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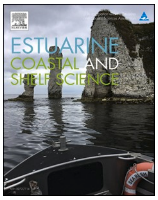

Tidewater glacier retreat in Antarctica: The table is set for fast-growing opportunistic species, is it?

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ABSTRACT

The rapid warming of the West Antarctic Peninsula (WAP) is causing an important expansion of marine coastal areas due to glacier retreat. These new ice-free areas offer additional habitats for the colonization of benthic species in areas formerly occupied by ice. The establishment of benthic species can represent important negative feedback to the warming process due to the new carbon fixed and stored. Opportunistic, fast-growing, and high turnover species are expected to colonize these new emerging areas. At Potter Cove, the glacier retreat has opened wide areas of soft bottoms, which provides an excellent study area to assess the colonization process and the success of opportunistic species. Here, we examined the population response of the opportunistic soft coral *Malacobelemnon daytoni* species in the soft bottom area of Potter Cove with different exposure times due to glacier retreat. Our results show a significant variation of *M. daytoni* population among the sampled areas in terms of presence, abundances, and distribution. In the long-term ice-free areas, opened for more than 60 years, we observed a ~20-fold increase of *M. daytoni* densities within just 15 years. However, this extraordinary population outburst was not observed in the newer ice-free areas (≤15 years). We registered very low densities in areas of 15 years and no colonies in areas with 10 years of open sea conditions. These were unexpected results based on colonization capabilities showed by the species and habitat suitability of the new areas. Indeed, using Species Distribution Models (SDMs) we also obtained contrasting outputs. SDMs based on long-term areas presence data predicted high habitat suitability and the potential presence of the species in the newer areas. However, when based on newer and older areas data, SDMs showed low habitat suitability and potential absence of the species in the newer areas. This work suggests that species that can be considered as fast and efficient colonizers, could not perform in that way under certain conditions. This deepens the current knowledge on species natural history and environmental relationships, especially to improve our prediction capabilities under changing environmental conditions.

1. Introduction

Climate-driven expansion of new ice-free areas in Antarctica, mainly due to ice-shelf collapses and rapid glacier retreat, could be considered among the more crucial topics of polar research nowadays. These emerging ice-free areas are exposing a substantial amount of new substrates for biological production and therefore play an important role in carbon uptake that could be among the main negative feedbacks to climate change (Peck et al., 2010; Barnes, 2017; Barnes et al., 2020; Deregibus et al., 2020). Biological responses as changes in species distribution, expansion of distribution range of opportunistic species, extinction of less-competitive species and the potential spread of invasive species have been some of the predicted impacts postulated due to the ongoing increase of these new ice-free areas (Quartino et al., 2013;

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Sahade et al., 2015; Lagger et al. 2017, 2018; Lee et al., 2017). Furthermore, they are genuine places to study how polar ecosystems respond to the increasing environmental changes, especially those related to ice losses.

Under the strongest forcing scenario of climate change (RCP 8.5) over 17,000 km^2 could be free of ice coverage in the Antarctic Peninsula by the end of the century, representing nearly a 25% increase in total area (Lee et al., 2017). At 25 de Mayo/King George Island, the largest of the South Shetland Islands and where Potter Cove is located, most of the glaciers are retreating at an unprecedented speed, increasing the amount of newly ice-free areas to approx. 75 km^2 along the entire island between 1956 and 2008 (Osmanoğlu et al., 2013; Jerosch et al., 2018). In the particular case of Potter Cove, the Fourcade glacier shows a progressive and considerable retreat (approximately 1.5 km^2 over the last six decades), causing massive meltwater streams with sediment discharge into the cove. This discharge not only affects the hydrographical characteristics of the cove (Rückamp et al., 2011; Schloss et al., 2012; Bers et al., 2013; Monien et al., 2017) but also impacts the physiology of aquatic organisms (Philipp et al., 2011; Torre et al. 2012, 2014, 2014; Fuentes et al., 2016). This sediment discharge is currently recognized as a driver for changes at the community assemblage level, with long-term effects on the biomass and species composition (Thrush et al., 2004; Siciński et al., 2012; Gutt et al., 2015; Moon et al., 2015; Sahade et al., 2015; Valdivia et al., 2020).

To investigate benthic population responses to climate-induced environmental shifts, we focused on one of the most abundant species at Potter Cove, the Antarctic soft coral *Malacobelemnon daytoni.* This species was among those favored after the major shift registered on benthic assemblages at Potter Cove due to increased sediment runoff triggered by glacier retreat, significantly increasing their density and distribution area in a few years (Sahade et al., 2015). This was expected since *M. daytoni* showed a high tolerance to sedimentation and high reproductive output. It is also dominant in heavily ice-impacted areas suggesting a high population turnover and fast growth rates (Sahade et al., 1998; Servetto et al. 2013, 2017, 2017; Torre et al., 2014; Servetto and Sahade, 2016). However, this species was surprisingly not found in the new ice-free soft-bottom areas with ~5 years of exposition to open sea conditions, front to the Fourcade glacier (Lagger et al., 2017). Such observations, on one hand, suggest that *M. daytoni* has the necessary characteristics to perform as an efficient pioneer species in new ice-free habitats. However, on the other hand, the species did not colonize *a priori* favorable areas after five years. Therefore to test whether *M. daytoni* could be a successful colonizer of new ice-free areas, the aims of the present study were (1) to explore the presence, distribution and abundances of *M. daytoni* in three areas of Potter Cove exposed for different periods to open sea conditions (ice-free areas for > 60, 15 and 10 years), (2) to identify environmental indicators that determine distribution patterns of this species and (3) to map, using Species Distribution Models (SDMs), the habitat suitability for this species under different glacier conditions to predict possible distribution changes. Potter Cove can be considered a good sentinel of glacier retreat effects on Antarctic glaciomarine fjords, due to a multidisciplinary program running during the last decades. Therefore, these results will provide important insights into a key species of Potter Cove and represent an important contribution to the current knowledge on Antarctic coastal ecosystem responses to the ongoing Climate Change process.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted at Potter Cove (62°14′ S, 58°35′ W, Fig. 1),

