Vol. 750: 1–18, 2024
https://doi.org/10.3354/meps14731

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 5

Antarctic benthic species distribution models and compositional analysis in a coastal ecosystem under glacier retreat

Camila Neder[1,2], Kerstin Jerosch[3,*], Hendrik Pehlke[3], Luciana Torre[1,2], Ricardo Sahade[1,2,*]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto de Diversidad y Ecología Animal (IDEA), Ecosistemas Marinos y Polares, Córdoba 5000, Argentina

[2]Universidad Nacional de Córdoba (UNC), Facultad de Ciencias Exactas, Físicas y Naturales, Ecología Marina, Córdoba 5000, Argentina

[3]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, 27570 Bremerhaven, Germany

ABSTRACT: In the face of global climate change, the West Antarctic Peninsula has been identified as highly vulnerable due to rising temperatures and increased anthropogenic carbon emissions impacting its biodiversity. Species distribution models are useful tools for assessing habitat suitability and forecasting responses in a changing environment. At Potter Cove, glacier retreat has opened new ice-free areas for colonization while altering the environment through meltwater input and sediment run-off. This fjord serves as a case study to identify environmental predictors driving Antarctic zoobenthos distribution in a changing coastal ecosystem and to analyze the potential benthic colonization in areas strongly affected by glacier retreat. About 60% of the study area, equivalent to 5.45 km^2, was estimated to be suitable for zoobenthic occurrence. Potential spatial co-occurrence was identified in highly glacier-influenced areas. The interpretation of binary transformation thresholds emphasizes taxa-specific environmental requirements responding to glaciological, oceanographic, and sedimentological predictors, inferring particularities depending on their feeding strategies. A lower threshold value estimated a wider habitat extension. This study enhances our understanding of benthic responses to ongoing environmental shifts due to climate change in the Antarctic coastal ecosystem, emphasizing long-term research to increase our current predictive capacities and improve conservation and management strategies.

KEY WORDS: Habitat suitability models · Antarctic benthos · Polar regions · Coastal ecosystems · Climate change

1. INTRODUCTION

The Antarctic benthos can be identified as a distinct and relatively homogeneous unit, isolated from other oceans by the Antarctic Circumpolar Current and the Polar Front (Clarke & Crame 1992, Griffiths et al. 2009, Gutt et al. 2021). However, benthic assemblages show particular structural and diverse features driven by different local processes and environmental heterogeneity. For instance, fjord assemblages can be more complex and exhibit higher diversity patterns than their contiguous shelf counterparts at the West Antarctic Peninsula (WAP) and, therefore, are considered hotspots of benthic diversity (Grange & Smith 2013, Ziegler et al. 2017). The WAP is primarily affected by increasing atmospheric temperatures associated with anthropogenic CO$_2$ emissions, showing the highest Antarctic regional warming (Turner et al. 2020). This has led to significant oceanographic and cryosphere alterations, shaping the ecosystem structure of WAP fjords (Smale & Barnes 2008, Cook et al. 2016, Henley et al. 2019).

As a rule, environmental gradients act as filters for selecting species with appropriate traits, affecting

---

*Corresponding authors:
kerstin.jerosch@awi.de, rsahade@unc.edu.ar

Publisher: Inter-Research · www.int-res.com

functional divergence, and structuring the species composition assembly (Keddy 1992, Weiher & Keddy 1995, Sutton et al. 2021). Therefore, studying the environmental suitability and survival ability of different species in a changing environment has become crucial under the ongoing climate change process. In response to climate change, most WAP glaciers are retreating, resulting in increased terrigenous run-off, salinity variations, and frequent ice impacts structuring the benthic assemblages. This has a 2-fold effect on benthic ecosystems. On the one hand, it causes diversity and biomass losses (Smale & Barnes 2008, Moon et al. 2015). On the other hand, it opens up new ice-free areas, generating new habitats that can be colonized, gaining biomass, and possibly increasing diversity (Fillinger et al. 2013, Gutt et al. 2013). Notably, both processes were observed in Potter Cove, a fjordic ecosystem at the northern tip of the WAP, surrounded by the Fourcade glacier (Fig. 1). First, a sudden shift in the benthic assemblage was linked to increased sedimentation rather than ice scouring, suggesting that sedimentation rates could have surpassed a threshold forcing the ecosystem to a different equilibrium of species composition (Sahade et al. 2015, Torre et al. 2021), but glacier retreat opened newly available areas, allowing potential colonization (Campana et al. 2018, Lagger et al. 2018, Deregibus et al. 2023). Whether one process would prevail is an open question, emphasizing the need for predictive tools to assess potential biota responses.

In such a context, species distribution models (SDMs) are ecological niche-based models useful for assessing habitat suitability in time and space and forecasting possible responses in a changing environment (Soberón & Peterson 2005, Elith & Leathwick 2009, Peterson et al. 2011). These models capture the complexity of the ecosystem by assessing the associations of species with their environment, acknowledging their intrinsic physiological tolerance, biotic interactions, and spatial geographic distribution (Peterson & Soberón 2012). By linking the presence or absence of taxa with known environmental conditions, they also address data gaps in less accessible areas. Different platforms and studies enable the

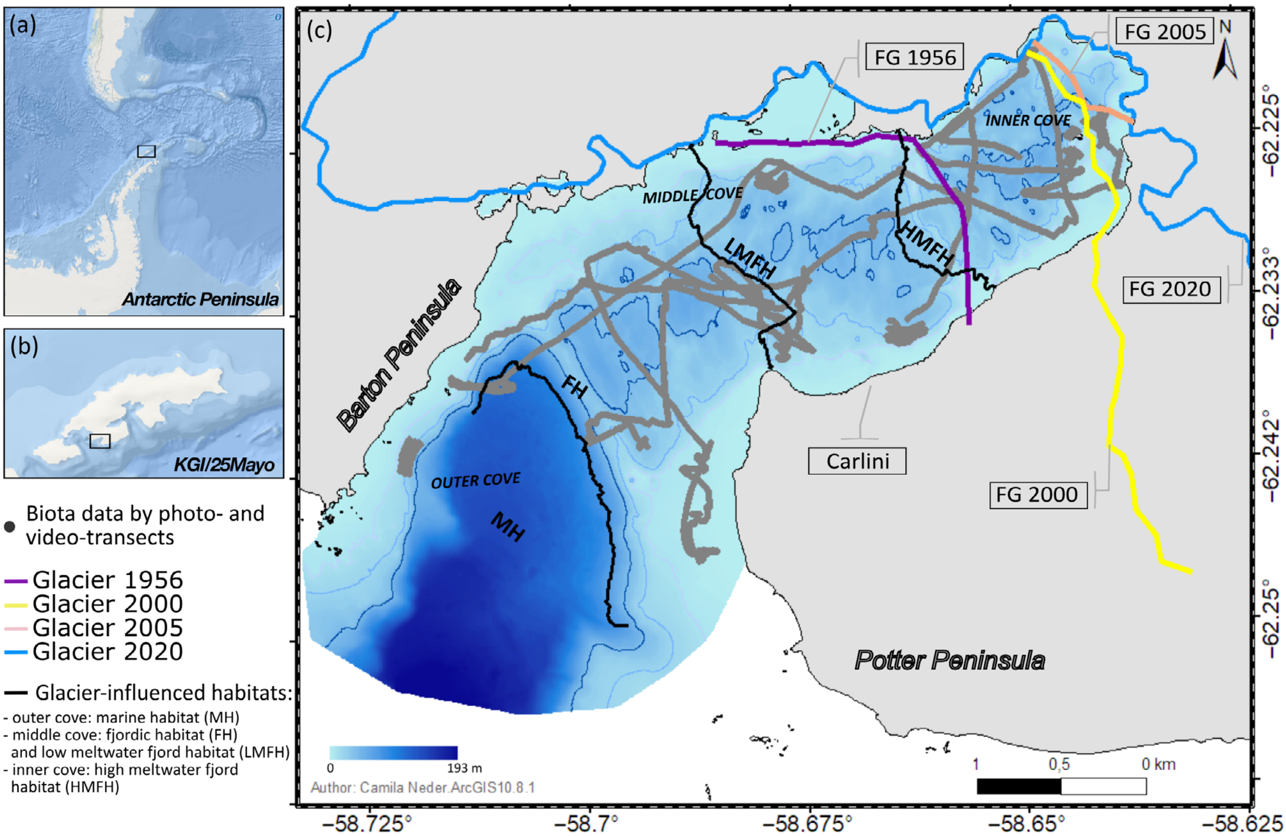


Fig. 1. Study area: (a) West Antarctic Peninsula, (b) King George Island (KGI)/25 de Mayo Island where Potter Cove is located, (c) Potter Cove ecosystem surrounded by Fourcade glacier (FG) and biota data imagery survey. FG retreats caused meltwater and sediment run-off input along the southern coast and the northern glacier front, dividing 4 different habitats in the outer, middle, and inner cove. Grey lines represent video surveys

development and application of single SDMs and ensemble models (Araújo & New 2007, Thuiller et al. 2009, 2021). However, calibration remains critical for effective model transferability, even when accounting for the error of simplifying complex processes at a particular scale and resolution (Araújo & Guisan 2006, Cerasoli et al. 2021, Guillaumot 2021). Therefore, using SDMs, we aimed to (1) identify the environmental predictors that drive Antarctic zoobenthos distribution in a changing coastal ecosystem and (2) analyze the potential colonization and co-occurrence of the benthic assemblage in areas strongly affected by glacial retreat.

2. MATERIALS AND METHODS

2.1. Study area

Potter Cove is a ~9 km^2 fjord in the 25 de Mayo/King George Island, South Shetlands, where the Argentine Carlini Station is located (Fig. 1). This ecosystem has been studied for more than 3 decades at different scales and organizational levels, using different approaches that point to a high glacier influence in configuring the ecosystem structure and function (Klöser et al. 1996, Quartino et al. 2001, Wiencke et al. 2008, Schloss et al. 2012, Torre et al. 2014, Sahade et al. 2015, Abele et al. 2017, Jerosch et al. 2019, Alurralde et al. 2020, Braeckman et al. 2021, Rodriguez et al. 2022, Latorre et al. 2023; among others). Fourcade glacier has been retreating, with an ice loss of almost 75% of the total ice cover recorded in 2000 (loss of 64 129 m^2 yr^{-1} in only 5 yr) and a maximum rate, considering only the last 2 decades, of 2.175 m yr^{-1} accounting for its perimeter (Neder 2023). Thus, according to the environmental characteristics, the cove has been categorized into 4 different habitats from outer to inner cove with increasing glacial influence: outer cove, consisting of (1) marine habitat (MH); middle cove, consisting of (2) fjordic habitat (FH) and (3) low meltwater fjord habitat (LMFH); and inner cove, consisting of (4) high meltwater fjord habitat (HMFH) (Jerosch et al. 2018, Neder et al. 2022).

