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Climate change effects on Antarctic benthos: a spatially explicit model approach

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Abstract The Antarctic Peninsula is one of the regions on the Earth with the clearest evidence of recent and fast air warming. This air temperature rise has caused massive glacier retreat leading to an increased influx of glacier meltwater which entails hydrological changes in coastal waters, increasing sediment input and ice-scouring impact regime. It has been hypothesized that an increase of sediment load due to glacier retreat resulted in a remarkable benthic community shift in Potter Cove, a small inlet of the South Shetland Islands. In order to test this hypothesis, we developed an explicit spatial model to explore the link between sedimentation and ice-scouring increase upon four of the most conspicuous benthic species. This is a valuable novel approach since disturbances are strongly dependent of the space. The model takes into account sediment and population dynamics with Lotka-Volterra competition, a sediment-dependent mortality term and a randomized ice-scouring biomass removal. With the developed algorithm, and using a MATLAB environment, numerical simulations for scenarios with different sedimentation and ice-impact rates were undertaken in order to evaluate the effect of this phenomenon on biological dynamics. Comparing simulation results with biological data, the model not only recreates the spatial community distribution pattern but also seems to be able to recreate the shifts in abundance

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under sedimentation enhancement, pointing out its importance as a structuring factor of polar benthic communities. Considering the challenges of Antarctic field work, this model represents a powerful tool for assessing, understanding, and predicting the effects of climate change on threatened Antarctic coastal ecosystems.

1 Introduction

There is a growing concern for understanding how climate change will affect polar ecosystems (Peck 2005; Smetacek and Nicol 2005; Barnes and Peck 2008; Kennicutt et al. 2014, 2015). In Antarctica, scientific priority setting is particularly important given the substantial cost and challenges of conducting research in the region. In a huge and international effort to establish these priorities, the first Antarctic and South Ocean Science Horizon Scan have recently identified the key scientific questions that need to be addressed in the following years. Among these questions, there is a clear concern about species and food web vulnerabilities at different spatial and temporal scales, under multiple stressors and environmental change drivers (Kennicutt et al. 2014, 2015). The west Antarctic Peninsula (WAP) is a region on the Earth with one of the most accelerated air warming trends. In fact, in the last few decades, it has shown a significant ice-mass loss as a consequence of ice shelf collapses and about 87% of its marine glaciers have been retreating and thinning (Cook et al. 2005; Pritchard and Vaughan 2007; Turner et al. 2009, 2016). This massive ice-mass imbalance entails hydrographical consequences including ice-scour and sedimentation increase (Bers et al. 2012; Schloss et al. 2012; Barnes et al. 2014) that could be considered the main benthic physical disturbance factors at coastal polar regions (Smale and Barnes 2008; Barnes and Peck 2008).

Ice-scour is a phenomenon in which icebergs pushed by wind, waves, or sea currents scrape the sea bottom removing and killing most of benthic fauna following a bathymetric pattern that becomes less intense with depth. Ice-scour has been intensively studied as a key structural force acting on benthic communities at high latitudes and essentially it decreases species abundance, richness, and coverage at a local scale but enhances regional diversity (Gutt 2001; Gutt and Starmans 2001; Brown et al. 2004; Teixidó et al. 2004; Gutt 2004; Barnes and Souster 2011).

