Metz et al. (2020) found similar relationships between sea ice and benthic carbon in the Weddell Sea and thus there is likely to be a large scale and valuable negative (mitigating) feedback on climate change around Antarctic coastal seas (Bax et al., 2021). A key element of increasing blue carbon there is likely to be the potential of increases in macroalgal growth and colonization, but to date this has been little explored in the polar regions. Possibly due to the high dispersion of macroalgal shredded fragments beyond these organism habitats (Clark et al., 2013), studies in Antarctica quantifying sequestration of macroalgal carbon is a difficult challenge but crucial when considering ecosystem services. Monitoring programs could be implemented at a regional scale (e.g. in the framework of the Southern Ocean Observing System) along the WAP to measure the expansion of such organisms in other locations, as well as their production, further export to other marine ecosystems, and build up in sediments.

#### Author statement

Conceptualization: Dolores Deregibus, Gabriela L. Campana, Camila Nader, David K. A. Barnes, Katharina Zacher, María Liliana Quartino, Data curation: Dolores Deregibus, Gabriela L. Campana, Camila Nader, Katharina Zacher, Kerstin Jerosch, María Liliana Quartino, Formal analysis: Dolores Deregibus, Gabriela L. Campana, David K. A. Barnes, Camila Nader, Katharina Zacher, Kerstin Jerosch, María Liliana Quartino.

Funding acquisition: María Liliana Quartino, Kerstin Jerosch.

Investigation: Dolores Deregibus, Camila Nader, Gabriela L. Campana, David K. A. Barnes, Katharina Zacher, María Liliana Quartino.

Methodology: Dolores Deregibus, Gabriela L. Campana, David K. A. Barnes, Camila Nader, Katharina Zacher, María Liliana Quartino, Juan Manuel Piscicelli.

Resources: María Liliana Quartino, Kerstin Jerosch.

Writing - original draft: Dolores Deregibus.

Writing - review and editing: Dolores Deregibus, Gabriela L. Campana, Camila Nader, David K. A. Barnes, Katharina Zacher, Kerstin Jerosch, María Liliana Quartino.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Dolores Deregibus reports equipment, drugs, or supplies and travel were provided by Ministerio de Ciencia y Tecnología. Dolores Deregibus reports travel was provided by Coastcarb.

#### Data availability

Data will be made available on request.

#### Acknowledgements

This work was performed at Carlini Station within the framework of the scientific collaboration between Instituto Antártico Argentino/ Dirección Nacional del Antártico, the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research and the British Antarctic Survey. This study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and by grants from DNA-IAA (PICTA 7/2008–2011), ANPCyT-DNA (PICTO 0116/2012–2015), PICT-2021-GRF-TI-00536, PICT 2017–2691, Deutsche Forschungsgemeinschaft (DFG, grant Za735/1-1), PICT-2018-01379, IAA-DNA H18 (GC), National University of Luján CDDCB N 69/2021 (GC) and PADI Foundation Grant No. 47918. 2020 (GC). These studies were also supported by MINCYT-BMBF Program (AL/17/06- 01DN18024) and ALEARG'18 Scholarship by DAAD/Ministerio de Educación de Argentina. The present manuscript also presents an outcome of the EU project IMCONet (FP7 IRSES, action no. 319718). This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 87269 CoastCarb. We are especially grateful to the divers, scientific and logistics groups of Carlini Station – Dallmann Laboratory for their technical assistance during the Antarctic expeditions. In addition, we gratefully acknowledge Thomas Mumford, J. Robert Waaland, Silvia Rodríguez and Eduardo Ruiz Barlett for their valuable comments that helped to improve the manuscript. I would like to offer special thanks to Dr. Doris Abele, who, although no longer with us, continues to inspire by her dedication to this Antarctic family she served over the course of her career.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106056>.