2.2. Benthic species records

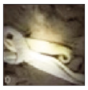
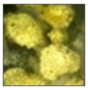
A data set of previously analyzed still photographs obtained in Potter Cove during the summers of 2008/2009 and 2010/2011 (Zamboni 2011, Sahade et al. 2015, Lagger et al. 2017, 2018, 2021) was extended with subaquatic video material captured during 2016 and processed using SANYO VMS 1.8 software, providing a final biota data set of 37 075 points (Fig. 1). The analysis identified and registered targeted macrobenthic invertebrate taxa and the sea floor structure within 1 s of video from a total of 18 h 34 min of video (622 341 still images). The analysis covers a diverse range of area sizes, as the distance to the seafloor was not constant. Images without a visible bottom were excluded. Subsequently, samples were georeferenced by matching GPS records from boat trips with recorded video time, following Weber (2017).

In this study, we focused on 8 conspicuous key macrobenthic taxa of Antarctic zoobenthos, emphasizing their ecosystemic importance in terms of their abundances, their shifts in response to climate change observed in Potter Cove, and their prevalence (Sahade et al. 2015, Lagger et al. 2017, 2018, 2021). The selected taxa were a pennatulid (*Malacobelemnon daytoni*), a sea star (*Odontaster validus*), a nemertean (*Parborlasia corrugatus*), an ascidian (*Molgula pedunculata*), a sponge (*Mycale acerata*), isopods (Serolidae spp.), a bivalve (*Laternula elliptica*), and a polychaete of the subclass Errantia (1 morphotype, species not identified). Table 1 shows some life traits of the investigated taxa. The presence/absence data of selected species in a pixel grid (5 m × 5 m) were deduplicated to avoid overprediction and improve transferability. All records outside the range of environmental predictors were removed. When records differed in the presence or absence of a taxon within the same pixel grid, presence was kept as an observation. Prevalence of each taxon was identified (Fig. 2). We used presence/absence records to enhance distribution prediction due to their proximity to natural environmental range boundaries and relatively easy accessibility (Wisz & Guisan 2009, Fernandes et al. 2019, Liao & Chen 2022, Neder 2023).

2.3. Environmental predictors

The environmental predictors were selected from a set of 41 variables with a spatial resolution of 5 m × 5 m (25 m^2) covering a study area of ~7 km^2 that characterized the environment of Potter Cove during summers between 2010 and 2015 and the glacier ice-free area for 2020 (Neder 2023). The variables were rasterized from original *in situ* data by applying geostatistical models, other interpolation tools in ArcGIS (ESRI) (Neder et al. 2020), and the dynamical FESOM-C model (Neder et al. 2022). Habitat characterization groups the environmental predictors based

Table 1. Life traits of selected benthic species: sea pen *Malacobelemnon daytoni*, sea star *Odontaster validus*, nemertean *Parborlasia corrugatus*, ascidian *Molgula pedunculata*, sponge *Mycale acerata*, isopod of the family Serolidae, bivalve *Laternula elliptica*, polychaete of the subclass Errantia (1 morphotype, species not identified)

	Benthic taxon	Substrate	Feeding strategy	Mobility	Reproduction and growth
	*M. daytoni* (Octocorallia)	Soft	Suspension-feeder	Sessile	Annual reproduction, rapid sexual maturity, high growth rate, lecithotrophic larvae
	*O. validus* (Asteroidea)	Hard and soft	Predator/ scavenger	Mobile	Annual reproduction, high fecundity, demersal planktotrophic larvae
	*P. corrugatus* (Pilidophora)	Soft	Predator/ scavenger	Mobile	Annual reproduction, planktotrophic larvae
	*M. pedunculata* (Ascidiacea)	Hard and soft	Filter-feeder	Sessile	Annual reproduction, lecithotrophic larvae
	*M. acerata* (Demospongiae)	Hard and soft	Filter-feeder	Sessile	Annual reproduction, fast-growing, planktonic larvae
	Serolidae (Malacostraca)	Soft	Scavenger/ deposit-feeder/ suspension-feeder	Vagile	Annual or biannual reproduction, sexual, incubated eggs
	*L. elliptica* (Bivalvia)	Soft	Filter-feeder	Sessile (infaunal)	Annual reproduction, lecithotrophic larvae
	Errantia (Polychaeta)	Soft	Deposit-feeder	Mobile	—

on similar processes or their comparable descriptions to characterize the habitat. This included ocean terrain (bathymetry, benthic position index, slope), limits of the marine area (distance to the coast), glaciology (distance to the glacier and age of ice-free habitat), sediment type (grain size and hard substrate probability), geochemical components (iron and silica), temperature and salinity at different water column levels, bed sheer at different levels of stress, current velocities at different ranges, and suspended particulate matter (SPM; minimum, mean, median, and maximum concentration).

For an optimum balance between the sensitivity and precision of the models, the initial set was reduced to 28 predictors based on ecological relevance for benthic species, importance analysis, correlation, multicollinearity, zero and near-zero variance, and spatial autocorrelation. To avoid overfitting and enhance predictive power, predictors were selected following the principle of parsimony. Environmental predictors with an importance of $<1\%$ assessed by a generalized boosting model (Guillaumot 2021), a high Spearman rank correlation coefficient ($r_S > 0.6$), and a variance inflation factor (VIF) >10 (Gokmen et al. 2022) were excluded, keeping only 1 predictor per group. Given the number of environmental predictors considered, the range of analysis of the VIF index was insufficient to determine the inflation factor. However, it allowed us to identify and eliminate covariates with high multicollinearity and to re-run the analysis to a successive reduction below the indicated limit (Zuur et al. 2010), finally reaching 9 selected predictors related to glacier dynamics, benthic morphology, water masses, and exogenous material input from terrestrial to marine ecosystems.

The 9 selected environmental predictors with ecological and statistical relevance (final $r_S < 0.7$; VIF < 5) characterizing the marine and periglacial ecosystem at Potter Cove for further input data in modeling were (1) oceanographic: bathymetry (m), mean temperature in the water column (°C), median velocity of current (m s^{-1}), distance to the coast (m), and slope (°); (2) glaciological: distance to Fourcade glacier in 2020 (m); and (3) sedimentological: the median and maxi-

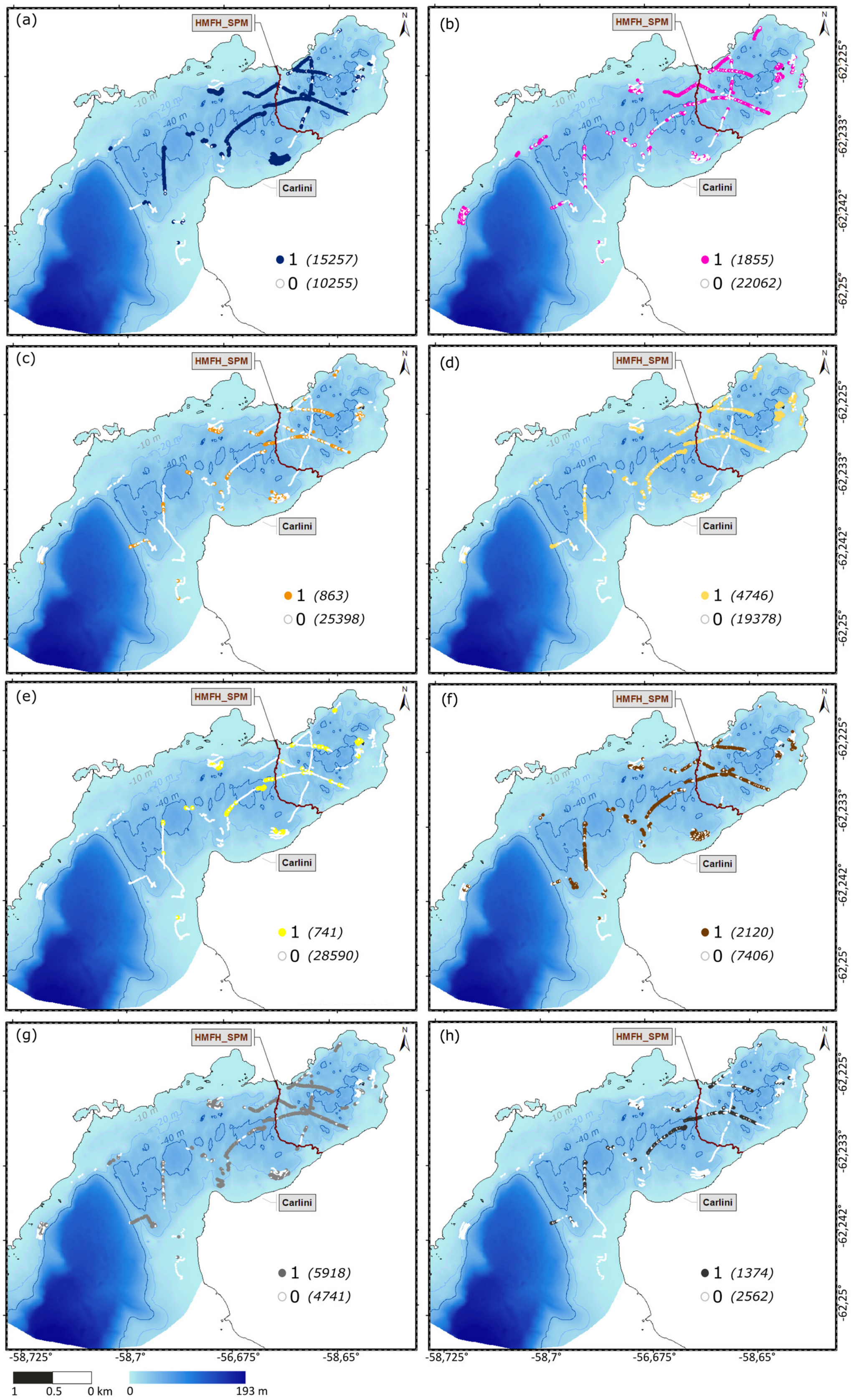


Fig. 2. Spatial distribution of presences (1) and absences (0) for benthic taxa with a resolution smaller than 5 m distance (the total numbers of presence and absence of records before deduplication of data for prevalence information are shown in *italics*). (a) Pennatulid *Malacobelemnon daytoni.* (b) Sea star *Odontaster validus.* (c) Nemertean *Parborlasia corrugatus.* (d) Ascidian *Molgula pedunculata.* (e) Sponge *Mycale acerata.* (f) Isopod (family Serolidae). (g) Bivalve *Laternula elliptica.* (h) Polychaete (subclass Errantia). In each panel, the brown line shows the division of the high glacier-influenced area delimited by the high meltwater fjord habitat (HMFH)

mum concentration of SPM (mg l^{-1}) and mean grain size (mm). For rasterization specifications and spatial resolutions of these selected predictors, refer to Fig. S1 and Table S1 in the Supplement at www.int-res.com/articles/suppl/m750p001_supp.pdf.