Together with ice action, most coastal environments, especially fjords, are also influenced by sedimentation caused by seasonal glacier runoff. An increase in sedimentation rates can negatively affect aquatic ecosystems at many different levels, for example, by suffocating filter feeders, or affecting primary production by reducing light penetration (Pakhomov et al. 2003; Thrush et al. 2004; Deregibus et al. 2016). Studies of sedimentation effects on polar coastal benthos have been conducted almost exclusively in the Arctic. These studies clearly point out that sediment discharge is an important structuring factor of benthic communities that generates horizontal zonation. Diversity and species richness decrease towards inner fjord and glacier fronts (Carney et al. 1999; Wlodarska-Kowalczuk and Pearson 2004; Wlodarska-Kowalczuk et al. 2005). However, in Antarctica, a different pattern has been described, showing higher diversities and a clear dominance of epibenthic suspension feeders even in soft bottoms closer to the glacier fronts. Indeed, WAP fjords can be considered benthic diversity hotspots (Sahade et al. 1998; Grange and Smith 2013) that are currently threatened by increased sedimentation rates and ice disturbance frequency caused by massive glacier retreat along the WAP (Cook et al. 2005; Smale and Barnes 2008; Grange and Smith 2013). We recently reported a sudden shift in an Antarctic fjord, probably related to glacier retreat and increased inorganic matter runoff. Our results also suggested that benthic ecosystems could cope with sedimentation until thresholds limits that once surpassed important shifts could be triggered (Sahade et al. 2015). The changes observed in the benthic community were decline of the species populations most vulnerable to sediment (mostly solitary ascidians) and population increase of the most tolerant ones, (like the bivalve *Laternula elliptica* and the pennatulid *Malacobelemnom daytoni*) (Philipp et al. 2011; Torre et al. 2012, 2014; Sahade et al. 2015), coinciding with the highest sedimentation rates recorded for the last 100 years (Monien et al. 2011).

Considering the inherent difficulties to experimentally test hypotheses in Antarctica, we used a modeling approach to explore this complex disturbance scenario and provide new insights on the underlying ecological processes. As it has been summarized by Turner et al. (2009), different Antarctic environmental changes have intensively been modeled at different time and spatial scales, either for current or geological climatic events. Nevertheless, the benthic system has barely been explored. For instance, there are only a few models exploring the combined effects of benthic species longevity under different ice-scouring intensities (Potthoff et al. 2005; Johst et al. 2006). We present here an explicitly spatial model that links ice-scour and sedimentation increase on population dynamics of four key species. Based on a simpler previous approximation that only considered competition between the same groups of species and differential sensitivities to ice and sediment impact (Momo et al. 2008), we developed a more complex, realistic, and spatially explicit model. This allows us to explore the benthic community structure along a bathymetric gradient exposed to different sediment and ice-scouring intensities. Finally, contrasting simulation results with real data, the model will also help to understand not only the importance of each factor in the spatial distribution of the considered species but also how ice and sediment changes could affect them.

2 Methods and models

2.1 Species considered

We selected four species that together represent approximately the 40% of the Potter Cove animal benthic community biomass: *Molgula pedunculata*, *Ascidia challengeri*, *M. daytoni*, and *L. elliptica*. These species have shown the most critical abundances and changes in distribution patterns in the last 20 years (Sahade et al. 1998; Sahade et al. 2015). All of them inhabit soft bottoms and are filter feeders, so they compete for substratum and food sources.

2.2 The model

We developed an explicit spatial model that includes population growth, dispersion, and Lotka-Volterra competition between the four species selected. The lethal effect of sedimentation is added as mortality rate. The basic dynamics is based on the model of Momo et al. (2008). The ice-scouring effect was temporally and spatially randomized within a given impacted area. A detailed formulation of the model is explained in Supplementary Material 1.

2.3 Parameters

Most parameters were inferred from empirical data that was taken from multiple expeditions at Carlini station since 1993. Most of the data have been already published. Parameters and its original sources are summarized in Table 1. Detailed calculation of parameters is explained in Supplementary Material 2.

2.4 Resolution method

To solve the equation system (3), a spatial discretization was performed with centered finite differences, and for time discretization, we used the Crank-Nicholson method (Strikwerda 2004; Leveque 2007; Burden and Faires 2010). As a result (after discretization), we found a nonlinear algebraic system that was solved by a predictor-corrector method. This method, originally implemented for solving parabolic problems with finite elements, is also adaptable for use with finite differences. Basically, the method consists of predicting the outcome by adjusting the system using nonlinear iterations of the algebraic system (Douglas et al. 1979).

2.5 Graphic representation

A two-dimensional spatial resolution is being analyzed where different depths are related to its distance to the coastline. We chose an area in Potter Cove which corresponds to the location of station 1 (E1) in the studies of Sahade et al. (1998, 2015) on benthic community structure changes over the years. This station also matches the hydrologic station of the inner cove, where salinity, MPS, chlorophyll, and temperature have been continuously recorded since 1991 (Bers et al. 2012; Schloss et al. 2012). This station is located on the south shore of the inner region of the cove, and it gets most glacier meltwater discharge through the two major runoff creeks (Fig. 1).