#### References

- Ahn, I.Y., Moon, H.W., Jeon, M., Kang, S.H., 2016. First record of massive blooming of benthic diatoms and their association with megabenthic filter feeders on the shallow seafloor of an Antarctic fjord: does glacier melting fuel the bloom? *Ocean Sci. J.* 51, 273–279. <https://doi.org/10.1007/s12601-016-0023-y>.
- Alurralde, G., Fuentes, V., Maggioni, T., Movilla, J., Olariaga, A., Orejas, C., Schloss, I., Tatián, M., 2019. Role of suspension feeders in antarctic pelagic-benthic coupling: trophic ecology and potential carbon sinks under climate change. *Mar. Environ. Res.* 152, 104790 <https://doi.org/10.1016/j.marenvres.2019.104790>.
- Amsler, C.D., Iken, K., McClintock, J.B., et al., 2005. Comprehensive evaluation of the palatability and chemical defenses of subtidal macroalgae from the Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* 294, 141–159. <https://doi.org/10.3354/meps294141>.
- 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. *J. Phycol.* 50 (1), 1–10. <https://doi.org/10.1111/jpy.12137>.
- Amsler, C., Amsler, M., Curtis, M., McClintock, J., Baker, B., 2019. Impacts of gastropods on epiphytic microalgae on the brown macroalgae *Himantothalpus grandifolius*. *Antarct. Sci.* 31 (2), 89–97. <https://doi.org/10.1017/S0954102019000014>.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E., Stier, A.C., Silliman, B.R., 2001. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193. <https://doi.org/10.1890/10-1510.1>.
- Barnes, D.K.A., Conlan, K.E., 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 362 (1477), 11e38. <https://doi.org/10.1098/rstb.2006.1951>.
- Barnes, D.K.A., Souster, T., 2011. Reduced survival of Antarctic benthos linked to climate-induced iceberg scouring. *Nat. Clim. Change* 1, 365–368. <https://doi.org/10.1038/nclimate1232>.
- Barnes, D.K.A., Fenton, M., Cordingley, A., 2014. Climate-linked iceberg activity massively reduces spatial competition in Antarctic shallow waters. *Curr. Biol.* 24 (12), R553–R554. <https://doi.org/10.1016/j.cub.2014.04.040>.
- Barnes, D.K.A., 2015. Antarctic sea ice losses drive gains in benthic carbon drawdown. *Curr. Biol.* 25, R789–R790. <https://doi.org/10.1016/j.cub.2015.07.042>.
- Barnes, D.K.A., Fleming, A., Sands, C.J., Quartino, M.L., Deregibus, D., 2018. Icebergs, blue carbon and Antarctic climate feedbacks. *Philos. Trans. A Math. Phys. Eng. Sci.* 376 (2122), 20170176. <https://doi.org/10.1098/rsta.2017.0176>.
- Barnes, D.K.A., Sands, C.J., Cook, A., Howard, F., Roman, A., Carlos, G., et al., 2020. Blue carbon gains from glacial retreat along Antarctic fjords: what should we expect. *Global Change Biol.* 27, 2750–2755. <https://doi.org/10.1111/gcb.15055>.
- Barrera Oro, E., Moreira, E., Seefeldt, M.A., et al., 2019. The importance of macroalgae and associated amphipods in the selective benthic feeding of sister rockcod species *Notothenia rossii* and *N. coriiceps* (Nototheniidae) in West Antarctica. *Polar Biol.* 42 (2), 317–334. <https://doi.org/10.1007/s00300-018-2424-0>.
- Bartsch, I., Paar, M., Fredriksen, S., Schwanz, M., Daniel, C., Hop, H., Wiencke, C., 2016. Changes in kelp forest biomass and depth distribution in Kongsfjorden, Svalbard, between 1996–1998 and 2012–2014 reflect Arctic warming. *Polar Biol.* 39, 2021–2036. <https://doi.org/10.1007/s00300-015-1870-1>.