2.4. Modeling: calibration and evaluation

Five SDM algorithms were applied. In earlier studies, 4 algorithms exhibited strong performance for marine species in particular: generalized linear model (GLM), generalized additive model (GAM), generalized boosting model (GBM, equivalent to boosted regression trees), random forest (RF), and surface range envelope (SRE, equivalent to BIOCLIM), a straightforward algorithm that is frequently used (Reiss et al. 2011, Neder 2016, Chaabani et al. 2019, Jerosch et al. 2019, Guillaumot et al. 2021). Data partitioning in model calibration followed default settings as defined by the R package 'biomod2' v3.5.1 (Thuiller et al. 2021), but has implications for model performances (Guillaumot et al. 2019). To improve model performance, we adjusted the classic 70–30 cross-validation (Thuiller et al. 2009) to a block partitioning calibration (Muscarella et al. 2014, Guillaumot et al. 2021). Such calibration accounted for spatial autocorrelation and spatial distribution of biological records using the 'blockCV' v2.1.4 package by applying specific functions (Valavi et al. 2019). The function 'SpatialAutoRange' calculated the optimal block size over which observations are independent, distinguishing alternative environmental conditions for potential habitat distinction, and the 'spatialBlock' generated blocks exclusively where biological records exist. As a result, an optimal block size of 1439 m enables a maximum partition of 12 blocks for Potter Cove, which was halved for improved time efficiency (Fig. S2). This calibration led to the computation of 30 single models (5 algorithms × 6 iterations), each subjected to 10 permutations using R software v.4.1.2 (R Core Team 2022). The workflow is shown in Fig. S3. Computational R networking is available in Neder & Pehlke (2024).

The performance of the model was estimated by 2 evaluation metrics: true statistics skills (TSS) and relative operating characteristic. TSS compares the number of correctly predicted presences and absences against a random distribution, and is frequently used to assess and combine SDMs according to their performance. SDMs with a TSS >0.5 are considered fair+, while SDMs with a TSS >0.6 are good (Allouche et al. 2006, Thuiller et al. 2010). A final ensemble model (EM) was selected employing a weighted mean approach ('EWmean' function) with a TSS threshold set above 0.5, 0.6, or 0.7, dependent on the maximum evaluation metrics of the single models per taxon (Thuiller et al. 2021). Such an EM was chosen because it resulted in better overall performance by weighing the single models that scored higher during the evaluation process (Marmion et al. 2009, Neder 2023). Additionally, we evaluated the impact of environmental predictors on species' habitats following Thuiller et al. (2021) by assessing the importance and response of such predictors. The importance of each environmental predictor was calculated per taxon for all single algorithms and ensemble models (maximum predictor value: 100%) and accumulated for all analyzed taxa. Response curves were used to determine the range of variability in environmental predictors that constrained habitat suitability for each taxon.

2.5. Post-processing analysis: binary transformation and compositional analysis

Habitat suitability analysis for each taxon was conducted to estimate potential benthic presence, colonization after glacier retreat, and co-occurrence of taxa following the 'predict first, assemble later' procedure (Ferrier & Guisan 2006). Habitat suitability (values between 0 and 1000) was transformed into a binary map to indicate suitable (1) or unsuitable (0) habitats for taxon potential presence or absence, respectively, within the study area. Since the threshold value for transformation can influence the extent of predicted distribution, 3 binary transformation methods were assessed as thresholds: (1) sensitivity and specificity maximization, defined as the sum of mentioned metrics from the EM, where sensitivity and specificity measure the proportion of observed presence and observed absences that the model correctly predicts, respectively; (2) mean habitat suitability, calculated as an average of the predicted value at each pixel of the study area; and (3) the 'cut-off' parameter from the 'FindOptim.Stat' function of 'biomod2,' which assesses a sequence of 100 thresholds ranging from the minimum to the maximum of the predicted habitat suitability into binary data, and compares the outcome with data observations for TSS evaluation, and sensitivity and specificity calculations (Liu et al. 2005, Torres & Jayat 2010, Thuiller et al. 2021). The last method was selected for the final binary transformation since it applies multiple threshold simulations, keeping the one that maximizes the TSS value, resulting in the most conservative method. Each presence pixel was assumed to represent at least 1 individual. The potential benthic colonization after the Fourcade glacier retreat until 2020 was estimated by calculating such suitable habitat within the ice-free area from 1956 to 2000 using the 'Clip' tool (ESRI 2016).

Further, taxa distribution analysis within a shared habitat enables inferences on potential taxa co-occurrences and associations. Thus, compositional analysis involves overlapping binary maps of all studied taxa and counting the analyzed taxa that might occur at each pixel in the study area. Finally, compositional information was represented as (1) a map highlighting the hotspot suitable for the higher amount of analyzed taxa (i.e. co-occurrence map) and (2) an exclusive habitat map that shows the suitable area for the presence of only 1 taxon.

3. RESULTS

3.1. Species occurrences and environmental range

The benthic taxa registered in this study co-occurred throughout the cove, mainly in the middle and inner coves (Fig. 2). Initial analysis of benthic records revealed notable occurrences of the pennatulid *Malacobelemnon daytoni* (Fig. 2a), followed by the bivalve *Laternula elliptica* (Fig. 2g) and the ascidian *Molgula pedunculata* (Fig. 2d). The sea star *Odontaster validus* (Fig. 2b) had the broadest distribution, occurring within areas with different substrates (both soft and hard substrates). A potential habitat overlap was evident considering a mean depth of ~25 m and <1 km away from the glacier front, with frequent occurrences in areas estimated to be ice-free for at least a century (Table 2). None of the analyzed taxa was exclusively observed in recently ice-free (since 2000) or old ice-free areas (before 1956).

Environmental variability range among initial predictors, such as salinity, water temperature, current velocity, and sediment iron and silica content, was similar for zoobenthic presence (Table S2). However, species such as *M. pedunculata* were present at a higher current velocity, while others such as Serolidae, Errantia polychaetes, and *Mycale acerata* were present in calmer waters. Serolidae were particularly frequent in calm waters but tolerated higher currents as well. Six of 8 taxa were observed in areas with a

Table 2. Mean ± SD of environmental predictors for the presence of 8 benthic taxa (full names given in Table 1). Environmental predictors were input for species distribution models (SDMs), adding the exposure time of the ice-free area. SPM: suspended particulate matter

	M. daytoni	*O. validus*	*P. corrugatus*	*M. pedunculata*	*M. acerata*	Serolidae	*L. elliptica*	Errantia (Polychaeta)
Bathymetry (m)	31.24 ± 9.45	24.27 ± 9.68	32.81 ± 8.64	33.49 ± 10.34	38.22 ± 8.72	30.89 ± 8.26	29.00 ± 9.33	38.20 ± 7.44
Distance to coast (m)	410.54 ± 165.88	272.57 ± 188.85	394.82 ± 163.67	367.88 ± 213.37	456.02 ± 177.48	431.90 ± 168.70	347.32 ± 176.64	479.46 ± 132.39
Distance to glacier (m)	674.36 ± 319.06	475.18 ± 328.68	640.74 ± 352.24	581.77 ± 328.77	631.14 ± 242.18	817.32 ± 367.76	699.64 ± 449.75	670.75 ± 238.63
Mean grain size (mm)	0.03 ± 0.22	0.89 ± 3.27	0.03 ± 0.47	0.09 ± 0.99	0.01 ± 0.02	0.14 ± 1.26	0.23 ± 1.39	0.01 ± 0.01
Slope (°)	8.83 ± 5.82	13.53 ± 9.43	10.29 ± 7.05	10.67 ± 8.36	9.07 ± 7.07	7.60 ± 4.86	8.48 ± 5.46	7.48 ± 4.82
Maximum SPM (mg l^{-1})	268.64 ± 89.10	289.71 ± 96.37	257.75 ± 61.56	317.18 ± 130.60	421.39 ± 176.58	250.39 ± 55.03	286.47 ± 98.26	335.61 ± 150.69
Median SPM (mg l^{-1})	7.75 ± 8.27	10.78 ± 8.83	7.04 ± 6.91	11.14 ± 10.54	17.42 ± 13.60	5.59 ± 6.37	8.89 ± 8.20	11.08 ± 12.27
Weighted mean water column temperature (°C)	1.19 ± 0.05	1.21 ± 0.05	1.19 ± 0.06	1.20 ± 0.04	1.18 ± 0.04	1.19 ± 0.04	1.20 ± 0.06	1.19 ± 0.04
Median current velocity (m s^{-2})	0.04 ± 0.02	0.05 ± 0.04	0.03 ± 0.02	0.04 ± 0.03	0.06 ± 0.04	0.03 ± 0.02	0.04 ± 0.02	0.04 ± 0.03
Ice-free time (habitat age) (yr)	119 ± 65	84.22 ± 67.30	112.70 ± 68.06	98.99 ± 66.93	112.84 ± 44.94	146.11 ± 77.70	114.93 ± 79.99	117.35 ± 53.23