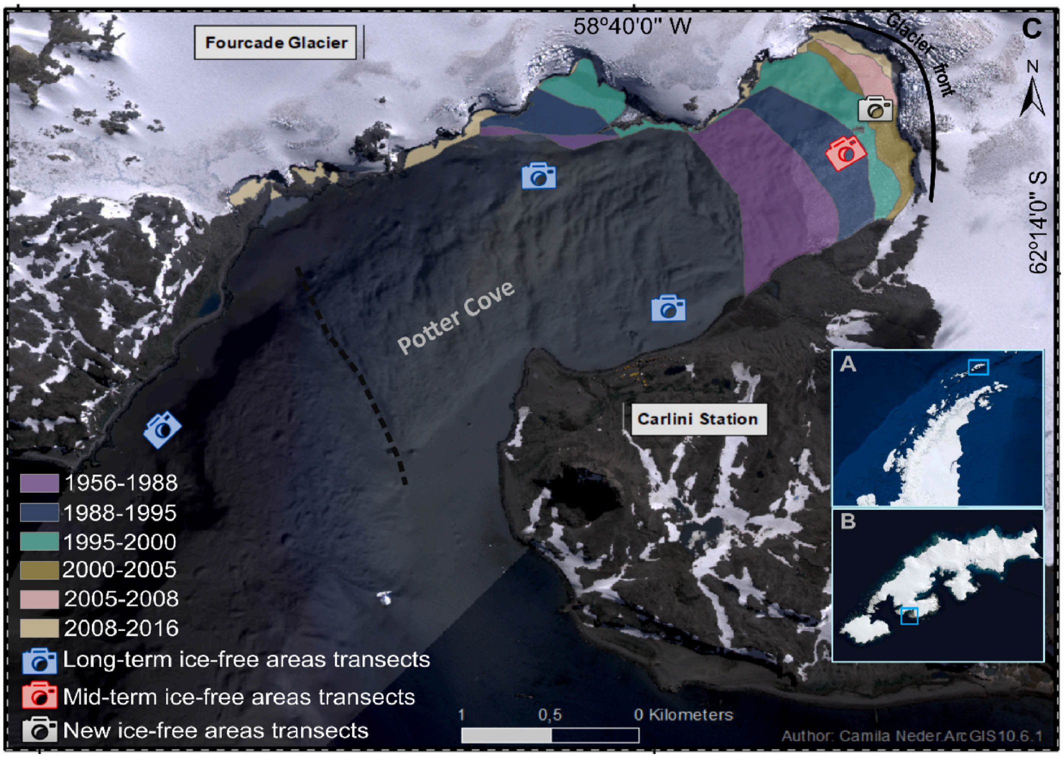

Fig. 1. Location of the study area. (A) Isla 25 de Mayo/King George Island on the Antarctic Peninsula (blue square) (B) Location of Potter Cove in Isla 25 de Mayo/King George Island (blue square) and (C) Satellite image of Potter Cove (ESRI, 2017; Digital Globe, 2014), showing the sampling stations: Long-Term Ice-Free Areas are marked with a blue camera symbol (LTIFA), Mid-Term Ice-Free Areas with a red camera symbol (MTIFA) and New Ice-Free Areas with a grey camera symbol (NIFA). The black dotted line indicates the position of the sill which divides the cove into the outer and inner parts. Fourcade glacier front lines, represented by the color gradients, were taken from Rückamp et al., (2011) and Weber (2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

where the Argentine Antarctic Carlini Station and the Argentine-German Dallmann laboratory are located. Potter Cove is a small glacial fjord in the southwest of Isla 25 de Mayo/King George Island, South Shetland Islands, Antarctica. The cove has an area of approximately 8 km^2 (~4 km long and ~2 km wide) and is divided into an inner and outer part by a 30 m deep underwater sill. In the inner cove, soft-sediments dominate mainly composed of silt and water depths do not exceed about 50 m, whereas the outer part is typified by hard substrate and depths reaching ~200 m (Klöser et al., 1994; Eraso and Dominguez, 2007; Wölfl et al., 2014). The cove is partly surrounded by the Fourcade glacier, which has shown a progressive retreat over the last 60 years exposing new areas free of ice in the inner part and leaving almost the entire bottom of the cove ice-free (Rückamp et al., 2011). A noticeable gradient of sediment influence can be observed through the cove, mainly during the summer melt season. In the inner part of the cove, large amounts of suspended particulate matter (SPM) are deposited from sediment-laden surface plumes generated by glacial discharge, meltwater streams, and surrounding snowfields, whereas the outer part is the least influenced by sedimentation (Jerosch et al., 2018; Neder et al., 2020). The rapid glacial melting also results in salinity and temperature changes between areas, seasons, and years (Schloss et al., 2012). Ecological impacts associated with Fourcade glacier's retreat have been reported on the local biodiversity, species distribution, and benthic community composition (Torre et al., 2014; Pasotti et al., 2015; Sahade et al., 2015; Deregibus et al., 2016). The existing data on the physical and biological features of the cove are summarized in Wiencke et al., (2008). Detailed information of pelagic and benthic communities is described in Quartino et al., (2013); Passotti et al., (2015); Sahade et al., (2015); Deregibus et al., (2016); Abele et al., (2017); Lagger et al., (2017) and Lagger et al., (2018).