- Bax, N., Sands, C.J., Gogarty, B., Downey, R.V., Moreau, C.V., Moreno, B., Held, C., Paulsen, M.L., McGee, J., Haward, M., Barnes, D.K.A., 2021. Perspective: increasing blue carbon around Antarctica is an ecosystem service of considerable societal and economic value worth protecting. *Global Change Biol.* 27, 5–12.
- Beuchel, F., Gulliksen, B., 2008. Temporal patterns of benthic community development in an Arctic fjord (Kongsfjorden, Svalbard): results of a 24-year manipulation study. *Polar Biol.* 31 (8), 913–924. <https://doi.org/10.1007/s00300-008-0429-9>.
- Braeckman, U., et al., 2021. Glacial melt disturbance shifts community metabolism of an Antarctic seafloor ecosystem from net autotrophy to heterotrophy. *Comm. Biol.* <https://doi.org/10.1038/s42003-021-01673-6>.
- Campana, G.L., Zacher, K., Fricke, A., et al., 2009. Drivers of colonization and succession in polar benthic macro- and microalgal communities. *Bot. Mar.* 52, 655–667. <https://doi.org/10.1515/BOT.2009.076>.
- Campana, G.L., et al., 2020. Successional processes in antarctic benthic algae. In: Gómez, I., Huovinen, P. (Eds.), *Antarctic Seaweeds*. Springer, Cham. [https://doi.org/10.1007/978-3-030-39448-6\\_9](https://doi.org/10.1007/978-3-030-39448-6_9).
- Campana, G.L., Zacher, K., Deregibus, D., Momo, F., Wiencke, C., Quartino, M.L., 2018. Succession of Antarctic benthic algae (Potter Cove, South Shetland Islands): structural patterns and glacial impact over a four-year period. *Polar Biol.* 41 (2), 377–396.
- CCAMLR-41/34, 2022. Updated Conservation Measure Proposal for the Establishment of a Marine Protected Area in Domain 1 (Western Antarctic Peninsula and Southern Scotia Arc) – Delegations of Argentina and Chile.
- Chung, I.K., Beardal, J., Mehta, S., et al., 2011. Using marine macroalgae for carbon sequestration: a critical appraisal. *J. Appl. Phycol.* 23 (5), 877–886. <https://doi.org/10.1007/s10811-010-9604-9>.
- Chown, S.L., Leihy, R.I., Naish, T.R., Brooks, C.M., Convey, P., Henley, B.J., Mackintosh, A.N., Phillips, L.M., Kennicutt II, M.C., Grant, S.M. (Eds.), 2022. *Antarctic Climate Change and the Environment: A Decadal Synopsis and Recommendations for Action*. Scientific Committee on Antarctic Research, Cambridge, United Kingdom. [www.scar.org](http://www.scar.org).
- Clark, G.F., Stark, J.S., Johnston, E.L., et al., 2013. Light-driven tipping points in polar ecosystems. *Global Change Biol.* 12, 3749–3761. <https://doi.org/10.1111/gcb.12337>.
- Clark, G.F., Stark, J.S., Palmer, A.S., Riddle, M.J., Johnston, E.L., 2017. The roles of sea-ice, light and sedimentation in structuring shallow Antarctic benthic communities. *PLoS One* 12 (1), e0168391. <https://doi.org/10.1371/journal.pone.0168391>.
- Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K., Bindoff, N.L., et al., 2014. Climate change and Southern Ocean ecosystems. I: how changes in physical habitats directly affect marine biota. *Global Change Biol.* 20, 3004–3025. <https://doi.org/10.1111/gcb.12623>.
- Cook, A.J., Holland, P.R., Meredith, M.P., Murray, T., Luckman, A., Vaughan, D.G., 2016. Ocean forcing of glacier retreat in the western Antarctic Peninsula. *Science* 353 (6296), 283–286. <https://doi.org/10.1126/science.aac0017>.