2.6 Simulated scenarios

Three sediment intensities were used: 70, 140, and 280 kg of sediment discharge distributed weekly and corresponding to S+, S++, and S+++, respectively. In the absence of accurate data about weekly or daily sediment loading in Potter Cove, these amounts were chosen in order to mimic water column sediment concentrations similar to those recorded between 1991 and 2009 (Schloss et al. 2012).

Three ice-scouring intensities were tested: 50, 200, and 400 impact events, corresponding to I+, I++, and I+++, respectively. As there is no data on ice impact for this area, many numbers of impacts were tested and the ones chosen were arbitrary, chosen to represent low, intermediate, and high impact levels. There were no differences in the final output over 400 impacts.

To compare the effect of both factors (ice and sediment) together, we evaluated many combinations of them. Nevertheless, for simplification and to compare with real data, we only consider analyzing those conditions reported for the area in the last 20 years. We had consistent data about sedimentation increase (Bers et al. 2012; Schloss et al. 2012; Sahade et al. 2015), but there was a lack of ice-scouring records for the area. However, bare substratum distribution was similar to the one obtained with the low ice-impact intensity scenario (I+). Thus, to create realistic sediment load simulations, we evaluated them maintaining a low ice-impact condition (low ice-impact + low sedimentation (I + S+); low ice-impact + high sedimentation (I + S+++)). An extra intermediate condition low ice-impact + medium sedimentation (I + S++) and its comparison with real data are detailed in Supplementary material 3.

Table 1 Summary of model species parameters and its sources

Parameter	*M. pedunculata*	*A. challengeri*	*M. daytoni*	*L. elliptica*	Source
Average individual biomass (g AFDM)	2.23	2.75	0.07	4.05	Sahade (1999), Urban and Mercuri (1998), Servetto et al. (2013)
Maximum population biomass registered (g AFDM m^{-2})	60	20	0.5	80	Sahade (1999), Urban and Mercuri (1998), Servetto et al. (2013), Servetto and Sahade (2016)
Carrying capacity (g AFDM m^{-2})	85				Sahade et al. 1998, 2008, 2015
Dispersion coefficient km^2 w^{-1}	1×10^{-5}	2×10^{-5}	1×10^{-4}	1×10^{-4}	This work
Intrinsic growth rate (year^{-1})	0.512	0.395	0.26	0.129	Rauschert (1991) Kühne (1997) Kowalke et al. (2001), Sahade et al. 2008, 2015[a]. Urban and Mercuri
Competition coefficient	$\beta_{Mp\text{-}Ac} = 1.868$ $\beta_{Mp\text{-}Md} = 1.760$ $\beta_{Mp\text{-}Le} = 1.129$	$\beta_{Ac\text{-}Mp} = 2.079$ $\beta_{Ac\text{-}Md} = 1.862$ $\beta_{Ac\text{-}Le} = 1.146$	$\beta_{Md\text{-}Mp} = 1.967$ $\beta_{Md\text{-}Ac} = 1.620$ $\beta_{Md\text{-}Le} = 1.142$	$B_{Le\text{-}Mp} = 1.972$ $\beta_{Le\text{-}Ac} = 1.556$ $\beta_{Le\text{-}Md} = 1.781$	Sahade et al. 1998[a]
Sediment mortality coefficient	5.53×10^{-2}	5.57×10^{-3}	–	2.7×10^{-4}	Torre et al. 2012, Philipp et al. 2011[a]

[a] Calculation of these parameters has been made as part of this work based on this previous work data