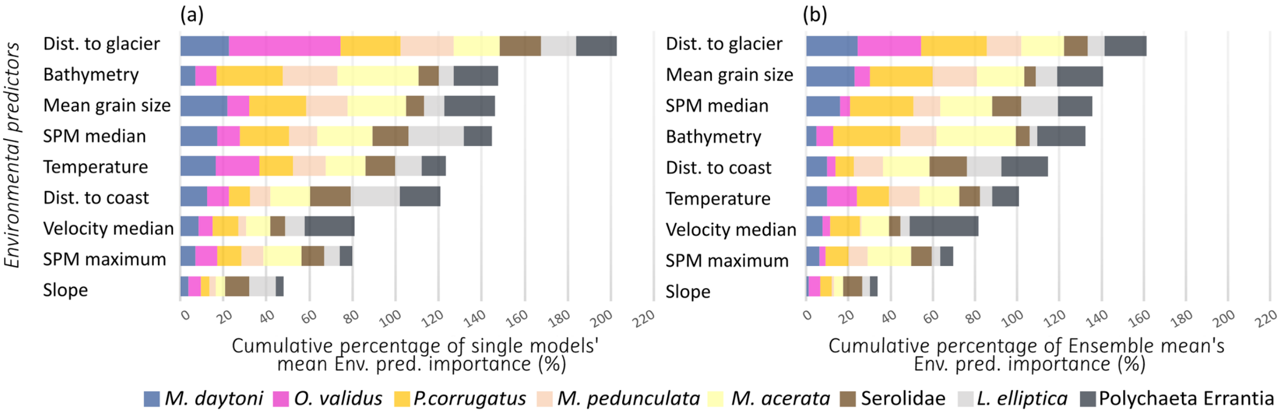


Fig. 3. Environmental predictor importance. (a) Cumulative percentage of mean environmental predictor importance per taxon considering the 5 single models and (b) cumulative percentage of environmental predictor importance by ensemble weighted mean model. Full taxon names are given in Fig. 2

high maximum concentration of suspended particulate matter (~694 mg l^{-1}) but a median concentration ranging from ~29 to 43 mg l^{-1} (Table S2). The majority of records were from fine-soft substrates like silt and clay, with variations in mean grain size ranges (Table S1).

3.2. Importance of environmental predictors and benthic habitat suitability

Both single and ensemble weighted mean models effectively identified the environmental predictors influencing benthic taxa distribution, with variations in predictor importance among species. The most important was distance to the glacier, followed by mean grain size, the mean concentration of SPM, bathymetry (or bathymetric position index associated with topography in the case of the initial analysis of environmental predictors), and distance to the coast (Fig. 3). In particular, distance to the glacier was the most important predictor for *M. daytoni* and *O. validus*, bathymetry for *Parborlasia corrugatus* and *M. acerata*, mean grain size for *M. pedunculata*, distance to the coast for Serolidae, SPM mean concentration for *L. elliptica*, and mean current velocity for Errantia polychaetes.

The benthic taxa analyzed showed high habitat suitability at the center of the cove, ~200 m away from the coast. Serolidae showed the highest mean habitat suitability (423.7), while *M. acerata* had the lowest (209.5; Table 3). *M. daytoni* showed an extensive suitable area in the middle cove, while habitat suitability for mobile or vagile species such as *O. validus* and Serolidae was more homogeneous throughout the entire cove. Notably, *O. validus* inhabited both hard and soft sediment, with higher habitat suitability along the northwest coast compared to Serolidae (Fig. 4).

EMs outperformed single models for all analyzed taxa, although with varying standard deviations

Table 3. Threshold for binary conversion of habitat suitability (values of 0–1000) to suitable habitat for potential taxa presences (values of 0–1) by 3 different methods. Asterisk (*) marks the selected method. The high meltwater fjordic habitat (HMFH) delimits the high glacier-influenced area. Full names of benthic taxa are given in Table 1. TSS: true statistics skills

	Total suitable habitat (km^2)	Suitable habitat in HMFH area after glacier retreat (km^2)	Sensibility and specificity maximization	Mean habitat suitability	Cut-off threshold*	Evaluation of ensemble model (TSS)
M. daytoni	1.990	0.451	192.637	391.465	744	0.927
O. validus	2.430	0.558	182.640	370.276	451	0.886
P. corrugatus	1.134	0.329	185.895	305.072	556	0.860
M. pedunculata	4.235	0.739	188.668	380.472	504	0.887
M. acerata	0.853	0.291	187.969	209.470	464	0.893
Serolidae	3.373	0.678	175.663	423.718	408	0.757
L. elliptica	2.675	0.762	187.894	405.885	457	0.882
Errantia	1.486	0.226	179.492	319.716	570	0.795

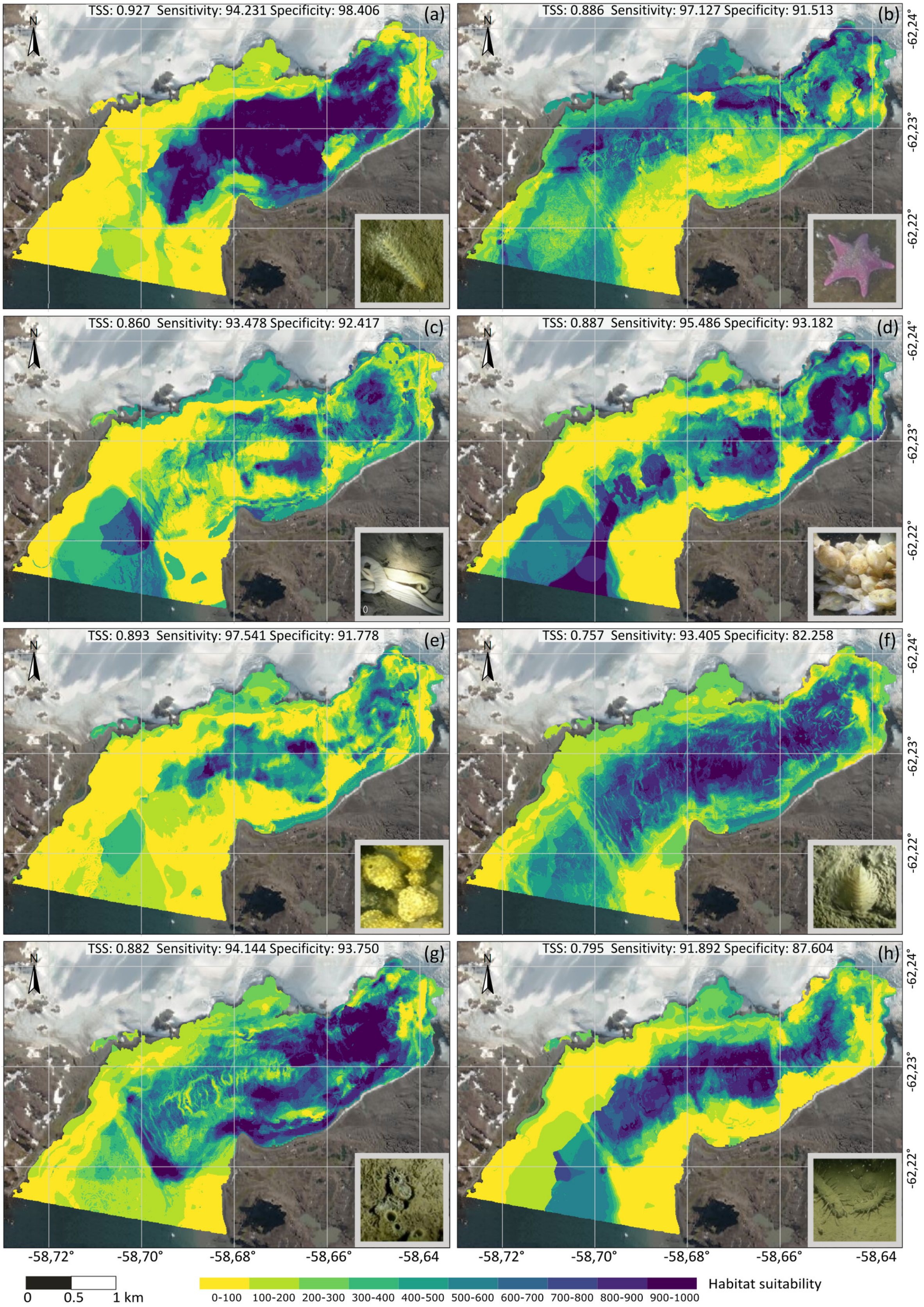


Fig. 4. Habitat suitability maps for modeled taxa by a weighted mean ensemble model based on single models surpassing the TSS evaluative metric threshold defined per taxon. (a) Pennatulid *Malacobelemnon daytoni*. (b) Sea star *Odontaster validus*. (c) Nemertean *Parborlasia corrugatus*. (d) Ascidian *Molgula pedunculata*. (e) Sponge *Mycale acerata*. (f) Isopod (family Serolidae). (g) Bivalve *Laternula elliptica*. (h) Polychaete (non-identified species, subclass Errantia). Satellite image source: OpenStreetMap, Projection EPSG 4326

among them (Fig. S4). Achieving TSS values indicating very good to excellent models (TSS 0.756–0.927; Fig. 4), significant deviations occurred in the unsampled outer cove (>50% suitability error), particularly for *P. corrugatus* and the polychaete (Fig. S4c,h). Intermediate deviations (20–35%) were observed along the northwest coast, close to the glacier front. Conversely, *O. validus* and *L. elliptica* showed minor deviations throughout the study area. Variations in TSS thresholds among algorithms and taxa influenced the constitution of the EM (Fig. S5). Machine learning algorithms, particularly GBM and RF, outperformed linear and additive approximations such as GLM and GAM. Meanwhile, straightforward algorithms such as SRE demonstrated poor or deficient performance. GLM consistently estimated responses, including those to bathymetry and distance to the glacier and coast (see Fig. S6). Species with different feeding strategies (i.e. *O. validus*, *P. corrugatus*, and Serolidae) showed minor variation in their habitat suitability, with intermediate–high values observed across the different cove habitats (Fig. 4). Although single models for predators or scavenger-generalist species showed less accuracy (TSS 0.01–0.71; Fig. S5), the EM performed very well (>0.85; Table 3).

3.3. Suitable habitat for potential presence and compositional analysis

A total area of ~5.45 km^2 resulted in a suitable habitat for the studied taxa in Potter Cove (Figs. 5 & 6, Table 3). All performed models led to a homogeneous 'cut-off' value (between 408 and 570) except for the pennatulid, which had a higher threshold of 744. Regarding the total suitable habitat extent in Potter Cove, *M. pedunculata* showed the most extensive area, followed by Serolidae and *L. elliptica*. *M. acerata* showed the smallest extent (Table 3).