- Deregibus, D., Quartino, M.L., Campana, G.L., Momo, F.R., Wiencke, C., Zacher, K., 2016. Photosynthetic light requirements and vertical distribution of macroalgae in newly ice-free areas in Potter Cove, South Shetland Islands, Antarctica. *Polar Biol.* 39 (1), 153–166. <https://doi.org/10.1007/s00300-015-1679-y>.
- Deregibus, Dolores, 2017. Efecto del retroceso glaciario inducido por el cambio climático sobre la comunidad de macroalgas en nuevas áreas libres de hielo en un ecosistema costero antártico (Caleta Potter, 1.25 de Mayo, I. Shetland del Sur). Tesis Doctoral. Universidad de Buenos Aires. Facultad de Ciencias Exactas y Naturales. [http://hdl.handle.net/20.500.12110/tesis\\_n6241\\_Deregibus](http://hdl.handle.net/20.500.12110/tesis_n6241_Deregibus).
- Deregibus, D., Quartino, M.L., Zacher, K., Campana, G.L., Barnes, D.K.A., 2017. Understanding the link between sea ice, ice scour and Antarctic benthic biodiversity: the need for cross station and nation collaboration. *Polar Rec.* 53, 143–152. <https://doi.org/10.1017/S0032247416000875>.
- Deregibus, D., et al., 2020. Carbon balance under a changing light environment. In: Gómez, I., Huovinen, P. (Eds.), *Antarctic Seaweeds*. Springer, Cham. [https://doi.org/10.1007/978-3-030-39448-6\\_9](https://doi.org/10.1007/978-3-030-39448-6_9).
- DigitalGlobe, 2014. *WorldView-2 Scene 103001001F612100, 07/03/2013* under a CC BY License, with Permission from Maxar-EU Space Imaging-DigitalGlobe original copyright 2013.
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., et al., 2008. *InfoStat version 2008*. Grupo InfoStat, Facultad de Ciencias Agropecuarias. Universidad Nacional de Córdoba, Córdoba.
- Dolliver, J., O'Connor, N., 2022. Whole system analysis is required to determine the fate of macroalgal carbon: a systematic review. *Jun J. Phycol.* 58 (3), 364–376. <https://doi.org/10.1111/jpy.13251>. PMID: 35397178; PMCID: PMC9325415.
- Eggert, A., Wiencke, C., 2000. Adaptation and acclimation of growth and photosynthesis of five Antarctic red algae to low temperatures. *Polar Biol.* 23, 609–618. <https://doi.org/10.1007/s003000000>.
- Foster, M.S., Harrold, C., Hardin, D.D., 1991. Point vs. photo quadrat estimates of the cover of sessile marine organisms. *J. Exp. Mar. Biol. Ecol.* 146, 193–203. [https://doi.org/10.1016/0022-0981\(91\)90025-R](https://doi.org/10.1016/0022-0981(91)90025-R).
- García, M.D., Dutto, M.S., Chazarreta, C.J., Berasategui, A.A., Schloss, I.R., Hoffmeyer, M.S., 2020. Micro- and mesozooplankton successions in an Antarctic coastal environment during a warm year. *PLoS One* 15 (5), e0232614. <https://doi.org/10.1371/journal.pone.0232614>.
- Gogarty, B., McGee, J., Barnes, D.K.A., et al., 2019. Protecting Antarctic blue carbon: as marine ice retreats can the law fill the gap? *Clim. Pol.* <https://doi.org/10.1080/14693062.2019.1694482>.
- Gómez, I., Weykam, G., Klöser, H., Wiencke, C., 1997. Photosynthetic light requirements, metabolic carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). *Mar. Ecol. Prog. Ser.* 148, 281–293. <https://doi.org/10.3354/meps148281>.
- Gómez, I., Pirjo, H., 2020. Antarctic Seaweeds Diversity Adaptation and Ecosystem Services. Springer, Cham. <https://doi.org/10.1007/978-3-030-39448-6>.