During the austral summer of 2010, a photographic survey at 15, 20, 25, and 30 m depths by SCUBA diving was performed in the Mid-Term Ice-Free Areas (MTIFA) and analyzed in the present work. The MTIFA were defined as ice-free since 1995, thus, it was approximately exposed for 15 years when the survey was done (Fig. 1; Table 1). To complete all analyses presented here, we used the data obtained in different photographic surveys performed during the summer seasons of 1994, 1998, and 2009 in the Long-Term Ice-Free Areas (LTIFA) and a photographic survey carried out during summer 2010 in the New Ice-Free Areas (NIFA) (Fig. 1; Table 1). Furthermore, we used high definition videos obtained during summer 2015 in the same NIFA sites sampled in 2010 to detect the presence/absence of *M. daytoni* colonies (Table 1). A high definition digital camera housed in a waterproof case and fitted with two led lights was used to take the pictures. An aluminum ruler of 10 cm was attached to the housing and used to quantify the sampled area. Along the fixed transects, a total of 45–50 images (40 × 30 cm = 0.12 m^2) were taken, resulting in a total sampled area of ~25 m^2. At each depth profile, photographs were taken every ca. 2 m along the fixed transect.

Table 1

Summary photographic surveys carried on between 1994 and 2015 at Potter Cove. Long-Term Ice-Free Areas (LTIFA), Mid-Term Recently Ice-Free Areas (MTIFA), and New Ice-Free Areas (NIFA). Distances of the stations to the glacier front were determined using the glacier front (the eastern glacier termini) in the year 2016 as a baseline.

Sampling year	Area	Ice-free for ~	Distance to the glacier front (m)	Source
1994	LTIFA	>60 years	~1500	Sahade et al. (1998)
1998	LTIFA	>60 years	~1500	Sahade et al. (2008)
2009	LTIFA	>60 years	~1500	Sahade et al. (2015)
2010	MTIFA NIFA	15 years 5 years	~300 ~100	Present study Lagger et al. (2017)
2015	NIFA	10 years	~100	Present study

2.2. Data analysis and statistical treatment

Photographs were projected onto grids of 100 points evenly distributed and those underlying each colony were counted to estimate percentage cover. Colonies in each photograph were counted (abundance) and the total number divided by the area sampled to estimate densities (col.m^{-2}). Abundance and percentage cover were analyzed from the photographs with ImageJ. The resolution of images was sufficiently fine to detect colonies of *M. daytoni* smaller than 10 mm in diameter. Identification and quantification were always conducted by the same person (CL) to reduce methodological bias.

A General Linear Model (ANOVA) was performed to test for mean differences among areas and years in density, percentage cover, and estimated sizes. In all cases, normality assumptions were tested using the Shapiro-Wilk test (Rahman and Govindarajulu, 1997), also with a visual inspection of diagnostic plots (residual vs. fitted and normal Q-Q) (Kozak and Piepho, 2018). Homogeneity of variance was tested by applying Levene's test (Montgomery, 2007) and by visual inspection of residual plots. Non-homogeneous variances were Log-transformed to achieve homogeneity. When differences were detected (ANOVA), post hoc multiple means comparisons were performed using the DGC test (Di Rienzo et al., 2002). Statistical analyses were carried out using the Infostat software package (Di Rienzo et al., 2015).

2.3. Environmental predictors and model calibration

We assessed the potential effect of four environmental parameters and their interaction on the sea pen *M. daytoni* suitability using species distribution models (SDMs). For the SDMs approach, Guisan and Zimmermann's methodology was implemented with the biomod2 platform (Guisan and Zimmermann, 2000; Thuiller et al. 2009, 2016). The environmental parameters statistically selected were: bathymetry (m), benthic position index (BPI, a measure of the depth on site relative to the mean depth of the surrounding 15 m area: positive values means depressions, equal to zero are constant slope or flat areas and negatives for elevations), distance to glacier front (m) and percentage of fine sediment content in sea-floor (%, fine sediment is defined as clay and silt proportion) (Sup. Material, Fig. S1) (Jerosch et al., 2018). The biological data of presence/absence to simulate the sea pen distribution in Potter Cove over time and during glacier retreat were divided into two sets: the first performed based on presence/absence data from the LTIFA to test the predicted distribution of *M. daytoni* on newer habitats and the second using all data available from the LTIFA, MTIFA and NIFA survey in 2009 and 2010 to test the possible differences when actual data of newer habitats are included (Sup. Material, Fig. S2). Nine SDM algorithms proposed by the R package biomod2 able to deal with presence/absence data have been taken into account (for SDM algorithms, see Sup. Material, Section 3 and 4). Spatial autocorrelation was assessed by eliminating duplicates and dividing the data records randomly into 70% for model calibration and 30% for model evaluation. To evaluate the model performance, sensitivity and specificity were calculated based on the probability threshold for which their sum was maximized. The predictive performance of each model and the hierarchy of environmental parameters importance were assessed by True Skill Statistics (TSS) and Receiver Operating Characteristic curve (ROC) calculated by 10-fold cross-validation. SDMs were run 20 times for each algorithm and data set (9 algorithms x 20 repetitions = 180 SDMs for each *M. daytoni* data set). Subsequently, those SDMs qualified as "good" by meeting the requirements (TSS value $>$ 0,7 and a ROC $>$ 0.8) according to other studies by Araújo et al. (2005), Thuiller et al. (2010) and Zhang et al. (2019), where used to combine them as a weighted mean to one ensemble habitat suitability model.