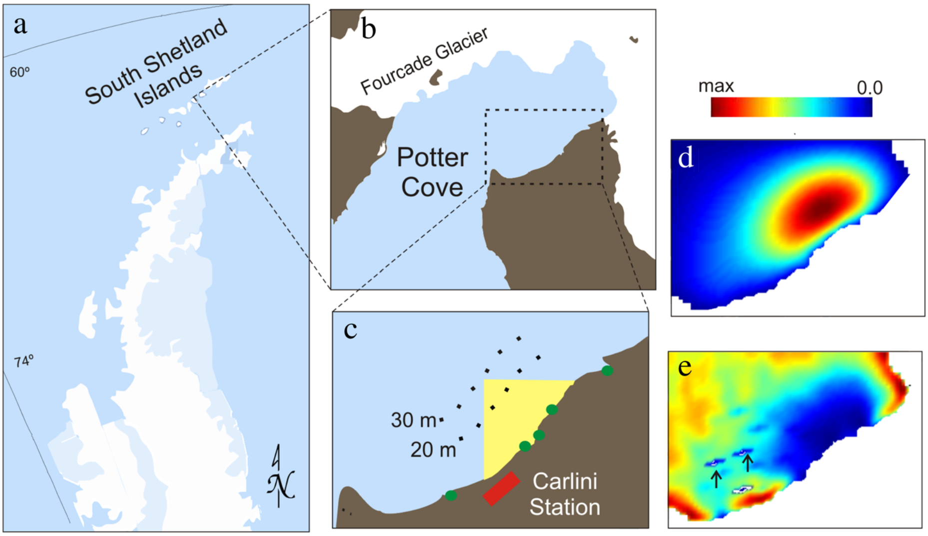

Fig. 1 Location of the studied area in the Antarctic Peninsula (**a**). Map of Potter Cove with Fourcade Glacier (*white*) and ice-free areas (*darker brown*) (**b**). Closer view of the simulated area, *green dots* are pointing the main sediment sources (meltwater creeks); *yellow marked* correspond to the "ice-impacted zone" that mimics bathymetric ice-impact probability gradient. Transects of 20 and 30 m depth are also showed as *pointed lines* (**c**). Sediment simulated plume distribution example (**d**). Species-simulated distribution under sedimentation and ice-scouring example (*arrows point* ice-scouring event of biomass removal) (**e**). Colorimetric scale is auto-scaled from minimum (*dark blue*) to maximum (*dark red*) in each graph

2.7 Simulation output analysis

At the end of each simulation under different intensities of disturbance (ice, sediment, or both), we analyzed the resulting species distribution pattern. The graphs generated by the program were colored from light blue (minimum) to dark red (maximum) abundance values, but each graph is auto-scaled; therefore, the colors have only a relative meaning and they are not comparable across species. Therefore, to study the effect of different disturbance intensities or between species, we needed to directly analyze biomass values at the same selected points of each species grid. In order to get an output comparable with the photo-transects performed by Sahade et al. (2015), we selected points aligned parallel to the coastline representing the different transect depths (Fig. 1b). We compared real data with predictions of the model through nonparametric correlation Spearman analyzed with InfoStat version 2016 (Di Rienzo et al. 2016).

3 Results

3.1 Ice-scouring impact and sedimentation effect on species distribution pattern

Removal of biomass by ice-impact did generate a relatively similar distribution pattern for all the simulated species, all showing their lower abundance in the near shore zone. As expected, the effect on each population did not exceed the impact area (Fig. 2a).

Simulated sediment discharge triggered a completely different distribution pattern between species. *M. pedunculata* was more abundant in deeper areas while *A. challengeri* seemed to be