- Grange, L.J., Smith, C.R., 2013. Megafaunal communities in rapidly warming fjords along the West Antarctic Peninsula: hotspots of abundance and beta diversity. *PLoS One* 8 (12), e77917. <https://doi.org/10.1371/journal.pone.0077917>.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.
- Ha, S.Y., Ahn, I.Y., Moon, H.W., Choi, B., Shin, K.H., 2019. Tight trophic association between benthic diatom blooms and shallow-water megabenthic communities in a rapidly deglaciated Antarctic fjord. *Estuar. Coast Shelf Sci.* 218, 258–267. <https://doi.org/10.1016/j.ecss.2018.12.020>.
- Heijden, L.H., Kamenos, N.A., 2015. Calculating the global contribution of coralline algae to carbon burial. *Biogeosci. Discuss.* 12 (10), 7845–7877. <https://doi.org/10.5194/bgd-12-7845-2015>.
- Hendry, K.R., Meredith, M.P., Ducklow, H.W., 2018. The marine system of the West Antarctic Peninsula: status and strategy for progress. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 376, 1–6. <https://doi.org/10.1098/rsta.2017.0179>.
- Hoffmann, R., Al-Handal, A.Y., Wulff, A., Deregibus, D., Zacher, K., Quartino, M.L., Wenzhöfer, F., Braeckman, U., 2019. Implications of glacial melt-related processes on the potential primary production of a microphytobenthic community in potter cove (Antarctica). *Front. Mar. Sci.* 6, 655. <https://doi.org/10.3389/fmars.2019.00655>.
- Huang, Y.M., Amsler, M.O., McClintock, J.B., et al., 2007. Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula. *Polar Biol.* 30, 1417–1430. <https://doi.org/10.1007/s00300-007-0303-1>.
- IPCC, 2021. Regional fact sheet—polar regions. In: MassonDelmotte, V., Zhai, P., Pirani, A., et al. (Eds.), *Climate Change 2021: the Physical Science Basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. <https://www.ipcc.ch/report/ar6/wg1/resources/factsheets>.
- Jerosch, K., et al., 2018. Benthic Meltwater Fjord Habitats Formed by Rapid Glacier Recession on King Subject Areas, vol. 376. *Philosophical transactions of the Royal Society A*, 20170. <https://doi.org/10.1098/rsta.2017.0178>.
- Jerosch, K., Scharf, F.K., Deregibus, D., Campana, G.L., Zacher, K., Pehlke, et al., 2019. Ensemble modeling of Antarctic macroalgal habitats exposed to glacial melt in a polar fjord. *Front. Ecol. Evol.* 7, 207. <https://doi.org/10.3389/fevo.2019.00207>.
- Karsten, U., Wiencke, C., Kirst, G.O., 1991a. The effect of salinity changes upon physiology of epilittoral green macroalgae from Antarctica and Southern Chile. I. Cell viability, growth, photosynthesis and dark respiration. *J. Plant Physiol.* 138, 667–673.
- Karsten, U., Wiencke, C., Kirst, G.O., 1991b. The effect of salinity changes upon physiology of epilittoral green macroalgae from Antarctica and Southern Chile II. Inorganic ions and organic compounds. *J. Exp. Bot.* 42, 1533–1539.
- Kim, D., 2001. Seasonality of marine algae and grazers of an Antarctic rocky intertidal, with emphasis on the role of the limpet *Nacella concinna* Strebel (Gastropoda: patellidae). *Berichte zur Polar-und Meeresforschung* 397, 1–136.
- Kirk, J.T.O., 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511263370>.
- Klöser, H., Quartino, M.L., Wiencke, C., 1996. Distribution of macroalgae and macroalgal communities in gradients of physical conditions in Potter Cove, King George Island, Antarctica. *Hydrobiologia* 333, 1–17. <https://doi.org/10.1007/BF00020959>.