3. Results

The LTIFA showed marked temporal variations with a significant increment in *M. daytoni* densities from 1994 to 2009 (Table 2, Fig. 2). In the inner station, density increased in an order of magnitude at 20 m depth in just four years, and three orders of magnitude at 30 m depth in ~10 years (Table 2; Fig. 2). The highest densities in the entire cove were registered in the LTIFA in 2009, where in the middle station at 30 m we registered 466 col.m^{-2}, followed by the densities observed at 20 m (314 col.m^{-2}, Table 2). Significant differences were found among depths in the last sampled survey in the LTIFA, where *M. daytoni* densities were significantly higher than in the MTIFA and NIFA (ANOVA, F = 34.54, $p < 0.01$; Table 2). At the MTIFA, very low densities between 0.3 and 2.3 col.m^{-2} were registered, whereas no colonies were observed in the NIFA (Table 2; Fig. 3).

M. daytoni also showed marked differences among areas and stations in terms of percentage cover (Table 3). The coverage in the last sampling survey (2009) on LTIFA was significantly higher compared to the MTIFA, and NIFA where no colonies were registered (ANOVA; F = 36.92; $p < 0.0001$; Table 3). Significant differences were also found among depths in LTIFA, where the highest coverage was observed at 30 m at the middle station (ANOVA; F = 33.08; $p < 0.0001$; Table 3). The coverage in the LTIFA also showed marked temporal variations with a significant increment between 1994 and 2009 at all depths. The coverage was significantly higher in 2009 compared with 1994 and 1998 in the inner station (ANOVA; F = 29.30; $p < 0.0001$) and also in the middle station (ANOVA, F = 37.06; $p < 0.0001$). This extraordinary percentage of coverage in the LTIFA was not registered in the MTIFA and NIFA. Indeed, the MTIFA registered very low coverage from 0.01 to 0.02% between 10 and 25 m, with a maximum value of 0.12 in at 30 m (Table 3). No colonies were observed in the NIFA neither in a second exploratory video survey performed in 2015 (5 years after the first survey in the same soft-bottom area) (Table 3).

3.1. *Species distribution models (SDMs)*

Taking into account the low colonization registered in the MTIFA and the absence of *M. daytoni* in the NIFA, the SDMs were generated for two data sets (one with LTIFA data only and another also including the MTIFA and NIFA stations) applying every nine algorithms (Sup. Material, Section 3 and 4 for the evaluation and mean model projection of single algorithm). Considering SDMs based on LTIFA data only (Fig. 4A, Sup. Material Fig. S3.1A), 119 of 180 resulted in models with high predictive accuracy meeting the requirements (TSS > 0.9) for the ensemble modeling (Sup. Material Fig. S3.2A). For a current projection of *M. daytoni* distribution in the year 2010 using the MTIFA and NIFA (Fig. 4B, Sup. Material Fig. S3.1B), 61 of 180 models contribute to the ensemble SDM (Sup. Material Fig. S3.2B). For the LTIFA ensemble model, the distance to the glacier front with an importance index value of 0.88 was identified as the most important environmental parameter influencing the distribution of sea pens in Potter Cove, followed by the bathymetry (0.31), the percentage of fine sediment (0.08) and the benthic position index (0.078). For the current *M. daytoni* distribution, the order of the parameters was the same with an importance index value of 0.77, 0.19, 0.15, 0.06, respectively. The cut-off threshold which converts the predicted habitat suitability vector into a binary value of presence/absence (Thuiller et al., 2016) was higher for the current distribution model (87.6%) than the one based on the LTIFA data only (70.6%).