A remarkable potential co-occurrence arose approximately between 100 and 300 m from the coast, particularly for those taxa with similar feeding types (Fig. 6b). The middle and inner coves showed a complex assemblage formed by 4–8 benthic taxa with potential co-occurrence, becoming more complex at greater depths (24–45 m). *M. acerata* and the polychaete showed the highest habitat overlap with negligible areas of exclusive presence (500 and 1850 m^2, respectively). The largest exclusive habitat among the analyzed taxa was identified for *O. validus* in the middle cove along the northern coast and for *L. elliptica*, Serolidae, and *M. daytoni* along the southern coast. Along the northwest coast towards the outer cove, *M. pedunculata* had an exclusive habitat, partly shared with Serolidae and *P. corrugatus* at deeper depths (Fig. 6a).

Between 1956 and 2020, glacial retreat resulted in approximately 1.6 km^2 of ice-free area, of which 1.35 km^2 could be colonized by benthic taxa, primarily in the inner cove. Considering the high glacier-influenced area delimited by the HMFH, *L. elliptica* had potentially colonized the most extensive area, followed by *M. pedunculata* and Serolidae (0.762, 0.739, and 0.678 km^2, respectively), while the polychaete had the narrowest extent (0.226 km^2; Table 3). Serolidae potentially dominated newly ice-free areas that had been open for at least 2 decades but were predicted to be absent in areas free of ice for the past 10 yr, where *M. pedunculata* and *O. validus* may colonize. The ice-free area that opened between 2018 and 2020 at the north of the cove, within <150 m from the glacier front, was unsuitable for all analyzed taxa (Fig. 6a).

4. DISCUSSION

4.1. Benthic habitat suitability

The 8 analyzed taxa distributed across the cove showed intermediate to high habitat suitability in the inner and middle cove areas, leading to a potential coexistence of sessile species that could form a mixed benthic assemblage with sessile suspension- and filter-feeders together with mobile predators and scavengers. These areas are characterized by soft sediment, shallow water (<40 m), intense water dynamics, and high SPM concentrations (Neder et al. 2022). Most of the samples were collected in soft-sediment areas within the cove, with fewer samples collected in higher-risk zones near the northern glacier front or across the outer coast in the southern cove (Fig. 1), leading to higher deviation in such zones. However, model calibration allows for an accurate transferability.

A high habitat suitability indicates a greater likelihood of taxa occurrence rather than encountering their actual presence. However, the binary transformation analysis can facilitate the prediction of species distributions. A pixel with habitat suitability higher than the 'cut-off' value indicates potential presence, while one lower than this threshold indicates potential absence. The chosen cut-off threshold also hints at the ecological requirements of the taxa in a given area, potentially serving as an environmental filter index while maximizing model sensitivity and

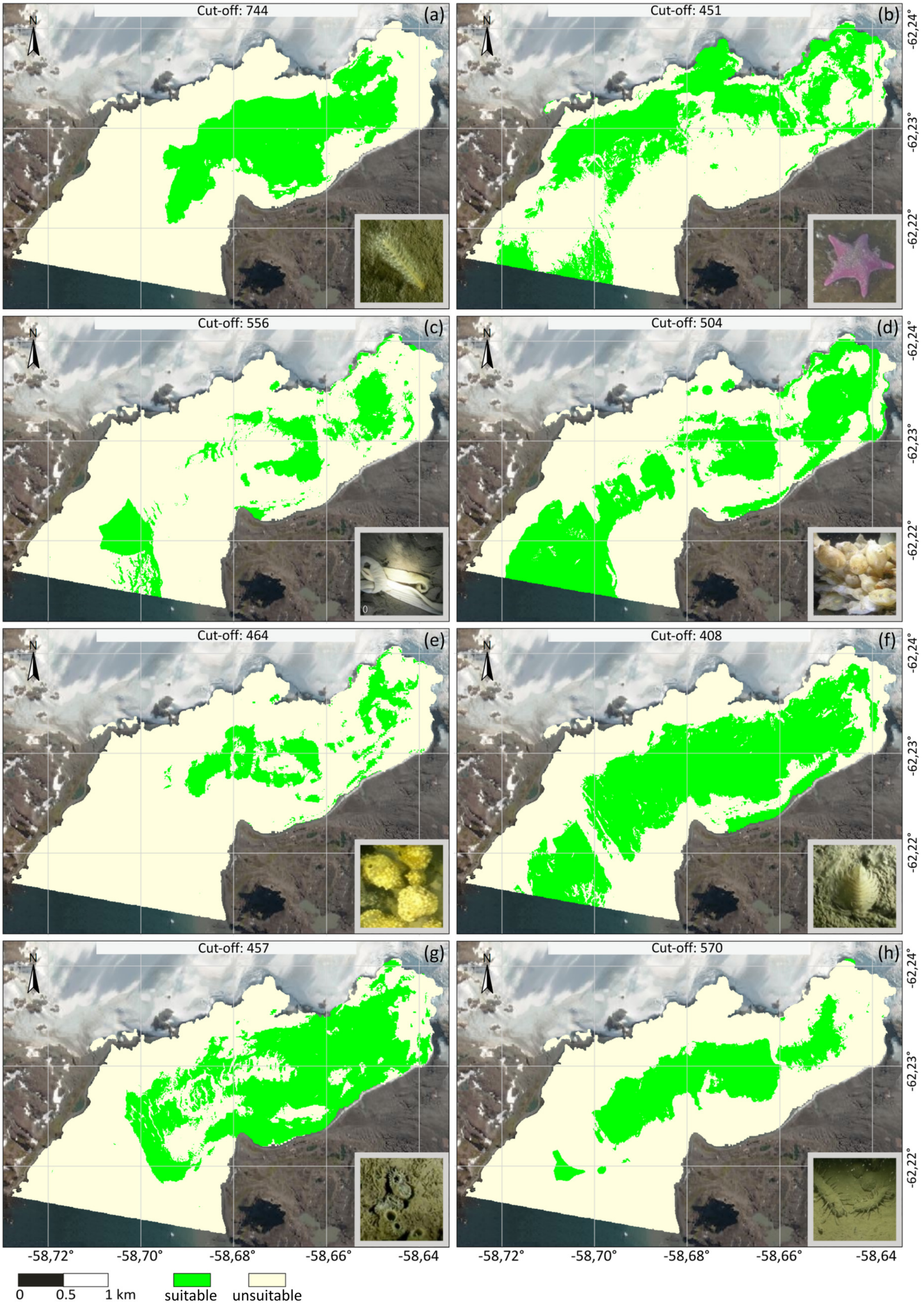


Fig. 5. Binary maps based on the taxon-specific environmental suitability threshold (cut-off) to determine the suitable habitat of the analyzed fauna taxa. (a) Pennatulid *Malacobelemnon daytoni*. (b) Sea star *Odontaster validus*. (c) Nemertean *Parborlasia corrugatus*. (d) Ascidian *Molgula pedunculata*. (e) Sponge *Mycale acerata*. (f) Isopod (family Serolidae). (g) Bivalve *Laternula elliptica*. (h) Polychaete (non-identified species, subclass Errantia)

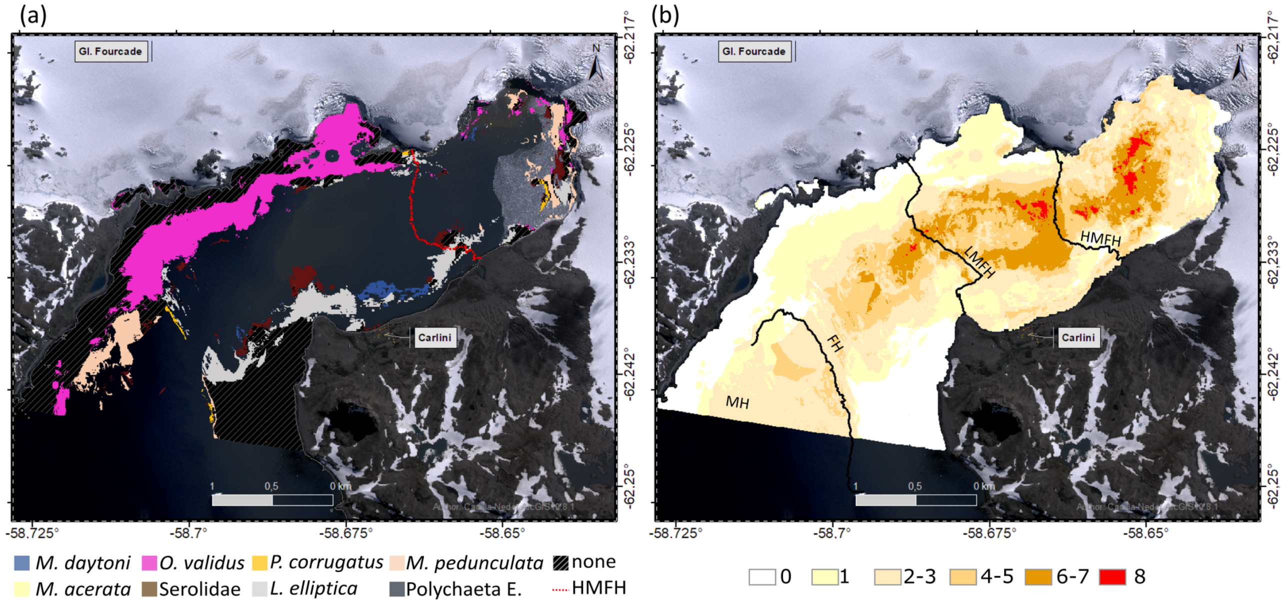


Fig. 6. Benthic compositional information from taxa habitat overlap. (a) Exclusive habitat for single taxon presence. Indistinguishable areas for *Mycale acerata* and the polychaeta (subclass Errantia). (b) Hotspot areas of potential co-occurrence of analyzed taxa. Glacial-influenced areas are indicated: marine habitat (MH), fjordic habitat (FH), low meltwater fjord habitat (LMFH), and high meltwater fjord habitat (HMFH)

specificity. A lower cut-off value increases the likelihood of estimating taxa presence even under 'less favorable' conditions. For example, if the cut-off score is 110 and the habitat suitability at a location is 200 (out of 1000), it means that 20% of environmental conditions are favorable, but still sufficient to estimate species presence. Less restrictive ecological requirements can result in more extensive distributions. Moreover, the alternative threshold, which averages the habitat suitability of a taxon across all pixels, could provide the frequency of encountering that taxon — in other words, the mean probability that a chosen pixel estimates the presence of the taxon (Liu et al. 2005, Torres & Jayat 2010). This could be linked to local abundance studies (Sahade et al. 2015, Lagger et al. 2018). For example, *Mycale acerata* occurred less frequently than *Malacobelemno daytoni*; these 2 species have type localities in Potter Cove with mean habitat suitability of 209.47 and 391.47, respectively (based on a maximum value of 1000; Table 3). This infers an encounter frequency of approximately 0.2 for *M. acerata* compared to 0.4 for *M. daytoni* but under less restrictive environmental conditions. Cut-off values of 464 vs. 744, respectively, indicate that 46.4 and 74.4% of their environmental requirements must be met for their presence, increasing the chances that habitat suitable for *M. acerata* could be shared by other taxa and resulting in a higher area of exclusive presence for *M. daytoni* (47 550 m^2 vs. 500 m^2).