- Krause-Jensen, D., Duarte, C.M., 2016. Substantial role of macroalgae in marine carbon sequestration. *Nat. Geosci.* 9 (10), 737. <https://doi.org/10.1038/ngeo2790>.
- Krause-Jensen, D., Lavery, P., Serrano, O., Marbà, N., Masque, P., Duarte, C.M., 2018. Sequestration of macroalgal carbon: the elephant in the blue carbon room. *Biol. Lett.* 14, 20180236 <https://doi.org/10.1098/rsbl.2018.0236>.
- Laffoley, D., Grimsditch, G., 2009. *The Management of Natural Coastal Carbon Sinks*. IUCN, Gland, Switzerland.
- Lagger, C., Servetto, N., Torre, L., Sahade, R., 2017. Benthic colonization in newly ice-free soft-bottom areas in an Antarctic fjord. *PLoS One* 12, e0186756. <https://doi.org/10.1371/journal.pone.0186756>.
- Lagger, C., Nime, M., Torre, L., Servetto, N., Tatián, M., Sahade, R., 2018. Climate change, glacier retreat and a new ice-free island offer new insights on Antarctic benthic responses. *Ecography* 40, 1–12. <https://doi.org/10.1111/ecog.03018>.
- Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116, 25–44. <https://doi.org/10.1086/283610>.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Science Ltd.
- Mateo, R.G., Felicísimo, Á.M., Muñoz, J., 2012. Modelos de distribución de especies y su potencialidad como recurso educativo interdisciplinar. *Reduca (Biología)* 5 (1), 137–153. Available from: <http://www.revistareduca.es/index.php/biologia/article/view/881>.
- Matula, C.V., Quartino, M.L., Nuñez, J.D., et al., 2022. Effects of seawater temperature and seasonal irradiance on growth, reproduction, and survival of the endemic Antarctic brown alga *Desmarestia menziesii* (Phaeophyceae). *Polar Biol.* 45, 559–572. <https://doi.org/10.1007/s00300-021-02991-5>.
- Marina, T.L., Salinas, V., Cordone, G., Campana, G.L., Moreira, E., Deregibus, D., Torre, L., et al., 2018. The food web of Potter Cove (Antarctica): complexity, structure and function. *Estuar. Coast Shelf Sci.* 200, 141–151. <https://doi.org/10.1016/j.ecss.2017.10.015>.
- Meredith, M.P., King, J.C., 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* 32, L19604 <https://doi.org/10.1029/2005GL024042>.
- Meredith, M.P., Falk, U., Bers, A.V., Mackensen, A., Schloss, I.R., Barlett, E.R., et al., 2018. Anatomy of a glacial meltwater discharge event in an Antarctic cove. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 376 <https://doi.org/10.1098/rsta.2017.0163>.
- Moreira, E., Juárez, M., Barrera-Oro, E., 2014. Dietary overlap among early juvenile stages in an Antarctic notothenioid fish assemblage at Potter Cove, South Shetland Islands. *Polar Biol.* 37, 1507–1515. <https://doi.org/10.1007/s00300-014-1545-3>.
- Morley, S.A., Souster, T.A., Vause, B.J., Gerrish, L., Peck, L.S., Barnes, D.K.A., 2022. Benthic biodiversity, carbon storage and the potential for increasing negative feedbacks on climate change in shallow waters of the antarctic Peninsula. *Biology* 11, 320. <https://www.mdpi.com/2079-7737/11/2/320>.
- Neder, Camila, 2016. *El bentos de Caleta Potter (Antártida): Un meta-análisis usando modelos de distribución de especies*. Tesis Doctoral. Universidad Nacional de Córdoba.
- Neder, C., et al., 2020. Default versus ConFigured-geostatistical modeling of suspended particulate matter in potter cove, West Antarctic Peninsula. *Fluid.* <https://doi.org/10.3390/fluids5040235>.
- Noël, L.M.-L.J., Griffin, J.N., Moschella, P.S., Jenkins, S.R., Thompson, R.C., Hawkins, S. J., 2009. Changes in diversity and ecosystem functioning during succession. In: Wahl, M. (Ed.), *Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change*, Ecological Studies, vol. 206. Springer, Heidelberg, pp. 213–223. <https://doi.org/10.1007/b76710.15>.