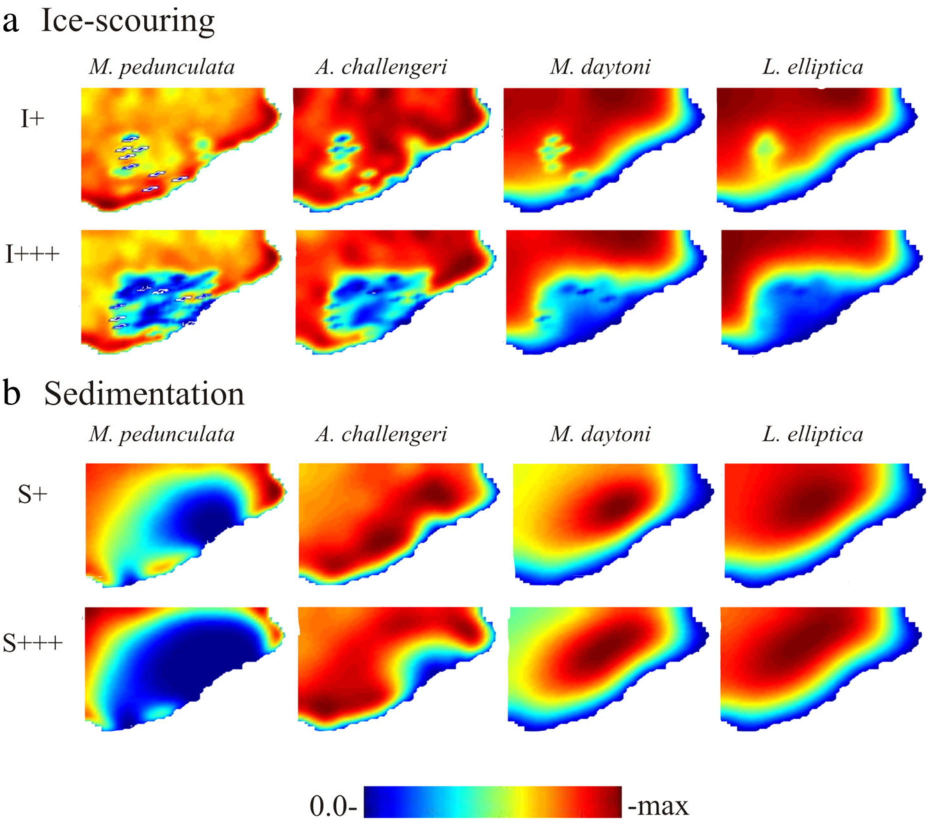

Fig. 2 Final simulated distribution pattern of *M. pedunculata*, *A. challengeri*, *M. daytoni*, and *L. elliptica* under two ice-scouring impact conditions, low (I+) and high (I+++) (**a**) and under two sedimentary loads condition, low (S+) and high (S+++) (**b**). The colorimetric scale is auto-scaled from minimum (*dark blue*) to maximum (*dark red*) in each graph

more abundant at intermediate depths. Clearly, under higher sedimentation input, both retreated their distribution depths. On the contrary, *M. daytoni* and *L. elliptica* were both more abundant at shallower areas. The increase of sediment input showed an expansion of their distribution depth pattern (Fig. 2b). This apparently "positive" effect of sedimentation over the population of the last two species was actually an indirect consequence of the negative effect of sedimentation over their competitors (the ascidians). In the absence of a competitor, the distribution pattern of both species was completely different with almost no specific pattern or change at increasing sediment loads (data not shown).

3.2 Combined effect of ice-scouring and sedimentation against real data

The simulated sedimentation increase resulted in a decrease in the abundance of *M. pedunculata* changing their distribution pattern, almost disappearing at 20 m depths under the highest simulated concentration (Fig. 3b). This change had a very similar result to that one observed in Potter Cove for this species in the last 15 years ($R^2 = 0.66$) (Fig. 3a). Although changes in *A. challengeri* biomass were not as dramatic as in *M. pedunculata*, they were well correlated with real data ($R^2 = 0.71$). We could see a slight biomass increase from low to