In Antarctic fjords, environmental conditions influencing and resulting from glacier retreat are gaining importance in predicting dynamics of polar benthic assemblages. In Potter Cove, the analyzed zoobenthos distribution responded to glaciological predictors, followed by sedimentological and oceanographic predictors. The distance to the glacier is strongly correlated to habitat age, moderately correlated to salinity and temperature, and inversely correlated to median SPM. This suggests a proxy for meltwater input, sediment run-off, and ice impacts, which in turn structure the polar benthic assemblage (Moon et al. 2015, Kim. et al. 2022, Neder 2023). The mean grain size is closely linked to seabed morphology shaped by glacier retreat, water mass circulation, and deposition (Wölfl et al. 2016). Also, it correlates with life traits such as feeding strategy, mobility, and body size (Wölfl et al. 2016, Sutton et al. 2021), which influence benthic composition and diversity (Kim et al. 2021).

4.2. Taxonomic associations estimated by benthic co-occurrence

The SDMs developed in this study aim to contribute to the realized niche knowledge of the analyzed taxa in an Antarctic fjord ecosystem affected by glacier retreat. The relationship between distribution and niche is closely linked, as the geographic distribution of a species is associated with and influenced by factors — not directly considered by SDMs — such as mobility, dispersal potential, and biotic interactions (Phillips 2008). These factors could contribute to identifying the assemblage's complexity and diversity patterns explaining the observed spatio-temporal changes in the Antarctic benthic structure. Beyond SDM results, further interpretation can be carried out to understand potential interactions or ecological relationships among the taxa using compositional information, co-occurrence maps, and habitat-overlap analysis.

Differences in the importance of environmental predictors among analyzed taxa could reflect taxa-specific requirements, such as distinguishing suspension- and filter-feeding strategies from those of predators, scavengers, deposit-feeders, or species with combined strategies. Filter-feeders like *Molgula pedunculata* and *Laternula elliptica* showed habitat suitability influenced by sedimentological predictors — particularly sediment type for *M. pedunculata* and SPM for *L. elliptica* — followed by oceanographic predictors. Conversely, *M. acerata* habitat suitability showed the opposite order. Suspension-feeders, such as *M. daytoni*, depend primarily on a combination of glaciological predictors followed by sedimentological predictors. This highlights their distribution in the glacier-influenced areas, suggesting a greater tolerance to SPM run-off attributed to the absence of a filter system, which reduces the risk of clogging (Torre et al. 2012). For mobile species with different feeding strategies, such as predators or scavengers like *Odontaster validus* and *Parborlasia corrugatus*, the most important environmental predictors were glaciological and oceanographic factors such as distance to the glacier and bathymetry, whereas for deposit-feeders such as the Errantia polychaete, only oceanographic predictors were important, reflecting potential links with food supply along the cove. Serolidae habitat was influenced by a combination of all 3 predictor types, primarily oceanographic (distance to the coast), followed by sedimentological and glaciological, likely due to the interplay of their combined feeding strategies. Environmental predictors that were most important for certain taxa but not for others included mean current velocity for the polychaete and the water column temperature for *O. validus* (Fig. 3). These differences in the habitat distribution and importance of predictors could be linked to life traits of the taxa, such as feeding and reproductive strategies, and their responses to parameters associated with movements of water masses, such as food availability, sediment particle transport, and substrate type, influencing their distribution (Pineda-Metz et al. 2019).

In Potter Cove, *O. validus* and *M. acerata* share habitat in the inner cove center and in the transition zone from low glacier-influenced to fjordic habitat in the outer cove. SPM concentrations, particularly their responses to maximum and median concentrations, could influence realized niche diversification for both species. *M. acerata* presented optimal suitability at 100 mg l^{-1} lower values of maximum SPM concentration and slightly deeper areas (10–50 m) compared to *O. validus* (8–45 m). Also, it showed a direct relation to median SPM concentrations in contrast to an indirect one for *O. validus* (Table 4; Fig. S6.5). This suggests the ability of *M. acerata* to cope with SPM by releasing mucus to prevent its osculum from clogging (Dayton et al. 1974, Barthel & Gutt 1992). Additionally, *O. validus* and *P. corrugatus* share similar feeding strategies and hold high positions in the food web (Rodriguez et al. 2022), but differ in the substrate type that they inhabit (soft for the nemertean, while the sea star inhabits both soft and hard ones). Varied feeding strategies and reducing food sources could reduce competition and lead to niche differentiation (McClintock et al. 2008, Rodriguez et al. 2022), explaining why suitable areas in the middle and inner cove for *P. corrugatus* were unsuitable for *O. validus*. Assessing habitat suitability for other non-modeled species could provide valuable insights into the complexity of the benthic assemblage and interspecific competition, as exemplified by interactions involving *Perknaster* and *O. validus*).

Among sessile suspension- and filter-feeders, habitats extensively overlapped spatially for *M. daytoni*, *M. acerata*, *M. pedunculata*, and *L. elliptica*. Differences in their distribution were primarily driven by habitat suitability responses to SPM and distance to the coast (Fig. S6). *M. pedunculata*, *M. daytoni*, and *L. elliptica* showed increased or constant habitat suitability at higher SPM concentrations, in contrast to *M. acerata*. The maximum SPM concentration limit for *M. daytoni* (600 mg l^{-1}) coincided with that registered experimentally without significant physiological response (Torre et al. 2012, Servetto et al. 2013). Strikingly, *M. pedunculata* showed high habitat suitability at even higher SPM concentrations than all other taxa, exceeding the expected value (650 mg l^{-1}), contrary to its low measured physiological tolerance (Torre et al. 2012).

Except for *L. elliptica* (<10 mm), sessile suspension- and filter-feeders showed high suitability for muddy substrate with a grain size of ~0.02 mm. Specifically, *M. pedunculata* showed low suitability in areas with a

Table 4. Optimal value of selected environmental predictors that determine high habitat suitability with the potential occurrence of zoobenthos. Arrows indicate the association between the parameters, where ↑ is a direct relation, ↓ is inverse, and → is horizontal, without variation in response to the different values taken by the environmental predictor. Full names of benthic taxa are given in Table 1. SPM: suspended particulate matter

	M. daytoni	*O. validus*	*P. corrugatus*	*M. pedunculata*	*M. acerata*	Serolidae	*L. elliptica*	Errantia polychaete
Bathymetry (m)	↓~12–45	↓~8–45	↑~10–45	↑~12–45	↑~10–50	↓~12–45	↓~10–45	↑~12–45
Distance to coast (m)	↑50–700	↑< 700	↑~50–800	↓< 800	↓< 600	↑100–750	↑100–700	↑~50–800
Distance to glacier (m)	↓~100–1400	↓<1600	↓~250–1500	↓<1500	↓<1400	↓~200–1500	↓~100–1600	↓~250–1500
Mean grain size (mm)	↓0–0.02	→~0–14	↓0–0.01	↓0–0.02	→0–0.01	→0–0.01	↓0–10	↓0–0.01
Slope (°)	↓<25	↑<40	↓<30	↑<40	↑<45	↓<20	↓<22	→<25
SPM_max (mg l^{-1})	→~200–600	↑~200–600	↑~200–600	↑~200–650	↑200–500	↓~200–550	↑~200–600	→~200–400
SPM_med (mg l^{-1})	↓<30	↓<30	↑<32	↑<30	↑<25	↑<25	↓<30	↓<20
Water column temperature (°C)	↓<1.3	↑<1.5	↓<1.35	↑<1.35	↓<1.3	↓<1.3	↑<1.35	↓~1.15–1.3
Median velocity (m s^{-1})	→<0.12	→<0.15	↓<0.10	↓<0.15	↓<0.15	↓<0.1	↓<0.12	↓<0.07

mean grain size between ~0.25 and 16 mm. However, this contradicts its suitable habitat in high-slope and deep areas (50 m) of the outer cove and its occurrence on a rocky island in the inner cove. Even if we acknowledge that the mean grain size raster could be improved by increasing environmental variability considering a larger grain size range, the results likely underestimate the ascidian's suitability for hard bottoms. Hard substrates are dominated by macroalgae on the northwest coast (Quartino et al. 2001), suggesting potential spatial competition between ascidians and algae, supported by their distribution patterns on the rocky island. Under favorable light, macroalgae dominate, while ascidians prevail in the rock walls (Lagger et al. 2018).

Smaller and more dispersedly distributed *M. daytoni* and *L. elliptica* were observed near ascidian patches, while they were more concentrated in benthic diatom-dominated areas. Despite potential competition for food resources (Kowalke 1999, Servetto et al. 2017), the observed pattern suggests that varying spatial feeding strategies facilitate their co-occurrence. *M. pedunculata*, with its 30 cm peduncle, could filter water higher in the column, doubling the height of *M. daytoni*, which reaches 14 cm (Monniot & Monniot 1994, Servetto 2014). Both species are potential pioneers, with the ascidian colonizing both soft and hard substrates, while the pennatulid colonizes only soft substrates, giving the ascidian a broader suitable habitat. Furthermore, high pumping rates of *M. pedunculata* enable it to filter large volumes of water, influencing the quality and quantity of available food for nearby *M. daytoni* or *L. elliptica*. This filtration efficiency may cause other species to consume different particles, such as benthic diatoms (Urban & Mercuri 1998, Servetto et al. 2017). This was also observed in our video data, which showed a clear halo around *M. daytoni* or *L. elliptica* on brownish diatom mats.