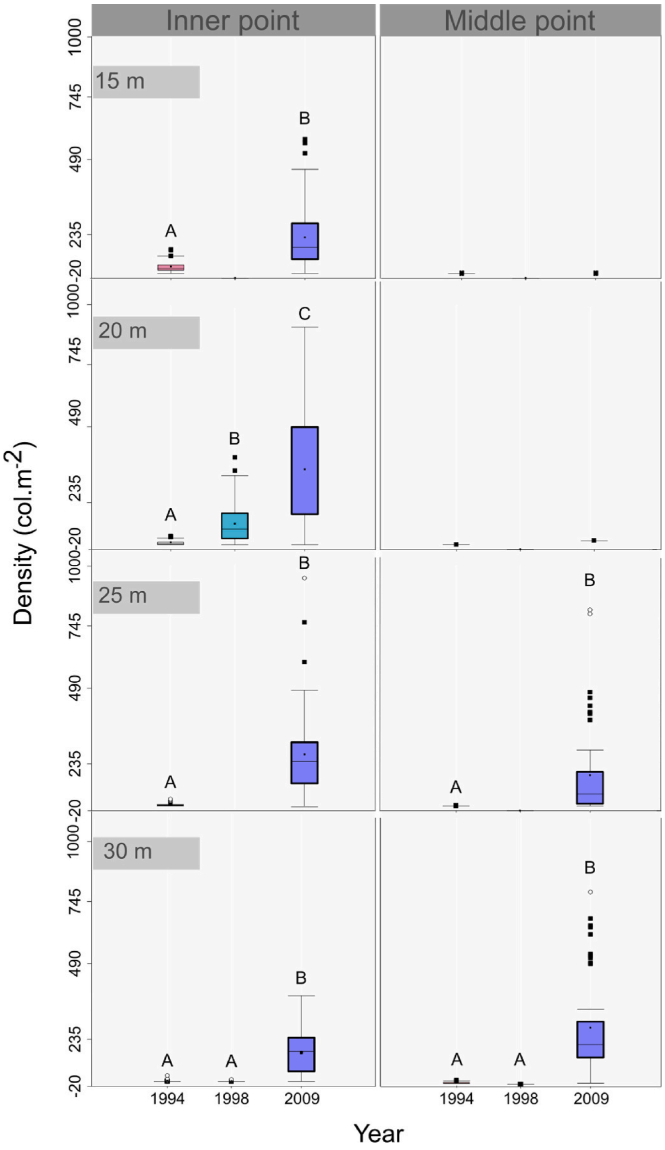

Fig. 2. Box plot of *Malacobelemnon daytoni* density in 1994, 1998 and 2009 at different depths, showing inner and middle stations in the Long-Term Ice-Free Areas (LTIFA) in Potter Cove. Different letters represent DGC test significant differences ($p < 0.05$). Box plot illustrates median, second and third quartile (upper and lower limit, respectively).

SDMs using the LTIFA data only shows habitat suitability higher than 75% for *M. daytoni* in the inner cove area close to the glacier current

Table 2
Densities of *Malacobelemnon daytoni* at 15, 20, 25 and 30 m in each sampled area between 1994 and 2015 at Potter Cove. Long-Term Ice-Free Areas (LTIFA); Mid-Term Ice-Free Areas (MTIFA) and New Ice-Free Areas (NIFA). – means no data.

Depth/Site	LTIFA						MTIFA	NIFA	
	Middle			Inner					
	1994	1998	2009	1994	1998	2009	2010	2010	2015
15	0	–	0	27.76 ± 23.08	–	149.5 ± 136.47	0.34 ± 1.67	0	0
20	0	4.17 ± 9.97	0	8.64 ± 10.88	86.84 ± 84.82	314.17 ± 265.11	0.68 ± 4.76	0	0
25	0	–	127 ± 192.5	4 ± 6.57	–	214 ± 183.59	0.51 ± 2.64	0	0
30	4.51 ± 6.71	0	466.2 ± 399.7	1.36 ± 4.01	0.44 ± 1.45	119.5 ± 86.74	2.3 ± 6.08	0	0

Data are expressed as col.m^{-2} mean ± Standard Deviation (SD).

front (Fig. 4A). With less exposure time to oceanic conditions, the current species distribution model shows low suitability for the species in these newer areas (Fig. 4B). In the outer cove and mainly near to the coast, for both models, the suitability is low or null, less than 25%. Standard deviation values (Stdv) are higher in the LTIFA model than in the current SDM (mean 36.8% of suitability error against 23.0%, respectively). However, both models are in between ±3 Stdv (Sup. Material, Fig. S3.1).

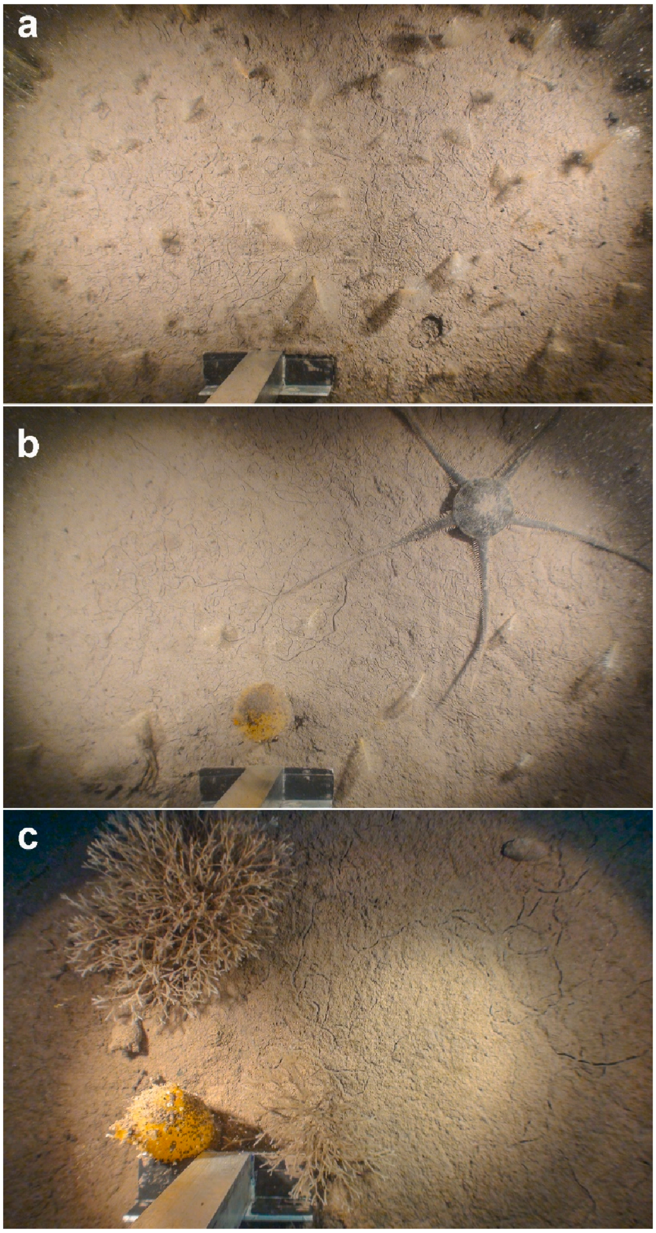

Fig. 3. Photographs taken in 2010 from (a) Long-Term Ice Free-Areas (LTIFA: > 60 years free of ice), showing a high density and % cover of *Malacobelemnon daytoni* (b) Mid-Term Ice Free-Area (MTIFA: 15 years free of ice), showing medium density values and (c) New Ice Free-Areas (NIFA), where no colonies were registered even after 10 years free of ice.