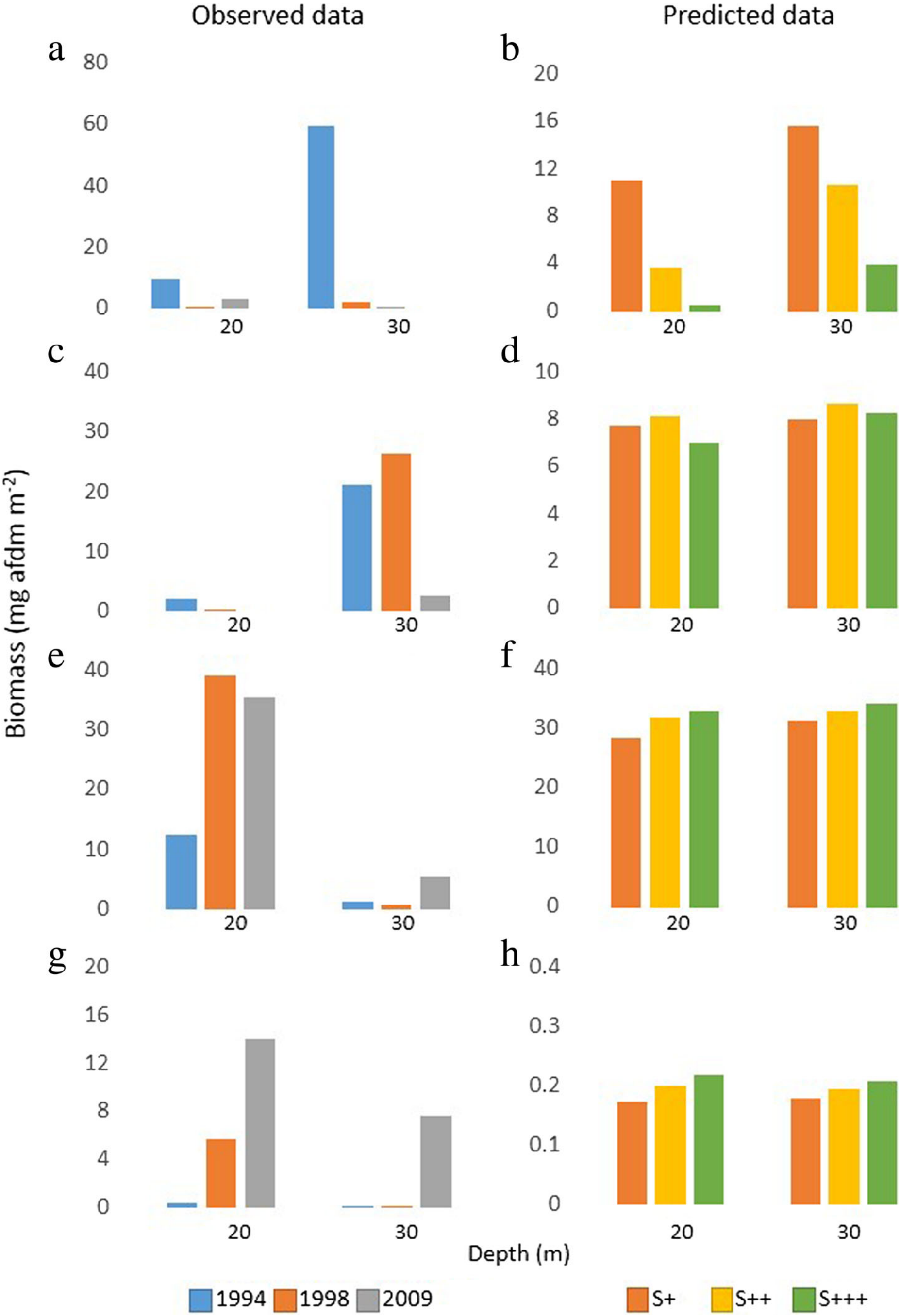

Fig. 3 Comparison between observed data in 1994, 1998, and 2009 surveys (Sahade et al. 1998, 2015) and modeled predicted data of three scenarios of low ice-impact (I+) and three sedimentary loads condition (S+, S++, S+++) on distribution pattern and abundance of *M. pedunculata* (**a**, **b**), *A. challengeri* (**c**, **d**), *L. elliptica* (**e**, **f**), and *M. daytoni* (**g**, **h**) at 20 and 30 m depth

intermediate concentration to finally decrease at the higher one (Fig. 3d). This pattern of change coincided with observations in Potter Cove where, at 30 m depth, a biomass increase was recorded from 1994 to 1998 and finally decreased to a value below initial ones in 2009 (Fig. 3c). Both *L. elliptica* and *M. daytoni* showed biomasses increase proportional to sediment input increasing at every depth (Fig. 3f, h, respectively). This pattern coincided with the observed biomass change of these two species in the studied area (Fig. 3e, g, respectively) but was only significantly correlated for *M. daytoni* ($R^2 = 0.77$).