- Oliveira, E.C., Absher, T.M., Pellizzari, F.M., Oliveira, M.C., 2009. The seaweed flora of admiralty Bay, king George island, antarctic. *Polar Biol.* 32, 1639–1647. <https://doi.org/10.1007/s00300-009-0663-9>.
- Oliveira, M., Pellizzari, F., Medeiros, A., Yokoya, N.S., 2020. Diversity of Antarctic Seaweeds. [https://doi.org/10.1007/978-3-030-39448-6\\_2](https://doi.org/10.1007/978-3-030-39448-6_2).
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>.
- Pasotti, F., Manini, E., Giovannelli, D., Wöfl, A.C., Monien, D., Verleyen, E., Braeckman, U., Abele, D., Vanreusel, A., 2015. Antarctic shallow water benthos in an area of recent rapid glacier retreat. *Mar. Ecol.* 36, 716–733. <https://doi.org/10.1111/maec.12179>.
- Pellizzari, F., Santos-Silva, M.C., Medeiros, A., Oliveira, M.C., Yokoya, N.S., Pupo, D., Rosa, L., 2017. Diversity and spatial distribution of seaweeds in the South Shetland Islands, Antarctica: an updated database for environmental monitoring under climate change scenarios. *Polar Biol.* <https://doi.org/10.1007/s00300-017-2092-5>.
- Pellizzari, F., Rosa, L.H., Yokoya, N.S., 2020. Biogeography of Antarctic Seaweeds Facing Climate Changes. [https://doi.org/10.1007/978-3-030-39448-6\\_5](https://doi.org/10.1007/978-3-030-39448-6_5).
- Peters, et al., 2005. A comparative analysis of the nutritional and elemental composition of macroalgae from the western Antarctic Peninsula. *Phycologia* 44 (4), 453–463. [https://doi.org/10.2216/0031-8884\(2005\)44\[453:ACAOTN\]2.0.CO;2](https://doi.org/10.2216/0031-8884(2005)44[453:ACAOTN]2.0.CO;2).
- Pineda Metz, S.E.A., Gerdes, D., Richter, C., 2020. Benthic fauna declined on a whitening Antarctic continental shelf. *Nat. Commun.* 11, 2226. <https://doi.org/10.1038/s41467-020-16093-z>.
- Quartino, M.L., Zaixso, H.E., Boraso de Zaixso, A.L., 2005. Biological and environmental characterization of marine macroalgal assemblages in potter cove, South Shetland islands, Antarctica. *Bot. Mar.* 48 (3), 187–197. <https://doi.org/10.1515/BOT.2005.029>, 2005.
- Quartino, M.L., Boraso de Zaixso, A.L., 2008. Summer macroalgal biomass in potter cove, South Shetland islands, Antarctica: its production and flux to the ecosystem. *Polar Biol.* 31 (3), 281–294. <https://doi.org/10.1007/s00300-007-0356-1>.
- Quartino, M.L., Deregibus, D., Campana, G.L., Latorre, G.E.J., Momo, F.R., 2013. Evidence of macroalgal colonization on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica. *PLoS One.* <https://doi.org/10.1371/journal.pone.0058223>.
- Quartino, M.L., et al., 2020. Production and Biomass of Seaweeds in Newly Ice-free Areas: Implications for Coastal Processes in a Changing Antarctic Environment. *Antarctic Seaweeds*. Springer, Cham. [https://doi.org/10.1007/978-3-030-39448-6\\_8](https://doi.org/10.1007/978-3-030-39448-6_8).
- Queirós, A.M., Stephens, N., Widdicombe, S., et al., 2019. Connected macroalgal-sediment systems: blue carbon and food webs in the deep coastal ocean. *Ecol. Monogr.* 89 (3), e01366 <https://doi.org/10.1002/ecm.1366>.
- Rückamp, M., Braun, M., Suckro, S., Blindow, N., 2011. Observed glacial changes on the King George Island ice cap, Antarctica, in the last decade. *Global Planet. Change* 79, 99–109. <https://doi.org/10.1016/j.gloplacha.2011.06.009>.
- Runcie, J.W., Riddle, M.J., 2012. Estimating primary productivity of marine macroalgae in East Antarctica using in situ fluorometry. *Eur. J. Phycol.* 47 (4), 449–460.
- Ruiz Barlett, et al., 2021. Interannual variability of hydrographic properties in Potter Cove during summers between 2010 and 2017. *Antarct. Sci.* <https://doi.org/10.1017/S0954102020000668>.
- Sahade, R., Lagger, C., Torre, L., Momo, F.R., Monien, P., Schloss, I., et al., 2015. Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. *Sci. Adv.* 1, e1500050 <https://doi.org/10.1126/sciadv.1500050>.