4. Discussion

The Antarctic soft-coral *M. daytoni* showed a distribution pattern at Potter Cove with marked differences in densities among areas with similar environmental conditions, especially substrate and depth, but with different exposure times to open sea conditions due to glacier retreat. Our results revealed the presence of a distinct spatial variation of this soft coral within areas separated by rather short distances (<1.3 km). High densities were found, as expected, in the LTIFA; in contrast, the MTIFA and NIFA showed very low abundances and complete absence of the species respectively. A marked shift at the assemblage level was recently reported in Potter Cove benthic systems, where the pennatulid *M. daytoni* was one of the species that contributed more to this change (Sahade et al., 2015). This sea pen became more prevalent and among the most abundant species in the new assemblage due to its significant increment in densities and distribution range. In just four years, between 1994 and 1998, *M. daytoni* showed a density increase of almost an order of magnitude, from ~9 to ~87 col.m^{-2} at 20 m depth in the inner cove but it was almost absent at deeper depths. Then, ten years later, ca. 15 from the first survey, a repeated sampling showed another 4-fold increase in its abundance at 20 m depth and three orders of magnitude increment at 30 m depth. Thus, in the LTIFA, we observed a ~20-fold increase of total *M daytoni* densities in 15 years (see Table 2). Therefore, *M. daytoni* not only showed an extraordinary outburst in its population growth but also extended its distribution to depths where previously it did not reach greater abundances. These results showed the capacity of the species of a high population turnover suggesting also a great colonization potential.

On the other hand, the sampling conducted in the MTIFA, areas with ca. 15 years of exposure to open sea conditions, showed that despite the species was present it had very low densities between 10 and 30 m depth. Indeed, *M. daytoni* densities values and percentage cover found here are between the lowest reported for the species in the cove. Similarly, the video survey were taken at the same locations and depth profiles of the NIFA five years after the first sampling of the area, so 10 years of exposure, did not show any colonization signal of *M. daytoni*. Therefore, the absence of *M. daytoni* colonies in soft-bottom areas with 10 years free of ice as well as the very low densities values in 15 years ice-free areas emphasize the necessity of answers to new questions such as 1) Why this species that show features of a colonizer and pioneer species did not colonize the NIFA? and 2) Why did it show such low abundance in the MTIFA when it is a short distance away from LTIFA? The questions become even more relevant considering that both areas could be considered environmentally suitable for their settlement and

Table 3
Percentage cover of *Malacobelemnon daytoni* at 15, 20, 25 and 30 m in Potter Cove in each sampled area between 1994 and 2015. Long-Term Ice-Free Areas (LTIFA); Mid-Term Ice-Free Areas (MTIFA) and New Ice-Free Areas (NIFA). – means no data.

Depth/Site	LTIFA						MTIFA	NIFA	
	Middle			Inner					
	1994	1998	2009	1994	1998	2009	2010	2010	2015
15	0	–	0	1.88 ± 2.05	–	2.60 ± 3.17	0.02 ± 2.12	0	0
20	0	0.06 ± 0.28	0	0.90 ± 1.33	4.25 ± 4.82	6.21 ± 6.35	0.01 ± 2.83	0	0
25	0	–	3.14 ± 4.64	0.38 ± 6.6	–	3.85 ± 3.53	0.02 ± 3.53	0	0
30	0.74 ± 1.05	0	11.08 ± 9.19	1.4 ± 4	0	2.56 ± 2.55	0.12 ± 4.23	0	0

Data are expressed as % mean ± Standard Deviation (SD).