4 Discussion

Antarctic benthic communities have been considered good sentinels for detecting environmental changes due to their relative stability and low velocities in biological processes. Although it was previously predicted, just recently, a sudden shift in a benthic community that could be related to the ongoing climate change has effectively been reported (Sahade et al. 2015), despite ice-scouring previously being considered the main factor structuring the Potter Cove benthic community (Sahade et al. 1998). Considering the physiological responses to sediments of the main species affected, and in the absence of other potential driving factor data, authors pointed to sedimentation increase as the possible causal factor. The results of this model support this idea.

4.1 Ice-scouring impact and sedimentation effect on species distribution pattern

It is widely known that Antarctic patchy distribution and depth zonation are mainly generated by ice biomass removal and substratum heterogeneity (Gutt and Starmans 2003; Gerdes et al. 2003; Smale 2008). Environments where organisms are grouped in patches generally show greater density variance than those homogeneously distributed (Margalef 2005). In our simulations, where all substratum is equally available for colonization, the decreasing density variance along depths could be considered an indicator of a bathymetric pattern of patchiness generated by ice influence. The model did not reproduce this expected ice caused pattern, where ice has always been considered the most important factor of species vertical distribution in almost all coastal polar environments (Dayton et al. 1969, 1974; Sahade et al. 1998; Nonato et al. 2000; Smale et al. 2007). It is known that ice effect diminishes with depth (Dayton et al. 1969, 1974; Smale 2008) and that most Antarctic coastal communities have zonation patterns along the bathymetric gradient. It is then supposed that highly impacted areas would determine the success of a good colonizer (a fast growing, highly reproductive, and high dispersal capacity species), while at deeper or less impacted areas, biological interactions will determine the dominance of the best competitors (Gutt and Starmans 2001; Poulin et al. 2002; Teixidó et al. 2004; Gutt et al. 2011). However, our model output was not completely consistent with this well-supported paradigm and neither the community studied in Potter Cove where *M. pedunculata*, having a higher growth rate and largely considered a pioneer species (Kowalke et al. 2001; Teixidó et al. 2004; Potthoff et al. 2005; Barnes and Conlan 2007, 2014; Gutt et al. 2011; Fillinger et al. 2013; Gutt et al. 2013), does not succeed in these shallower highly ice-impacted areas. Instead, *L. elliptica*, which is the species with the slowest growth and turnover rates (Urban and Mercuri 1998), dominates this more disturbed area together with *M. daytoni*. The success of *L. elliptica* in shallower zones could be related to its ability to burrow, avoiding ice removal and the faster growth rate of *M. pedunculata* would not be enough to cope with this disturbance frequency. Nevertheless, this probably also indicates a synergic effect of other factors such as sedimentation, since *L. elliptica* and *M. daytoni* are more tolerant to it than *M. pedunculata* and these shallower areas are also more affected by sediments (Philipp et al. 2011; Torre et al. 2012). Nevertheless, a model is always an over simplification of reality, and in this case, it recreates the only aspects we know for sure about the ice-scouring phenomenon, the randomness of its occurrence, and its bathymetric occurrence pattern (Barnes 2016). The expectation was that ice could, as it has been hypothesized, recreate zonation pattern of this species in Potter Cove (Sahade et al. 1998). These results point out that we probably need to know more about the ice-impact phenomenon as the knowledge we have is not enough to recreate it effects on the benthic communities or that there could be other factors and interactions that should be taken into account that may intensify its effects.

Simulated sedimentation regenerated the distribution pattern of the species considered at Potter Cove. While it was expected for the most sensitive species *A. challengeri* and *M. pedunculata*, the distribution pattern of the other two species, *L. elliptica* and *M. daytoni* was an unexpected output of the model. Although *L. elliptica* is also affected by sedimentation (in a much lower extent than ascidians), in the model, it dominates the shallower areas together with *M. daytoni*. The result makes clear that this species distribution pattern is the result of an indirect effect of sedimentation that strongly affects ascidians. Meaning that its dominance at shallower areas depends on its higher tolerance to sedimentation, and the absence (due to sediment impact) of their stronger competitors, the ascidians.