- Sanches, P.F., Pellizzari, F.M., Horta, P.H., 2016. Multivariate analyses of Antarctic and sub-Antarctic seaweed distribution patterns: an evaluation of the role of the Antarctic Circumpolar Current. *J. Sea Res.* 110, 29–38. <https://doi.org/10.1016/j.seares.2016.02.002>.
- Schloss, I.R., Ferreyra, G.A., Ruiz-Pino, D., 2002. Phytoplankton biomass in antarctic shelf zones: a conceptual model based on potter cove, king George island. *J. Mar. Syst.* 36, 129–143.
- Schloss, I.R., Abele, D., Moreau, S., Norkko, A., Cummings, V., Thrush, S., 2012. Response of phytoplankton dynamics to 19 year (1991–2009) climate trends in Potter Cove (Antarctica). *J. Mar. Syst.* 92, 53–66. <https://doi.org/10.1016/j.jmarsys.2011.10.006>.
- Schloss, I.R., Wasilowska, A., Dumont, D., Almandoz, G.O., Hernando, M.P., Michaud-Tremblay, C.-A., Saravia, L., Rzepecki, M., Monien, P., Monien, D., Koczyńska, E.E., Bers, A.V., Ferreyra, G.A., 2014. On the phytoplankton bloom in coastal waters of southern King George Island (Antarctica) in January 2010: an exceptional feature? *Limnol. Oceanogr.* 59 (1), 195–210. <https://doi.org/10.4319/lo.2014.59.1.0195>.
- Servetto, N., Rossi, S., Fuentes, V., Alurralde, G., Lagger, C., Sahade, R., 2017. Seasonal trophic ecology of the dominant antarctic coral malacobelemnon daytoni (octocorallia, pennatulacea, kophoblemnidae). *Mar. Environ. Res.* 130, 264–274. <https://doi.org/10.1016/j.marenvres.2017.08.003>.
- Sousa, W.P., Connell, J.H., 1992. Grazing and succession in marine algae. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), *Plant-animal Interactions in the Marine Benthos*. Oxford University Press, New York, pp. 425–441.
- Stammerjohn, S., Massom, R., Rind, D., Martinson, D., 2012. Regions of rapid sea ice change: an inter-hemispheric seasonal comparison. *Geophys. Res. Lett.* 39, 1–8. <https://doi.org/10.1029/2012GL050874>.
- Torre, L., Servetto, N., Eöry, M.L., Momo, F., Tatián, M., Abele, D., et al., 2012. Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. *Polar Biol.* 35, 1743–1748. <https://doi.org/10.1007/s00300-012-1208-1>.
- Turner, J., Bindschadler, R.A., Convey, P., Di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D.A., et al., 2009. *Antarctic Climate Change and the Environment*. SCAR, Cambridge.
- Wiencke, C., Clayton, N., 2002. Antarctic seaweeds. In: Wagele, J.W. (Ed.), *Synopses of the Antarctic Benthos*. Ruggell, Lichtenstein: A.R.G. Gantner Verlag KG.
- Wiencke, C., Amsler, C.D., 2012. Seaweeds and their communities in polar regions. In: Wiencke, C., Bischof, K. (Eds.), *Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization*, Ecological Studies, vol. 219. Springer, Heidelberg, pp. 265–292. <https://doi.org/10.1007/978-3-642-28451-9>.
- Wöfl, A.C., et al., 2014. Distribution and characteristics of marine habitats in a subpolar Bay based on hydroacoustics and bed shear stress estimates-potter cove, king George island, Antarctica. *Geo Mar. Lett.* 34 (5), 435–446. <https://doi.org/10.1007/s00367-014-0375-1>.
- Wulff, A., Iken, K., Quartino, M.L., et al., 2009. Biodiversity, biogeography and zonation of marine benthic micro- and macroalgae in the Arctic and Antarctic. *Bot. Mar.* 52 (6), 491–507. <https://doi.org/10.1515/BOT.2009.072>.
- Zacher, K., Rautenberger, R., Hanelt, D., Wulff, A., Wiencke, C., 2009. The abiotic environment of polar marine benthic algae. *Bot. Mar.* 52, 483–490. <https://doi.org/10.1515/BOT.2009.082>.
- Zwerschke, N., Sands, C.J., Roman Gonzalez, A., Barnes, D.K.A., Guzzi, A., Jenkins, S., Muñoz Ramírez, C., Scourse, J., 2022. Quantification of blue carbon pathways contributing to negative feedback on climate change following glacier retreat in West Antarctic fjords. *Global Change Biol.* 28 (1), 8–20.