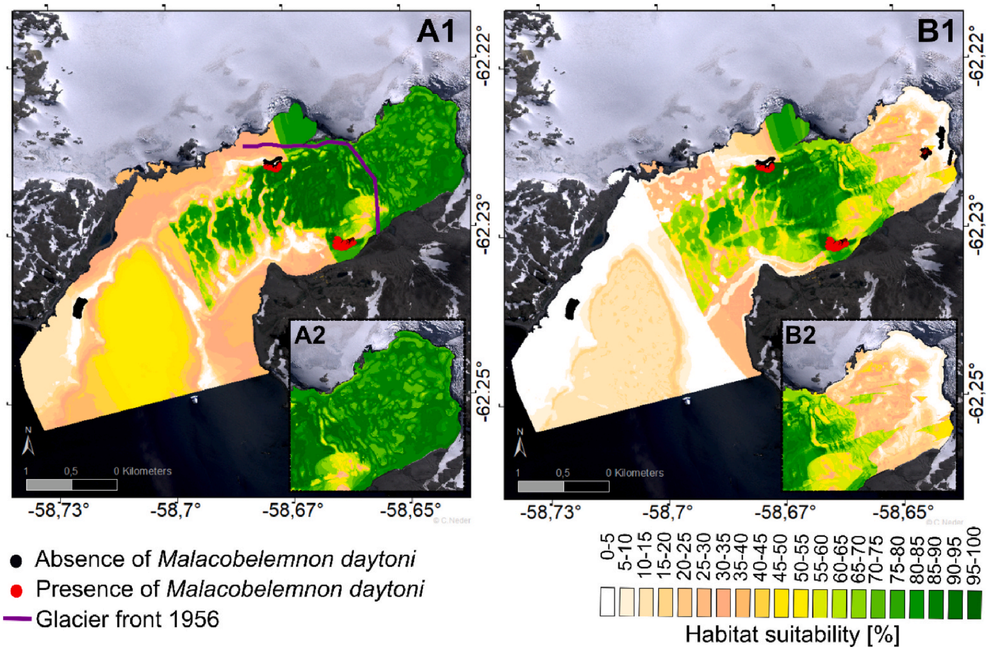

Fig. 4. Species distribution models for the two data sets showing the habitat suitability (from white-pink to yellow-green) at Potter Cove for *Malacobelemnon daytoni*. **A)** SDM is based on the LTIFA data **B)** SDM including the LTIFA, MTIFA, and NIFA data (all available data). Inner cove zooms in **A2** and **B2**. For standard deviation maps, refer to Sup. Material, Fig. S3.1. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

population development.

The exposure time of the seabed to open sea conditions of the newer areas, the MTIFA and NIFA, would have been an appropriate answer, especially considering low velocities of biological processes in Antarctic ecosystems, including colonization and population turnover (Stanwell-Smith and Barnes, 1997; Bowden et al., 2006; Barnes and Conlan, 2007). However, in the other examined area, the LTIFA, *M. daytoni* showed impressive population growth at time scales similar to the available in the MTIFA and NIFA. Due to the short distances separating the areas, it would be possible to think of the LTIFA as a population source for the other two areas. Moreover, a new island located close to the glacier front in the NIFA showed after 6 years of exposure a rich and well-developed assemblage suggesting that benthic colonization and succession can be faster than previously thought in Antarctica (Lagger et al., 2018). *M. daytoni* was not registered, and not expected, in these assemblages due to the rocky substrate of the island. Lagger et al. (2017) also reported high abundances values of epibenthic filter feeders such as ascidians and bryozoans on soft-bottom areas of the NIFA after just five years exposure periods. For these reasons, exposure times, particularly the 15 years of the MTIFA, seem to be enough for the establishment and development of this sea pen population and would not explain the scarcity of the species in these areas.

Closeness to the glacier front of the NIFA and MTIFA concerning LTIFA could indicate higher physical disturbances and stress as those caused by ice scour and sedimentation rates, intensified in turn by glacier retreat driven by the rapid climatic change of the Antarctic Peninsula (Cook et al., 2014). A recent work monitoring ice impact at Potter Cove showed higher scouring rates closer to Fourcade glacier termini, suggesting that calving growlers are an important factor for seabed disturbance (Deregibus et al., 2017). However, the ice that falls from the glacier cliffs usually produces floating brash and growlers with a diameter of no more than a few meters (Klöser et al., 1994). Thus, it would not represent a disturbance factor for the seabed deeper than 10 m. Ice-scour marks were not registered in the NIFA during the sampling work in the sediments below 15 m depth confirming that idea (pers. obs.). On the other hand, *M. daytoni* populations seem to effectively respond to ice disturbance as suggested by its abundances at 15 m depth of the LTIFA where ice action is considered an important disturbance keeping benthic assemblages with reduced diversity and dominated by *M. daytoni* and the bivalve *Laternula elliptica* (Sahade et al., 1998). Finally, considering that the glacier tongue is almost entirely land-based since 2016 (Jerosch et al., 2018), ice disturbance, by locally produced growlers, will be significantly reduced.

Sedimentation caused by the increased meltwater runoff from the retreating Fourcade glacier is also more intense close to the glacier front, where higher sedimentation rates were measured (Monien et al., 2011; Schloss et al., 2012; Pasotti et al., 2014). An increase in sedimentation rates can negatively affect filter feeders (Pakhomov et al., 2003; Thrush et al., 2004; Włodarska-Kowalczuk et al., 2005; Renaud et al., 2007; Włodarska-Kowalczuk and Węsławski, 2008; Pawłowska et al., 2011; Torre et al., 2012; Moon et al., 2015). Indeed, the major shifts reported on the assemblages of LTIFA were related to increased sedimentation rates at Potter Cove. However, *M. daytoni* was among the winning species in the new assemblages, suggesting sedimentation would not be an important stressor for these animals, at least at the present rates (Sahade et al., 2015). Similarly, experiments carried out at increasing concentrations of sediment up to 600 mg L^{-1}, had no significant effect on *M. daytoni* oxygen consumption, also suggesting this species can cope with high sediment concentrations in the water column (Torre et al., 2012). A reduction in food availability could be considered as a secondary effect of sedimentation since inorganic matter can effectively reduce primary production and associated secondary production (Deregibus et al., 2017; Hoffman et al., 2018). However, this sea pen is a species that can make use of a wide spectrum of resources (Servetto et al., 2017). That together with the allochthonous origin of the majority of the energetic resources for the benthic system at Potter Cove (Quartino et al., 2008, Marina et al., 2018), suggest sedimentation would not be an important factor preventing the establishment of *M. daytoni*. Then, unless sediment concentration can surpass a threshold limit of tolerance for the species, which is unknown at the moment, this factor and the ice disturbance would not satisfactorily explain the low colonization of this sea pen in the newer areas of Potter Cove.