4.2 Combined effect of ice-scouring and sedimentation against real data

In general, the simulated sediment increase recreates very well the form of the change suffered by these four species in the last 20 years, but they fail in adjusting or achieving biomass values against real data. Most of these differences are related to the complexity of a system with more than 50 species where only four are being consider, ignoring the competitive or trophic interaction that could be taking place in nature. One of the most relevant differences is on the predicted biomass of *M. daytoni*, which may be indicating other phenomena that could be taking place and the model is not considering like a surprising episodic recruitment (Dayton et al. 2016a, b). Nevertheless, the model supported our hypothesis that increased sedimentation could be the causal factor of the observed sudden shift in Potter Cove benthic communities. Although the model developed is quite simple, it reproduced very well the main changes observed in Potter Cove benthic communities between 1994 and 2009 based on dynamic competition of four species with different sediment sensitivities.

This model did not intend to simulate sediment burial, which is one of the possible effects of sedimentation over benthic fauna but mainly associated to landslides or other massive sedimentation events described in Antarctica (Dayton et al. 2016a, b; Slattery and Bockus 1997), it was not the case of the community we studied. A slumping event would have provoked first a diminish in flat-shaped organisms (the ones that get more easily covered), though by the contrary showed an increase in the early stages of community shift, but as sedimentation increased in the system and in the model, these flat form sensitive ascidians were also affected (i.e., *A. challengeri* 1998 at 30 m depth (Fig. 3c)) (Sahade et al. 2015).

The idea of sediment generating horizontal zonation patterns on marine benthos is well extended in Arctic and temperate fjords (Thrush et al. 2004). It has been proposed as a factor that negatively affects diversity and richness. Wlodarska-Kowalczuk and Weslawski (2001) reported that as a consequence of turbidity, a primary production diminish near the sediment discharge also affects benthic biomass by reducing system capacity (*K*). More recently, the same group found that species that dominate the nearest sediment discharge areas are far from the typical opportunistic species expected in highly disturbed areas. Instead, these species have lecithotrophic larvae and low offspring but seems to be the best adapted to resist sediment disturbance (Wlodarska-Kowalczuk et al. 2005). However, due to the evolutionary history of the Antarctic continent, sedimentation was not taken into account until recently. Indeed, the existence of complex epibenthic communities on soft bottoms were explained by the absence of important sedimentary events such as those experienced by Arctic and temperate coastal and shelf systems during deglaciations (Gili et al. 2006). Unlike the rest of the world's coastlines, including the Arctic, Antarctica has virtually no sediment discharge from inland rivers. In fact, there are almost no estuaries because virtually the entire coast is covered with ice, and the low sediment supply comes primarily from the slow erosion of glaciers (Clarke et al. 2004). In the present scenario, where the retreating glaciers of the Antarctic Peninsula (Cook et al. 2005) are changing hydrography and the sedimentation regime not only locally (Monien et al. 2011; Schloss et al. 2012), but also extending their influence over 100 km from the coast (Dierssen et al. 2002), the importance of understanding sedimentary effects is acquiring a high relevance. It has been described that sediment influence decreases with its distance to the discharge source, but the sensitivity of filter-feeding species may increase with this distance. This means that specimens of species inhabiting areas frequently affected by sedimentation would deal better with sediment impact than the ones inhabiting pristine environments (Lohrer et al. 2006). If this were the case of susceptible Antarctic species, it is likely that the effect in more remote areas will be even more severe than that observed at the tip of Antarctic Peninsula, even at lower concentrations.

One of the biggest challenges for modelers nowadays is to enhance quality, resolution, and prediction capacity of global and regional models (Refsgaard et al. 2013; Boyd et al. 2014). However, to reach that goal, studies developed at local level, like the case of Potter Cove, are useful, since there is an extensive data set to contrast and test model outputs allowing an efficient feedback among models output, experimental work, and biological observations. These small but more detailed models will then point out which variables or interactions we should consider to enhance the quality of the regional ones.

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Author attribution LT: developed the model and parameters, carried out analyses, and wrote the original manuscript
PCCT: developed the model program and writing
FM: developed the model, discussed the results and writing.
JFCAM: developed the model program and writing.
RS: designed the project discussed the results and writing.
All authors discussed the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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