Binary overlap and the percentage of the sum of probabilities for EM showed a similar co-occurrence pattern (Fig. S7). The most notable potential benthic co-occurrence was observed in the middle and the inner coves at intermediate-low and high glacial-influenced areas, respectively, within a distance of <1 km from the glacier (Fig. S8). Conversely, a 1.44 km^2 area in the outer cove, particularly along the south and northwest coast, was unsuitable for all analyzed taxa, which could be attributed to higher wave impact and intense water dynamics in Potter Cove (Lim 2014, Neder et al. 2022). Larval type, settlement patterns, food availability, and growth of benthic organisms are likely influenced by physical oceanographic conditions and substrate type, especially affecting filter- and suspension-feeders. Therefore, the hotspot habitat in the middle cove could be linked to factors such as space availability, water circulation, and vortices, which could increase the supply and transport of pelagic larvae to new environments. The patchy 3-dimensional structure of the assemblage could affect system turbulence, increasing local food variability and supporting the coexistence of epibenthic fauna without restricting the number of potential competitors (Gutt 2006, Rossi et al. 2017).

4.3. Newly available habitat in glacier-influenced areas

Between 1956 and 2020, glacial retreat released an ice-free area of 1.55 km^2 available for species colonization, with 1.22 km^2 in the HMFH. This habitat is strongly influenced by the Fourcade glacier, which maintains high constant values of SPM (Neder et al. 2022). All analyzed benthic taxa showed potential to inhabit HMFH, benefiting from distinct abilities to cope with the suspended sediment (Dayton et al. 1974, Ahn 1993, Torre et al. 2012, Servetto et al. 2017). Comparatively, *L. elliptica* occupies a slightly more extensive area in the HMFH than *M. pedunculata* (0.76 vs. 0.74 km^2, respectively), while Serolidae occupy a third (0.68 km^2). Despite the inverse relation between habitat suitability and distance to the glacier (Table 4), none of the taxa analyzed showed suitable habitat within ~150 m of the glacier in the inner cove (Fig. S6). This was unexpected for *M. daytoni* and the polychaete due to their pioneer ability and SPM tolerance. This prediction reflects the influence of other factors, such as SPM tolerance limit, disturbance frequency, and the time since the area became free of ice, which in turn shapes the sea floor structure and benthic assemblage complexity. In a fjordic area undergoing glacier retreat, benthic taxa SDMs should be interpreted by considering the effect of environmental predictors and combining taxonomic associations, life traits, successional patterns, and habitat availability.

Sahade et al. (2015) found that sponge abundance increased and ascidian abundance decreased after an SPM peak, which contrasts our results showing suitable habitat for *M. pedunculata* and narrow habitat for *M. acerata* in highly influenced SPM and meltwater areas close to the glacier (Fig. 5). Assuming at least one individual could colonize the estimated suitable habitat, our results suggest a higher abundance of ascidians compared to sponges in the inner cove. Abundance variations by depth rather than solely presence/absence will improve the assessment of the hypothesis of an SPM threshold shifting to a different equilibrium (Torre et al. 2021). Additionally, the observed differences could support the hypotheses of sluggish colonization of recent ice-free areas following glacier retreat (Lagger et al. 2021), highlighting factors such as the duration of ice-free exposure or habitat age, which is linked to glaciological, oceanographic, sedimentological, and biogeochemical variables (Neder 2023) that could shape the benthic assemblage structure.

Newly available areas allow for new colonization and the succession of benthic assemblages. Species such as *M. pedunculata, M. daytoni, L. elliptica, M. acerata,* and *O. validus* exhibit characteristics that define potential roles across different colonization and successional stages, from pioneers to maturing, depending on species' abilities to reach and establish in the new habitat. Habitat colonization of new ice-free areas may not occur as the area becomes exposed, as several factors could interfere with this process. The influence of habitat age extends beyond glacier retreat to include substrate stability and water mass dynamics, impacting particle transport, food quality, sedimentation, and sediment grain size, which in turn play a primary role in colonization success, shaping benthic taxa composition (Campana et al. 2018, Pineda-Metz et al. 2019, Sutton et al. 2021, Beauchard et al. 2022). Our results highlight the need to understand pelagic larval transport, growth, reproductive strategies, and food dynamics concerning distribution and colonization processes adapted to local disturbance.

5. CONCLUSIONS

Benthic distribution, primarily influenced by oceanographic and sedimentological predictors in Potter Cove following glacier retreat, leads to various hypotheses that may drive the composition of species assemblages differently. On the one hand, SPM tolerance and values exceeding species sensitivity limits could select functional composition (Torre et al. 2014, 2021). On the other hand, food supply can decrease in glacier-influenced areas through intense hydrological dynamics (Neder et al. 2022). Such changes may affect competition among suspension-feeders, causing distribution shifts. Furthermore, sluggish colonization can result from a lag between habitat availability and species arrival, influenced by larval lifespan, dispersal ability, and reproductive strategies. Habitat age, environmental filtering, life traits, and substrate stability also play key roles in the establishment of sessile species in a newly available area. The question remains: does glacier retreat increase environmental disturbances causing biodiversity shifts and biomass loss, or does it create new available areas for colonization? It is still a matter of life traits, space, and time. An interdisciplinary approach that integrates biodiversity studies with ongoing long-term research and modeling tools is essential for deepening our understanding of Antarctic species distribution, coexistence, and habitat changes, as well as for informing conservation strategies in polar ecosystems affected by glacier retreat.

Acknowledgements. This project was partly supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-Res. No. 4252/116 and Project ASIEBA-SDMs RESOL-2023-1026-APN), SECYT-UNC, and PICT-2020-SERIEA-02956. This research received funding from the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No. 872690 (CoastCarb) under secondment of C.N. in agreement with Deliverables D1.2 and D2.1. We also acknowledge support by the Open Access Publication Funds of Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung. The present work was part of C.N.'s PhD thesis. We gratefully acknowledge the crew members of CAV 2016 and the Instituto Antártico Argentino for logistical and financial support of the Antarctic Scientific Expedition, and Sara Schlagenhauf, Prof. Cristina Gómez, and 3 anonymous reviewers for their thoughtful comments on an earlier version of this paper.

LITERATURE CITED

Abele D, Vasquez S, Buma AGJ, Hernandez E (2017) Pelagic and benthic communities of the Antarctic ecosystem of Potter Cove: genomics and ecological implications. Mar Genomics 33:1–11

Ahn IY (1993) Enhanced particle flux through the biodeposition by the Antarctic suspension-feeding bivalve *Laternula elliptica* in Marian Cove, King George Island. J Exp Mar Biol Ecol 171:75–90

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Alurralde G, Fuentes VL, De Troch M, Tatián M (2020) Suspension feeders as natural sentinels of the spatial variability in food sources in an Antarctic fjord: a stable isotope approach. Ecol Indic 115:106378

Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. J Biogeogr 33:1677–1688

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Barthel D, Gutt J (1992) Sponge associations in the eastern Weddell Sea. Antarct Sci 4:137–150

Beauchard O, Mestdagh S, Koop L, Ysebaert T, Herman PMJ (2022) Benthic synecology in a soft sediment shelf: habitat contrasts and assembly rules of life strategies. Mar Ecol Prog Ser 682:31–50

Braeckman U, Pasotti F, Hoffmann R, Vázquez S and others (2021) Glacial melt disturbance shifts community metabolism of an Antarctic seafloor ecosystem from net autotrophy to heterotrophy. Commun Biol 4:148

Campana GL, Zacher K, Deregibus D, Momo FR, Wiencke C, Quartino ML (2018) Succession of Antarctic benthic algae (Potter Cove, South Shetland Islands): structural patterns and glacial impact over a four-year period. Polar Biol 41:377–396

Cerasoli F, Besnard A, Marchand MA, D'Alessandro P, Iannella M, Biondi M (2021) Determinants of habitat suitability models transferability across geographically disjunct populations: insights from *Vipera ursinii ursinii*. Ecol Evol

Chaabani S, López-González PJ, Casado-Amezua P, Pehlke H, Weber L, Martínez-Baraldés I, Jerosch K (2019) Ecological niche modelling of cold-water corals in the Southern Ocean (N Antarctic), present distribution and future projections due to temperature changes. Mar Ecol Prog Ser 628:73–93

Clarke A, Crame JA (1992) The Southern Ocean benthic fauna and climate change: a historical perspective. Philos Trans R Soc B 338:299–309

Cook AJ, Holland PR, Meredith MP, Murray T, Luckman A, Vaughan DG (2016) Ocean forcing of glacier retreat in the western Antarctic Peninsula. Science 353:283–286

Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol Monogr 44:105–128

Deregibus D, Campana GL, Neder C, Barnes DKA and others (2023) Potential macroalgal expansion and blue carbon gains with northern Antarctic Peninsula glacial retreat. Mar Environ Res 189:106056

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

ESRI (Environmental Systems Research Institute) (2016) ArcGIS Desktop 10.4.1/10.6.1/10.8.1. ESRI, Redlands, CA. https://support.esri.com/es/Products/Desktop/arcgis-desktop/arcmap/10-4-1 (accessed 17 Dec 2023)

Fernandes RF, Scherrer D, Guisan A (2019) Effects of simulated observation errors on the performance of species distribution models. Divers Distrib 25:400–413

Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. J Appl Ecol 43:393–404

Fillinger L, Janussen D, Lundälv T, Richter C (2013) Rapid glass sponge expansion after climate-induced Antarctic ice shelf collapse. Curr Biol 23:1330–1334

Gokmen S, Dagalp R, Kilickaplan S (2022) Multicollinearity in measurement error models. Commun Stat Theory Methods 51:474–485

Grange LJ, Smith CR (2013) Megafaunal communities in rapidly warming fjords along the West Antarctic Peninsula: hotspots of abundance and beta diversity. PLOS ONE 8:e77917

Griffiths HJ, Barnes DKA, Linse K (2009) Towards a generalized biogeography of the Southern Ocean benthos. J Biogeogr 36:162–177

Guillaumot C (2021) Modelling the response of Antarctic marine species to environmental changes. Methods, applications and limitations. PhD thesis, Université Bourgogne Franche-Comté, Besançon