Species Distribution Models proved to be valuable tools to predict the potential presence of a species under determined environmental conditions, including future scenarios of the same areas affected by environmental shifts (Beaumont et al., 2008; Guisan and Thuiller, 2005).

Here, SDMs were used to test the predicted distributions of *M. daytoni* in newly ice-free areas based on species occurrences in LTIFA and known environmental data of the newer areas. The idea was to test the model performance for these new habitats, which are rapidly increasing in Antarctica due to glacier retreat and ice shelves collapses. The model predicted high habitat suitability for *M. daytoni* in the inner cove including the newer areas. This was coincident with the initial thought of *M. daytoni* performing efficiently as a pioneer species and coincident with our current knowledge on the species biology and its responses to environmental shift suggesting potential rapid colonization for *M. daytoni*. Then, the model was run using distribution data of *M. daytoni* including also the newer areas (LTIFA, MTIFA, and NIFA). Contrary to the first case, this model predicted low habitat suitability for the new areas, despite the environmental similarities among the three sampled areas. Comparing both model outputs (see Fig. 4), there is coincident low habitat suitability for *M. daytoni* at the west coast in the mid- and outer stations of the LTIFA. However, major differences were evident in the inner area of Potter Cove between the LTIFA only data-based model and the model including also MTIFA-NIFA. The slight increase in the variable importance for the percentage of fine sediment within the models highlights this variable even when ranking the third position, to expose differences in the habitat suitability, whereas for both models high suitability of *M. daytoni* was related with a high percentage of fine sediment of among 65–80%. Distance to the glacier front took the first place in both models with a higher importance value in the LTIFA model, predicting high suitability for *M. daytoni* closer to the glacier front (Sup. Material, Section 5). Distance to the glacier can be associated with higher sedimentation and higher ice disturbance, that due to *M. daytoni* tolerance to sedimentation and a high population turnover rate (Torre et al., 2012; Servetto and Sahade, 2016; Servetto et al., 2017) would explain the success of the species under these conditions and the output of the LTIFA model predicting high suitability in the newer areas. However, when data of the newer areas that show a scarce or null presence of the species are included, the model predicted low suitability in these newer areas close to the glacier front. In this case, the variable can be associated with the period of sea-bottom exposure, e.g. habitat age, especially under a glacier retreat process like the one taking place at Potter Cove. Since the exposure time is not included in the modeling as a predictor, the difference between both models could be related to this variable or another random factor not considered. The LTIFA model predicted high habitat suitability for these newer areas, but since the LTIFA were free of glacier coverage for at least more than 60 years, the model could project a species distribution that included that time-lapse of the species population dynamics. Modeling the complete data set, the actual distribution in these newer areas predicted low suitability. Differences between models could be due to a time-lag between habitat availability and colonization. Then, a comparison between models could project a lethargy time for colonization of ca. 50 years for *M. daytoni.* The LTIFA model could be properly predicting the distribution in that time frame but failing in predicting distribution at this short-time of habitat availability. It could be possible, but this required that the colonization time would not be consistent with the registered population outburst, the dominance in heavily ice affected areas, and the reproductive strategy of this species with a rapid sexual maturation and more than one spawning per year, which suggest a high population turnover and also explain the population growth and dominance in highly disturbed areas (Sahade et al. 1998, 2015; Servetto et al. 2013, 2016, 2017). These results suggest that using SDMs to predict colonization processes in Antarctic new ice-free areas is still challenging and requires not only up-to-date observations and long-term researches but probably also, more caution than with other better-known environments.

The results of this study were unexpected since a species with all the characteristics to perform as an efficient pioneer, did not effectively colonize the newly available habitats. Moreover taking into account that in a fjord nearby (Marian Cove), two ascidian species *Molgula pedunculata* and *Cnemidocarpa verrucosa*, signed also as pioneer species performed well in a similar situation of new habitats opened after glacier retreat (Moon et al., 2015). Both ascidians species also colonized rapidly new rocky habitats in Potter Cove (Lagger et al., 2017). If time seems to be enough for *M. daytoni*, as previously discussed, and disturbance factors tolerable for the species, then what prevented the colonization process is still an open question. New hypotheses can be related to distance from source populations or still unknown tolerance limits of the species to physical factors like sedimentation. Another approach might consider that *M. daytoni* presented an episodic recruitment event between the sampling surveys on LTIFA, due to still unknown favorable conditions, which was not repeated in the following years. Episodic recruitments were also observed in Mc Murdo Sound where sponges showed important recruitment and growth during a decade following 2 or 3 decades of very low recruitment. Moreover, and strikingly, the settlement of these new sponges took place on artificial substrates but not on natural ones. A shift in food particle sizes and supply was hypothesized, but assessing the actual causal factors will demand more uninterrupted long-term data programs and experimental works (Dayton, 1989; Dayton et al. 2016, 2019). All these results suggest that predicting recruitment and colonization processes of the increasing Antarctic new ice-free areas is still far from being a straightforward task, even using valuable tools as SDMs. Despite a well-provisioned table, some guests fail to arrive.

4.1. *CRediT authorship contribution statement*

Cristian Lagger: Conceptualization, Methodology, Formal analysis, Investigation. Camila Neder: Conceptualization, Methodology, Software, Formal analysis, Visualization. Pablo Merlo: Photographic analysis, Formal analysis. Natalia Servetto: Conceptualization, Formal analysis, Supervision. Kerstin Jerosch: Methodology, Software. Ricardo Sahade: Conceptualization, Methodology, Supervision. All authors contributed to the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107447.

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