Guillaumot C, Jean A, Thomas S, Laura D and others (2019) Broad-scale species distribution models applied to data-poor areas. Prog Oceanogr 175:198–207

Guillaumot C, Danis B, Saucède T (2021) Species distribution modelling of the Southern Ocean benthos: a review on methods, cautions and solutions. Antarct Sci 33: 349−372

Gutt J (2006) Coexistence of macro-zoobenthic species on the Antarctic shelf: an attempt to link ecological theory and results. Deep Sea Res II 53:1009−1028

Gutt J, Cape M, Dimmler W, Fillinger L and others (2013) Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic Peninsula. Polar Biol 36:895−906

Gutt J, Isla E, Xavier JC, Adams BJ and others (2021) Antarctic ecosystems in transition — life between stresses and opportunities. Biol Rev Camb Philos Soc 96:798−821

Henley SF, Schofield OM, Hendry KR, Schloss IR and others (2019) Variability and change in the west Antarctic Peninsula marine system: research priorities and opportunities. Prog Oceanogr 173:208−237

Jerosch K, Pehlke H, Scharf F, Weber L, Braun MH, Abele D (2018) Benthic meltwater fjord habitats formed by rapid glacier recession on King George Island, Antarctica. Philos Trans R Soc A 376:20170178

Jerosch K, Scharf FK, Deregibus D, Campana GL and others (2019) Ensemble modeling of Antarctic macroalgal habitats exposed to glacial melt in a polar fjord. Front Ecol Evol 7:207

Keddy PA (1992) Assembly and response rules: two goals for predictive community ecology. J Veg Sci 3:157−164

Kim DU, Khim JS, Ahn IY (2021) Patterns, drivers and implications of ascidian distributions in a rapidly deglaciating fjord, King George Island, West Antarctic Peninsula. Ecol Indic 125:107467

Kim DU, Ahn IY, Noh J, Lee C, Khim JS (2022) Shifts in benthic megafauna communities after glacier retreat in an Antarctic fjord. Commun Earth Environ 5:438

Klöser H, Quartino ML, 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

Kowalke J (1999) Filtration in Antarctic ascidians — striking a balance. J Exp Mar Biol Ecol 242:233−244

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

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 41:579−591

Lagger C, Neder C, Merlo P, Servetto N, Jerosch K, Sahade R (2021) Tidewater glacier retreat in Antarctica: The table is set for fast-growing opportunistic species, is it? Estuar Coast Shelf Sci 260:107447

Latorre MP, Iachetti CM, Schloss IR, Antoni J and others (2023) Summer heatwaves affect coastal Antarctic plankton metabolism and community structure. J Exp Mar Biol Ecol 567:151926

Liao CC, Chen YH (2022) The effects of true and pseudo-absence data on the performance of species distribution models at landscape scale. Taiwania 67:9−20

Lim CH (2014) Modelling waves and currents in Potter Cove, Antarctica. PhD dissertation, Carl von Ossietzky Universität, Oldenburg

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385−393

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Divers Distrib 15:59−69

McClintock JB, Angus RA, Ho C, Amsler CD, Baker BJ (2008) A laboratory study of behavioral interactions of the Antarctic keystone sea star *Odontaster validus* with three sympatric predatory sea stars. Mar Biol 154: 1077−1084

Monniot C, Monniot F (1994) Ascidians collected in the Weddell Sea by the RV ‘Polarstern’ (EPOS cruise leg 3). Bull Mus Natl Hist Nat Sect A Zool Biol Ecol Anim 16: 13−37

Moon HW, Wan Hussin WMR, Kim HC, Ahn IY (2015) The impacts of climate change on Antarctic nearshore mega-epifaunal benthic assemblages in a glacial fjord on King George Island: responses and implications. Ecol Indic 57: 280−292

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol Evol 5:1198−1205

Neder C (2016) El bentos de Caleta Potter (Antártida): un meta-análisis usando modelos de distribución de especies. MSc thesis, Universidad Nacional de Córdoba

Neder C (2023) El bentos antártico y su respuesta al cambio climático: una aproximación usando modelos de distribución de especies como caso de estudio en caleta Potter. PhD thesis, Universidad Nacional de Córdoba

Neder C, Pehlke H (2024) SDM_biomod2 v3.5 for benthic distribution in an Antarctic fjord area under glacier retreat. https://doi.org/10.5281/zenodo.14236049

Neder C, Sahade R, Abele D, Pesch R, Jerosch K (2020) Default versus configured-geostatistical modeling of suspended particulate matter in Potter Cove, West Antarctic Peninsula. Fluids 5:235

Neder C, Fofonova V, Androsov A, Kuznetsov I and others (2022) Modelling suspended particulate matter dynamics at an Antarctic fjord impacted by glacier melt. J Mar Syst 231:103734

Peterson AT, Soberón J (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. Nat Conserv 10:102−107

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martinez-Meyer E, Nakamura M, Bastos Araujo M (2011) Ecological niches and geographic distributions. Monographs in Population Biology, Vol 49. Princeton University Press, Princeton, NJ

Phillips SJ (2008) Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 31:272−278

Pineda-Metz SEA, Isla E, Gerdes D (2019) Benthic communities of the Filchner Region (Weddell Sea, Antarctica). Mar Ecol Prog Ser 628:37−54

Quartino ML, Klöser H, Schloss IR, Wiencke C (2001) Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. Polar Biol 24:349−355

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reiss H, Cunze S, König K, Neumann H, Kröncke I (2011) Species distribution modelling of marine benthos: a North Sea case study. Mar Ecol Prog Ser 442:71−86

Rodriguez ID, Marina TI, Schloss IR, Saravia LA (2022) Marine food webs are more complex but less stable in sub-Antarctic (Beagle Channel, Argentina) than in Antarctic (Potter Cove, Antarctic Peninsula) regions. Mar Environ Res 174:105561

Rossi S, Bramanti L, Gori A, Orejas C (2017) Animal forests of the world: an overview. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine animal forests. Springer, Cham, p 1–30

Sahade R, Lagger C, Torre L, Momo FR and others (2015) Climate change, glacier retreat and shifts in an Antarctic benthic ecosystem. Sci Adv 1:e1500050

Schloss IR, Abele D, Moreau S, Demers S, Bers AV, González O, Ferreyra GA (2012) Response of phytoplankton dynamics to 19-year (1991–2009) climate trends in Potter Cove (Antarctica). J Mar Syst 92:53–66

Servetto N (2014) Rol ecosistémico de *Malacobelemnon daytoni* (Octocorallia, Pennatulacea, Kophobelemnidae) en comunidades bentónicas de Caleta Potter, Isla 25 de Mayo, Antártida. PhD thesis, Universidad Nacional de Córdoba

Servetto N, Torre L, Sahade R (2013) Reproductive biology of the Antarctic "sea pen" *Malacobelemnon daytoni* (Octocorallia, Pennatulacea. Polar Res 32:20040

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, Kophobelemnidae). Mar Environ Res 130:264–274

Smale DA, Barnes DKA (2008) Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century, based primarily on evidence from the West Antarctic Peninsula region. Ecography 31:289–305

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform 2:1–10

Sutton L, Mueter FJ, Bluhm BA, Iken K (2021) Environmental filtering influences functional community assembly of epibenthic communities. Front Mar Sci 8:736917

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD — a platform for ensemble forecasting of species distributions. Ecography 32:369–373

Thuiller W, Lafourcade B, Araújo MB (2010) Presentation manual for BIOMOD. Université Joseph Fourier, Grenoble

Thuiller W, Georges D, Gueguen M, Engler R, Breiner FT (2021) Biomod2: ensemble platform for species distribution modeling. R package version 3.5.1. https://CRAN.R-project.org/package=biomod2

Torre L, Servetto N, Eöry ML, Momo F, Tatián M, Abele D, Sahade R (2012) Respiratory responses of three Antarctic ascidians and a sea pen to increased sediment concentrations. Polar Biol 35:1743–1748

Torre L, Abele D, Lagger C, Momo F, Sahade R (2014) When shape matters: strategies of different Antarctic ascidians morphotypes to deal with sedimentation. Mar Environ Res 99:179–187

Torre L, Alurralde G, Lagger C, Abele D, Schloss IR, Sahade R (2021) Antarctic ascidians under increasing sedimentation: physiological thresholds and ecosystem hysteresis. Mar Environ Res 167:105284

Torres R, Jayat JP (2010) Para cuatro especies de mamíferos típicas del Chaco en Argentina. Mastozool Neotrop 17: 335–352

Turner J, Marshall GJ, Clem K, Colwell S, Phillips T, Lu H (2020) Antarctic temperature variability and change from station data. Int J Climatol 40:2986–3007

Urban HJ, Mercuri G (1998) Population dynamics of the bivalve *Laternula elliptica* from Potter Cove, King George Island, South Shetland Islands. Antarct Sci 10: 153–160

Valavi R, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2019) BlockCV: an R package for generating spatially or environmentally separated folds for *k*-fold cross-validation of species distribution models. Methods Ecol Evol 10:225–232

Weber L (2017) Macroalgal distribution shifts during the climate change induced glacier retreat in Potter Cove, West Antarctic Peninsula, 1993–2016. BSc thesis, Hochschule Karlsruhe

Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74:159–164

Wiencke C, Ferreyra GA, Abele D, Marenssi S (eds) (2008) The Antarctic ecosystem of Potter Cove, King-George Island (Isla 25 de Mayo) Synopsis of research performed 1999–2006 at the Dallmann Laboratory and Jubany Station. Ber Polar Meeresforsch 571

Wisz MS, Guisan A (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecol 9:8

Wölfl AC, Wittenberg N, Feldens P, Hass HC, Betzler C, Kuhn G (2016) Submarine landforms related to glacier retreat in a shallow Antarctic fjord. Antarct Sci 28: 475–486

Zamboni N (2011) Comunidades epibentónicas de Caleta Potter, Antártida: estructura, distribución y dinámica espacio-temporal. MSc thesis, Universidad Nacional de Córdoba

Ziegler AF, Smith CR, Edwards KF, Vernet M (2017) Glacial dropstones: islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. Mar Ecol Prog Ser 583:1–14

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Editorial responsibility: Stephen Wing,
Dunedin, New Zealand
Reviewed by: 3 anonymous referees

Submitted: January 29, 2024
Accepted: October 8, 2024
Proofs received from author(s): November 30, 2024